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Nutritional diversity in leaves of various amaranth (*Amaranthus* spp.) genotypes and its resilience to drought stress

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Summary

The nutritional diversity in leaves of twelve accessions of four amaranth species (*Amaranthus caudatus*, *A. cruentus*, *A. hybridus*, *A. hypochondriacus*) was studied in a randomized complete block design (n = 5). The accessions revealed high contents of the macronutrients K, Ca, Mg, and P, while the micronutrients Fe and Zn were comparatively low (542 – 717, 304 – 497, 131 – 230, 74 – 166, 0.9 – 1.3, 0.4 – 0.9 mg 100 g^{-1} fresh weight, respectively). Protein contents were found to be higher (23 – 32%) compared to other commonly consumed leafy vegetables in Sub-Saharan-Africa. Phenolic acid and flavonoid contents strongly varied between accessions and to some extent were lower in comparison to those reported in literature. Amaranth is reported to be drought tolerant, thus, one accession of each species was subjected to two different drought stress conditions (moderate – 35 – 45% field capacity, severe – 15 – 25% field capacity, n = 3). Well-watered plants were used as control (60 – 70% field capacity). A significant reduction in plant height and fresh matter occurred in all accessions with increasing drought stress, whereas contents of nutritional compounds increased. Phenolic acids and flavonoid contents in all accessions/species were not affected by drought stress except for *A. cruentus* where total phenolic acids significantly increased.

Introduction

The world at present is facing major challenges. Global population is increasing exponentially, yet already around one billion people of the global population suffer malnutrition and hunger or experience regular food insecurity (FAO, 2016). The urgency to reduce poverty has been recognized by the United Nations launching Sustainable Development Goals in 2015 (AGENDA, 2030). Extreme poverty continues to be mainly concentrated in rural areas of developing countries, affecting primarily subsistence producers. Malnourishment and malnutrition are often directly connected to hunger and poverty. In Sub-Saharan Africa, these challenges are particularly high (WFP, 2018) as a large number of African families are depending principally on subsistence farming.

Micronutrient deficiency is closely related to the increasing problem of malnutrition, often referred to "hidden hunger" (Miller and Welch, 2013). Micronutrients are important for the human body immunity, neurological functions, metabolism, growth, and development; thus, the effects of prolonged deficiency are known to be irreversible (Gilbert, 2001; UNICEF, 2003). According to UNICEF (2003), about 80 – 98% of children reveal iron deficiency in arid and semi-arid areas and millions of children therefore suffer from stunted growth, cognitive delays, weakened immunity, and disease as a result of lack of micronutrient supply. Micronutrient deficiencies develop gradually over time and their devastating impact is not seen until irreversible damage. Although micronutrient supplementation and fortification have been in place for a long time (UNICEF, 2003; Voster et al., 2007), they have been found to be costly, not sustainable and not accessible to all population (Miller and Welch, 2013). In return, food-based approaches through dietary diversification and modification are considered to be more sustainable strategies to improve the consumption of micronutrients (FAO, 1997; Keding et al., 2009). Crops like maize which still dominate agricultural production and daily nutrition in many resource-poor countries have only a low nutritional value. At the same time, these water consuming crops provide poor harvests during drought. It is therefore of high relevance to promote production and consumption of micronutrient rich foods among populations with health and nutrition deficiencies (Chege, 2012).

There is a high diversity of vegetable crops that have potential to improve human health but have been neglected so far (Bokelmann et al., 2022). Traditional crops are extremely important for food production and fighting malnutrition in low income, food-deficit countries where they continue to be maintained by traditional uses and cultural preferences (Bokelmann et al., 2022; Slabbert and Krüger, 2014). To ensure food security and dietary diversification for smallholder farmers in Sub-Saharan Africa, focus on the use of drought resistant crops has been recommended (Esilaba et al., 2011), since drought is one of the major threats to food production and nutritional food security, specifically in recent years due to unexpected climate change events. Consequently, there is a need to explore suitable and high-quality crops that are nutrient-rich and that are adapting well to climate changes, and thus might thrive in drier regions under poor conditions and with lower production costs.

Amaranth is one of the underutilized but very promising and nutritious food crops (Rastogi and Shukla, 2013). Although the cultivation of amaranth was initiated in the prehistoric period with a promising note, later it lagged behind conventional crop and was mainly seen as a weedy plant (Ebert, 2014). Only recently, a number of research activities on nutritive value rediscovered amaranth and projected it as potential crop of the future with special emphasis on food security of the increasing world population (e. g. Ebert, 2014; Joshi and Verma, 2020). Amaranth shows a wide geographical distribution, evolution of landraces and domestication in many areas. It is a fast-growing plant that reveals a high drought tolerance and can be easily cultivated in garden and fields (Rastogi and Shukla, 2013). Furthermore, amaranth is reported to have higher nutrient contents compared to many exotic vegetables like kale and collard greens, and thus can meet malnutrition deficiencies (Das, 2016; Ruth et al., 2021). Most attention in research has been concentrating on species of grain amaranth and only limited studies are reported on leafy amaranth species. However, amaranth leaves are known for their high nutritional value (Das, 2017). Therefore, it is important to evaluate the nutritional value of leafy amaranth species for deciding on its genetic improvement, production, consumption, and marketing in terms of food security also under climate change, i. e. drought stress conditions (Muriuki et al., 2014).

For that purpose, various amaranth accessions were selected from Bio Innovation Zimbabwe (BIZ) in Harare, Zimbabwe and grown under controlled greenhouse conditions at Humboldt-Universität zu Berlin, Germany. The objectives were 1) to evaluate the nutritional

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value of leaves of different amaranth accessions (genotype diversity) and 2) to determine the drought tolerance of selected accessions.

Materials and Methods

Genotype trial

Seeds of twelve accessions of four *Amaranthus* species, i. e. *A. caudatus*, *A. cruentus*, *A. hybridus*, and *A. hypochondriacus*, were obtained from Bio Innovation Zimbabwe Institute (BIZ) in Harare, Zimbabwe (Tab. 1). Sowing was conducted in germination trays (Piki-Box model 68, Meyer, Germany) containing peat soil (Substrat 5, Klasmann-Deilmann GmbH, Germany) in the experimental greenhouse in Berlin-Dahlem at Humboldt-Universität zu Berlin. One week after germination, seedlings of 6–8 cm in height were transplanted into round, free-draining brown plastic pots (Poeppelmann, TEKU MCL 24, 6 L) containing 2 kg of peat soil with 1 plant per pot (Substrat 1, Klasmann-Deilmann GmbH, Germany). The temperature in the greenhouse was kept at 22/20 °C day/night during the entire experimental period for ten weeks. Additional lighting was used when sun radiation intensity was falling under 50 kLx (overhead metal-halide lamps, 600 mmol photon m^{-2} s^{-1} light intensity). The plants were supplied with NPK fertilizer (YaraTera Krista K plus) four and seven weeks after planting. Irrigation of plants was conducted every second to third day based on pre-experiments. For the study, a randomized complete block design with five replications of each amaranth accession was used.

To analyze differences in growth and nutrient profile of diverse amaranth accessions, the following parameters were analyzed: plant leaf biomass, plant height, leaf water content, leaf macro- and micronutrient content, profile of phenolic acids and flavonoids in amaranth leaves.

Tab. 1: Information of amaranth accessions used for the genotype trial (Bio Innovation Zimbabwe)

Accession number	*Amaranthus* species	Comments
288279	*A. caudatus*	edulis type
22379	*A. cruentus*	all green advanced line from Nepal
538255	*A. cruentus*	variety 'AMONT'
538319	*A. cruentus*	all green
604666	*A. cruentus*	orange, South Africa
636182	*A. cruentus*	large and bright seeds
641047	*A. cruentus*	white seeds from Nigeria
642734	*A. cruentus*	high yield in Chile
538324	*A. hybridus*	early in Nebraska
538325	*A. hybridus*	short advanced variety
649305	*A. hypochondriacus*	early maturity
667174	*A. hypochondriacus*	golden seeds from Zimbabwe

Determination of plant growth parameters

At the end of the experiment (10 weeks after planting), plant height was measured from upper soil layer to the top of the flag leaf. To determine the leaf biomass of the different amaranth accessions, the total surface biomass of each plant was harvested, and leaves were separated to weight leafy fresh weight. Water content of leaves was determined by calculating the ratio of fresh weight and dry weight of amaranth leaf material determined after oven-drying for 48 h at 105 °C. At harvest, the plants of all accessions were at the stage of vegetative growth.

To analyze macro- and micronutrients as well as selected secondary plant metabolites in the leaves of the different amaranth accessions, harvested leaf material was frozen in liquid nitrogen, lyophilized (Lyo Cube, Alpha 1–4, Martin Christ Gefriertrocknungsanlagen GmbH, Germany), grounded to fine powder, and kept in a desiccator for further analysis.

Determination of plant macro- and micronutrients

The following contents of macro- and micronutrients were analyzed in the leaves of amaranth species: potassium (K), calcium (Ca), magnesium (Mg), phosphorus (P), iron (Fe) and zinc (Zn). The mineral content of species was quoted on fresh weight basis [mg/100 g fresh weight].

Basis for the detection of macro- and micronutrients was a spectroscopic method (VDLUFA 1976) using the microwave digestion system "Inductively Coupled Plasma – Optical Emission Spectrometry" (ICP-OES). Therefore, 0.5 g dried grounded leaf material was weighed into microwave absorbing vessels. Afterwards, 5 mL of 65% nitric acid and 3 mL 30% hydrogen peroxide were added to the tissue samples, and the solutions were placed into the microwave (MARS Xpress, CEM, USA). In the microwave, the material was heated (800 W) to a temperature of 220 °C over a period of 37 min. Solutions were cooled down to room temperature, transferred into volumetric flasks, and filled up 50 mL with distilled water. After filtration (SM grade 389, white spot, 125 mm), solutions were analyzed spectroscopically with an ICP emission spectrometer (iCAP 6300 Duo MFC, Thermo Scientific, USA) at wavelength ranges between 166 and 847 nm (P at 213.6 nm, K at 766.5 nm, Ca at 317.9 nm, Mg at 279.0 nm, Fe at 259.9 nm, Zn at 213.8 nm). The analysis was performed with the following operating conditions: 1150W RF power, 0.55 L min^{-1} nebulizer gas flow with argon used as plasmogen as well as carrier gas and performed with a cross flow nebulizer (MIRA MIST, Thermo Scientific; England), in addition to radial (Ca and Mg) and axial (Fe and Zn) view. Quantitative and qualitative determination of elements was conducted based on a single element standard solution (1000 mg L^{-1} in 1.4 mol L^{-1} HNO_3, Carl Roth GmbH & Co. KG, Germany) and calibrations curves.

Determination of protein

The quantitative determination of the total nitrogen content (N_t) of leafy plant material was conducted according to DIN-ISO-10694 (1995) and DIN-ISO-13878 (1998). Approximately 0.5 g dried leaf powder was weighed into reaction vessels and mixed with 50 mL 1M NH_4NO_3. The solution was filtered through a membrane filter and poured into test tubes. The samples were combusted at 900 °C in an oxygen atmosphere (Vario MAX CNS, Elementar Analysensysteme GmbH, Germany). Nitrogen is quantitatively converted to N_2 via subsequent oxidation and reduction tubes and measured through a thermal conductivity detector (CONTHOS 3–TCD, LFE GmbH & Co. KG, Germany). Results are given as percentage of nitrogen, which is converted into protein by using the conversion factor 6.25 (Sosulski and Imafidon, 1990).

Determination of phenolic acids and flavonoids

Phenolic acids and flavonoids were extracted from 20 mg lyophilized powder. Based on a slightly modified method described by Förster et al. (2015), the material was extracted in 300 µL 70% methanol (pH 4, acetic acid) for 15 min in ice water using sonification (Bandelin Sonorex, BANDELIN electronic GmbH & Co. KG, Germany). The pellet was re-extracted twice with 300 µL of the extraction solvent for 10 min. After each extraction step the samples were centrifuged for 5 min at 6,800 × g (Thermo Scientific, Heraeus Megafuge X1R Centrifuge, Germany) at 4 °C and the supernatants were combined. Supernatants were concentrated (vacuum concentrator, Thermo Scientific Savent SPD111V Concentrator, vacuum

pump: Vacuumbrand PC 3001 series, CVC3000, Germany) to near dryness, dissolved in 50% methanol, and filled up to 1 mL. The samples were shortly vortexed and centrifuged for 5 min at 4,000 ×g, filtered (polypropylene centrifuge tube filters, 0.22 µm), and transferred to HPLC vials.

Extracts were qualitatively and quantitatively analyzed by HPLC (Ultimate 3000 equipped with an autosampler WPS-3000TR, pump LPG-3400RS, column compartment TCC-3000RS, diode array detector DAD-3000RS, Thermo Scientific, Germany). A volume of 10 µL extract was injected and separated using a 150 × 2.1 mm C16 column (AcclaimPA, 3 µm, Thermo Scientific, Germany) with the following gradient program: 0 – 1 min: 0.5% B, 1 – 10 min: 0.5 – 40% B, 10 – 12 min: 40% B, 12 – 18 min: 40 – 80% B, 18 – 20 min: 80% B, 20 – 24 min: 80 – 100% B, 24 – 30 min: 100% B, 30 – 34 min: 100 – 0.5% B, and 34 – 39 min 0.5% B at a flow rate of 0.4 mL min^{-1}. Two solvents were used for analysis: solvent A: H_2O (0.5% formic acid), B: 40% acetonitrile. The oven temperature was 35 °C. Detection of phenolic acids and flavonoids was carried out at 290 nm on a photodiode array detector against the internal standard 4-methoxycinnamic acid (1 mM, Sigma Aldrich, Germany). Commercially available standards of single compounds were used as reference (p-coumaryl acid, trans-ferulic acid, caffeic acid, quercetin 7-*O*-glucoside, and quercetin 3-*O*-rutinoside). Relative response factors of compounds with a similar chemical structure were used to correct for absorbance difference. Results were expressed in µmol g^{-1} dry weight.

Drought stress tolerance trial

To characterize the impact of water deficiency on leaf amaranth in terms of growth (biomass) and nutritional value, one accession out of each of the four different species was chosen: *A. caudatus* (accession no. 288279), *A. cruentus* (accession no. 667174), *A. hybridus* (accession no. 641047), and *A. hypochondriacus* (accession no. 538324).

To assess plant responses to variations in water deficiency, accessions were exposed to drought conditions at two different levels: 1) plants of the moderate drought stress treatment were kept at 35 – 45% field capacity (DSI); 2) plants of severe drought stress treatment were kept at 15 – 25% field capacity (DSII); well-watered plants were used as control and kept at 60 – 70% field capacity (C = Control). The determination of the specific drought stress treatments was obtained by own previous experiments (Köhler et al., 2020) and reported studies (e. g. Lei et al., 2017; Li et al., 2015; Zhang et al., 20212).

The species were grown for a period of six weeks under well-watered conditions. After an acclimatization period of one week (plants had adjusted to their level of field capacity in this period, the plants were grown under the different drought stress conditions, i. e. respective irrigation regimes for three weeks. Three plants per species (n = 3) and drought stress level were harvested after three weeks. Soil moisture levels were controlled by weighting the pots every two days. Evaporation of water was calculated, and water deficit was balanced to maintain the desired drought stress level.

The same quality parameters used for the genotype trial were also measured for the drought tolerance trial, however additionally, the leaf proline content was determined.

Analysis of free proline

Determination of free proline was based on a photometrical and slightly modified method described by Bates et al. (1973). Leaf powder (total of 80 mg) was extracted with 1.5 mL 3% 5-sulfosalicylic acid. The homogenate was centrifuged (Thermo Scientific, Heraeus Megafuge X1R Centrifuge, Germany) at 23,000 ×g at 0 °C for 30 min. After collecting 300 µL of the supernatant, 300 µL acid ninhydrin (2.5 g ninhydrin in 60 mL glacial acetic acid and 40 mL 6 M ortho-phosphoric acid) and 300 µL glacial acetic acid were added. Samples were incubated in a water bath at 90 °C for 60 min. The reaction was terminated on ice. A volume of 900 µL toluene was added to the sample and the mixture was vortexed and centrifuged at 23,000 ×g at 0 °C for 10 min. Toluene phase was transferred into micro cuvettes and the absorbance was determined at 520 nm with a spectrophotometer (Sequoia-Turner, Sequoia-Turner Corporation, USA). Free proline content [µg g^{-1} dry weight] was calculated by reference to a standard curve with L-proline (Carl Roth GmbH + Co. KG, Germany).

Statistical analysis

Analysis of data was conducted through the statistical software SPSS (IBM SPSS Statistics 25) and subjected to one-way analysis of variance (ANOVA) followed by Tukey's HSD test to measure statistical differences ($p \leq 0.05$ or $p \leq 0.1$).

Results

Genotype trial

In order to determine the nutritional value of leaves of the different amaranth species, cultivated samples were observed for growing patterns, subsequently harvested and finally analyzed for characteristic nutritional compounds (Tab. 2). Plant height of all analyzed accessions of the four amaranth species ranged between 84 and 149 cm. Four accessions, all belonging to the species *A. cruentus*, were significantly higher in growth in comparison to all other amaranth accessions. Average leaf fresh weight ranged between 99 (*A. hypochondriacus* 649305) and 168 g (*A. cruentus* 538255), leaf dry weight between 12 (*A. hypochondriacus* 649305) and 22 g (*A. cruentus* 22379, 538255), and water content of leaves between 85% (*A. caudatus* 288279) and 89% (*A. cruentus* 604666) (Tab. 2). Amaranth leaf nutrients, i. e. protein, contents of potassium (K), calcium (Ca), magnesium (Mg), phosphorus (P), iron (Fe), and zinc (Zn) were determined (Tab. 2). Protein contents of one *A. cruentus* accession (604666), the two *A. hypochondriacus* accessions (649305 and 667174), and one *A. hybridus* accession (538325) were significantly higher than in four *A. cruentus* accessions (538319, 636182, 641047, and 642734) and one *A. hybridus* accession (538324). In general, protein of all analyzed amaranth accessions ranged between 23 and 32% dry weight. In respect to all macro- and micronutrients analyzed, *A. caudatus* (288279) revealed tendentiously the highest contents. Some accessions had consistently significantly lower contents (*A. cruentus* 604666, 641047; *A. hybridus* 538325) in comparison to other accessions showing significantly higher contents (*A. caudatus* 288279). For all accessions, K content ranged between 541.8 and 716.8, Ca between 304.4 and 497.0, Mg between 131.1 and 230.4, P between 73.8 and 165.9, Fe between 0.91 and 1.34, and Zn content between 0.42 and 0.86 mg 100 g^{-1} fresh weight.

To evaluate the nutritional value of leaves of the different amaranth species and accessions, also phenolic acids and flavonoids were determined (Tab. 3). The contents of phenolic acids ranged between 5.22 (*A. hypochondriacus* 649305) and 14.89 µmol g^{-1} dry weight (*A. hybridus* 538325). *A. hybridus* (538325) showed a significantly higher total phenolic acid content in comparison to all other accessions. In all four species different ferulic acid derivates and two different isomers of caffeoyl quinic acid were detected. Additionally, also another caffeic acid derivate was found in *A. hypochondriacus*. Coumaryl quinic acid was not identified in *A. caudatus*, but in the other three amaranth species. Total flavonoid contents ranged between 0.19 (*A. hypochondriacus* 667174 and *A. cruentus* 604666) and 1.16 µmol g^{-1} dry weight (*A. hybridus* 538324). However, in all accessions just one flavonoid compound was identified, i. e. quercetin-3-*O*-rutinoside.

Tab. 2: Growing parameters and nutrient contents of different accessions of four *Amaranthus* spp.

Amaranth species	Accession number	Plant height [cm]	Fresh weight [g]	Water content [%]	Dry weight [g]	Protein [% dry weight]	K	Ca	Mg	P	Fe	Zn
							[mg 100 g^{-1} fresh weight]					
A. caudatus	288279	125 ^{bc} ± 6.5	127 ^{b} ± 12.1	85 ^{b} ± 0.7	19 ^{ab} ± 2.1	28 ^{bc} ± 2.7	679.9 ^{a} ± 10.0	476.4 ^{a} ± 16.3	201.2 ^{a} ± 13.8	165.9 ^{a} ± 6.5	1.34 ^{a} ± 0.13	0.86 ^{a} ± 0.07
A. cruentus	22379	148 ^{a} ± 3.4	149 ^{ab} ± 28.9	86 ^{ab} ± 1.5	22 ^{a} ± 4.7	27 ^{bc} ± 1.8	711.7 ^{a} ± 78.7	497.0 ^{a} ± 45.5	193.6 ^{ab} ± 26.0	110.8 ^{c} ± 7.6	1.31 ^{a} ± 0.13	0.72 ^{b} ± 0.08
	538255	145 ^{a} ± 2.9	168 ^{a} ± 22.8	87 ^{a} ± 1.4	22 ^{a} ± 3.4	28 ^{bc} ± 2.4	624.4 ^{ab} ± 35.1	439.4 ^{ab} ± 37.7	169.3 ^{b} ± 4.2	126.6 ^{b} ± 8.2	1.24 ^{ab} ± 0.16	0.71 ^{bc} ± 0.18
	538319	149 ^{a} ± 4.5	133 ^{b} ± 3.3	87 ^{a} ± 0.4	18 ^{abc} ± 2.0	24 ^{cd} ± 2.4	541.8 ^{c} ± 42.9	466.7 ^{ab} ± 32.3	230.4 ^{a} ± 38.5	133.4 ^{b} ± 19.4	1.03 ^{b} ± 0.02	0.63 ^{bc} ± 0.05
	604666	84 ^{d} ± 3.3	164 ^{a} ± 15.7	89 ^{a} ± 1.3	18 ^{abc} ± 2.0	32 ^{a} ± 1.5	660.6 ^{ab} ± 64.7	304.4 ^{d} ± 20.9	131.4 ^{d} ± 9.6	73.8 ^{d} ± 5.4	0.91 ^{c} ± 0.03	0.42 ^{d} ± 0.05
	636182	144 ^{a} ± 3.5	147 ^{a} ± 4.3	87 ^{a} ± 0.8	20 ^{ab} ± 0.6	25 ^{c} ± 1.3	595.0 ^{b} ± 9.6	442.9 ^{ab} ± 41.8	158.1 ^{bc} ± 11.4	130.3 ^{b} ± 7.4	1.17 ^{ab} ± 0.13	0.86 ^{a} ± 0.13
	641047	135 ^{b} ± 6.1	149 ^{ab} ± 8.9	88 ^{a} ± 1.3	19 ^{ab} ± 1.2	23 ^{d} ± 0.9	564.4 ^{c} ± 22.4	385.2 ^{c} ± 28.1	156.0 ^{c} ± 9.9	98.9 ^{c} ± 10.0	1.08 ^{b} ± 0.09	0.55 ^{bc} ± 0.13
	642734	137 ^{b} ± 1.5	129 ^{b} ± 20.9	86 ^{ab} ± 1.3	18 ^{abc} ± 3.2	23 ^{d} ± 1.5	654.4 ^{ab} ± 64.4	421.6 ^{b} ± 2.0	185 ^{ab} ± 11.8	139.0 ^{b} ± 12.3	1.14 ^{b} ± 0.10	0.78 ^{ab} ± 0.11
A. hybridus	538324	132 ^{b} ± 4.1	135 ^{b} ± 9.2	87 ^{a} ± 0.2	17 ^{abc} ± 1.3	25 ^{c} ± 1.7	574.3 ^{bc} ± 30.1	437.3 ^{b} ± 22.6	160.6 ^{bc} ± 10.8	107.7 ^{c} ± 3.3	1.09 ^{b} ± 0.04	0.54 ^{c} ± 0.06
	538325	116 ^{c} ± 3.0	121 ^{b} ± 11.7	88 ^{a} ± 1.2	15 ^{bc} ± 1.6	29 ^{ab} ± 2.9	665.5 ^{a} ± 29.1	360.4 ^{c} ± 33.7	143 ^{cd} ± 9.1	100.4 ^{c} ± 8.0	1.17 ^{ab} ± 0.06	0.53 ^{c} ± 0.03
A. hypochondriacus	649305	110 ^{c} ± 15.2	99 ^{c} ± 2.6	88 ^{a} ± 0.2	12 ^{c} ± 3.6	32 ^{ab} ± 3.0	649.1 ^{ab} ± 57.1	387.6 ^{c} ± 16.0	131.1 ^{d} ± 7.0	100.9 ^{c} ± 13.2	1.00 ^{b} ± 0.05	0.83 ^{a} ± 0.05
	667174	120 ^{c} ± 4.9	137 ^{ab} ± 30.1	86 ^{ab} ± 0.9	19 ^{ab} ± 4.7	29 ^{b} ± 1.5	716.8 ^{a} ± 84.3	448.6 ^{ab} ± 13.3	203.9 ^{a} ± 11.9	109.6 ^{c} ± 10.2	1.11 ^{b} ± 0.05	0.42 ^{d} ± 0.03

Mean ± standard deviation; different letters indicate significant differences between accessions and within one parameter (Tukey's HSD test, $p \leq 0.05$).

Tab. 3: Phenolic acid and flavonoid contents [µmol g^{-1} dry weight] of different accessions of four *Amaranthus* spp.

Phenolic acids and flavonoids	Amaranth species and accessions											
	A. caudatus	*A. cruentus*							*A. hybridus*		*A. hypochondriacus*	
	288279	22379	538255	538319	604666	636182	641047	642734	538324	538325	649305	667174
Ferulic acid derivates	7.12 ^{ab} ± 0.78	5.43 ^{bcd} ± 1.04	6.58 ^{abc} ± 0.74	7.41 ^{bcd} ± 0.64	4.56 ^{cd} ± 1.11	6.10 ^{bcd} ± 0.45	5.50 ^{cd} ± 1.08	5.68 ^{cd} ± 0.49	5.76 ^{bcd} ± 0.93	8.43 ^{a} ± 1.14	4.06 ^{d} ± 1.51	5.17 ^{bcd} ± 1.55
Caffeoyl quinic acid I	0.18 ^{e} ± 0.03	0.46 ^{abc} ± 0.11	0.49 ^{ab} ± 0.07	0.36 ^{cd} ± 0.06	0.33 ^{cd} ± 0.08	0.38 ^{bcd} ± 0.05	0.51 ^{ab} ± 0.04	0.58 ^{a} ± 0.08	0.40 ^{bcd} ± 0.06	0.26 ^{de} ± 0.08	0.14 ^{e} ± 0.08	0.17 ^{e} ± 0.02
Caffeoyl quinic acid II	1.22 ^{e} ± 0.43	2.50 ^{bcde} ± 0.42	2.58 ^{bcde} ± 1.53	1.76 ^{de} ± 0.52	3.71 ^{bcd} ± 1.70	2.14 ^{cde} ± 1.31	2.00 ^{cde} ± 0.97	4.21 ^{abc} ± 1.43	2.00 ^{cde} ± 0.40	6.17 ^{a} ± 1.56	0.77 ^{e} ± 0.27	4.60 ^{ab} ± 0.68
Caffeic acid derivate	0.00 ^{b} ± 0.00	0.00 ^{b} ± 0.00	0.00 ^{b} ± 0.00	0.00 ^{b} ± 0.00	0.00 ^{b} ± 0.00	0.00 ^{b} ± 0.00	0.00 ^{b} ± 0.00	0.00 ^{b} ± 0.00	0.00 ^{b} ± 0.00	0.00 ^{b} ± 0.00	0.20 ^{a} ± 0.04	0.23 ^{a} ± 0.09
Coumaryl quinic acid	0.00 ^{d} ± 0.00	0.08 ^{ab} ± 0.02	0.08 ^{a} ± 0.02	0.09 ^{a} ± 0.03	0.08 ^{a} ± 0.02	0.07 ^{ab} ± 0.01	0.05 ^{bc} ± 0.01	0.10 ^{a} ± 0.02	0.01 ^{cd} ± 0.01	0.02 ^{cd} ± 0.02	0.02 ^{cd} ± 0.01	0.02 ^{cd} ± 0.01
Total content phenolic acids	8.53 ^{b} ± 0.66	8.47 ^{b} ± 0.86	9.73 ^{b} ± 0.99	9.62 ^{b} ± 0.67	8.68 ^{b} ± 1.39	8.68 ^{b} ± 1.18	8.06 ^{bc} ± 1.21	10.56 ^{b} ± 1.62	8.18 ^{b} ± 0.96	14.89 ^{a} ± 1.23	5.22 ^{c} ± 1.63	10.18 ^{b} ± 2.15
Quercetin-3-*O*-rutinoside (Total content flavonoids)	0.23 ^{cd} ± 0.01	0.71 ^{b} ± 0.26	0.54 ^{bcd} ± 0.18	0.59 ^{bcd} ± 0.28	0.19 ^{d} ± 0.03	0.57 ^{bcd} ± 0.13	0.65 ^{bc} ± 0.20	0.51 ^{bcd} ± 0.06	1.16 ^{a} ± 0.50	0.37 ^{bcd} ± 0.07	0.21 ^{cd} ± 0.12	0.19 ^{d} ± 0.08

Mean ± standard deviation; different letters indicate significant differences between accessions and within one compound (Tukey's HSD test, $p \leq 0.05$).

Drought stress tolerance trial

To assess plant responses to variations in water supply, a drought stress tolerance trial was performed to investigate the impact of drought on the nutritional value of amaranth species. Results of proline, an amino acid being known to accumulate in plants under drought stress, showed a significant increase for *A. cruentus*, *A. hybridus*, and *A. hypochondriacus* under limited water supply conditions (Tab. 4). In contrast, a significant increase from control plants (C) to moderate drought stress (DS1) was only found for *A. cruentus*. A reduction

of plant biomass with the increasing levels of drought stress was clearly indicated by a decrease in plant height and leaf fresh weight (DSII < DSI < C). For all species, a significant decrease in plant height was found in the more severe drought stress variant (DSII) in comparison to the control (C), whereas leaf fresh weight was only affected for *A. cruentus*, *A. hybridus*, and *A. hypochondriacus*. Additionally, plants under severe drought stress (DSII) showed signs of leaf wilting and yellowing of the lower mature leaves, indicating a significant decline in leaf water contents (Tab. 4). However, leaf dry weight was not significantly influenced by drought stress.

Protein content of leaves ranged between 23 and 32% with no significant differences found between the drought stress variants for all species. A tendency of an increase of K, Ca, Mg, P, Fe, and Zn contents with decreasing water availability was detected for all species, even so significant differences could not always be found. For K contents in *A. cruentus*, *A. hybridus*, and *A. hypochondriacus,* significant differences were found between the control (C) and the severe drought stress (DSII) treatment. For Ca and Mg contents, this significance was detected in *A. caudatus*, *A. hybridus*, and *A. hypochondriacus*, for P content in *A. caudatus* and *A. cruentus*, for Fe content in all species, and for Zn content in *A. cruentus* and *A. hybridus*.

The total content of phenolic acids as well as the contents of single phenolic acids were not significantly affected by the drought stress variants (C, DSI, DSII) for *A. caudatus*, *A. hybridus*, and *A. hypochondriacus* (Tab. 5). The contents of different ferulic acid derivates, a coumaric acid derivate, and caffeoyl quinic acid in *A. caudatus* as well as the contents of coumaric acid derivate and two caffeoyl quinic acids in *A. hybridus* (exception caffeoyl quinic acid I) and *A. hypochondriacus* were not significantly different in the different drought stress regimes. However, in *A. cruentus,* all single phenolic acids as well as the total phenolic acid content were significantly increased with decreasing water availability (DSII in comparison to C). In terms of total flavonoids and single flavonoids (quercetin-3-*O*-rutinoside and quercetin-coumaryl hexoside), none of the drought stress treatments showed an effect in the four amaranth species.

Discussion

Impact of genotypes on growth pattern and nutritional value

Due to the lack of knowledge about differences in the nutritional levels of leaves among different amaranth genotypes, one objective of the study was to evaluate the characteristic growth patterns and nutrient compositions in different amaranth species and accessions. Inter- as well as intraspecific differences in the respective amaranth species could be identified for growth parameters and nutrient contents in the leaves. As also stated in literature (Singh and Whitehead, 1996), *A. cruentus* developed generally high leaf fresh weight in comparison to the other species. However, a single accession (*A. cruentus* 604666) exhibited small growth, and plants developed high amounts of leaves. This is in accordance with literature citing that plant height does not necessarily contribute to either grain or leaf yields (Hoidal et al., 2019). In general, amaranth is known to be a fast-growing plant species which takes 1 – 2 months to mature (leaf harvest), while grain take up to 3 months (grain harvest) (Das,

Tab. 4: Growing parameters and nutrient contents of different *Amaranthus* spp. under two drought stress treatments

Amaranth species	Irrigation variant	Proline content [µg g^{-1} dry weight]	Plant height [cm]	Fresh weight [g]	Water content [%]	Dry weight [g]	Protein [% dry weight]	K	Ca	Mg	P	Fe	Zn
								[mg 100 g g^{-1} fresh weight]					
A. caudatus	C	108 ^{a} ± 5.6	106 ^{a} ± 6.9	68 ^{a} ± 12.9	87 ^{a} ± 1.0	9 ^{a} ± 2.5	27 ^{a} ± 0.8	673.0 ^{a} ± 35.0	377.9 ^{b} ± 39.8	134.7 ^{c} ± 15.1	130.5 ^{b} ± 7.8	1.13 ^{b} ± 0.04	0.70 ^{a} ± 0.04
	DSI	99 ^{a} ± 10.6	112 ^{a} ± 5.6	80 ^{a} ± 14.3	85 ^{b} ± 0.7	12 ^{a} ± 2.4	27 ^{a} ± 1.2	764.8 ^{a} ± 59.1	468.7 ^{ab} ± 33.7	173.4 ^{b} ± 4.7	145.0 ^{ab} ± 3.7	1.25 ^{ab} ± 0.05	0.79 ^{a} ± 0.08
	DSII	122 ^{a} ± 26.7	95 ^{b} ± 5.0	63 ^{a} ± 2.2	83 ^{c} ± 0.3	11 ^{a} ± 0.3	29 ^{a} ± 3.1	775.8 ^{a} ± 49.5	488.9 ^{a} ± 10.9	191.2 ^{a} ± 3.4	161.9 ^{a} ± 8.7	1.26 ^{a} ± 0.02	0.82 ^{a} ± 0.04
A. cruentus	C	109 ^{a} ± 7.8	152 ^{a} ± 3.9	131 ^{a} ± 24.2	87 ^{a} ± 0.2	17 ^{a} ± 3.9	26 ^{a} ± 1.9	601.3 ^{c} ± 32.2	411.9 ^{c} ± 12.7	150.5 ^{b} ± 20.2	102.8 ^{b} ± 8.3	1.17 ^{b} ± 0.12	0.74 ^{b} ± 0.09
	DSI	141 ^{b} ± 18.5	135 ^{b} ± 5.3	111 ^{a} ± 22.5	85 ^{a} ± 1.3	17 ^{a} ± 5.8	23 ^{a} ± 4.0	697.4 ^{b} ± 21.4	483.6 ^{b} ± 25.5	179.6 ^{b} ± 40.6	97.9 ^{b} ± 5.5	1.19 ^{b} ± 0.12	0.84 ^{ab} ± 0.11
	DSII	281 ^{c} ± 25.1	110 ^{c} ± 2.1	64 ^{b} ± 2.2	80 ^{b} ± 0.3	13 ^{a} ± 0.5	26 ^{a} ± 0.3	903.9 ^{a} ± 57.4	624.1 ^{a} ± 18.9	258.4 ^{a} ± 7.3	123.8 ^{a} ± 6.4	1.44 ^{a} ± 0.01	1.02 ^{a} ± 0.02
A. hybridus	C	117 ^{a} ± 4.8	138 ^{a} ± 7.1	127 ^{a} ± 7.1	87 ^{a} ± 0.6	16 ^{a} ± 1.8	24 ^{a} ± 1.2	595.6 ^{b} ± 33.9	455.6 ^{a} ± 63.5	170.1 ^{a} ± 30.5	119.4 ^{a} ± 7.6	1.04 ^{b} ± 0.07	0.51 ^{b} ± 0.08
	DSI	114 ^{a} ± 6.5	131 ^{a} ± 1.4	116 ^{a} ± 1.4	85 ^{b} ± 0.5	16 ^{a} ± 2.8	24 ^{a} ± 1.3	661.0 ^{ab} ± 7.9	517.2 ^{a} ± 36.0	198.2 ^{a} ± 19.1	110.6 ^{a} ± 1.9	1.14 ^{b} ± 0.04	0.62 ^{ab} ± 0.01
	DSII	154 ^{b} ± 23.8	110 ^{b} ± 2.8	78 ^{b} ± 1.8	83 ^{c} ± 0.6	13 ^{a} ± 0.4	24 ^{a} ± 1.6	826.7 ^{a} ± 108.1	530.3 ^{a} ± 16.7	197.4 ^{a} ± 24.0	129.0 ^{a} ± 15.3	1.27 ^{a} ± 0.04	0.70 ^{b} ± 0.04
A. hypochondriacus	C	120 ^{a} ± 19.6	119 ^{a} ± 6.2	130 ^{a} ± 3.2	87 ^{a} ± 0.8	17 ^{a} ± 1.7	32 ^{a} ± 1.5	633.5 ^{b} ± 32.0	411.4 ^{b} ± 24.3	170.8 ^{b} ± 12.5	109.3 ^{a} ± 8.7	1.09 ^{b} ± 0.11	0.49 ^{a} ± 0.02
	DSI	139 ^{a} ± 15.2	115 ^{a} ± 1.4	98 ^{b} ± 11.2	87 ^{a} ± 0.3	13 ^{a} ± 2.1	26 ^{a} ± 1.4	678.5 ^{b} ± 21.6	417.6 ^{b} ± 7.9	169.7 ^{b} ± 5.8	105.0 ^{a} ± 2.4	1.03 ^{b} ± 0.04	0.51 ^{a} ± 0.09
	DSII	204 ^{b} ± 49.4	99 ^{b} ± 0.5	73 ^{c} ± 2.0	85 ^{b} ± 1.7	14 ^{a} ± 2.0	28 ^{a} ± 2.8	957.4 ^{a} ± 87.7	616.1 ^{a} ± 90.1	255.2 ^{a} ± 41.6	109.4 ^{a} ± 8.8	1.41 ^{a} ± 0.09	0.54 ^{a} ± 0.04

Mean ± standard deviation; different letters indicate significant differences between irrigations variants within each species and parameter (Tukey's HSD test, $p \leq 0.05$); C: Control, DS: Drought stress; C = control, 60 - 70% field capacity; DSI = drought stress variant I, 35 - 45% field capacity; DSII = drought stress variant II, 15 - 25% field capacity

Tab. 5: Phenolic acid and flavonoid contents [μmol g^{-1} dry weight] of different *Amaranthus* spp. under two drought stress treatments

	Amaranth species in different irrigation variants											
	A. caudatus			*A. cruentus*			*A. hybridus*			*A. hypochondriacus*		
Phenolic acids and flavonoids	C	DSI	DSII	C	DSI	DSII	C	DSI	DSII	C	DSI	DSII
Ferulic acid derivates	6.82 ^{a} ± 2.63	7.53 ^{a} ± 2.81	5.49 ^{a} ± 2.31	2.54 ^{b} ± 0.15	3.52 ^{ab} ± 1.21	4.07 ^{a} ± 0.24	5.76 ^{a} ± 1.24	3.27 ^{b} ± 0.47	5.06 ^{ab} ± 1.38	6.07 ^{a} ± 2.43	3.69 ^{a} ± 1.12	5.31 ^{a} ± 0.10
Coumaric acid derivate	0.05 ^{a} ± 0.02	0.07 ^{a} ± 0.01	0.07 ^{a} ± 0.03									
Caffeoyl quinic acid I	0.97 ^{a} ± 0.26	1.63 ^{a} ± 0.65	1.20 ^{a} ± 0.36	0.04 ^{b} ± 0.00	0.24 ^{a} ± 0.12	0.31 ^{a} ± 0.02	0.33 ^{a} ± 0.08	0.21 ^{b} ± 0.01	0.35 ^{a} ± 0.03	2.22 ^{a} ± 1.04	2.60 ^{a} ± 1.70	4.27 ^{a} ± 0.61
Caffeoyl quinic acid II				1.20 ^{b} ± 0.26	1.49 ^{ab} ± 0.80	2.47 ^{a} ± 0.50	1.93 ^{a} ± 0.92	1.39 ^{a} ± 0.18	2.36 ^{a} ± 0.50	0.10 ^{a} ± 0.04	0.14 ^{a} ± 0.09	0.19 ^{a} ± 0.02
Total content phenolic acids	7.83 ^{a} ± 2.79	9.22 ^{a} ± 3.40	6.76 ^{a} ± 2.70	3.78 ^{b} ± 0.32	5.24 ^{ab} ± 2.07	6.84 ^{a} ± 0.72	8.02 ^{a} ± 2.00	4.87 ^{a} ± 0.65	7.77 ^{a} ± 1.90	8.39 ^{a} ± 3.37	6.43 ^{a} ± 2.91	9.78 ^{a} ± 0.70
Quercetin-3-*O*-rutinoside	0.10 ^{a} ± 0.01	0.09 ^{a} ± 0.00	0.08 ^{a} ± 0.01	0.25 ^{a} ± 0.03	0.52 ^{a} ± 0.45	0.38 ^{a} ± 0.03	0.68 ^{a} ± 0.08	0.39 ^{a} ± 0.07	0.69 ^{a} ± 0.30	0.22 ^{a} ± 0.06	0.17 ^{a} ± 0.03	0.18 ^{a} ± 0.03
Quercetin-coumaryl hexoside	0.16 ^{a} ± 0.06	0.20 ^{a} ± 0.01	0.18 ^{a} ± 0.03									
Total content flavonoids	0.26 ^{a} ± 0.05	0.29 ^{a} ± 0.01	0.26 ^{a} ± 0.05	0.25 ^{a} ± 0.03	0.52 ^{a} ± 0.45	0.38 ^{a} ± 0.03	0.68 ^{a} ± 0.08	0.39 ^{a} ± 0.07	0.69 ^{a} ± 0.30	0.22 ^{a} ± 0.06	0.17 ^{a} ± 0.03	0.18 ^{a} ± 0.03

Mean ± standard deviation; different letters indicate significant differences between irrigations variants within each species and compound (Tukey's HSD test, $p \leq 0.10$); C: Control, DS: Drought stress; C = control, 60 - 70% field capacity; DSI = drought stress variant I, 35 - 45% field capacity; DSII = drought stress variant II, 15 - 25% field capacity.

2016; Muriuki, 2015). In our experiment, earliest possible harvest of leaves was 10 weeks after planting.

Compared to other leafy vegetables like spinach (88 – 94% water content) and chard (91 – 94% water content), leaves of the amaranth species and accessions studied were found to have lower water contents ranging from 85 – 89%, which is consistent with findings by Mahawar and Jalgaonkar (2012). Based on the higher levels of fiber and ash (Das, 2016) with less fresh leaf material, target nutrient intake can be achieved.

Protein contents of the amaranth accessions (23 – 32%) were higher than or comparable to that reported in literature, i. e. 15% (USDA, 2018), 14 – 21% (Muriuki, 2015), 28 – 32% (Salim, 1999), 28% (Kwenin et al., 2011). Additionally, protein contents of all accessions were higher than in some of the vegetables commonly consumed in Sub-Saharan Africa, e. g. spinach 18%, chard 11% (USDA, 2018), making amaranth leaves a suitable species for consumption to defy protein deficiency as one of Sub-Saharan Africa's main nutritional problems which affects a large proportion of the poor populations (FAO, 2016). The consumption of 100 g leafy amaranth could contribute 10% of the required daily intake (46 – 56 g; WHO, 2002). Additionally, amaranth leaf protein for use as human food is highly extractable (Ghaly and Alkoaik, 2010) and shows an excellent amino acid composition, digestibility, and nutritional effectiveness (Shukla et al., 2010), especially traced back to a high lysine content as essential amino acid (Andini et al., 2013). Therefore, including lysine into the diet is crucial for health purposes and shortage can lead to several diseases stated including defective connective tissues (Ngugi et al., 2017). Amaranth is therefore a high qualitative protein rich vegetable, even in comparison to maize with comparably high lysine contents (Beswa et al., 2016), which might be a solution to fight protein deficiency.

All amaranth species studied revealed considerably high contents of potassium compared to those reported in literature and to other vegetables consumed in Sub-Saharan-Africa (Tab. 6). Calcium contents of the amaranth species of the present study were mostly higher compared to the values found in literature (Tab. 6). In comparison to spinach and chard, amaranth leaves can be considered as a calcium-rich source of food. As also stated for calcium, amaranth is an excellent source of magnesium (Tab. 6). Compared to phosphorus contents in literature, the amaranth accessions analyzed in this study showed high contents. All amaranth accessions had lower iron contents compared to contents found in literature (Tab. 6). According to these results, iron content is also relatively low compared to spinach and chard. Even when zinc contents of most of the amaranth accessions studied were lower compared to literature, studied amaranth species still had higher amounts in comparison to other leafy vegetables consumed in Sub-Saharan-Africa like spinach and chard (Tab. 6). Since amaranth is often referred in literature to be rich in zinc and iron (Mnkeni et al., 2007), zinc and iron contents of the present species and accessions were rather low. Differences can be explained by the growth stage of the plant at harvest, showing that iron, zinc, and potassium accumulating to a lower extent as the plant enters reproductive stage (Flyman and Afolayan, 2008; Khader and Rama, 1998; Nyonje, 2015). Magnesium and calcium showed an opposite trend (Khader and Rama, 2003; Nyonje, 2015). According to the fact that deficiencies of iron and zinc are the most prevalent forms of micronutrient malnutrition in the world (FAO, 2015; WHO, 2012), the selection of the appropriate harvest time of amaranth leaves is an important criterium. Therefore, Showemimo and Olarewaju (2004) recommended a maturity period of six weeks for optimal contents of all nutritional valuable compounds.

A clear pattern of nutrient contents among species could generally not be determined in the present study. Plants of *A. caudatus* (288279) showed significantly high contents of all nutritional compounds analyzed. Although *A. caudatus* is mainly known as a grain source, leaves are highly nutritional and might therefore be a suitable species for nutritious purposes. Accessions of *A. cruentus*, *A. hybridus*, and *A. hypochondriacus* showed a highly diverse nutrient profile. Whereas in some accessions generally high nutrient contents and fresh weight could be detected (e. g. *A. cruentus* 22379, 538255), other were generally low in most nutrient levels but revealed high fresh weights (e. g. *A. cruentus* 604666, 641047) or low fresh weights

Tab. 6: Content of nutrients in the analyzed amaranth leaves, including values for RDI, literature values and nutrient contents of other vegetables

	Values own research [mg 100 g^{-1} FW]	Proportion of recommended daily amount by consuming 100 g FW		Comparison to literature		Comparison to other vegetables consumed in Sub-Saharan-Africa (Reference: USDA, 2018)
			Recommended daily intake (RDI) – Ministry of Health, 2017	Values [mg 100 g^{-1} FW]	Reference	Values [mg 100 g-1 FW]
Potassium	542 – 717	14 – 25%	3,800 (2,800 mg*)	611	USDA, 2018	spinach: 558 chard: 379 maize: 254
Calcium	304 – 497 3	0 – 50%	1,000 (1,000 mg*)	215 287 131 – 337 225 – 400	USDA, 2018 Larsen et al., 2003 Muriuki, 2015 Nyonje, 2015	spinach: 99 chard: 51
Magnesium	131 – 230	31 – 72%	420 (320 mg*)	55 177	USDA, 2018 Nyonje, 2015	
Phosphorus	74 – 166	7 – 17%	1,000 (1,000 mg*)	50	USDA, 2018	
Iron	0.9 – 1.3	5 – 16%	8 (18 mg*)	2.32	USDA, 2018	spinach: 2.71 chard: 1.8
Zinc	0.4 – 0.9	3 – 11%	14 (8 mg*)	0.9 0.6 – 1.7	USDA, 2018 Muriuki, 2015	spinach: 0.5 chard: 0.4

FW = fresh weight
*men/women 31-50 yr.

(e. g. *A. hybridus* 538324, *A. hypochondriacus 649305*). Therefore, a specific selection of accession is necessary to produce amaranth leaves with a high nutritional value along with high yields of leaf material.

Additionally to protein and macro-/micronutrients, secondary plant metabolites, i. e. phenolic acids and flavonoids in leaves of the amaranth species and accession were analyzed. Health promoting effects of amaranth (used in traditional medicine to treat e. g. fever, pain) are attributed to these metabolites (Nana et al., 2012), which were also found to correlate with the antioxidant capacity (Gogo et al., 2018). Therefore, consuming amaranth species and accessions with high contents is one possibility to improve human health. The contents of phenolic acids and flavonoids in the analysed amaranth accessions were highly variable with *A. hybridus* showing the highest phenolic acid (14,89 µmol g^{-1} dry weight) and flavonoid (1,16 µmol g^{-1} dry weight) contents for accessions 538325 and 538324, respectively. Furthermore, both accessions of *A. hypochondriacus* revealed generally lower contents of flavonoids among the species studied. In general, the polyphenol contents were found to be lower in comparison to those reported in literature, especially for flavonoids (Gogo et al., 2018; Sarker and Oba, 2018). Explanatory approaches are multifarious as secondary plant metabolites are highly influenced by abiotic (i. e. environmental factors, like temperature, fertilization) and biotic factors (i. e. pathogen infestation) as well as by the genetic constitution (selection of species/genotype) or developmental stage of a plant (Joshi et al., 2018; Podsedek, 2007; Yang et al., 2018).

Impact of drought stress on growth pattern and nutritional value

Scarcity of water is a severe environmental constraint to plant growth and productivity and therefore the most critical threat to world's food security (FAO, 2016). Amaranth is known as a plant that can grow under environmental adverse conditions, where most of the basic crops are not able to develop and therefore a suitable crop for semi-arid regions (Das, 2017). Amaranth can avoid water stress through restricted growth due to the closure of stomata to prevent water loss and maintaining a leaf water potential that keeps the leaf turgor in order to avoid wilting (Bello, 2013; Santella and Lawson, 2016). Additionally, osmo-protection can be achieved by the accumulation of free proline under drought stress (Heidaiy and Moaventi, 2009). Present results revealed a clear evidence of a significant increase of proline accumulation at severe exposure to drought stress (DSII) in comparison to control (C) for *A. cruentus* (increase of 157%), *A. hybridus* (increase of 32%), and *A. hypochondriacus* (increase of 71%). These results are in accordance with literature, where authors detected a proline accumulation in water stressed amaranth plants (Slabbert and Krüger 2014; Umebese, 2009) and correlate this increase with a higher capacity to absorb water from the soil and therefore improved drought tolerance (Chun et al., 2018). Additionally to the accumulation of free proline in leaves, a significant growth restriction was detected for the analyzed amaranth species under severe drought stress (DSII) for plant height and fresh weight. Therefore, a tendency of reduction with increasing levels of drought stress (C > DSI > DSII) could be observed which is in accordance with literature (Masariramb et al., 2012; Wang et al., 2003). Wang et al. (2003) also reported a yield reduction of 30 – 50% of amaranth plants under drought stress conditions. In comparison to rice plants, amaranth survived a drought stress treatment of 12.5% and 25% of field capacity in a study conducted by Chauhan and Abugho (2013), whereas plants cultivated on less than 25% field capacity did not survive longer than 35 days after transplanting demonstrating that the duration of drought stress is another important factor. Interestingly, the content of free proline as well as the leaf fresh weight of *A. caudatus* were not significantly affected by any of the drought stress treatments, indicating that this species seems to be highly drought tolerant.

The study revealed a general tendency of nutritional increase with increment of drought stress severity (C < DSI < DSII) for K (*A. cruentus*, *A. hybridus*, *A. hypochondriacus*), Ca and Mg (*A. caudatus*, *A. cruentus*, *A. hypochondriacus*), P (*A. caudatus*, *A. cruentus*), Zn (*A. cruentus*, *A. hybridus*), and Fe (all four species) (Tab. 4). Results of this study are in accordance with findings of Sarker and Oba (2018) for Ca, K, and Mg, where contents in leaves of *Amaranthus tricolor* increased with drought stress severity showing highest contents at 30% field capacity and lowest contents on controlling level. For Fe and Zn contradictory findings were observed (Sarker and

Oba, 2018). In comparison to literature stating negative effects of drought stress on phosphorus availability (He and Dijkstra, 2014), in the conducted study increasing P contents were observed. Literature refers results of diminished nutrient concentration in plant tissues to limited total nutrient uptake and translocation due to a reduced transpiration rate and therefore decreased water availability under drought stress (Farooq et al., 2009). However, plant species and genotypes may vary in their response to mineral uptake under drought stress. Especially *A. cruentus* developed significantly high contents of all nutrients at severe drought stress (DSII) and could therefore be a suitable species cultivated in drought prone areas, although at the expense of lower yields, i. e. leaf fresh weight. Additionally, drought can depress plant growth by reducing N and P uptake, transport, and redistribution (Rouphael et al., 2012), and furthermore might result in a significant decline in total protein content of plants. Whereas Sarker and Oba (2018) found an increase of protein in amaranth under drought stress, significant differences of protein content in the analyzed four species could not be detected.

In comparison to the findings of Sarker and Oba (2018), the phenolic acid and flavonoid contents of three out of the four selected species and accessions were not significantly influenced by drought stress. Only the total phenolic acid content of *A. cruentus* significantly increased with increasing drought stress. The effects of drought stress on secondary plant metabolites strongly depend on genotype, maturity at harvest, weather, cultivation, and storage conditions (Podsedek, 2007). Studies on lettuce also demonstrated that only one cultivar among others responded to different water regimes via increasing of phenolic compounds, whereas the other cultivars/varieties remained unaffected (Eichholz et al., 2014).

Focus of this work was placed on the nutritional value of amaranth leaves. Nevertheless, amaranth is a crop grown for dual uses, for high foliage and high grain yields. Therefore, it is recommended to use amaranth species as well as accessions where harvest of leaves and grains is targeted. Whereas Dinssa et al. (2018) detected this negative interaction in different amaranth species, Hoidal et al. (2019) found that defoliation up to 50% did not result in a decrease of seed yield and quality for different varieties of *A. cruentus*, *A. hypochondriacus*, and *A. caudatus*. According to Joshi et al. (2018), *Amaranthus* spp. showed a high genetically diversity, which make it an ideal crop for breeding, identifying species and accessions combining high yields of leaves and seeds.

The present study demonstrated that leafy amaranth species revealed high nutritional and health-promoting properties. Nevertheless, the different species and accessions studied showed diverse profiles (contents and compositions) of nutrients and secondary plant metabolites which might be considered in respective production areas. Furthermore, *Amaranthus* ssp. showed a high drought stress tolerance, and even with an increasing drought stress, a tendentious increase of nutrient compounds was observed. Therefore, due to its high nutritional value, drought tolerance, easy cultivation, and high biodiversity, *Amaranthus* spp. is an ideal crop for food security, especially in Sub-Saharan Africa, where problems like droughts and malnutrition are ubiquitous.

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Conflict of interest

No potential conflict of interest was reported by the authors.

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