

# Domestication syndrome of *Amaranthus cruentus* (Amaranthoideae, Amaranthaceae) at its putative domestication centres

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Academic editor: Elmar Robbrecht ♦ Received 28 May 2025 ♦ Accepted 19 December 2025 ♦ Published 31 March 2026

## Abstract

**Background and aims** – *Amaranthus cruentus*, native to Mexico and Guatemala, has significant cultural, medicinal, and ornamental uses and growing agricultural relevance. However, little research has focused on its origin and domestication. To determine its domestication syndrome, we identified a set of domestication-linked traits in cultivated *A. cruentus* and compared them with its wild ancestor *A. hybridus* and with *A. cruentus* accessions from different regions. We assessed whether the domestication syndrome enables us (1) to differentiate between the wild and cultivated species and (2) to determine the level of domestication in populations of *A. cruentus* from different putative centres of domestication.

**Material and methods** – Populations of *A. cruentus* and *A. hybridus* were sampled from Mexico and Guatemala. Ten morphological traits related to vegetative stage, anthesis, and seed maturation were evaluated to identify patterns linked to domestication. PERMANOVA was used to analyse differences in traits between cultivated and wild populations.

**Key results** – Basal stem size, plant height, inflorescence length, and seed yield (total mass) differed significantly between *A. cruentus* and *A. hybridus*. *Amaranthus cruentus* had a broader range of seed and inflorescence colours. The Mexican accessions had taller plants, longer inflorescences, and greater seed yield than the Guatemalan.

**Conclusion** – The selected set of characters unambiguously distinguishes the wild *A. hybridus* from the cultivated *A. cruentus*, enables differentiation of domestication levels, suggesting that Mexican accessions are more domesticated than the Guatemalan.

## Keywords

*Amaranthus hybridus*, artificial selection, grain amaranth, Guatemala, Mexico, morphological traits, selection pressure

## INTRODUCTION

Amaranthaceae sensu lato (s.l.) includes Amaranthaceae sensu stricto (s.s.), Chenopodiaceae, and other related genera (APG IV: The Angiosperm Phylogeny Group 2016). Amaranthoideae was formerly classified as a subfamily of Amaranthaceae s.s. (sensu Schinz 1893), but in the

present, Amaranthoideae (= Amaranthaceae s.s.) is one of the five subfamilies that comprise Amaranthaceae s.l. (Morales-Briones et al. 2021). However, *Amaranthus* L. is well preserved in the taxonomic history of Amaranthaceae and appears to be monophyletic (Sandoval-Ortega et al. 2017; Xu et al. 2024). The genus comprises 60–75 species, including the cultivated “grain amaranths” (Iamónico

2015; Wolosik and Markowska 2019; Adhikary et al. 2020); *Amaranthus caudatus* L., *A. cruentus* L., and *A. hypochondriacus* L. (Sauer 1950, 1967).

Grain amaranths have grain-like seeds, that are used in a similar way as the fruits (grains) of Poaceae. Their dry fruits are either indehiscent (utricles) or dehiscent (pyxidial), containing a single seed (Sánchez-del Pino et al. 2025). In the Americas, grain amaranths have been cultivated for thousands of years (Purugganan and Fuller 2011; Purugganan 2019) and, with maize (*Zea mays* L.) and beans (*Phaseolus vulgaris* L.), formed part of the staple diet of the Aztecs, Incas, and Mayas (Das 2014; Joshi et al. 2018; Zeece 2020). Although there is consensus that the three grain amaranths evolved from wild *A. hybridus* L., which is distributed throughout Mexico, Central America, northern South America, and in the Mediterranean region of Europe (Das 2016a), there is less consensus about their domestication process (Sánchez-del Pino et al. 2025). However, despite the recognition of the grain amaranths as Intangible Cultural Heritage by UNESCO, their future in Mexico is uncertain due to its limited cultivation (Hernández-Hernández et al. 2018). Efforts are underway to reestablish the value of the grain amaranths (Curiel 2022).

### Domestication of plants

Plant domestication dates back more than 10,000 years (Pickersgill 2016). It is an evolutionary process; a wild species is gradually transformed into a cultivated species via artificial trait selection instead of natural selection (e.g. Blanckaert et al. 2012; Chacón-Sánchez 2018; Gonçalves-Dias et al. 2023). Several categorization systems have been proposed to describe the different degrees of domestication, but the two most widely cited are Clement's (1999) system, which includes wild, incidentally co-evolved, incipiently domesticated, semi-domesticated, and fully domesticated; and that of Meyer et al. (2012), who reduced the categories to domesticated, semi-domesticated, and undomesticated.

### Domestication syndrome

Other authors defined the concept of domestication syndrome as a set of morphological traits that differentiate domesticated plants from their wild ancestors and are usually modifications that resulted from human selection (Harlan 1971; Hammer 1984; Meyer et al. 2012; Denham et al. 2020; Pacheco-Huh et al. 2021). Typical features of a domestication syndrome, often resulting from selection for preferred characteristics include changes to secondary metabolism (e.g. reduced bitter compounds, increased sugars, and pigment changes), plant architecture (e.g. modified branching, stem or inflorescence structure, plant height, apical dominance), leaves (e.g. size, shape, arrangement), and fruits (e.g. increased seed retention, larger seeds/fruits, loss of seed dormancy, fruit/seed colour) (Brenner et al. 2000; Rana et al. 2005; Meyer et al. 2012; Joshi et al. 2018; Purugganan 2019; Denham

et al. 2020; Mboujda et al. 2022). Plant species have undergone different degrees of domestication, usually in relation to their economic importance. Some are fully domesticated such as maize, which has large seeds that have lost their dormancy and dispersal capacity, and reduced branching and photoperiod sensitivity (Stetter et al. 2017). Other crops such as lentils, quinoa, sorghum, and grain amaranths apparently have poorly demarcated domestication syndromes (Li and Siddique 2018; Ruth et al. 2021; Chapman et al. 2022).

### Domestication of grain amaranths

The domestication syndrome of the grain amaranths is still under debate. Some have noted that traits such as seed size and seed retention are shared with their wild relatives (Sauer 1967; Stetter et al. 2020). Stetter et al. (2017) reported that seed colour in *A. caudatus* is associated with domestication: most cultivated species have pale seeds, while wild amaranth species have dark brown seeds. These authors also revealed a significant loss of genetic variation in domesticated amaranths, suggesting strong agricultural and cultural selection. Based on domestication traits (inflorescence shape, seed shattering, and seed size), which are shared by both wild and cultivated species in Amaranthaceae, Stetter et al. (2017) suggested that the domestication of amaranths may not fit neatly into the traditional model of domestication for well-established crops, proposed by Hammer (1984). Moreover, the phylogenetic and taxonomic status of the putative ancestors of the grain amaranths, *A. hybridus* and *A. quitensis* Kunth, is in question (Kietlinski et al. 2014; Sánchez-del Pino et al. 2025). Stetter et al. (2017) concluded that weak artificial selection for seed colour and a high level of gene flow between *A. caudatus* and *A. quitensis* has counteracted the fixation of domestication traits.

### *Amaranthus cruentus*

*Amaranthus cruentus* is an annual plant native to Mexico and Guatemala but is also currently cultivated in the United States, Argentina, and China (Das 2016a; Wolosik and Markowska 2019). In Mexico, the cultivation of *A. cruentus* declined notably after the arrival and conquests of the Spaniards, relegating it to an underutilized crop with restricted cultivation and limited economic relevance (Joshi et al. 2018).

Archaeological findings, such as in the Coxcatlán caves of Tehuacán, Mexico, suggest that amaranth was crucial to the Aztec civilization and as such extensively cultivated in Mexico by the 15<sup>th</sup> century. The domestication probably began more than 6000 years ago (Joshi et al. 2018; Turner et al. 2021). Sauer (1967: 123) mentioned: “*Amaranthus cruentus* evidently originated as domesticated grain crop somewhere in southern Mexico or Guatemala, the only region where it is found in aboriginal cultivation within the range of its probable progenitor, *Amaranthus hybridus*”. He also proposed that each grain amaranth has

its own “progenitor” at a different centre of domestication. Although the precise origin of cultivated amaranths remains unclear, *A. hybridus* has been widely recognised as the most likely ancestor (Kietlinski et al. 2014; Stetter et al. 2020; Gonçalves-Dias et al. 2023).

*Amaranthus cruentus* produces seeds (pseudo-grains, Sánchez-del Pino et al. 2025) that are consumed like a cereal grain and are of high value (Aguilar et al. 2015; Das 2016b; Adeniji 2018; Manyelo et al. 2020; Araujo-León et al. 2023). The International Union for the Protection of New Varieties of Plants (UPOV 2024) reports 29 varieties of *A. cruentus* from Mexico, Russia, France, the European Union, among others. The National Plant Germplasm System of the United States Department of Agriculture (USDA) holds 428 accessions of *A. cruentus* (364 active, 349 available), including “landraces” [sic] from Mexico, Guatemala, the United States, India, and China. Additionally, Kauffman (1992) described “morphological groups” of *A. cruentus* from Guatemala and Mexico, which are clusters of accessions with distinctive traits resulting from traditional selection and might each represent distinct “landraces” [sic] (National Plant Germplasm System 2025).

Three local races of *A. cruentus* (Mexican, African, and Guatemalan) have also been described, each with specific “phenological” and phenotypic characteristics generated through artificial selection in diverse cultural contexts (Kauffman 1992; Espitia-Rangel et al. 2010). Kauffman’s (1992) “morphological groups” refer to variation at the accession or “landrace” level, whereas the three local races correspond to broader, geographically structured categories recognised later. These local races illustrate how hybridization and selection have shaped the diversity and adaption of *A. cruentus* across different regions (Espitia-Rangel 2018).

### Aim of the study

Although we introduced features that are associated with the domestication syndrome in plants, only seed colour has consistently been identified as a domestication trait for grain amaranths (Sauer 1967; Stetter et al. 2017, 2020; Sánchez-del Pino et al. 2025). Attempts to define a domestication syndrome for the grain amaranths have mostly described generalities, neglecting that each crop has its own evolutionary history and thus its own domestication syndrome. Martínez-Núñez et al. (2019) proposed a method to use amaranths as model plants based on their life cycle. We propose that observations and measurements of traits at different phenological stages can be used to identify a set of characters that pertain to the domestication syndrome.

Studies to assess morphological traits of cultivated amaranths (e.g. Hauptli and Jain 1978; Sogbohossou and Achigan-Dako 2014; Thapa and Blair 2018) did not systematically evaluate traits that resulted from domestication in any of the proposed domestication centres. Our work is the first comparative morphometric

analysis of *A. cruentus* in its postulated centres of domestication (Mexico and Guatemala) including both wild (*A. hybridus*) and cultivated accessions. Using populations of *A. cruentus* from Mexico and Guatemala, we sought to identify a set of characteristics based on measurements of morphological characters at different developmental stages of the plant. We then tested their usefulness, in particular considering Sauer’s (1950, 1967) main hypothesis, by evaluating whether this set of traits can reveal different degrees of domestication in the putative centres of domestication proposed by Sauer. We also formulated the following questions: Can we identify a set of traits that unambiguously separates wild, ancestral *A. hybridus* from cultivated *A. cruentus*? Can this set be used to determine the level of domestication in populations from different centres of domestication of *A. cruentus*?

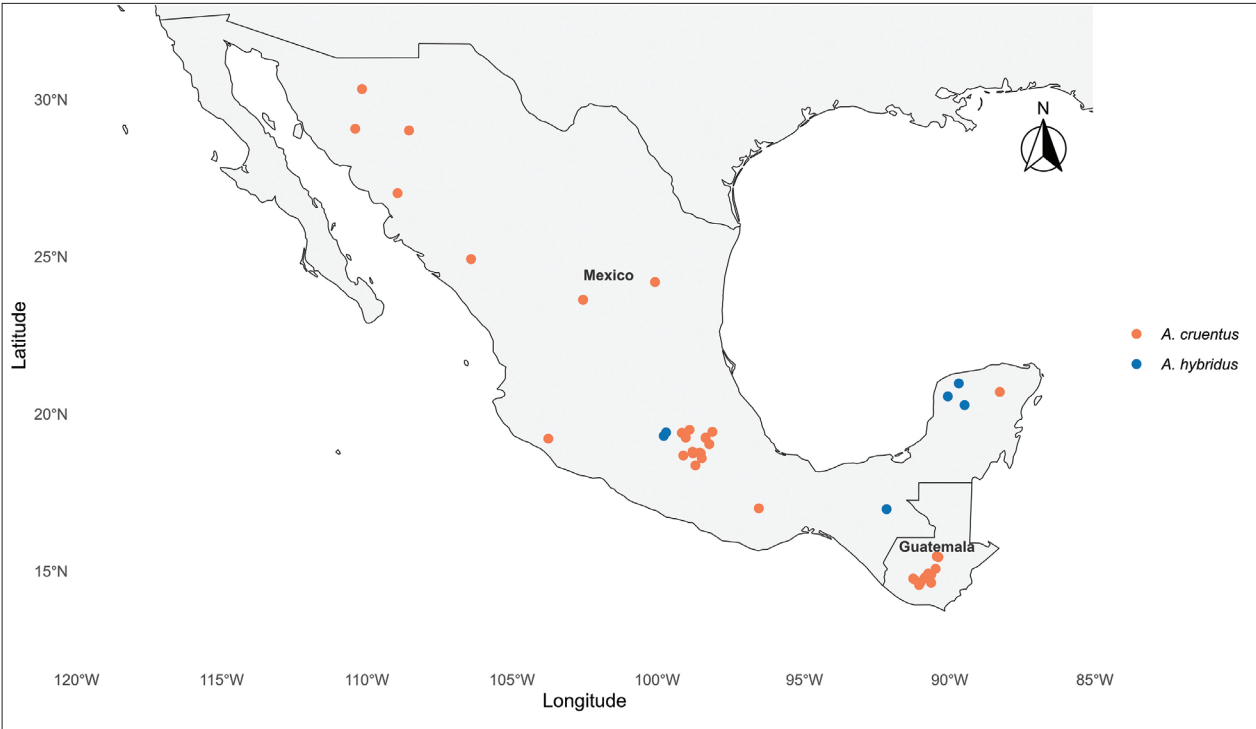
## MATERIAL AND METHODS

### Plant material




Among the 221 individuals belonging to 60 accessions from Mexico and Guatemala that were used, 54 accessions were *Amaranthus cruentus* (169 individuals) and six accessions were its wild relative *Amaranthus hybridus* (52 individuals). Fifty-one accessions of *A. cruentus* were obtained from the National Plant Germplasm System of the United States Department of Agriculture-Agricultural Research Service (National Plant Germplasm System 2025), and three were collected in situ. Thirty-six accessions are from Mexico and 18 from Guatemala. Material of the wild species *A. hybridus* is challenging to obtain due to limited representation in seed banks and herbarium collections, and because it is often considered a weed, it has received less attention. The six accessions of *A. hybridus* were collected in Mexico and served as reference species (voucher information: Suppl. material 1; distribution: Fig. 1). Plant identifications were based on the original sources (seed banks and personal collections). Once the plants were cultivated and reached maturity, the original source was checked using the diagnostic keys developed by Sánchez-del Pino et al. (2019). Herbarium specimens of the collected plants were deposited in CICY and UVAL (Thiers 2025).

### Plant growth conditions

The study was conducted at the Centro de Investigación Científica de Yucatán (CICY) from January to June 2023. Fifteen seeds for each accession (Suppl. material 1) were germinated under controlled conditions in a greenhouse (22–27°C). After 15 days, up to five of the most-developed seedlings of *A. cruentus* and a maximum of 10 of *A. hybridus* were transplanted into a terraced area in a randomized block design to minimise the effect of differences in natural light, that could influence plant size. Plants were observed and measured at three



**Figure 1.** Collection localities of accessions for the *Amaranthus* species used in this study.

	Vegetative stage	Reproductive stage	
Stages of development			
	Vegetative	Anthesis	Seed maturation
Days post-seeding	21 – 32	69 – 79	85 – 153
	20 *	60 – 150 *	90 – 180 *
	18 – 23 **	27 – 87**	35 – 122 **
Domestication-linked characters	Plant height Basal stem diameter Leaf length Leaf width	Plant height Basal stem diameter Leaf length Leaf width Duration of the vegetative stage Length of the terminal inflorescence Inflorescence color	Plant height Basal stem diameter Length of the terminal inflorescence Inflorescence color Dry mass of inflorescence Seed production Seed color

**Figure 2.** Plant stages, defined by Martínez-Núñez et al. (2019), of *Amaranthus cruentus* when morphological traits were measured (“Days post-seeding”), as described by Martínez-Núñez et al. (2019, grey row) and in this study (blue rows). Values with an asterisk are for *A. cruentus*; those with two asterisks are for *A. hybridus*.



stages: vegetative, anthesis, and seed maturation (Fig. 2; Martínez-Núñez et al. 2019). Although amaranths are predominantly autogamous, to prevent cross-pollination between the cultivated and wild species, we covered each inflorescence of both species with a 30 × 38 cm glassine bag during anthesis. In the greenhouse, plants were irrigated every third day throughout their life cycle. No fertilizers were applied. Pest control was implemented only when infestations were observed (for further details, see Xingú-López 2024).

### Assessment of domestication-linked morphological characters

All 221 plants available for the 60 accessions were measured at the vegetative stage (20 days post-seeding), anthesis stage (60 and 150 days post-seeding), and seed maturation (90 and 180 days post-seeding; Fig. 2).

Eight quantitative and two qualitative traits that are associated with domestication syndromes were considered. Quantitative traits were 1) plant height, 2) basal stem diameter, 3) leaf length, 4) leaf width, 5) terminal inflorescence length, 6) duration of the vegetative stage, 7) dry mass of inflorescence, and 8) seed yield (total mass). Qualitative traits were inflorescence and seed colour. Plant height (1) was measured with a standard tape measure using the method of Vazquez et al. (2011) and Ortiz-Torres et al. (2018). Basal stem diameter (2) was measured 5 cm above the ground using a digital micrometre (0–0.25 mm, Fowler, Massachusetts USA) as specified by Reinaudi et al. (2011). Leaf length (3) and width (4) were measured at the vegetative stage and anthesis. Starting at anthesis on, the leaves begin to senesce, then fall. Three to four randomly selected, well-developed leaves were marked to track length and width during both developmental stages. If the marked leaf had abscised, the closest leaf was used. Terminal inflorescence length (5) (from the last foliage leaf to the tip of the inflorescence) was measured at anthesis and seed maturation (Vazquez et al. 2011). Duration of the vegetative stage (6) was based on daily observations until the plant reached anthesis. Dry mass of inflorescences (7) was measured at seed maturation. The inflorescences were harvested individually and dried in a climate-controlled room at  $38 \pm 1^\circ\text{C}$  and 25–30% relative humidity. After drying under controlled room conditions (approximately 12% relative humidity), seed and dried inflorescences were weighed using a precision balance (220 g/ 0.1 mg, Ohaus Explorer, EX224, USA). Seed yield (total mass) (8) was weighed when seeds were mature. All seeds were removed manually from the inflorescences on one plant and weighed using a precision balance (220 g/ 0.1 mg, Ohaus Explorer, EX224, USA). Values were recorded in grams of total seed per plant.

The qualitative traits were assessed using the guidelines in the “Graphic Handbook for Variety Description in Amaranth (*Amaranthus* spp.)” by the National Seed Inspection and Certification Service (CP-SNICS 2006).

### Statistical analyses

PERMANOVA was used to test for significant differences in values for the morphological traits at each developmental stage between *A. cruentus* and *A. hybridus*, and among *A. cruentus* populations from different regions, because it is a non-parametric approach that does not rely on distributional assumptions, such as normality or homogeneity of variances. This method is particularly useful for analysing complex, high-dimensional datasets or when the assumptions of an ANOVA are not met (Dwivedi et al. 2019; Hamidi et al. 2019), as was the case for our data. Our samples comprised 169 individuals of *A. cruentus* and 52 of *A. hybridus*, which might cause a bias when using ANOVA; therefore, the small number of *A. hybridus* accessions did not influence the outcome of this study results when using PERMANOVA. Moreover, PERMANOVA was used to detect differences between Mexican and Guatemalan accessions of *A. cruentus*.

Minimum, maximum, and mean values and standard deviations were determined for each trait and compared between *A. cruentus* and *A. hybridus* at each of the three developmental stages using PERMANOVA in the R package *vegan* v.2.6-10 (Oksanen et al. 2025).

Nonmetric multidimensional scaling (NMDS) in the R package *vegan* v.2.6-10 (Oksanen et al. 2025) was used to visualise the similarity structure among samples of 1) *A. cruentus* and *A. hybridus*, 2) Mexican and Guatemalan populations of *A. cruentus*, in a lower-dimensional space based on the morphological traits at each stage. Pearson’s correlation analysis in R package *stats* v.4.4.0 (R Core Team 2024) was used to analyse how the traits are correlated within and between both species (Morales Saavedra et al. 2019; Ciccarelli and Bona 2022).

Plant height, basal stem diameter, leaf length and width, terminal inflorescence length, inflorescence dry mass, and seed yield were included in multivariate statistical analyses. Duration of the vegetative stage, inflorescence and seed colour were evaluated as qualitative descriptors and not included in the multivariate tests. The frequency of the occurrence of the qualitative characters was determined in each accession.

## RESULTS

### Morphometric analyses of wild and cultivated *Amaranthus* species

Our results revealed substantial morphological differences between the cultivated and wild species in plant height, leaf length and width at the vegetative stage; inflorescence length and duration of the vegetative stage at anthesis; and plant height, dry mass of the inflorescence, and seed yield (total mass) at seed maturation (Table 1). At the vegetative stage, plants of *A. cruentus* were taller and had larger and wider leaves compared to *A. hybridus*. The duration of the vegetative stage in *A. hybridus* was 49 days after transplant, compared to 100 days for *A. cruentus*.

**Table 1.** Minimum (Min), maximum (Max), and mean  $\pm$  SD for plant height, basal stem diameter, leaf dimensions, terminal inflorescence length, inflorescence dry mass, and seed yield of assessed *Amaranthus* species at different growth stage. \* d = days until anthesis.

Species name	Stage	Statistic	Plant height (cm)	Basal stem diameter (cm)	Leaf length (cm)	Leaf width (cm)	Duration of vegetative stage (d)*	Terminal inflorescence length (cm)	Inflorescence dry mass (g)	Seed yield (g)
<i>Amaranthus cruentus</i>	Vegetative	Min	2.50	0.11	1.90	0.83	60			
		Mean $\pm$ SD	16.02 $\pm$ 10.30	0.53 $\pm$ 0.27	6.08 $\pm$ 3.16	3.59 $\pm$ 1.95	100			
		Max	54.00	1.40	24.30	11.00	150			
	Anthesis	Min	42.30	0.50	3.60	1.70		2.00		
		Mean $\pm$ SD	118.01 $\pm$ 35.20	1.58 $\pm$ 0.49	14.60 $\pm$ 6.88	7.01 $\pm$ 5.93		10.74 $\pm$ 2.81		
		Max	247.00	2.58	53.43	13.66		53.50		
	Seed maturation	Min	33.50	0.52				16.00	5.00	1.81
		Mean $\pm$ SD	160.40 $\pm$ 45.60	1.66 $\pm$ 0.62				40.75 $\pm$ 11.60	45.7 $\pm$ 26.30	12.35 $\pm$ 9.49
		Max	262.60	6.00				74.00	119.00	43.54
<i>Amaranthus hybridus</i>	Vegetative	Min	2.40	0.11	1.03	0.47	27			
		Mean $\pm$ SD	11.00 $\pm$ 10.10	0.30 $\pm$ 0.20	3.90 $\pm$ 2.62	2.17 $\pm$ 1.40	49			
		Max	35.00	0.85	10.67	6.17	74			
	Anthesis	Min	9.50	0.16	1.20	0.73		1.60		
		Mean $\pm$ SD	59.19 $\pm$ 54.9	0.74 $\pm$ 0.63	5.90 $\pm$ 5.25	2.91 $\pm$ 4.31		7.55 $\pm$ 1.84		
		Max	177.00	2.22	14.83	6.83		22.30		
	Seed maturation	Min	18.00	0.66				7.50	7.00	1.76
		Mean $\pm$ SD	105.20 $\pm$ 66.30	0.97 $\pm$ 0.54				30.00 $\pm$ 11.60	18.08 $\pm$ 26.30	5.28 $\pm$ 5.05
		Max	225.00	2.04				69.00	62.00	18.56

**Table 2.** PERMANOVA of morphological traits at different growth stages of the two *Amaranthus* species.

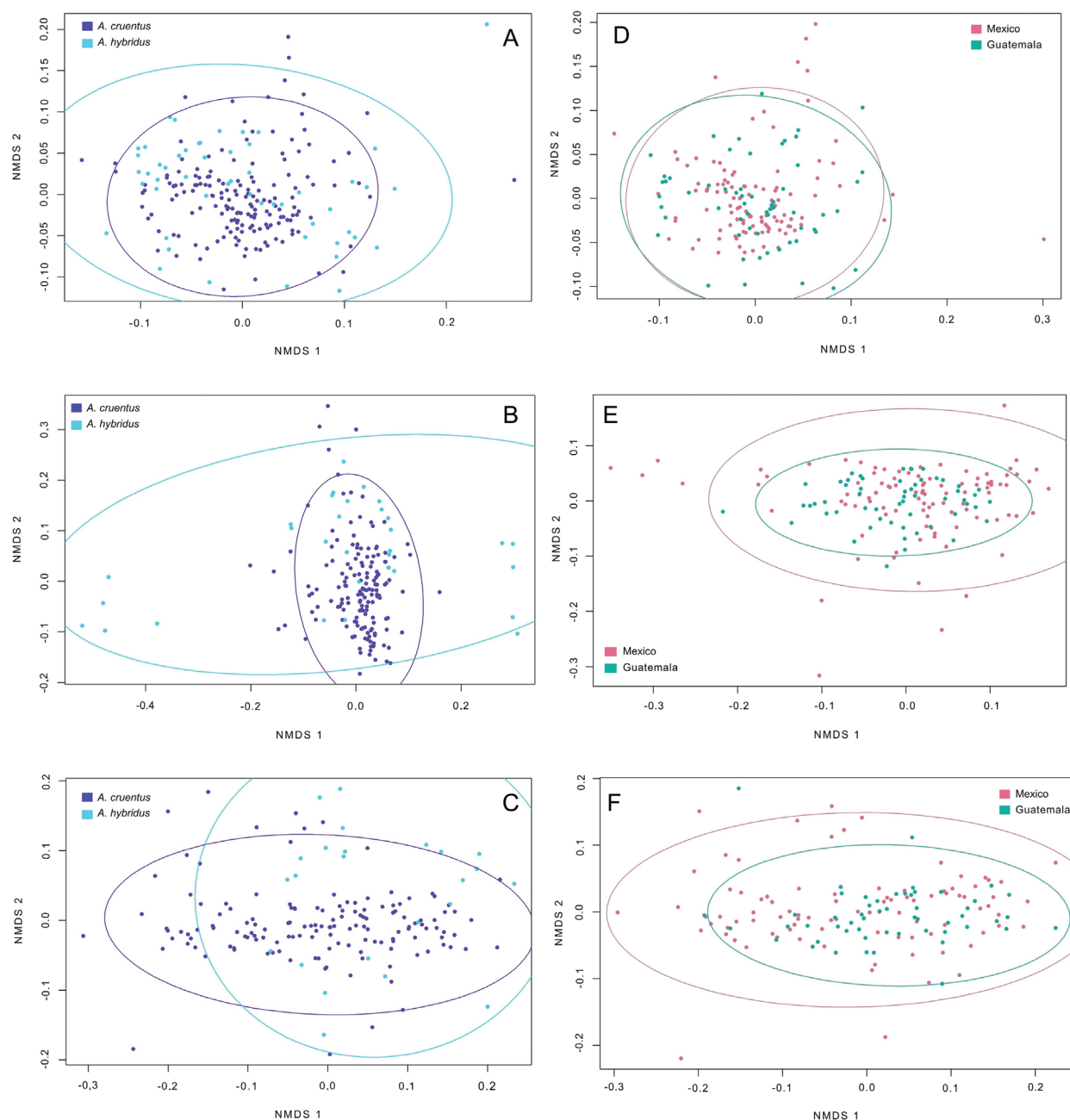
Stage	d.f.	SS	R <sup>2</sup>	F	Pr(>F)
Vegetative	1	1.95	0.12	30.22	0.001
Anthesis	1	3.76	0.35	103.61	0.001
Seed maturation	1	1.29	0.20	42.04	0.001

*Amaranthus cruentus* developed significantly larger inflorescences than *A. hybridus*. At seed maturation, mean plant height for *A. cruentus* was significantly greater than for *A. hybridus* and *A. cruentus* had substantially greater inflorescence dry mass and seed yield (total mass) compared to *A. hybridus*.

The PERMANOVA results (Table 2) showed the greatest differentiation between the two species at anthesis ( $F = 103.61$ ;  $p < 0.001$ ). At seed maturation, the differences remained significant ( $F = 42.049$ ;  $p < 0.001$ ), but the variance decreased to 20.1%. The vegetative stage

had the lowest level of differentiation ( $F = 30.226$ ;  $p < 0.001$ ), with only 12.18 % of the variance explained. The NMDS scatter diagram (Fig. 3) illustrates the variation between the two species across the growth stages: the traits of the cultivated species appear more clustered than those of the wild relative.

Several positive correlations were found between morphological traits of individual plants for the two *Amaranthus* species at different stages of growth (Table 3), reflecting trait variation across the two species. At the vegetative stage, plant height, stem diameter, and leaf

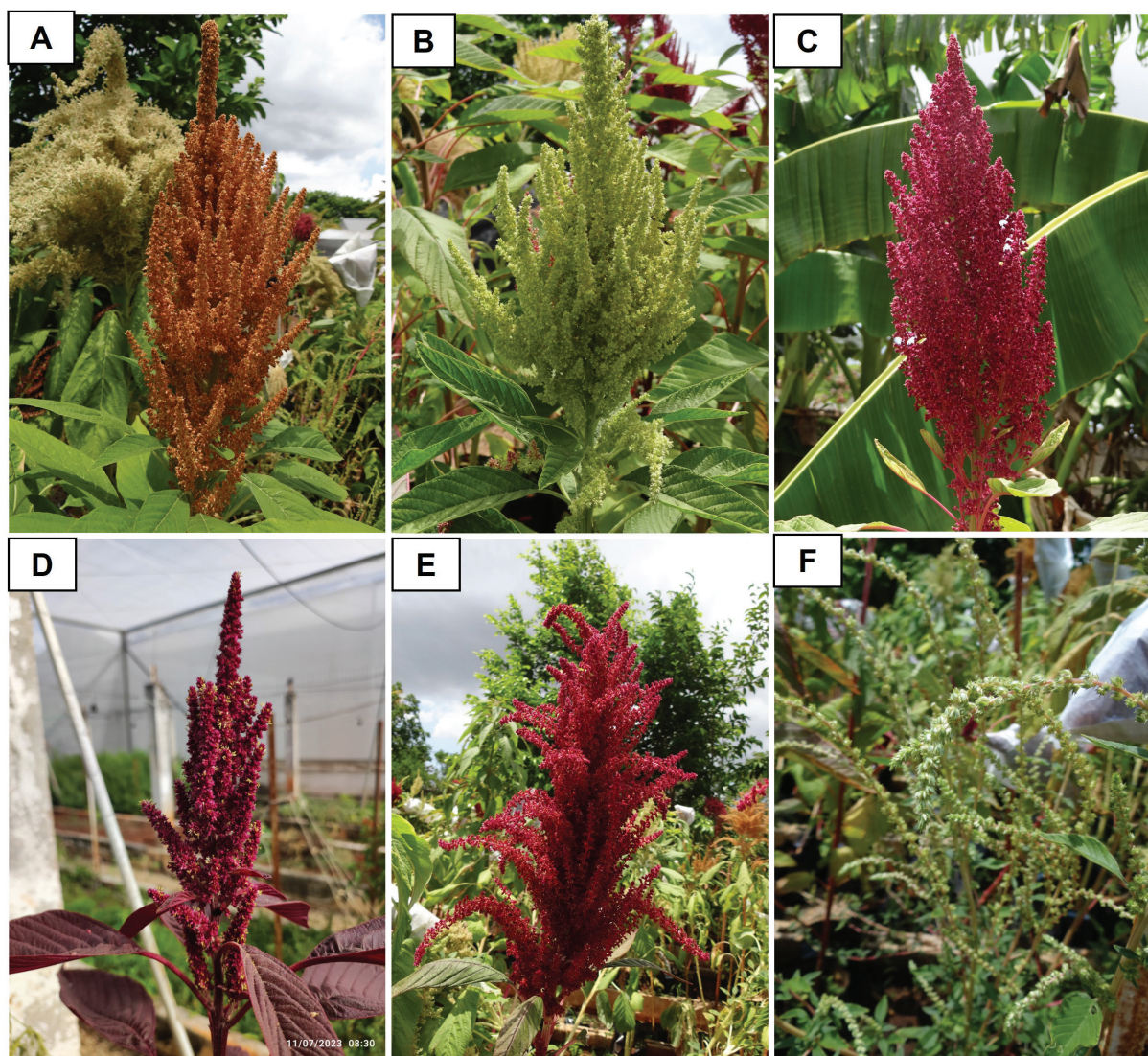


**Figure 3.** NMDS plots of traits. **A–C.** *Amaranthus cruentus* (blue dots) and *A. hybridus* (cyan dots) during different growth stages. **A.** Vegetative. **B.** Anthesis. **C.** Seed maturation. **D–F.** *A. cruentus* from Mexico (pink dots) and Guatemala (green dots) at different growth stages. **D.** Vegetative stage. **E.** Anthesis. **F.** Seed maturation.



**Table 3.** Pearson's correlation values of traits for the two *Amaranthus* species during different growth stages.

Stage	Trait	Plant height	Basal stem diameter	Leaf length	Leaf width	Terminal inflorescence length	Inflorescence dry mass	Seed yield
Vegetative	Plant height	1.00	0.89	0.77	0.77			
	Basal stem diameter	0.89	1.00	0.80	0.83			
	Leaf length	0.77	0.84	1.00	0.76			
	Leaf width	0.77	0.31	0.76	1.00			
Anthesis	Plant height	1.00	0.55	0.07	0.73	0.13		
	Basal stem diameter	0.55	1.00	0.57	0.65	-0.04		
	Terminal inflorescence length	0.13	-0.04	-0.001	-0.002	1.00		
	Leaf length	0.71	0.57	1.00	0.85	-0.001		
	Leaf width	0.72	0.65	0.85	1.00	-0.002		
Seed maturation	Plant height	1.00	0.67			0.47	0.46	0.31
	Basal stem diameter	0.67	1.00			0.48	0.63	0.58
	Terminal inflorescence length	0.47	0.48			1.00	0.63	0.56
	Inflorescence dry mass	0.49	0.63			0.63	1.00	0.78
	Seed yield	0.31	0.58			0.56	0.78	1.00

**Figure 4.** Colour variations in inflorescences of the two *Amaranthus* species studied. A–E. *A. cruentus*. F. *A. hybridus*.



length and width were positively correlated. At anthesis, positive correlations persisted between plant height and leaf length and width. At seed maturation, inflorescence dry mass and seed yield were strongly correlated, and stem diameter was also positively correlated with inflorescence dry mass and seed yield.

Furthermore, correlations among the morphological traits were examined within each species separately to explore trait interrelationships. Plant height, stem diameter, leaf length, and leaf width were strongly positive correlated at the vegetative stage in *A. cruentus* and *A. hybridus*. At anthesis, positive correlations among plant height, leaf length, and leaf width persisted in both species except for stem diameter, which was only positively correlated at this stage for *A. cruentus*. During the seed maturation stage, positive correlations among plant height, stem diameter, terminal inflorescence length, inflorescence dry mass, and seed mass were present in both species. However, the correlation between terminal inflorescence length and seed mass was comparatively weaker in *A. hybridus* (Suppl. material 2).

At anthesis, inflorescences of *A. cruentus* had a wider range of colours (shades of green, purple, pink, and red) than those of *A. hybridus*, which are green (Fig. 4). However, the most common inflorescence colour in *A. cruentus* was green (Fig. 5A).

Mature seeds of *A. cruentus* exhibited a wide range of colours (white to yellow, brown, and black), but white was most common. Seeds of *A. hybridus* were always black (Figs 5B, 6).

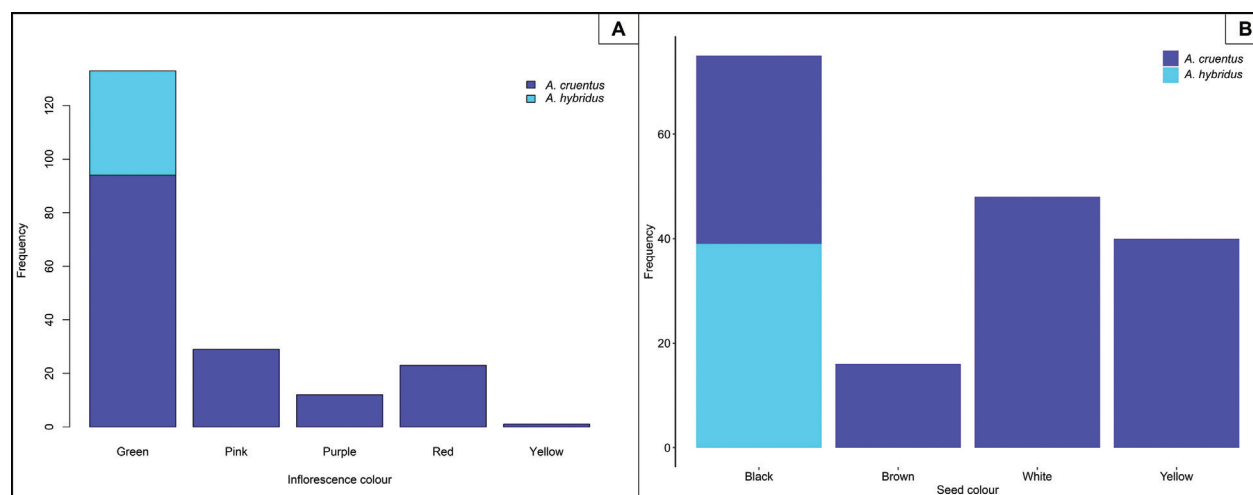
### Traits of *A. cruentus* accessions from Mexico and Guatemala

The comparative morphometric analysis of the traits at three growth stages showed significant differences between the accessions from Mexico and Guatemala

(Table 4) in leaf length and width at the vegetative stage; plant height, basal stem diameter, leaf length, leaf width, and terminal inflorescence length during anthesis; and plant height, basal stem diameter, terminal inflorescence length, inflorescence dry mass, and seed yield at seed maturation stage. During the vegetative stage, Mexican accessions had larger and wider leaves than the Guatemalan (Table 4). At anthesis, Mexican accessions had taller plants, thicker basal stems, larger leaves, and considerably longer terminal inflorescences (43 vs 37 cm in Guatemalan accessions; Table 4). At seed maturation, Mexican accessions consistently produced taller plants (262.6 vs 213.0 cm in the Guatemalan accessions; Table 4), thicker basal stems, and longer and heavier inflorescences, resulting in greater dry biomass (51 vs 37 g, respectively; Table 4). The Mexican accessions also had higher seed yields (mean 13.5 g, max 43.5 g) compared to the Guatemalan accessions.

The PERMANOVA analysis (Table 5) comparing the Mexican and Guatemalan accessions of *A. cruentus* revealed significant differences during the vegetative stage ( $F = 7.98$ ;  $p < 0.004$ ) and seed maturation ( $F = 5.57$ ;  $p < 0.012$ ), but not during anthesis ( $F = 2.39$ ;  $p > 0.1$ ). In the NMDS ordination analysis (Fig. 3), individuals of *A. cruentus* from Mexico and Guatemala during the vegetative stage were not clearly separated by country (Fig. 3D). In contrast, at anthesis (Fig. 3E) and seed maturation (Fig. 3F), individuals were more dispersed in the ordination space, reflecting increased morphological variation within the species.

Several positive correlations among the accessions of *A. cruentus* were observed (Table 6): at the vegetative stage, plant height, stem diameter, and leaf length and width; at anthesis, plant height, stem diameter and leaf length and width; at seed maturation inflorescence dry mass with seed yield, terminal inflorescence length and stem diameter with inflorescence dry mass and seed yield.



**Figure 5.** Frequency distribution of (A) inflorescence colours at anthesis and (B) mature seed colours for *Amaranthus cruentus* and *A. hybridus*.

**Table 4.** Minimum (Min), maximum (Max), and mean  $\pm$  SD for plant height, basal stem diameter, leaf dimensions, terminal inflorescence length, inflorescence dry mass, and seed yield of assessed *Amaranthus cruentus* from Mexico and Guatemala at different growth stages.

Species	Stage	Statistic	Plant height (cm)	Basal stem diameter (cm)	Leaf length (cm)	Leaf width (cm)	Terminal inflorescence length (cm)	Inflorescence dry mass (g)	Seed yield (g)
Mexico	Vegetative	Min	6.00	0.11	1.91	1.06			
		Mean $\pm$ SD	16.00 $\pm$ 8.08	0.55 $\pm$ 0.23	6.28 $\pm$ 3.11	3.76 $\pm$ 1.79			
		Max	46.00	1.29	24.30	11.00			
	Anthesis	Min	42.30	0.50	3.60	1.80	2.00		
		Mean $\pm$ SD	121.90 $\pm$ 38.00	1.64 $\pm$ 0.50	14.68 $\pm$ 6.69	7.58 $\pm$ 3.04	10.52 $\pm$ 7.35		
		Max	247.00	2.57	53.43	13.66	53.50		
	Seed maturation	Min	36.00	0.62			16.00	12.00	1.81
		Mean $\pm$ SD	163.80 $\pm$ 48.90	1.76 $\pm$ 0.66			42.88 $\pm$ 12.00	50.92 $\pm$ 27.00	13.55 $\pm$ 10.40
		Max	262.60	2.14			74.00	119.00	43.54
Guatemala	Vegetative	Min	2.50	0.10	2.00	0.83			
		Mean $\pm$ SD	16.18 $\pm$ 13.40	0.50 $\pm$ 0.33	5.74 $\pm$ 3.23	3.30 $\pm$ 2.20			
		Max	54.00	1.40	13.80	10.29			
	Anthesis	Min	42.50	0.53	4.47	1.70	3.70		
		Mean $\pm$ SD	125.00 $\pm$ 28.50	1.45 $\pm$ 0.45	13.93 $\pm$ 4.12	6.04 $\pm$ 1.99	11.10 $\pm$ 5.91		
		Max	180.00	2.55	22.60	11.57	28.00		
	Seed maturation	Min	33.50	0.52			18.50	5.00	1.82
		Mean $\pm$ SD	155.20 $\pm$ 38.80	1.51 $\pm$ 0.50			37.21 $\pm$ 9.84	36.48 $\pm$ 22.40	10.22 $\pm$ 7.28
		Max	213.00	2.60			58.30	116.00	35.89

**Table 5.** PERMANOVA of morphological traits at different growth stages of *Amaranthus cruentus* from Mexico and Guatemala.

Stage	d.f.	SS	R <sup>2</sup>	F	Pr(>F)
Vegetative	1	0.43	0.04	7.97	0.004
Anthesis	1	0.04	0.01	2.38	0.100
Seed maturation	1	0.12	0.03	5.57	0.012

**Table 6.** Pearson's correlation values of traits for *Amaranthus cruentus* from Mexico and Guatemala at different growth stages.

Stage	Trait	Plant height	Basal stem diameter	Leaf length	Leaf width	Terminal inflorescence length	Inflorescence dry mass	Seed yield
Vegetative	Plant height	1.00	0.89	0.71	0.75			
	Basal stem diameter	0.89	1.00	0.75	0.80			
	Leaf length	0.71	0.75	1.00	0.71			
	Leaf width	0.75	0.80	0.71	1.00			
Anthesis	Plant height	1.00	0.68	0.58	0.61	-0.06		
	Basal stem diameter	0.68	1.00	0.58	0.69	-0.18		
	Terminal inflorescence length	-0.06	-0.18	-0.16	-0.16	1.00		
	Leaf length	0.58	0.58	1.00	0.79	-0.16		
	Leaf width	0.61	0.69	0.79	1.00	-0.16		
Seed maturation	Plant height	1.00	0.59			0.39	0.41	0.19
	Basal stem diameter	0.59	1.00			0.41	0.56	0.52
	Terminal inflorescence length	0.39	0.41			1.00	0.64	0.85
	Inflorescence dry mass	0.41	0.56			0.64	1.00	0.78
	Seed yield	0.19	0.52			0.58	0.78	1.00

## DISCUSSION

### Justification for the set of domestication-linked characters

#### *Plant height, leaf length and width*

According to Joshi et al. (2018), features of plant architecture such as plant height and leaf length and width distinguish cultivated amaranths species from their wild relatives. Moreover, in the grain amaranths, seed yield is positively correlated with increasing plant height (Masaku et al. 2018). Rana et al. (2005) identified plant height and leaf size in *A. hypochondriacus* as characters that influence its agricultural performance. Humans probably selected for leaf dimensions as well as plant height in *Amaranthus*, but even if they did not, cultivated plants typically are taller and have larger leaves than their wild ancestors (Pérez-Pérez et al. 2010; Xiao et al. 2014; Milla and Matesanz 2017; Sánchez-del Pino et al. 2025). For example, the leaves and shoot tips of *A. cruentus* are also harvested for consumption before the inflorescence appear (Mapes et al. 1996; Sooriyapathirana et al. 2021), which may have led to selection of plants with larger leaves and taller plants. According to Brenner et al. (2000), vegetable amaranth cultivars, often appreciated locally for their high protein content and remarkable leaf production, are extensively grown throughout Africa, Asia, the Caribbean, and Central America.

#### *Basal stem diameter*

Stem diameter is a vital agronomic trait related to robustness of plants (Li et al. 2020). Wider stems are usually associated with healthier plants, tolerance to environmental stress, and structural strength and stability.

Thick, sturdy stems can support the heavy seed loads that are produced on the large terminal inflorescence (Mapes et al. 1996; Sooriyapathirana et al. 2021; De Melo et al. 2023; Fabris et al. 2023) and are particularly relevant in reducing lodging (permanent bending/breaking of crop stem), which can severely impact seed yield.

#### *Terminal inflorescence length, inflorescence colour, inflorescence dry mass, and duration of vegetative stage*

In cereals and several other crops including amaranths (Rana et al. 2005; Joshi et al. 2018), inflorescence length is correlated positively with seed yield (Boden et al. 2015; Feng et al. 2017; Nirubana et al. 2021; Manugade et al. 2023). In addition, inflorescence length is associated with efficient harvesting, genetic diversity, and adaptation to environmental conditions (Joshi et al. 2018). Also, inflorescence length and seed production are positively correlated. In amaranths, crop management, breeding, cultural preferences and agricultural performance affect the inflorescence colour, which also serves as a visual indicator of maturity, and may be associated with stress tolerance and pest resistance (Joshi et al. 2018). In cereal crops, inflorescence architecture determines both the quantity and the quality of seed production (Feng et al. 2017; Yamburenko et al. 2017). Also in amaranths, inflorescence dry mass is closely associated with seed yield, so it is an indicator of overall plant health and vigour (Joshi et al. 2018). Inflorescence biomass can be considered as a consequence of selection conditions that promote vigorous growth (Zhang and Yuan 2014; Studer et al. 2017). Artificial selection on different traits influences the time from germination to anthesis (Feng et al. 2017) (called “flowering time” by Joshi et al. 2018: 1813 vs “duration of vegetative stage” here). According



to Joshi et al. (2018), in grain amaranths, flowering time is correlated with factors such as species characteristics, environmental conditions, and management practices.

### Seed yield and colour

In many cultivated crops, seed yield is 50% higher than in their wild relatives (Rehman et al. 2014; Preece et al. 2017; Thakur and Prasad 2021). Grain amaranths such as *A. hypochondriacus* have higher seed yields, reflecting selection for enhanced grain productivity (Brenner et al. 2000; El Gendy et al. 2017). In *Amaranthus*, seed colour appears to also be a trait explicitly linked to domestication (Stetter et al. 2020). In *A. cruentus*, seed colour varies from light to dark, a pattern also observed in other crops (Sultan et al. 2014). Such variability suggests that seed colour is influenced by consumer preferences, leading to differences in uses. Not only is seed colour an aesthetic trait, but it is also associated with perceived quality attributes (e.g. flavour and nutritional content; Stetter et al. 2017; Abtahi et al. 2022).

In summary, the selected domestication-linked characters in this study are justified and supported by the literature. The traits plant height, leaf length and width, basal stem diameter, terminal inflorescence length, inflorescence colour, inflorescence dry mass, duration of vegetative stage, seed yield and colour have been highlighted in studies on amaranths and other crops, particularly due to their relevance to agronomic performance, reproductive output, and human selection during domestication.

### Distinguishing *A. hybridus* and *A. cruentus* using the set of domestication-linked characters

In the NMDS plot of the 10 characters, the points for *A. hybridus* are in a very dispersed cloud, whereas the points for *A. cruentus* are concentrated inside the larger cloud for *A. hybridus* (Fig. 3). The higher number of *A. hybridus* points reflects our sampling strategy, in which up to 10 individuals were selected per accession, so that traits for 52 individuals were measured throughout their life cycle. This finding suggests that there is an overall distinction between the two species. *Amaranthus hybridus* and *A. cruentus* share some characters, which should not be surprising since *A. hybridus* is considered to be the ancestor of *A. cruentus*. However, several domestication-linked characters distinguish *A. cruentus* from *A. hybridus* (Sánchez-del Pino et al. 2025: fig. 8I–K). According to our results (Table 2), the vegetative stage exhibits the lowest level of differentiation between the two species, suggesting that in the earlier developmental stages there is little or no morphological distinctions between the two species studied. In *A. cruentus*, the vegetative phase appears to retain ancestral traits as observed for other crops (Jisha et al. 2011).

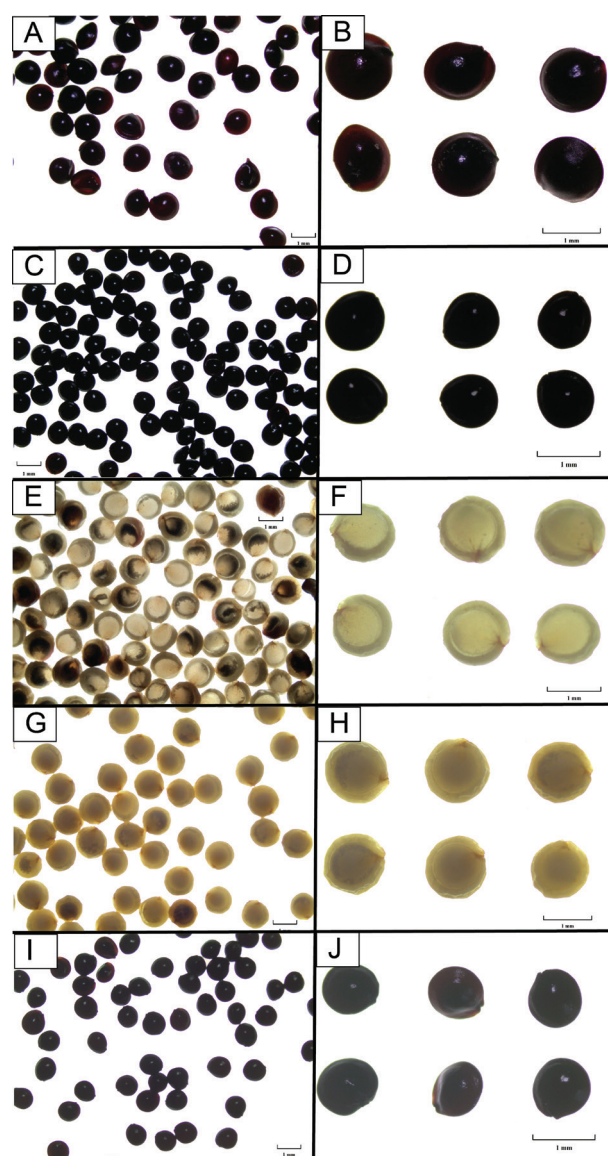
### Plant height and stem diameter

From anthesis on, *A. cruentus* tended to have a larger basal stem diameter and plants than *A. hybridus*, which fits

the common tendencies seen in other crops (Niklas and Enquist 2002; Herron et al. 2020; Kaur et al. 2023) (Table 1). By the time seeds are maturing, the thick, sturdy stems can support the heavy seed loads on the large terminal inflorescences, indicating more robust vegetative growth in the cultivated species. Our results are consistent with the findings of Maughan et al. (2011) and Akin-Idowu et al. (2016) in *A. cruentus*. The taller height of *A. cruentus* at all growth stages allows the plant to compete with weeds to maximize light interception for photosynthesis, as found in other domesticated crops (Cunniff et al. 2014; Peiffer et al. 2014). Brenner et al. (2000) and Spehar (2003) suggested a correlation between the height of *A. cruentus* and its photoperiod insensitivity.

### Leaf length and width

At anthesis, the leaves of *A. cruentus* tended to be larger than on *A. hybridus* (Table 2). Modifications of the leaves of *A. cruentus* later in development may help maximize



**Figure 6.** Colour variations in seeds of *Amaranthus cruentus* (A–H), and *A. hybridus* (I–J).

light absorbance and photosynthesis (Sooriyapathirana et al. 2021). Mapes et al. (1996) suggested humans selected for leaf size when they consumed the leaves. Indeed, the leaves of *A. hybridus* are eaten, mostly in Guatemala and Africa and those of *A. cruentus* in Mexico (Turreira-García et al. 2015; Cáceres and Cruz 2019; Gresta et al. 2020; Mapes et al. 2023). However, in our opinion, the larger leaf size is rather a side effect of selection for taller plants with larger inflorescences because leaves for eating are harvested before anthesis. For *A. cruentus*, measurements at seed maturation were not possible due to leaf senescence and shedding. As *A. cruentus* plants approached seed maturity, leaves began to senesce earlier than on *A. hybridus* (Table 1). These findings are consistent with those of Thapa et al. (2021), who also observed earlier leaf senescence in cultivated grain species of *Amaranthus*.

#### **Terminal inflorescence length, inflorescence colour, inflorescence dry mass, and duration of the vegetative stage**

*Amaranthus cruentus* tended to develop larger terminal inflorescences and smaller lateral inflorescences in contrast to *A. hybridus* (Table 1). These results concur with those of Mapes et al. (1996), Sogbohossou and Achigan-Dako (2014), El Gendy et al. (2017), and Thapa and Blair (2018). Denham et al. (2020) also suggested that selection for taller, more erect plants leads to fewer lateral branches. Such a growth pattern is common in many others crops (Doust 2007; Fuller 2010). Distal inflorescences facilitate seed retention and reduce premature seed dispersal during maturation (Adhikari et al. 2022). According to Thapa and Blair (2018), cultivated amaranths exhibit greater diversity in inflorescence traits, particularly in pigmentation. Our findings are consistent with this observation (Fig. 4), with *A. cruentus* displaying a broader range of colours compared to *A. hybridus*. This variation may reflect artificial selection for aesthetic features in cultivated species for commercial production (Altman et al. 2022). Our results for inflorescence dry mass (Table 1) are consistent with the findings of Gomes et al. (2024). According to Thapa and Blair (2018), the higher inflorescence dry mass of cultivated amaranths, particularly at higher planting densities, likely reflects an indirect consequence of artificial selection for larger or more productive inflorescences, rather than direct artificial selection for dry mass. In contrast, in wild amaranths inflorescence size and dry mass depend strongly on local growth conditions. According to our observations, the duration of the vegetative stage is shorter in *A. hybridus* than in *A. cruentus* (Table 1). This result agrees with those of Espitia-Rangel (2018) and Waselkov et al. (2020), who mentioned that early flowering in many wild species is a distinctive adaptation to environmental factors such as temperature and photoperiod.

#### **Seed yield and seed colour**

Our results showed that *A. cruentus* produced more seeds than *A. hybridus*, which is related to artificial selection on

seed production and domestication (Mapes et al. 1996). A similarly increased seed production is also observed in several cereal crops such as rice (*Oryza sativa* L.), wheat (*Triticum aestivum* L.), sorghum (*Sorghum bicolor* L.) Moench, and barley (*Hordeum vulgare* L.) (Garibaldi et al. 2021; He et al. 2023; Alam and Purugganan 2024). We observed pale seeds and dark seeds in *A. cruentus* (Figs 5B, 6), as also reported by Hauptli and Jain (1978), Espitia-Rangel et al. (2010), and Jacques et al. (2021). The other two grain amaranths have pale seeds, suggesting that *A. cruentus* is less domesticated. Other possible explanations are 1) hybridization between *A. cruentus* and *A. hybridus* because both species coexist in the same regions; 2) artificial selection in *A. cruentus* was not only concentrated on higher seed yield, but also on producing quality ornamentals or vegetables (Sauer 1967; Espitia-Rangel et al. 2010; Srivastava 2015).

#### **The set domestication-linked characters on *A. cruentus* from different centres of domestication**

At anthesis and seed maturation, the NMDS analysis (Fig. 7) showed a more dispersed cloud for the overall set of characters in *A. cruentus* from Mexico than in *A. cruentus* from Guatemala, suggesting that the two populations are distinct. At the vegetative stage, both populations are dispersed without distinction, which is not surprising considering that the relevant characters for domestication are mostly characters linked to the inflorescence or characters that are realised late in the life cycle. It should be noted that the Mexican dataset includes more accessions than the Guatemalan one, which may be related to the lower collection rates in Guatemala compared with Mexico (Ivonne Sánchez-del Pino pers. comm.).

#### **Plant height and stem diameter**

From the vegetative stage onward, stem diameters are larger for plants from Mexican accessions compared to the Guatemalan (Tables 4, 5).

#### **Leaf length and width**

Mexican *A. cruentus* tended to have longer and wider leaves at the vegetative stage. Guatemalan plants displayed smaller leaves on average, which may reflect either local environmental adaptations or less intensive selection (Espitia-Rangel et al. 2010, 2020).

#### **Terminal inflorescence length, inflorescence colour, inflorescences dry mass, and duration of vegetative stage**

At anthesis, Mexican accessions of *A. cruentus* exhibit longer terminal inflorescences compared to Guatemalan accessions, as observed by Espitia-Rangel (2018). According to this author, Mexican accessions typically have lateral inflorescences on the upper stem with a single dominant apical inflorescence, whereas Guatemalan accessions develop one smaller, inflorescence. Mexican accessions of *A. cruentus* display greater chromatic diversity, ranging from green to deep purple, consistent

with reports by Kauffman (1992) and Espitia-Rangel et al. (2010, 2020), and may reflect higher levels of genetic diversity and divergent selection pressures, potentially linked to cultural preferences or local uses. Mexican accessions of *A. cruentus* at seed maturation have greater inflorescence dry mass compared to Guatemalan accessions, which is indicative of artificial selection for grain yield in Mexico (Thapa and Blair 2018; Gomes et al. 2024). The duration of the vegetative stage of Mexican accessions of *A. cruentus* is within the flowering range for most *A. cruentus* plants reported (e.g. Baturaygil and Schmid 2022; Uriarte Ortiz et al. 2023). In comparison, Guatemalan accessions had a longer vegetative stage. According to Baturaygil and Schmid (2022), the duration of the vegetative stage in grain amaranths and wild relatives varies in temperate conditions, where accessions from regions with longer day lengths tend to flower earlier, demonstrating the species' sensitivity to photoperiod changes.

### Seed yield and colour

At seed maturation, Mexican accessions of *A. cruentus* had greater seed yield compared to Guatemalan accessions (Tables 4, 5), which is consistent with higher seed use in Mexico (Mapes 1997; Espitia-Rangel et al. 2010, 2018; Casini and La Rocca 2014). Seed colour in *A. cruentus* varied from black to white, as already reported by Espitia-Rangel et al. (2010, 2020). Seed colour also differed notably between populations: white seeds predominated in the Mexican accessions, reflecting historical selection for white seeds, in contrast to Guatemalan accessions. These patterns are consistent with previous reports (Mapes 1997; Espitia-Rangel et al. 2010, 2018, 2020) and suggest that differential human selection and cultural practices have played a key role in shaping seed traits across populations. Aguilera-Cauich et al. (2020) also found that the morphological traits of plants from Guatemala suggest there was less human intervention. The artificial selection of traits for different purposes in *A. cruentus* led to the development of local varieties in Guatemala and Mexico and to different degrees of domestication.

## CONCLUSION

We identified a set of domestication-linked characters for *A. cruentus*, based on measurements of morphological variables at different developmental stages. This set was tested as a domestication syndrome in populations of *A. cruentus* from Mexico and Guatemala in the context of Sauer's (1967) main domestication hypothesis.

Based on our results, we can answer our first question (determining a set of traits to separate unambiguously wild, ancestral *A. hybridus* and cultivated *A. cruentus*). An overall analysis of 10 selected characters linked to domestication separates *A. hybridus* from *A. cruentus*. The six most-diverse characters can be considered together as a domestication syndrome for *A. cruentus*: basal stem

diameter, plant height, inflorescence length, inflorescence colour, seed colour, and seed yield.

With regard to our second question (using the set of characters to determine levels of domestication in populations from different centres of domestication of *A. cruentus*), applying the set of characters to *A. cruentus* from two different centres of domestication allowed us to determine a difference in domestication level. In addition, when looking at individual characters, reproductive traits such as the length of the terminal inflorescence, dry inflorescence mass, and seed yield proved to be the most discriminative and relevant for domestication. Moreover, differences in seed colour in the populations of *A. cruentus* from Mexico and Guatemala suggest that the Mexican population is more domesticated than the Guatemalan population. Alternatively, the differences can be explained by artificial selection for different purposes or by hybridization between *A. cruentus* and *A. hybridus*.

## ACKNOWLEDGEMENTS

We thank the National Plant Germplasm System of the United States Department of Agriculture (USDA) for providing plant material. David Brenner's generous collaboration and review of the manuscript have been fundamental to our research. We are indebted to Edlin J. Guerra Castro (Escuela Nacional de Estudios Superiores, UNAM, Yucatán, México) for his contributions to PERMANOVA analyses. We thank Alejandra Paz (UNAM), Diana Mayreb (UNAM), Eduardo Gutiérrez (UADY), Jesús Ucan (ITSM), and Tabatha Cerna (UNAM) for their technical support. We are grateful to Allison Jazmín Téllez-Sánchez for preparing the illustrations for Fig. 3. We also thank CONAHCYT/SECIHTI for support under project FORDECYT-PRONACES-15319/2020 and CONAHCYT/SECIHTI for PhD scholarship 857164. We also are grateful to the anonymous reviewers and subject editor Elmar Robbrecht for their constructive feedback.

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## SUPPLEMENTARY MATERIALS

### **Supplementary material 1**

Voucher information and geographic origin of *Amaranthus cruentus* L. and *A. hybridus* L. accessions included in this study, indicating accession or voucher number, species, country, state or department of origin, source or herbarium, and geographic coordinates (latitude and longitude).

<https://doi.org/10.5091/plecevo.160401.suppl1>

### **Supplementary material 2**

Pearson's correlation coefficients among morphological traits of *Amaranthus cruentus* (Table S1) and *A. hybridus* (Table S2) across different growth stages (vegetative, anthesis, and seed maturation). Correlations were estimated for plant height, stem diameter, leaf length, leaf width, terminal inflorescence length, inflorescence dry mass, and seed mass.

<https://doi.org/10.5091/plecevo.160401.suppl2>