



Phenotypic plasticity of drought tolerance in tomato (*Solanum lycopersicum* L.) landraces and hybrid cultivars in Benin, Africa

Vincent Ezin ^{1*}, Felix Houessou ¹, David R. Bryla ² and Adam Ahanchede ¹

¹Department of Crop Production, Faculty of Agricultural Sciences, University of Abomey-Calavi 01 BP 526 Cotonou, Benin.

²United States Department of Agriculture, Agricultural Research Service, Horticultural Crops Research Unit, 3420 NW Orchard Avenue, Corvallis, Oregon, USA. *e-mail: ishola.vincent@yahoo.com

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Abstract

Drought is one of the most important abiotic stresses hampering crop productivity worldwide and is responsible for 20 percent of crop loss in Africa annually. Drought occurrence is likely to increase with climate change; therefore, the identification of drought resistance cultivars is an important tool in meeting food demands. New cultivars are needed that are tolerant to drought. The aim of the present study was to evaluate drought tolerance and its relation to vegetative, reproductive, and physiological characteristics of 20 tomato genotypes, including 14 local landraces, five hybrid cultivars, and a wild relative species (LA1579). The experiment was conducted at the International Institute of Tropical Agriculture in Benin, Africa. Each genotype was exposed to three treatments; a fully irrigated control, moderate drought (no water for 15 days during the vegetative stage and 7 days during the reproductive stage), and severe drought (no water for 21 days during the vegetative stage and 9 days during the reproductive stage). Plant height and leaf production were reduced by the initial episode of severe drought by 4-27% and 1-6%, respectively, but were unaffected in most genotypes by moderate drought. There was also no difference in leaf chlorophyll levels as a result of drought, but drought had a significant effect on leaf fluorescence in many genotypes. Diho and Dogbo landraces flowered first (57 days) and Tropimech hybrid flowered last (74 days). Both landraces and hybrids were equally affected by drought during flowering and fruit development. Heat was a limiting factor for some genotypes (LA1579) resulting in flower drop and yield loss by 100%. The landraces flowered earlier and more profusely than the hybrids but as a group both were equally affected by drought during flowering and fruit development. Some genotypes were also affected by heat, including LA1579, which aborted its flowers and produced no fruit in any treatment. Overall, two local landraces, Diho and Tovinklin, were most tolerant to drought amongst the genotypes and potentially could be used in breeding programs to improve drought tolerance in tomato.

Key words: *Solanum lycopersicum*, drought tolerance, fluorescence, flowering, fruit development, leaf chlorophyll, yield.

Introduction

Tomato is one of the most popular and important horticultural crops in the world, with a total production of 159 million tons in 2011 ¹. It ranks first amongst vegetables produced in Benin and worth a considerable amount of money to the national economy ². However, yields of tomato in West Africa, particularly Benin, have not been encouraging, especially when compared to production in developed countries. For example, yield per hectare in Benin was estimated to be only 14.3% of that produced in the United States ³.

Water plays a vital role in the production of tomatoes and can raise consumer costs when resources are low. In recent years, the price of tomatoes in Benin increased between the months of December and May, due to less precipitation and prolonged dry seasons. Moreover, climate change will increase current environmental challenges associated with tomato production in Benin, such as drought, heat, flooding, and soil salinity. Environmental stress is the primary cause of crop losses worldwide, reducing yield of most major crops by more than 50% ⁴ as reported by Bray *et al.* ⁵, Wang *et al.* ⁶ and Bayoumi *et al.* ⁷.

Drought is a major environmental factor limiting crop yields in West Africa. It is now undeniable that drought observed during the development cycle of plants directly influences yield. Today, the availability of water for agriculture is becoming scarce, while

food demand for the growing world population is projected to increase substantially. Henceforth, population growth and competition for water resources will make the effect of successive droughts more severe ⁸. Moreover, water deficits are also occurring unpredictably throughout the season as a result of less rainfall and the reduction of the number of days of rain in many regions.

To solve the problems of existing food insecurity and hunger, which the effects of climate change will exacerbate, it is necessary to identify cultivars for various crops that are tolerant to drought. Egea *et al.* ⁹ reported, that developing drought tolerant cultivars is of paramount importance due to the increasing rate of prolonged drought caused by changes in climate. The objective of this study was to screen existing tomato genotypes from Benin for resistance to drought during both vegetative and reproductive stages of development and identify those that are most tolerant.

Materials and Methods

Plant material and growth conditions: The experiment was conducted at the International Institute of Tropical Agriculture (IITA) in Benin, Africa. Twenty tomato genotypes, including fourteen local landraces, five hybrids, and one wild species were screened for their tolerance to drought. The landraces were collected originally in Benin and are named after the town or

region in which they were collected (Bante, Diho, Dogbo, Kpomasse, Lokassa, Malanville 1, Malanville 2, N'Dali, Natitangou, Ouesse, Parakou, TLCV15/PCM, Tori, and Toviklin). The hybrids tested are commonly grown in Benin, as well as other countries in Africa, and include F1 Mongal, Petomech, Rodeo 62, Roma VF and Tropimech. F1 Mongal is considered particularly well adapted to hot and tropical conditions and is reported to withstand temperatures over 42–45°C¹⁰. The wild species is *S. pimpinellifolium*, accession LA1579, obtained from the World Vegetable Center in Taiwan. This accession was previously identified to be tolerant to drought as reported by Kumar *et al.*¹¹. Seeds from each genotype were scarified with 5% sulfuric acid for 10 min and rinsed thoroughly with distilled water to remove any trace of the acid. The seeds were subsequently sown in trays filled with sterilized loamy soil (75% silt, 20% sand and 5% clay). The trays were kept in a greenhouse and watered daily. Once the seeds germinated, 3-week-old seedlings were transplanted into plastic pots containing 11.5 kg of loamy soil. Irrigation was applied by hand as needed. Granular NPK fertilizer (15-15-15) was applied at 15 days after transplanting, and urea (46-0-0) was applied just prior to flowering.

Plants were grown in the greenhouse under natural light conditions. Temperatures measured near the canopy of the plants ranged from 27–37°C during the day and 23–30°C at night (Table 1). Lower branches were pruned directly from the plants once they were placed in the greenhouse. The pots were hand-weeded daily, and were sprayed weekly with abamectin (18 g/L) and cyhalothrin (25 g/L) to prevent outbreaks of insect pests and plant pathogens.

Drought treatments and experimental design: Drought treatments were first initiated at 18 days after transplanting during the vegetative stage of plant development. Plants were either irrigated daily or exposed to drought (no water) for 15 (moderate) or 21 (severe) days. A second episode of drought was initiated at 60 days after transplanting during the reproductive stage of plant development. Again, plants were either watered daily or exposed to drought for 7 (moderate) or 9 (severe) days. The same plants were used for each treatment during both episodes of drought.

Treatments [20 genotypes×3 levels of drought (none, moderate and severe)] were arranged in a completely randomized block design with three replicate plants (pots) per treatment. Each block included five rows of 6.6 m each. The pots were spaced 0.6 m apart within the rows and 0.8 m apart between the rows. The center block was separated from the outside blocks by 1 m.

Measurements: Plant growth was measured at 6, 13, 20 and 27 days after the first episode of drought was initiated. These measurements included plant height (distance from the soil surface of the pot to the upper most growing tip of the plant), the total

number of leaves on the plants, and average length and width of the leaves. Leaf wilting and recovery was also measured during both episodes of drought and was estimated based on visual appearance of the leaves. The allocation of wilting rates was based on a scale defined for this purpose.

Days to low wilting = 10–49%

Days to moderate wilting = 50–70%

Days to severe wilting = 100%

Flowering was measured prior to and during the second episode of drought and included the number of days to flowering (from transplanting), the total number of flower clusters on each plant, and the total number of flowers produced on the second through sixth cluster of flowers produced by the plants (tagged during anthesis). Fruit were also counted on the first through the eighth cluster of flowers produced by the plants and were weighed at harvest (i.e. when the fruit turned completely red).

A portable chlorophyll meter (Minolta SPAD-502, Soil Plant Analysis Development, Minolta Co., Osaka, Japan) was used to measure leaf greenness, which is correlated to leaf chlorophyll and N content in many crops, including tomato with the reference to the work of Sandoval-Villa *et al.*¹² and Jiang *et al.*¹³. An average of triplicate readings was recorded on the third fully expanded leaflet on each plant. SPAD meter measurements were taken immediately following the first episode of drought between 8:00–10:00 HR Benin Standard Time. Chlorophyll fluorescence was also measured at that time using a continuous portable chlorophyll fluorometer (Model OS-30P; Opti-Sciences, New Hampshire, USA). Measurements were made on fully expanded leaflets clipped from the upper part of the plant canopy, after a 60-min dark adaptation period. Dark fluorescence (Fo), maximal fluorescence (Fm), and photochemical yield (Fv/Fm, where Fv = Fm – Fo) were recorded. The Fv/Fm ratio is an indicator of plant stress resulting from damage to photosystem II¹⁴.

Statistical analysis: Data were analyzed by analysis of variance (ANOVA) using R ver. 3.5¹⁵. Means were separated at the 5% level using Tukey's honest significant difference test. Quality traits were subjected to principal component analysis (PCA) to explore relationships among variables and treatments and to determine which quality traits were most related to drought tolerance within the genotypes¹⁶. The PCA outputs include variable loading to each selected component and treatment component scores. All the data obtained were converted to drought tolerance indexes before performing PCA and cluster analyses. A drought tolerance index was defined as the observation at severe drought divided by the average of the controls. Cluster group rankings were obtained based on Ward's minimum variance method and used to analyze the averages of the drought tolerance indices for 14 parameters, including plant height, leaf number per plant, leaf length, leaf width, chlorophyll meter readings, dark

Table 1. Mean monthly air temperatures in the greenhouse during the experiment (2017–2018).

Month	Air temperature (°C)					
	Morning (7:00–9:00 HR)		Afternoon (12:00–15:00 HR)		Night (1:00–2:00 HR)	
	Minimum	Maximum	Minimum	Maximum	Minimum	Maximum
October	29	29	30	34	25	30
November	28	29	32	36	26	29
December	27	29	34	37	23	27
January	27	29	32	35	25	26

fluorescence (Fo), maximum fluorescence (Fm), simultaneous variation in Fo and Fm (Fv/Fo), phytochemical yield (Fv/Fm), the number of flowers and flower clusters per plant, fruit set, fruit number per plant and yield.

Results and Discussion

Plant height and leaf development: The initial episode of drought reduced plant height in most genotypes, including eight landraces (Bante, Dogbo, Lokassa, Malanville 1, Malanville 2, N'Dali, Natitangou, and Parakou) and each hybrid (F1 Mongal, Petomech,

Rodeo 62, Romaf, and Tropimech) (Fig. 1). In all cases, this effect on plant height was only apparent with severe drought, although Dogbo, Malanville 2, N'Dali, and Parakou were also affected by moderate drought. Drought likewise affected leaf number and length across the genotypes but had no significant effect on leaf width (Fig. 2). Leaf production and growth was clearly inhibited by drought (moderate or severe) but recovered quickly once the plants were rewatered. Leaves tend to be very sensitive to drought in many plant species, including tomato as investigated by Petrović *et al.*¹⁷.

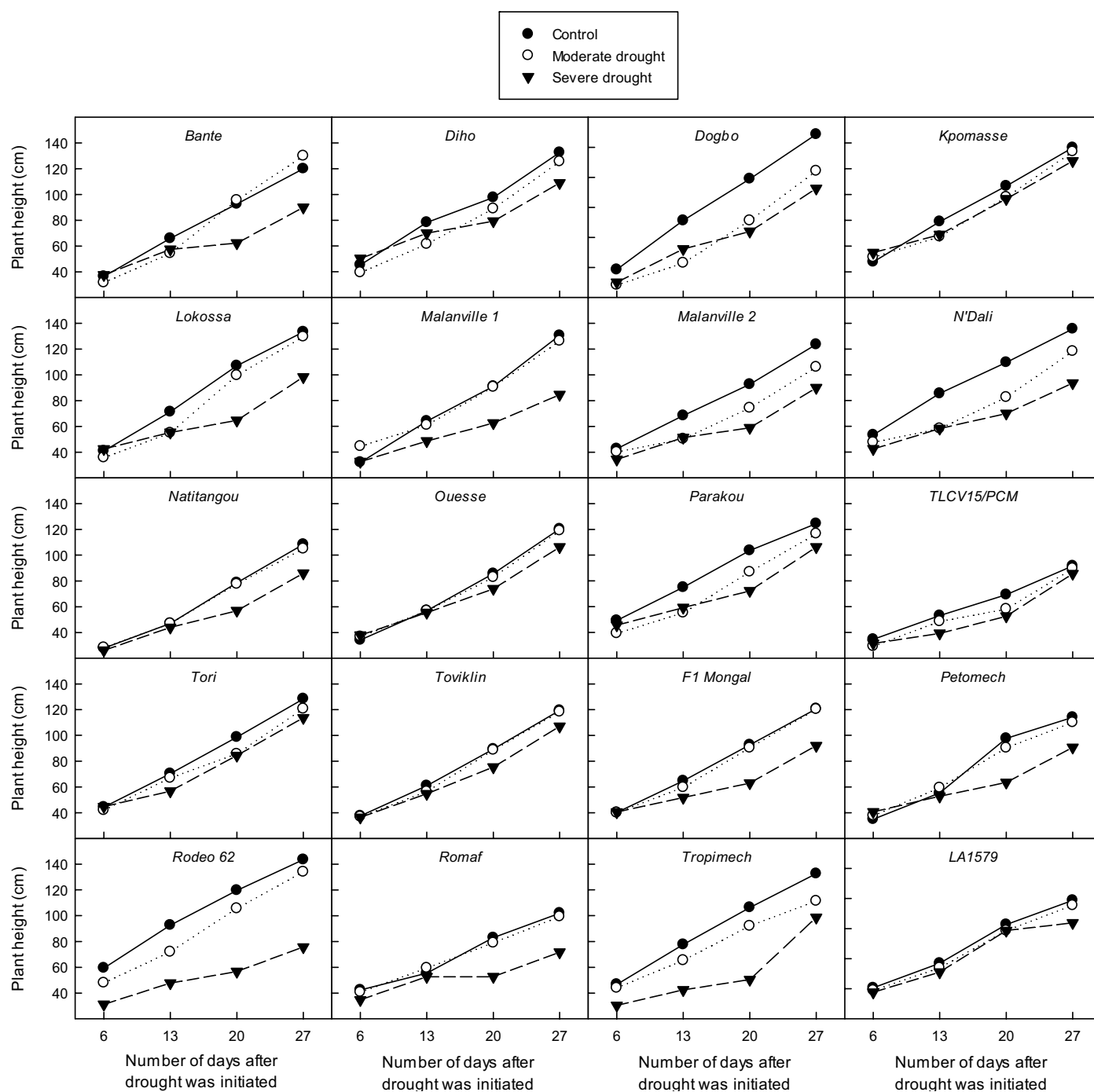


Figure 1. Effects of drought on plant height in 14 landraces (Bante, Diho, Dogbo, Kpomasse, Lokassa, Malanville 1, Malanville 2, N'Dali, Natitangou, Ouesse, Parakou, TLCV15/PCM, Tori, and Toviklin), five hybrid cultivars (F1 Mongal, Petomech, Rodeo 62, Roma VF, and Tropimech), and a wild species (LA1579) of tomato. Plants were exposed to moderate and severe drought during the vegetative stage of development (beginning 18 days after transplanting) and rewatered after 15 and 22 days, respectively.

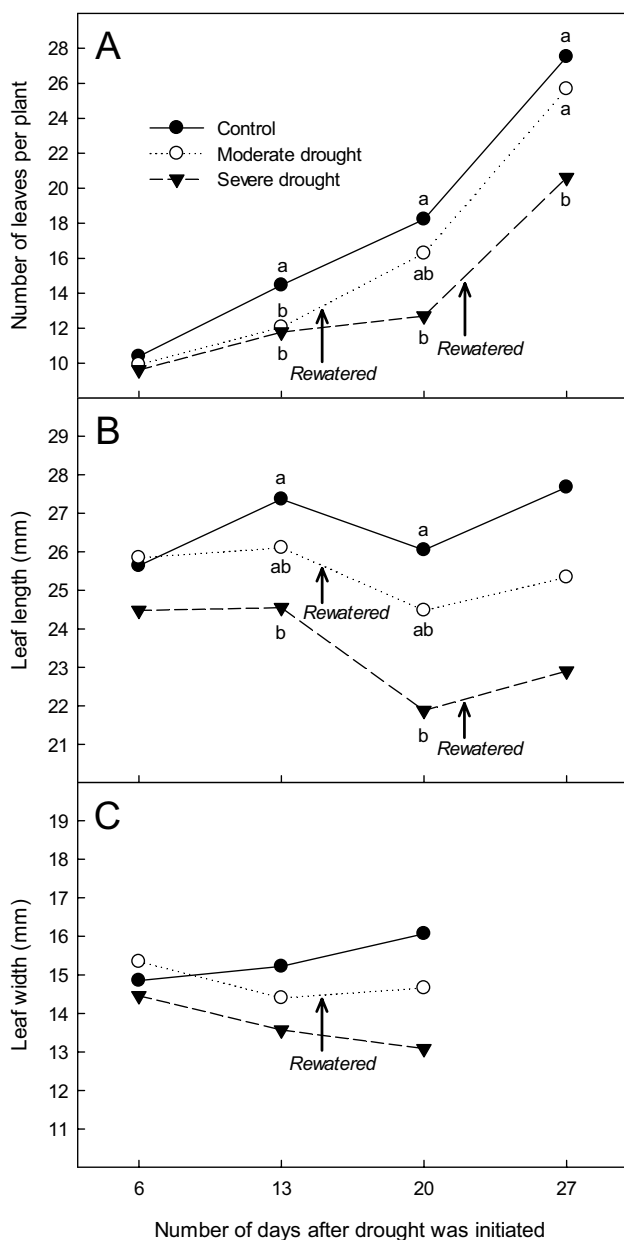


Figure 2. Effects of drought on leaf number and size in tomato (data are pooled across 20 genotypes). Plants were exposed to moderate and severe drought during the vegetative stage of development (beginning 18 days after transplanting) and rewatered after 15 and 22 days, respectively. Leaf width was not measured at 27 d after drought was initiated. Means were separated on each date using Tukey's honest significance test at $P = 0.05$; no letters indicate drought was non-significant ($P > 0.05$) on that given date.

Leaf wilting and recovery: The plants began wilting in an average of 11 days during the first episode of drought and were fully wilted in 15 days (Table 2). Each genotype wilted at a similar rate during the episode and recovered fully in < 3 days after moderate drought and in < 4 days after severe drought.

Each genotype also wilted at a similar rate during the second episode of drought, but in this case, they began wilting in an average of only 4 days (Table 2). The plants were much larger at this point and, as a result, transpired nearly three times more water per day (prior to wilting) than they did previously during the first

episode of drought. Interestingly, the plants exposed to moderate drought during the second episode were fully wilted a half day sooner than those exposed to severe drought. This slight delay in the latter treatment was due to less leaf area on the plants (caused by the first episode of drought) and perhaps osmotic adjustment in the leaves and roots¹⁸. Each wilted plant recovered from the second episode of drought within 5-6 days.

Leaf chlorophyll and fluorescence: SPAD meter readings, which are a function of leaf chlorophyll, differed among genotypes and were affected by drought (Table 3). The hybrids generally had higher SPAD meter readings than the landraces, while the wild accession, LA1579, had the lowest reading among the genotypes. The readings were also higher, on average, when the plants were exposed to drought. Apparently, drought had less effect on chlorophyll production than growth and therefore resulted in higher concentrations of chlorophyll in the leaves.

Quantum yield was similar among the genotypes under well-watered conditions but declined more so in some genotypes than others during drought (Table 3). In most cases, F_v/F_m was reduced by either moderate or severe drought; however, seven genotypes remained unaffected, including Diho, Dogbo, Kpomasse, Toviklin, F1 Mongal, Petomech, and Tropimech. A reduction in F_v/F_m is an indication of damage to the photosynthetic apparatus (photosystem II) in leaf chloroplasts^{19,20}.

Flowering and fruit production: Flowering began at 57-72 days after transplanting (Table 4). Dogbo was amongst the first to flower and began sooner than Malanville 1, TLCV15/PCM, F1 Mongal, Petomech, Rodeo 62, Roma VF and LA1579. Diho and Kpomasse likewise flowered early (58 days), and both produced more flower clusters or flowers than seven genotypes, including Malanville 1, Natitangou, TLCV15/PCM, and all but one hybrid cultivar, F1 Mongal. On average, the landraces began flowering in 63 days and produced a total of 11 flower clusters and 52 flowers per plant. The hybrids, on the other hand, began flowering in 71 days and together produced an average of only seven flower clusters and 39 flowers per plant.

Flowering was also affected across genotypes by drought (Table 4). Plants exposed to drought flowered 5 days earlier on average than those that were not droughted. They also produced fewer flower clusters and flowers, although the latter was only reduced by severe drought. Drought often has less effect on flower production than many other plant processes, including root and shoot growth and photosynthesis²¹. In some cases, drought can even induce flowering²². Fruit set and fruit growth, in contrast, tend to be very sensitive to drought²³.

Fruit set differed amongst the genotypes and was negatively affected by moderate and severe drought (Table 5). In each case, fruit set was low, averaging only 9% in the landraces and 13% in the hybrids. Temperatures were warm during flowering and reached values as high as 35-37°C during the day and 23-30°C at night (Table 1). The higher heat, coupled with drought, inhibited fruit set. Reduced fruit set was particularly evident in Bante, N'Dali, Natitangou, TLCV15/PCM and Roma VF, all of which produced no fruit when the plants were exposed to severe drought. LA1579 was also severely affected by heat and aborted 100% of the flowers on every plant in each irrigation. Ideal temperatures for tomato cultivation typically range from 25-30°C during the day and 20°C

Table 2. Effects of drought on leaf wilting and recovery by 20 genotypes of tomato.

Drought treatment	First episode of drought ¹					Second episode of drought ²				
	Days to wilting ³				Days to full recovery	Days to wilting ³				Days to full recovery
	First sign	10-40% of leaves	50-70% of leaves	Fully wilted		First sign	10-40% of leaves	50-70% of leaves	Fully wilted	
Moderate					2.7	4.1	4.1	4.3	4.7	5.6
Severe	10.7	11.0	11.9	15.2	3.5	4.1	4.1	4.4	5.2	5.2
Significance										
Genotype	0.634	0.893	0.906	0.396	0.316	0.759	0.999	0.121	0.234	0.125
Drought	–	–	–	–	0.004	0.639	0.685	0.451	0.032	0.468
G × D	–	–	–	–	0.288	0.424	1.000	0.409	0.084	0.977

¹ The first episode of drought was initiated during the vegetative stage of plant development (18 days after transplanting) and was applied for 15 and 21 days to the moderate and severe drought treatments, respectively. Since the drought treatments were identical during the first 15 days of drought, the number of days to “first sign”, “low”, and “moderate” wilting were pooled across drought treatments in each genotype. Furthermore, “severe” wilting did not occur with moderate drought, and therefore in this case, the treatment was excluded from the analysis. ² The second episode of drought was initiated during the reproductive stage of plant development (60 days after transplanting) and was applied for 7 and 9 days to the moderate and severe drought treatments, respectively.

Table 3. Effects of drought on leaf greenness (SPAD readings) and phytochemical yield (Fv/Fm) in 14 landraces, five hybrid cultivars, and a wild accession of tomato.

Treatment	SPAD meter readings	Fv/Fm		
		No drought	Moderate drought	Severe drought
Genotype				
<i>Landrace</i>				
Bante	39.5 abc ¹	0.74 a A	0.69 a A	0.51 f B
Diho	43.1 abc	0.71 a A	0.68 a A	0.67 a-e A
Dogbo	40.2 abc	0.69 a A	0.71 a A	0.68 abc A
Kpomasse	41.5 abc	0.69 a A	0.68 a A	0.61 b-f A
Lokossa	38.9 bc	0.70 a A	0.68 a AB	0.61 a-f B
Malanville 1	38.5 bc	0.76 a A	0.71 a AB	0.66 a-e B
Malanville 2	39.3 abc	0.71 a A	0.72 a A	0.62 a-g B
N'Dali	40.5 abc	0.72 a A	0.67 a A	0.50 g B
Natitingou	40.3 abc	0.71 a A	0.70 a A	0.49 g B
Ouesse	38.8 bc	0.75 a A	0.66 a B	0.55 def C
Parakou	39.3 abc	0.72 a A	0.67 a AB	0.61 b-f B
TLCV15/PCM	42.9 abc	0.70 a A	0.72 a A	0.52 f B
Tori	39.4 abc	0.77 a A	0.70 a AB	0.67 a-d B
Toviklin	38.4 bc	0.71 a A	0.68 a A	0.69 ab A
<i>Hybrid</i>				
F1 Mongal	45.8 a	0.69 a A	0.71 a A	0.72 ab A
Petomech	44.5 ab	0.72 a A	0.72 a A	0.72 ab A
Rodeo 62	43.5 abc	0.73 a A	0.72 a A	0.63 a-f B
Roma VF	43.6 ab	0.67 a A	0.72 a A	0.55 ef B
Tropimech	42.9 abc	0.72 a A	0.74 a A	0.74 a A
<i>Wild accession</i>				
LA1579	36.9 c	0.74 a A	0.70 a A	0.56 c-f B
Significance	<0.001		<0.001	
Drought				
None	38.0 c		0.72 a	
Moderate	41.1 b		0.70 ab	
Severe	43.6 a		0.62 c	
Significance	<0.001		<0.001	
Interaction				
G × D	0.986		<0.001	
Contrast				
Landraces vs. hybrids	<0.001		0.358	

¹ Means are separated within treatments using Tukey's honest significance test at $P = 0.05$. Small letters are used to compare means within columns and capital letters are used to compare means within rows.

Table 4. Effects of drought on flowering by 14 landraces, five hybrid cultivars, and a wild accession of tomato.

Treatment	Days to flowering	Number of flower clusters per plant	Number of flowers per plant ¹
Genotype			
<i>Landrace</i>			
Bante	63 a-f ²	10.3 a-d	49 a-e
Diho	58 ef	14.7 a	51 a-e
Dogbo	57 f	11.3 a-d	59 a-d
Kpomasse	58 c-f	13.2 ab	70 a
Lokossa	59 c-f	12.6 abc	56 a-e
Malanville 1	70 abc	8.3 bcd	35 de
Malanville 2	62 a-f	12.1 a-d	49 a-e
N'Dali	63 a-f	11.8 a-d	54 a-e
Natitingou	68 a-f	7.9 bcd	41 b-e
Ouesse	61 a-f	11.3 a-d	46 a-e
Parakou	60 b-f	13.6 ab	65 ab
TLCV15/PCM	70 abc	6.2 d	36 cde
Tori	64 a-f	10.0 a-d	61 abc
Toviklin	62 a-f	11.6 a-d	64 ab
<i>Hybrid</i>			
F1 Mongal	72 ab	10.2 a-d	47 a-e
Petomech	70 a-d	6.0 d	42 b-e
Rodeo 62	72 ab	6.1 d	33 de
Roma VF	70 a-e	6.8 cd	40 b-e
Tropimech	69 a-f	6.6 cd	32 e
<i>Wild accession</i>			
LA1579	73 a	13.9 ab	69 ab
Significance	<0.001	<0.001	<0.001
Drought			
None	69 a	12.7 a	55 a
Moderate	63 b	10.8 b	55 a
Severe	63 b	8.7 c	45 b
Significance	<0.001	<0.001	<0.001
Interaction			
G × D	0.361	0.830	0.850
Contrast			
Landraces vs. hybrids	<0.001	<0.001	<0.001

¹ Flowers were counted on the second through sixth cluster produced on each plant. ² Means are separated within treatments using Tukey's honest significance test at $P = 0.05$.

at night as claimed by Camejo *et al.* ²⁴. An increase of only 2-4°C above these optimal temperatures can interrupt gamete development and lead to flower abortion in tomato and other crops as investigated by Wang *et al.* ⁶, Sato *et al.* ²⁵, Thomas and Prasad²⁶, Wahid *et al.* ²⁷ and Ribeiro *et al.* ²⁸.

Fruit number, fruit weight, and yield also differed amongst the genotypes and declined with drought (Table 5). Diho, which had small tomatoes, produced the greatest number of fruit amongst the genotypes, including the hybrids. It was also one of the highest yielding genotypes. Diho appears to be under domestication, although the farmer from which the seeds were obtained testified that it was inherited from his forefather. Parakou, TLCV15/PCM, Tori and Roma VF, on the other hand, had amongst the lowest fruit number and yield due largely to very poor fruit set, as well as blossom end rot in Tori. These genotypes were particularly sensitive to drought and heat stress. On average, fruit number and yield declined by approximately half as a result of moderate drought and by 68% and 77%, respectively, due to severe drought. Fruit weight also declined, but in this case, by 25% with severe drought only.

Principal component analysis: Both individual genotypes and quantitative variables are represented in the PCA diagrams (Fig. 3). The first three principal components (PCs) were associated with eigenvalues > 1, while the fourth was equal to 1 and the remaining seven were < 1. Principal component 1 (PC1) describes 38.8% of the original information, and principal component 2 (PC2) describes 21.4%, which together revealed a high level of variation amongst the genotypes. Plant height, leaf length and width, SPAD readings, Fo, and the total number of flowers and flower clusters on the plants were positively correlated and grouped together on the upper rightside of the biplot. Leaf number, fruit set, fruit number, Fm, and yield were also correlated but with negative loading on the upper leftside of the biplot, while Fv/Fm and Fv/Fo were observed on the lower left portion of the biplot.

The genotypes were divided into four groups of drought tolerance (Fig. 4). The wild accession, LA1579, was the most susceptible genotype to drought (group 1), while Diho, Toviklin, Petomech, Rodeo, and Tropimech were ranked amongst the most tolerant genotypes (group 2). Roma VF, Bante, TLCV15/PCM, Natitingou, N'Dali, and Ouesse were also susceptible to drought

Table 5. Effects of drought on fruit production by 14 landraces, five hybrid cultivars, and a wild accession of tomato.

Treatment	Fruit set (%)	Number of fruit per plant ¹	Fruit wt. (g) ¹	Yield (g/plant) ¹
Genotype				
<i>Landrace</i>				
Bante	7 cde ²	3.7 bcd	13 bcd	49 a–d
Diho	34 a	16.7 a	7 d	115 a
Dogbo	8 cde	4.8 bcd	13 bcd	65 a–d
Kpomasse	8 cde	5.4 bcd	11 bcd	63 a–d
Lokossa	11 b–e	6.4 bc	13 bcd	93 abc
Malanville 1	10 b–e	3.7 bcd	15 bcd	56 a–d
Malanville 2	7 cde	3.2 bcd	16 bcd	51 a–d
N'Dali	5 de	2.7 cd	19 bc	49 a–d
Natitingou	6 de	2.4 cd	24 b	53 a–d
Ouesse	11 b–e	4.8 bcd	11 bcd	47 a–d
Parakou	5 de	2.7 cd	14 bcd	38 bcd
TLCV15/PCM	3 de	0.8 d	21 bc	16 d
Tori	4 de	2.2 cd	8 cd	22 d
Toviklin	11 b–e	6.7 bc	10 bcd	68 a–d
<i>Hybrid</i>				
F1 Mongal	7 cd	2.9 bcd	38 a	116 a
Petomech	22 ab	7.9 b	13 bcd	101 ab
Rodeo 62	19 bc	6.1 bc	17 bc	111 a
Roma VF	6 de	2.8 bcd	10 bcd	30 cd
Tropimech	14 bcd	5.8 bcd	12 bcd	70 a–d
<i>Wild accession</i>				
LA1579	0 e	—	—	—
Significance	<0.001	<0.001	<0.001	<0.001
Drought				
None	15 a	7.9 a	16 a	113 a
Moderate	8 b	4.1 b	15 ab	52 b
Severe	6 b	2.5 c	12 b	26 c
Significance	<0.001	<0.001	<0.001	<0.001
Interaction				
G × D	0.802	0.683	n.d. ³	0.350
Contrast				
Landraces vs. hybrids	<0.001	0.508	<0.001	0.020

¹ Fruit were counted and weighed from the first eight flower clusters on each plant. ² Means are separated within treatments using Tukey's honest significance test at $P = 0.05$. ³ n.d. – not determined; severe drought resulted in no fruit in several genotypes (Bante, N'Dali, Natitingou, TLCV15/PCM, and Roma VF), and the missing values do not allow analysis of the interaction between genotype and drought.

(group 3), whereas Mongal, Dogbo, Malanville 2, Parakou, Kpomasse, Tori, Lokossa, and Malanville 1 were somewhat tolerant in terms of their vegetative or reproductive traits (group 4).

Conclusions

Two local landraces, Diho and Toviklin, tolerated drought better than most other genotypes, including F1 Mongal, which is considered a good cultivar for production in the tropics. These landraces could potentially be used in breeding programs to improve drought and perhaps heat tolerance in tomato and are recommended to farmers as potential candidates to be sown during the dry season. Three hybrids, Petomech, Rodeo, and Tropimech, were also tolerant to drought.

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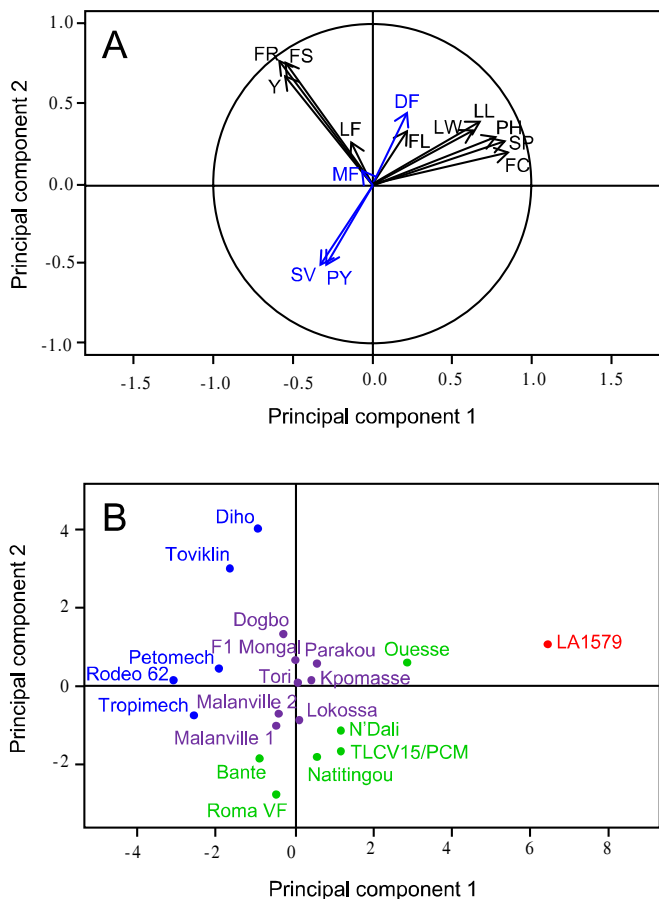


Figure 3. Principal component loading plot (A) and scores of principal component analysis (B) of tomato genotypes as a function of severe drought. The genotypes included 14 landraces (Bante, Diho, Dogbo, Kpomasse, Lokassa, Malanville 1, Malanville 2, N'Dali, Natitangou, Ouesse, Parakou, TLCV15/PCM, Tori, and Toviklin), five hybrid cultivars (F1 Mongal, Petomech, Rodeo 62, Roma VF, and Tropimech), and one wild species (LA1579). PH - plant height; LF - leaf number per plant; LL - leaf length; LW - leaf width; SP - SPAD meter readings; Fo - dark fluorescence; Fm - maximum fluorescence; Fv/Fo - simultaneous variation in Fo and Fm; Fv/Fm - phytochemical yield; FC - flower clusters per plant; FL - flower number per plant; FS - fruit set; FR - fruit number per plant; Y - yield.

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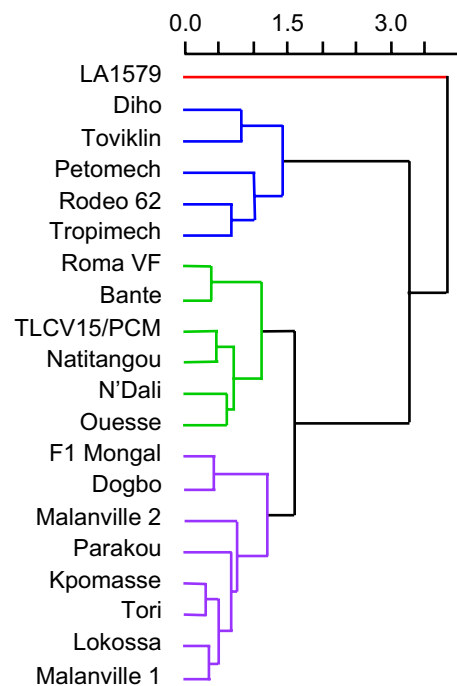


Figure 4. Cluster dendrogram of drought tolerance amongst 14 landraces (Bante, Diho, Dogbo, Kpomasse, Lokassa, Malanville 1, Malanville 2, N'Dali, Natitangou, Ouesse, Parakou, TLCV15/PCM, Tori, and Toviklin), five hybrid cultivars (F1 Mongal, Petomech, Rodeo 62, Roma VF, and Tropimech), and one wild species (LA1579) of tomato.

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