

Simulating the impact of projected West African heatwaves and water stress on the physiology and yield of three tomato varieties

C.F. Amuji ^{1,2(*)}, L.J. Beaumont ¹, M.E. Rodriguez ³

¹ Department of Biological Sciences, Faculty of Science and Engineering, Macquarie University, North Ryde NSW, 2109, Australia.

² Department of Crop Science, Faculty of Agriculture, University of Nigeria, Nsukka 41001, Enugu State, Nigeria.

³ Hawkesbury Institute for Environment, Western Sydney University, Locked Bag 1797, Penrith, NSW 2751, Australia.



Key words: fruit yield, heat stress, *Solanum lycopersicum*, tomato, water stress.

(*) **Corresponding author:**
felix.amuji@gmail.com

Citation:

AMUJI C.F., BEAUMONT L.J., ESPERON RODRIGUEZ M., 2020 - *Simulating the impact of projected West African heatwaves and water stress on the physiology and yield of three tomato varieties*. - Adv. Hort. Sci., 34(2): 147-156.

Copyright:

© 2020 Amuji C.F., Beaumont L.J., Esperon Rodriguez M. This is an open access, peer reviewed article published by Firenze University Press (<http://www.fupress.net/index.php/ahs/>) and distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Data Availability Statement:

All relevant data are within the paper and its Supporting Information files.

Competing Interests:

The authors declare no competing interests.

Received for publication 2 April 2019
Accepted for publication 5 March 2020

Abstract: Food security is a major issue in West Africa. As a consequence of climate change, increases in temperature and shifts in precipitation will have major ramifications for which crops can be grown in the region. Here we conducted an experiment to evaluate the impacts of short-term projected heat and water stress on three tomato varieties (*Solanum lycopersicum*): Oregon Spring, Roma VF, and Tropic. The plants were initially cultivated in the glasshouse programmed at 28/20°C day/night cycle. The treatments investigated were: control (CT); heat stress (Ht); water stress (Ws) and Heat + together with water stress (HtWs). For heatwave treatments, a 35/23°C day/night gradually taken up in a cycle was imposed. The water stress conditions were by decreasing the soil water field capacity by 50%. Leaf gas exchange and plant production parameters were measured. Our result indicated that all varieties suffered from significant declines in yield as consequence of the stresses. The heatwave treatment proved more detrimental on the tomato fruit yield than the water stress, except when these two treatments occurred in sequential cycles. The results of this study suggest that heatwaves and water stress, projected to occur more frequently due to climate change, may adversely impact the growth and yield of these three tomato varieties. Also, there was an unexpected fruit yield performance comparison among varieties tested in this experiment.

1. Introduction

Food security is a global issue that is projected to exacerbate as the human population grows (Godfray *et al.*, 2010). To meet the United Nations Millennium Development Goal of “eradicating extreme poverty and hunger”, considerable emphasis have to be placed on the developing regions of the world (Pingali *et al.*, 2006), such as West Africa. West Africa comprises 15 countries and is home to an estimated 350 million people

(30% of the African continent) (United Nations, 2018). The population of this region is increasing rapidly, and is expected to reach 490 million by 2030 (Hollinger and Staatz, 2015).

In some part of West Africa, more than sixty percent of the population are dependent upon rain-fed agriculture, which is characterised by low fertilizer use, poor seed quality, inadequate water management, and low soil fertility (Benin, 2016). Agriculture is also negatively influenced by extreme weather events, such as heatwaves and droughts (Asare-Kyei *et al.*, 2017). Indeed, the United Nations Food and Agricultural Organization reported that the drought occurred from June to August of 2019 in the Sahel region of West Africa, resulted in 9.7 million people being exposed to severe food insecurity, leading to 2 million children being under acute malnutrition (FAO, 2019).

Climate change poses additional concerns for food security in West Africa, particularly as the frequency and intensity of extreme weather events are projected to increase (Sylla *et al.*, 2016). Combined with climate change, the growing human population characterized by rain-fed agriculture in West Africa, suggest that the eradication of poverty and hunger from this region will be challenging. Thus, adaptation to future climate plays a crucial role in securing food production (Easterling *et al.*, 2007) and will require efficient adaptation strategies from the respective governments. While, some of these strategies have low or no cost and are already used in the region (e.g. shifting planting dates or selecting more resilient crop varieties), other strategies, such as developing new varieties or increasing irrigation, will require greater investment (Rosenzweig and Parry, 1994).

Tomato: a key horticultural crop in West Africa

Tomato (*Solanum lycopersicum* L.) provides substantial economic and nutritional benefits for humanity (Klunklin and Savage, 2017). This crop is one of the world's most highly consumed fruits (Arah *et al.*, 2015), with over 177 million tonnes of production across ~5 million hectares of harvested land globally (FAOSTAT, 2017). Within West Africa, tomato is among the top ten horticultural crops in terms of yield. In 2016, 3.7 million tonnes were produced across 0.7 million ha (FAOSTAT, 2017). This crop is typically grown throughout West Africa under rain-fed conditions, with the greatest yield being achieved in the Sudano-Sahelian zone of West Africa, located south of the Sahara Desert and north of the humid Guinea region (Perez *et al.*, 2017).

However, tomato growth and fruit production are affected significantly by climate (Petrozza *et al.*, 2014) and yield is generally reduced in areas with extreme weather events (Oladitan and Akinseye, 2014) such as heatwaves (Hatfield and Prueger, 2015), flooding (Ezin *et al.*, 2010), and drought, as well as pests and diseases (Ximénez-Embún *et al.*, 2016). The optimum growth rate for most tomato varieties require temperatures between 20 and 27°C (Nicola *et al.*, 2008) and 400-600 mm of water throughout their growing period (Jaria, 2012). Temperatures above 32°C can affect vegetative growth and reproduction of tomatoes (Pressman *et al.*, 2002; Abdelmageed *et al.*, 2003; Müller *et al.*, 2016), causing decreases in leaf area and plant development during the flowering stage (Nduwimana and Wei, 2017) and the failure of tomato fruit set (Sato *et al.*, 2000). Water stress may lead to poor tomato plant growth and productivity through inhibition of cell expansion and reduction of stomatal opening (Chaves *et al.*, 2003). Water stress also decreases the rate of photosynthesis, especially through stomatal conductance, as well as abundance of flowers and fruiting quality (Murshed *et al.*, 2013).

Due to the importance of tomato for the West African region and the potential threat of climate change on its production, in this work we assessed the effect of heatwave and water stress on three varieties of tomatoes. We hypothesised that: (1) heatwave and water stress (i.e. less than 50% of soil water field capacity) will have a negative influence on the tomato varieties, causing reductions in fruit yield even after recovery period exposure; (2) the effect of heatwaves followed by water stress will be more severe than either of these stresses alone, causing a significant reduction in fruit yield; and (3) seasonally adapted varieties of tomatoes will respond differently to heatwaves and water stress, with varieties from warmer regions having higher yield than a cool-region variety.

2. Materials and Methods

Plant material and environmental conditions

We selected three varieties of tomato, two of which are commercially grown in West Africa ('Roma' and 'Tropic'), while the third ('Oregon Spring') is typically grown in cooler regions of the world. 'Roma' variety has a strong, compact stem with determinate vines (Gelmessa *et al.*, 2010). This variety has been noted to be particularly suited to climatic conditions

in Savannah regions of West Africa (Ojo et al., 2013). *Tropic* was bred in the 1960's in the USA as an indeterminate variety adapted to warm, humid climates (Strobel, 1970). In contrast, *Oregon Spring* was bred as a determinate tomato for cold tolerance (Baggett and Kean, 1986).

The experiment was conducted under controlled environmental conditions at the Plant Growth Facilities glasshouse (PGF) at Macquarie University, Sydney, Australia. Seeds obtained from a seed distribution company called Eden Seeds, Australia, were germinated in a growth chamber at 22°C in commercial punnets. Six weeks after sowing, seedlings of similar height were transplanted to ten litres pots filled with 10 kg of soil mix that contained sand, topsoil, and rocky grey clay. Thirty-six plants of each variety were potted. The plants were initially cultivated in the glasshouse programmed at 28/20°C day/night cycle (temperature ambient, or TA). We kept a minimum night temperature of 20°C. Then from 04:00 h, temperature was increased by 0.5°C every 30 minutes, then remained constant at 28°C until 17:00 h. Following this, temperature was decreased by 0.5°C every 30 minutes to reach the minimum night-time temperature of 20°C. This temperature cycle was selected as it represents the conditions under which tomatoes are commonly grown in West Africa. In addition, a 12-hour photoperiod of 600 $\mu\text{molm}^{-2}\text{s}^{-1}$ and CO₂ concentration of 400 ppm (parts per million) were maintained in the glasshouses throughout the experiment.

After estimating the irrigation water capacity of the pots, all pots (with the exception of individuals in the water stress treatments, see details below) were watered daily to a 100% soil water field capacity (FC) which equated to a water holding capacity of 35%. The percentage water holding capacity was determined as the gain in the weight of the soil at saturation point divided by the dried weight of the soil x 100:

$$\% \text{ water holding cap.} = \frac{\text{gain in weight of the soil at saturation point}}{\text{dried weight of the soil}} \times 100$$

All plants were given the same quantity of fertilizer fortnightly using Yates Nutricote Standard Grey® fertilizer containing NPK (16:4:4) liquid fertilizer at the rate of 1 g L⁻¹.

Experimental design

Our goal was to assess the ecophysiological responses of the three tomato varieties to heatwave and water stress. For heatwave treatments, a 35/23°C day/night cycle (temperature high, or TH)

was imposed, where temperature increased 1°C per hour from the minimum night temperature of 23°C from 04:00 h (local time) to the maximum day temperature of 35°C then kept constant at this till 17:00 h. Before been decreased at the same rate until the minimum temperature was reached (23°C), were it stayed constant again till the 04:00 h, then the cycle continued. This temperature range was selected based on future heat projections for West Africa (Abiodun et al., 2013; Sylla et al., 2016).

Presently, there is no consensus regarding future rainfall patterns for West Africa (Roudier et al., 2011), however increases in the frequency of drought conditions have been projected for the western Sahel sub-region (west of ~0°E) (Monerie et al., 2013). Thus, in this study, we simulated water stress conditions by decreasing the soil water field capacity by 50%.

To avoid location specific effects, the position of plants within the glasshouse were randomly rearranged weekly. Once reaching the flowering stage (~six weeks after sowing), three treatments together with the control were initiated for a total duration of eight weeks. Nine individual plants of each variety were placed in each treatment.

Ct - Control. Plants were grown at an ambient temperature (TA) consisting of a 28/20°C day/night cycle. All individuals were watered daily to approximately 100% FC. This condition was maintained for these Ct plants for the whole duration of the experiment. The treatment conditions are explained below:

1. *Ws - Water stress treatment*. Plants were grown at TA. The soil water field capacity of each individual was measured daily using a soil moisture sensor (Campbell Scientific Australia Pty Ltd -Hydro sense11®). During the treatment, all individuals were watered daily to only 50% FC. This condition was maintained throughout the eight weeks of treatment application.

2. *Ht - Heat treatment*. Plants were exposed to a cycle of a 14-day heatwave (TH = 23/35°C night /day) followed by 14 days at TA, and were kept well-watered. This cycle of conditions was maintained throughout the eight weeks of treatment application.

3. *HtWs - Heat and water stress treatment*. Plants were exposed to a 7-day heatwave, during which they were well watered then followed by seven days of water stress (i.e. 50% FC) at TA. Also, this cycle of conditions was maintained throughout the eight weeks of treatment application.

After this treatments application period, all the plants were returned to the Ct conditions (see details

above) and allowed to recover for five weeks then the experiment terminated. The above conditions were simulated to imitate what normally happen in nature during a heatwave occurrence.

Ecophysiological and production measurements

Ecophysiological responses were assessed by measuring gas exchange traits, which included: transpiration rate, intracellular CO₂ concentration (Ci), stomatal conductance (gs), and net assimilation rate (E). These traits are widely used to evaluate physiological responses of plants to heat-water stress conditions (Nankishore and Farrell, 2016; Duan *et al.*, 2017). The traits were measured on three mature, fully expanded leaves without damage and in good health, from five plants per treatment and variety using a Licor 6800 portable photosynthesis system (Li COR, Lincoln Nebraska, USA). Gas exchange measurements were taken at the third week (i.e. first week after complete treatments cycle-W3) and eight weeks (i.e. last week of treatment application-W8) between 09:30-14:00 h (local time). Also at the same period the number of flowers per plant were counted from the nine sampling plants per treatment and variety. Subsequently, the number of fruits that developed on these plants was also recorded. Maturity of fruit was determined based on a standard USDA colour chart (e.g. 'light red', UCANR, 2011). During the termination of the experiment (i.e. after the five weeks of recovery period), matured fruits were collected and weighed. The fresh and dry above ground biomass of the sampled plants were weighed and recorded too, with drying undertaken in an oven at 70°C for seven days. Measurements were noted as Fresh Biomass Weight Without Fruit (FWWF), Fresh Fruit Weight (FFW), Total Fresh Biomass Weight (TFW).

Statistical analysis

A two-way Analysis of variance (ANOVA) model with a correction formula called Satterthwaite approximation was performed to determine the effects of all the treatments (i.e. water treatment vs heat treatment vs both in sequential combination) vs control on the tomato varieties, using the *lmerTest* Package (Kuznetsova *et al.*, 2017) in R version 3.4.3 (R Development Core Team, 2017). As measurements were taken on the same individuals over two different weeks, we used week as a covariate, with plant ID treated as a random effect. Post-hoc tests (Turkey contrasts) were used to compare means between treatments, and results were considered significant

when $p < 0.05$. Statistical differences were reported as different letters on each figure. All figures were drawn in R using the 'ggplot2' (Wickham, 2016) packages.

3. Results

Ecophysiological measurements

From figure 1 and Table 1 it can be observed that for all the three varieties, transpiration rate differed significantly across treatments and weeks. Transpiration was generally highest among Ht plants and lowest in the HtWs treatment. For 'Oregon Spring', transpiration rates among Ht plants did not differ significantly to Ct, whereas rates were significantly higher among 'Roma's Ht plants. For both *Roma* and *Tropic*, transpiration rates between Ct plants and Ws were not significantly different (Fig. 1).

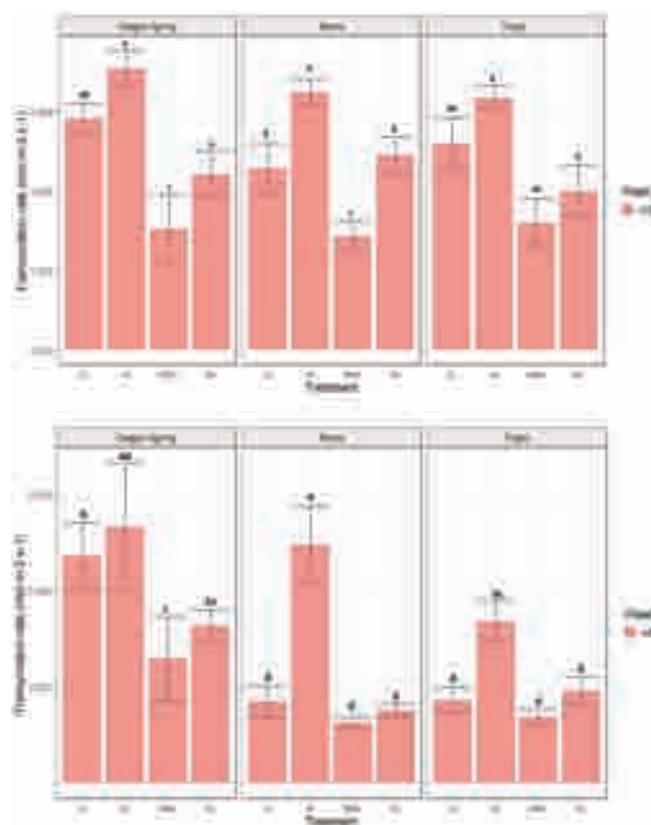


Fig. 1 - Transpiration rate ($\text{mol m}^{-2} \text{s}^{-1}$) of three tomato varieties (Oregon Spring, Roma and Tropic). The treatments consist of Control (Ct), Water stress (Ws), Heat + Water stress (HtWs) and Heat (Ht). W3 and W8 = weeks of treatments imposition with measurements. Bars with the same letter are not significantly different at $P < 0.05$ according to Turkey's test.

Table 1 - Intracellular CO₂ response (Pa) of the three tomato varieties (Oregon Spring, Roma and Tropic)

Tomato varieties	Treatments		Weeks		Interaction	
	F-value	P value	F-value	P value	F-value	P value
<i>Number of fruits</i>						
Oregon Spring	399.681	< 0.001	350.074	<0.001	0.0466	<0.001
Roma	206.190	< 0.001	243.735	< 0.001	61.612	0.019
Tropic	289.064	< 0.001	453.048	<0.001	84.548	< 0.001
<i>Number of flowers</i>						
Oregon Spring	27.092	0.07	19.494	0.177	10.069	0.409
Roma	19.226	0.1568	27.351	0.1130	36.571	0.0289
Tropic	76.114	0.001	74.866	0.001	62.638	0.0033
<i>Intracellular CO₂ response</i>						
Oregon Spring	15.867	0.231	766.736	<0.001	12.037	0.3126
Roma	46.786	0.015	1.007.011	< 0.001	41.736	0.007
Tropic	41.423	0.023	11.552	0.285	0.9491	0.420
<i>Assimilation Rates</i>						
Oregon Spring	25.944	0.088	295.82	<0.001	7.449	<0.001
Roma	0.2935	0.829	911.11	<0.001	27.802	<0.001
Tropic	21.725	0.131	1322.9	<0.001	25.296	<0.001
<i>Stomatal conductance</i>						
Oregon Spring	59.115	0.006	119.84	<0.001	72.924	<0.001
Roma	81.714	0.002	131.58	< 0.001	7.443	<0.001
Tropic	37.627	0.032	259.27	<0.001	11.078	< 0.001
<i>Transpiration Rates</i>						
Oregon Spring	65.636	0.04	253.232	<0.001	13.997	0.247
Roma	23.232	<0.001	237.1	<0.001	9.214	<0.001
Tropic	13.053	<0.001	241.49	<0.001	5.393	0.002

The treatments consist of Control (Ct), Water stress (Ws), Heat + Water stress (HtWs) and Heat (Ht). W3 and W8 = weeks of treatments imposition with measurements. Bars with the same letter are not significantly different at P<0.05 according to Turkey's test.

In general, plants exposed to heatwave stress had higher rates of intracellular CO₂ compared to plants in the other treatments. The lowest values occurred among HtWs plants, with similar patterns for the three varieties (Fig. 2). Stomatal conductance (g_s) across the three varieties was generally higher in Ht plants, and lowest in the HtWs treatment (Fig. 3, Table 1). However, treatment, week, and their interactions differed significantly for each variety. Among *Oregon Spring* and *Roma* varieties, Ct and Ht plants had significantly higher g_s than the HtWs plants. For *Tropic*, the Ht plants had significantly higher g_s than HtWs plants in the weeks observed (Fig. 3, Table 1). Net assimilation rate (E) differed significantly for the weeks and the interaction between treatments and weeks among all the three varieties (Fig. 4; Table 1).

Production measurements

For the three varieties, the number of flowers was greater in both of the heatwave treatments (Ht and HtWs) compared to the Ct and Ws treatments. Ht treated plants had significantly the highest number of flowers. Also, by the end of the treatment application (w8), 'Oregon Spring' had an average of 8.5 (± 0.6 SD) flowers among plants in the Ws treatment,

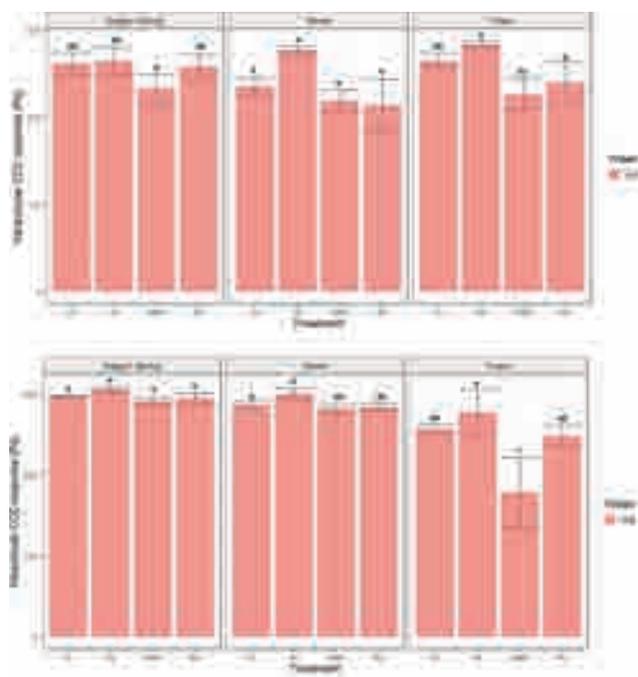


Fig. 2 - Intracellular CO₂ response (Pa) of the three tomato varieties (Oregon Spring, Roma and Tropic). The treatments consist of Control (Ct), Water stress (Ws), Heat + Water stress (HtWs) and Heat (Ht). W3 and W8 = weeks of treatments imposition with measurements. Bars with the same letter are not significantly different at P<0.05 according to Turkey's test.

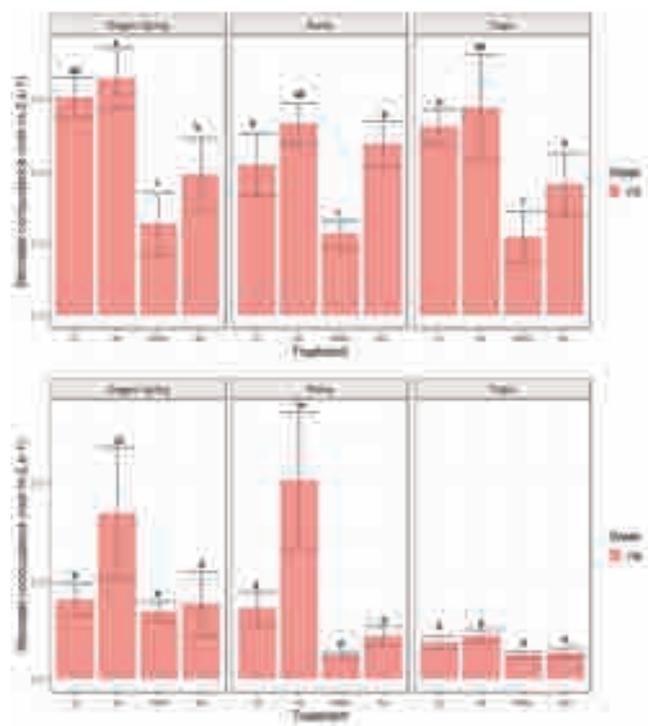


Fig. 3 - Stomatal conductance ($\text{mol m}^{-2} \text{s}^{-1}$) of the three tomato varieties (Oregon Spring, Roma and Tropic). The treatments consist of Control (Ct), Water stress (Ws), Heat + Water stress (HtWs) and Heat (Ht). W3 and W8 = weeks of treatments imposition with measurements. Bars with the same letter are not significantly different at $P < 0.05$ according to Turkey's test.

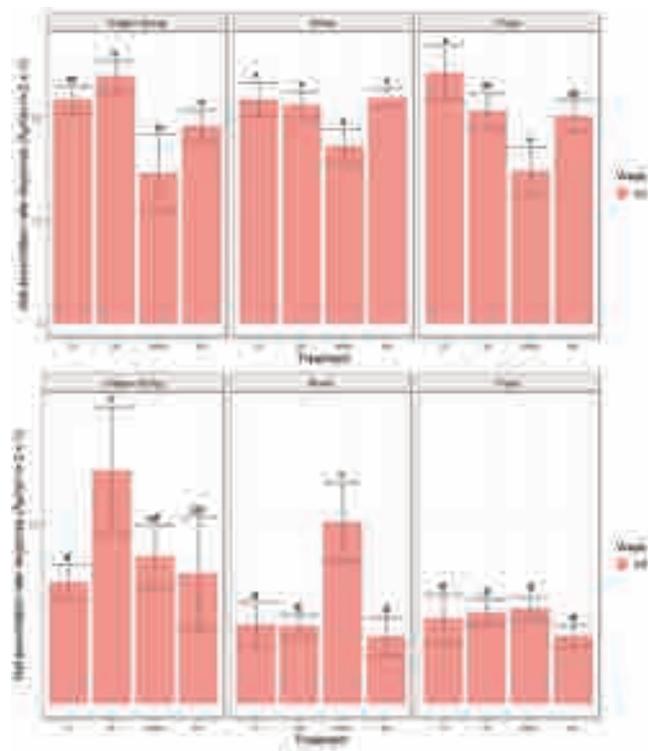


Fig. 4 - Net assimilation rate response ($\mu\text{mol m}^{-2} \text{s}^{-1}$) of the three tomato varieties (Oregon Spring, Roma and Tropic). The treatments consist of Control (Ct), Water stress (Ws), Heat + Water stress (HtWs) and Heat (Ht). W3 and W8 = weeks of treatments imposition with measurements. Bars with the same letter are not significantly different at $P < 0.05$ according to Turkey's test.

and $15 (\pm 4)$ and $20 (\pm 7)$ flowers on plants in the HtWs and Ht treatments, respectively (Fig. 5). For both 'Roma' and 'Tropic', the average number of fruits that developed per plant differed significantly across treatments, weeks, and their interactions (Table 1). All three varieties produced fewer fruits under both heatwave treatments. This effect was most pronounced for Roma where, by W8 of the treatment period, Ct plants had produced an average of $19.4 (\pm 8.9)$ fruits per plant compared to Ht plants (Ht: 2.6 ± 2.4 and HtWs: 0.8 ± 1.8), and significantly more fruits than plants in the Ws treatment (9.8 ± 4.4). Oregon Spring produced more fruits in the heatwave treatments compared to the warmer varieties (Fig. 6, Table 1).

In general, heatwave treatments resulted in greater reductions to the harvested fruit weight than the water stress treatment. However, harvested fresh fruit weight (FFW) was higher among Ct plants compared to the other treatments (Fig. 7). This difference was significant for 'Roma' and 'Tropic' (Table 2), although there was no significant difference between Ct and Ws treatments for 'Oregon Spring'.

For 'Roma' and 'Tropic' we found no significant differences among treatments when we compared Fresh Biomass weight without fruits (i.e. FWWF = Fresh Biomass excluding fruit). However, 'Oregon Spring' biomass was significantly greater for Ht plants than the other three treatments. For this variety, heatwave stressed plants were able to maintain growth at the expense of fruit production. We found a significant difference in the total biomass weight (TFW) (due to the adding of fruits weight) among treatments (Fig. 7, Table 2).

4. Discussion and Conclusions

We simulated the impacts of climate change by assessing the response of three varieties of tomato ('Roma', 'Tropic', 'Oregon Spring') to heatwave and water stresses. We found that assimilation rate, transpiration rate, intracellular CO₂ response, and stomatal conductance were all elevated under heatwave stress. In addition, we extended upon previous studies on tomatoes (e.g. Nankishore and Farrell, 2016;

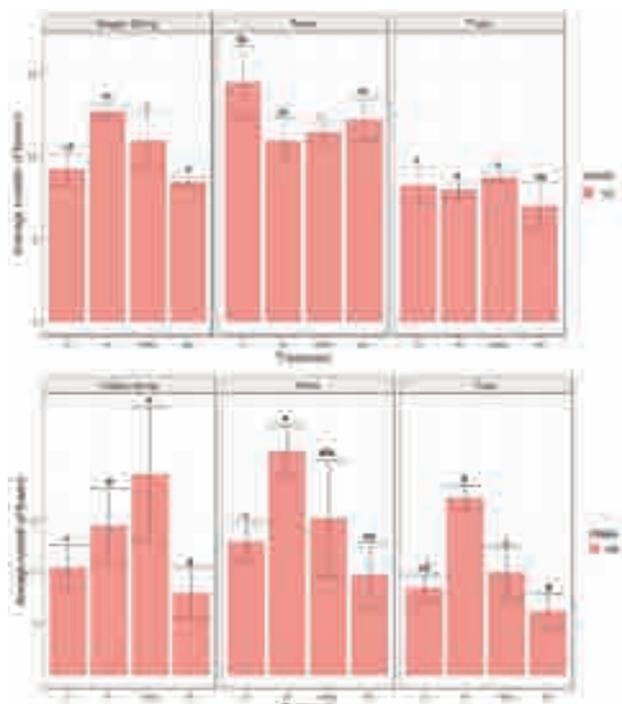


Fig. 5 - Average number of flowers per plant for the three tomato varieties (Oregon Spring, Roma and Tropic). The treatments consist of Control (Ct), Water stress (Ws), Heat + Water stress (HtWs) and Heat (Ht). W3 and W8 = weeks of treatments imposition with measurements. Bars with the same letter are not significantly different at $P < 0.05$ according to Turkey's test.

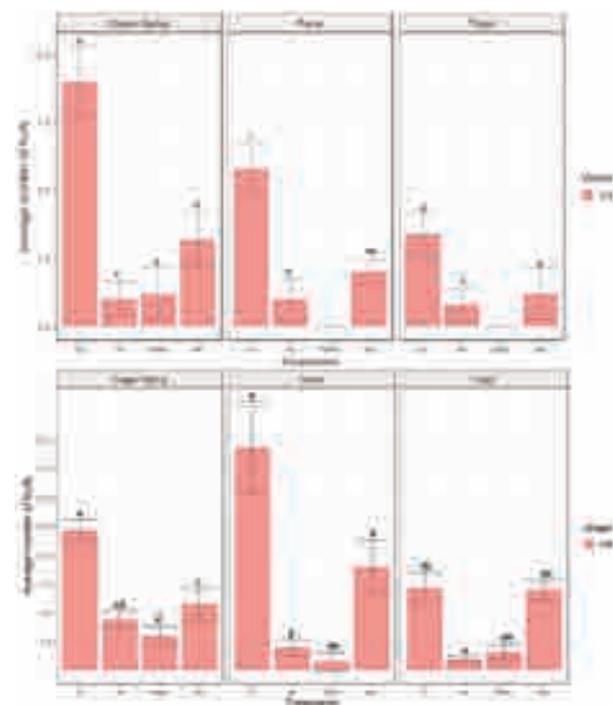


Fig. 6 - Average number of fruits per plant for the three tomato varieties (Oregon Spring, Roma and Tropic). The treatments consist of Control (Ct), Water stress (Ws), Heat + Water stress (HtWs) and Heat (Ht). W3 and W8 = weeks of treatments imposition with measurements. Bars with the same letter are not significantly different at $P < 0.05$ according to Turkey's test.

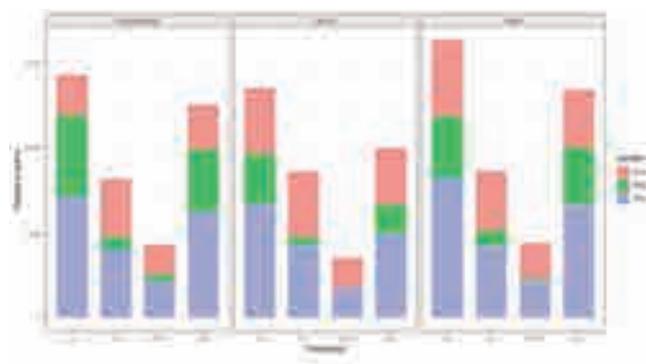


Fig. 7 - Fruit yield (marketable harvested fresh fruit) and aerial biomass accumulation response for the three tomato varieties (Oregon Spring, Roma and Tropic). The treatments consist of Control (Ct), Water stress (Ws), Heat + Water stress (HtWs) and Heat (Ht). Measured during the termination of experiment (i.e. after allowing for five weeks' recovery from the treatments). FWWF=Fresh Biomass weight without fruits; FFW=Fresh fruits weights; TFW= Total fresh biomass weight.

Table 2 - ANOVA (F-value and P-value) comparing the impact of the treatments on the harvested fresh fruits and aerial biomass measurements that developed on three varieties of tomato (OregonSpring, Roma and Tropic)

Tomato varieties	Treatments	
	F-value	P- value
<i>Fresh weight without fruits (FWWF)</i>		
Oregon Spring	3.04	0.046
Roma	1.18	0.335
Tropic	1.93	0.148
<i>Harvested fresh fruits weights (FFW)</i>		
Oregon Spring	14.66	<0.001
Roma	18.00	<0.001
Tropic	9.79	<0.001
<i>Total fresh weight (TFW)</i>		
Oregon Spring	6.75	0.002
Roma	19.89	<0.001
Tropic	10.96	<0.001

Sivakumar and Srividhya, 2016; Duan *et al.*, 2017; Zhou *et al.*, 2017) by assessing the impact of these stresses individually and sequentially on fruit yield, which is crucial from a socio-economic and food security perspective especially in region like West Africa. We found that these studied three tomato varieties experienced greater decline in yield (i.e. harvested fresh fruit weight) due to heat wave stress compared to water stress. However, under water stress fewer flowers were formed, indicating that heatwave stress results in a higher rate of aborted flowers compared with water stress, since its higher

number flowers did not transform to more fruits. Unsurprisingly, a greater impact on the plants fruit yield occurred when exposed to both stressors sequentially (i.e. heatwave then water stress together). Plants exposed to this treatment (i.e. HtWs) were unable to form fruit despite having more flowers than plants exposed to water stress only.

Water and heat stress affect photosynthesis and other physiological processes of tomatoes (Nankishore and Farrell, 2016; Duan *et al.*, 2017; Zhou *et al.*, 2017). Thus, as climate change intensifies, tomato yield in West Africa may decline due to the predicted higher frequency of heatwaves (Engelbrecht *et al.*, 2015). High temperature can deactivate enzyme activity involved in the photosynthetic process, reducing or inhibiting photosynthesis (Rennenberg *et al.*, 2006). This, in turn, has been reported to cause a 2.5% to 10% decline in yield for numerous crop species (Hatfield *et al.*, 2011). In tomatoes, heat stress also has the potential to affect the viability of pollen (Hatfield and Prueger, 2015) resulting in failure of fruit set (Sato *et al.*, 2000). Nevertheless, the impacts of heatwaves can be alleviated with irrigation. Here, we found that stomata closed when the plants in ambient temperature were under water stress, which invariably led to lower rates of leaf gas exchange. This was not the case for the plants under the heatwave treatment that remained well-irrigated, these plants consistently had higher values of stomatal conductance.

Crops differ in their capacity to recover from heatwave and water stress. For instance, some grains like maize (*Zea mays* L.) and rice (*Oryza spp.*) require a 10-day period of normal conditions (i.e. lower temperature and irrigation) after heat stress to enable the development of fruits (Hatfield and Prueger, 2015). For our experiment, a period of 14 days of normal conditions (i.e. 28/20°C day/night cycle and well-watered) between heatwave-imposed stress was not enough for plants to recover and produce fruits from the flowers formed, although the magnitude of the impacts on fruit production varied among the varieties. 'Tropic' and 'Oregon Spring' varieties had significantly higher fruit yield than 'Roma'. This finding highlights the vulnerability of these tomato varieties to heatwave and water stress. High temperature can affect allocation of resources, such as above- and below-ground tissues, with a tendency towards higher shoot-to-root ratios (Way and Oren, 2010). Neither heatwave or water stress, individually or sequentially, significantly affected vegetative biomass of the three tomato varieties, which con-

trasts to yield. Under all treatments within this experiment, the three varieties continued to have normal vegetative growth; however, flowers and the consequent fruit yield were drastically affected indicating the importance of optimal conditions (i.e. temperature and water) to facilitate plant reproduction (Peet and Welles, 2005; Parvej *et al.*, 2010).

Initially, we hypothesised that heat stress would have a greater negative impact on the yield of 'Oregon Spring', the cool region variety, compared to the warm region varieties, i.e. 'Roma' or 'Tropic'. However, our results indicate the opposite, suggesting that *Oregon Spring* may out-perform either 'Roma' and 'Tropic' under similar conditions. This finding may indicate a higher plasticity in 'Oregon Spring' and a higher adaptive capacity. We suggest future research to explore the genetic characteristics of 'Oregon Spring' in response to heatwave and water stress to validate this as a potential variety to use under stress climatic conditions in as used in this experiment.

This study indicated that under a simulated climate projection of 50% less soil water field capacity and a heatwave of 35/23°C-day night cycles for West Africa, leaf gas exchange and fruit yield of three varieties of tomatoes were negatively affected, although vegetative growth was unaffected. Individually, heatwave stress was more detrimental for fruit yield than water stress, although experiencing these two stresses in sequence had an even greater consequence. Hence, ensuring plants are well watered can ameliorate some of the negative impacts of heatwave stress. Further studies are necessary to confirm the relationship existing among the various combinations of the heatwave and water stress conditions on different reproductive stages, such as pollen formation, pollen development and fertilization of tomatoes. Interestingly, the cool adapted variety assessed in this work, 'Oregon Spring', might represent an alternative option in warm temperature regions where 'Roma' and 'Tropic' varieties are underperforming, provided that irrigation is not limited.

Acknowledgements

The authors wish to thank Professor B.J. Atwell and Dr. Alessandro Ossola for their technical inputs. This study was supported by a scholarship and research funding from the Macquarie University Australia's International Research Training Program (iRTP).

References

- ABDELMAGEED A., GRUDA N., GEYER B., 2003 - *Effect of high temperature and heat shock on tomato (Lycopersicon esculentum Mill) genotypes under controlled conditions*. - Deutscher Tropentag 2003, Göttingen, 8-10 October 2003. Conference on International Agricultural Research for Development, 34(10): 1064-1076.
- ABIODUN B.J., LAWAL K.A., SALAMI A.T., ABATAN A.A., 2013 - *Potential influences of global warming on future climate and extreme events in Nigeria*. - Regional Environ. Change, 13(3): 477-491.
- ARAH I.K., KUMAH E., ANKU E., AMAGLO H., 2015 - *An overview of post-harvest losses in tomato production in Africa: causes and possible prevention strategies*. - J. Biol., Agric. Healthcare, 5(16): 78-88.
- ASARE-KYEI D., RENAUD F.G., KLOOS J., WALZ Y., RHYNER J., 2017 - *Development and validation of risk profiles of West African rural communities facing multiple natural hazards*. PloS One, 12(3): e0171921.
- BAGGETT J., KEAN D., 1986 - *'Oregon Spring' and 'Santiam' parthenocarpic tomatoes*. HortScience, 21: 1245-1247.
- BENIN S., 2016 - *Impacts of comprehensive Africa Agriculture Development Programme (CAADP) on Africa's Agricultural-led Development*. - Intl Food Policy Research Institute, Vol. 1553, Washington DC, USA.
- CHAVES M.M., MAROCO J.P., PEREIRA J.S., 2003 - *Understanding plant responses to drought - from genes to the whole plant*. - Functional Plant Biology, 30(3): 239-264.
- DUAN H., WU J., HUANG G., ZHOU S., LIU W., LIAO Y., YANG X., XIAO Z., FAN H., 2017 - *Individual and interactive effects of drought and heat on leaf physiology of seedlings in an economically important crop*. AoB Plants, 9(1): plw090.
- EASTERLING W., AGGARWAL P., BATIMA P., BRANDER K., ERDA L., HOWDEN M., KIRILENKO A., MORTON J., SOUSSANA J.-F., SCHMIDHUBER S., TUBIELLO F.N., 2007 - *Food, fibre and forest products*, pp. 273-313. - In: PARRY M.L., O.F. CANZIANI, J.P. PALUTIKOF, P.J. VAN DER LINDEN, and C.E. HANSON (eds.) *Climate change 2007: Impacts, adaptation and vulnerability. Contribution of working group II to the fourth assessment report of the intergovernmental panel on climate change*. Cambridge University Press, UK.
- ENGELBRECHT F., ADEGOKE J., BOPAPE M.-J., NAIDOO M., GARLAND R., THATCHER M., MCGREGOR J., KATZFEY J., WERNER M., ICHOKU C., CHARLES G., 2015 - *Projections of rapidly rising surface temperatures over Africa under low mitigation*. Environmental Research Letters, 10(8): 085004.
- EZIN V., PENA R.D.L., AHANCHEDE A., 2010 - *Flooding tolerance of tomato genotypes during vegetative and reproductive stages*. - Brazilian Journal of Plant Physiology, 22(2): 131-142.
- FAO, 2019 - *Sahel - Regional overview (July 2019)*. - Food and Agriculture Organization of the United Nations; Resources documents. Rome, Italy.
- FAOSTAT F., 2017 - *Statistical data*. - Food and Agriculture Organization of the United Nations, Rome, Italy.
- GELMESA D., ABEBIE B., DESALEGN L., 2010 - *Effects of Gibberellic acid and 2, 4-dichlorophenoxyacetic acid spray on fruit yield and quality of tomato (Lycopersicon esculentum Mill.)*. - J. Plant Breeding Crop Sci., 2(10): 316-324.
- GODFRAY H.C.J., BEDDINGTON J.R., CRUTE I.R., HADDAD L., LAWRENCE D., MUIR J.F., PRETTY J., ROBINSON S., THOMAS S.M., TOULMIN C., 2010 - *Food security: the challenge of feeding 9 billion people*. - Science, 327(5967): 812-818.
- HATFIELD J.L., BOOTE K.J., KIMBALL B., ZISKA L., IZAURRALDE R.C., ORT D., THOMSON A.M., WOLFE D., 2011 - *Climate impacts on agriculture: implications for crop production*. - Agronomy Journal, 103(2): 351-370.
- HATFIELD J.L., PRUEGER J.H., 2015 - *Temperature extremes: Effect on plant growth and development*. - Weather and Climate Extremes, 10: 4-10.
- HOLLINGER F., STAATZ J.M., 2015 - *Agricultural Growth in West Africa. Market and policy drivers*. - FAO, African Development Bank, ECOWAS. Publication of the African Development Bank and the Food and Agriculture Organization of the United Nations, Rome.
- JARIA F., 2012 - *Irrigation Scheduling Strategies for Tomato Production in Southwestern Ontario*. PhD Thesis submitted at Department of Bioresources Engineering, McGill University Montreal, Quebec, Canada, pp. 40.
- KLUNKLIN W., SAVAGE G., 2017 - *Effect on quality characteristics of tomatoes grown under well-watered and drought stress conditions*. Foods, 6(8): 56.
- KUZNETSOVA A., BROCKHOFF P.B., CHRISTENSEN R.H.B., 2017 - *lmerTest package: tests in linear mixed effects models*. - J. Statistical Software, 82(13).
- MONERIE P.A., ROUCOU P., FONTAINE B., 2013 - *Mid-century effects of Climate Change on African monsoon dynamics using the A1B emission scenario*. - Int. J. Climatology, 33(4): 881-896.
- MÜLLER F., XU J., KRISTENSEN L., WOLTERS-ARTS M., DE GROOT P.F., JANSMA S.Y., MARIANI C., PARK S., RIEU I., 2016 - *High-temperature-induced defects in tomato (Solanum lycopersicum) anther and pollen development are associated with reduced expression of B-class floral patterning genes*. - PloS One, 11(12): e0167614.
- MURSHED R., LOPEZ-LAURI F., SALLANON H., 2013 - *Effect of water stress on antioxidant systems and oxidative parameters in fruits of tomato (Solanum lycopersicon L. cv. Micro-tom)*. - Physiology and Molecular Biology of Plants, 19(3): 363-378.
- NANKISHORE A., FARRELL A.D., 2016 - *The response of contrasting tomato genotypes to combined heat and drought stress*. - J. Plant Phys., 202: 75-82.
- NDUWIMANA A., WEI S.M., 2017 - *Effects of high tempera-*

- ture regimes on cherry tomato plant growth and development when cultivated in different growing substrates systems. - Biol. Clinical Res., 4(1): 1-17.
- NICOLA S., TIBALDI G., FONTANA E., 2008 - *Tomato production systems and their application to the tropics*. - Acta Horticulturae, 821: 27-33.
- OJO G., EKOJA E., UKPOJU O., 2013 - *Evaluation of tomato (Lycopersicon lycopersicum Mill.) for fruit yield and yield components in the southern guinea Savanna ecology of Nigeria*. - Int. J. Agron. Agric. Res., 3(3): 1-5.
- OLADITAN T.O., AKINSEYE F.M., 2014 - *Influence of weather elements on phenological stages and yield components of tomato varieties in Rainforest Ecological Zone, Nigeria*. - J. Nat. Sci. Res., 4(12): 19-24.
- PARVEJ M.R., KHAN M.A., AWAL M.A., 2010 - *Phenological development and production potentials of tomato under polyhouse climate*. - J. Agric. Sci. Sri Lanka, 5(1): 19-31.
- PEET M.M., WELLES G.W.H., 2005 - *Greenhouse tomato production*. - Crop Production Sci. Hortic., 13: 257.
- PEREZ K., FROIKIN-GORDON J.S., ABDOURHAMANE I.K., LEVASSEUR V., ALFARI A.A., MENSAH A., BONSU O., HABSATOU B., ASSOGBA-KOMLAN F., MBAYE A.A., NOUSSOUROU M., 2017 - *Connecting smallholder tomato producers to improved seed in West Africa*. - Agric. Food Security, 6(1): 42.
- PETROZZA A., SANTANIELLO A., SUMMERER S., DI TOMMASO G., DI TOMMASO D., PAPARELLI E., PIAGGESI A., PERATA P., CELLINI F., 2014 - *Physiological responses to Megafol® treatments in tomato plants under drought stress: a phenomic and molecular approach*. - Scientia Hort., 174: 185-192.
- PINGALI P., STAMOULIS K., STRINGER R., 2006 - *Eradicating extreme poverty and hunger: towards a coherent policy agenda. The Development Dimension Trade, Agriculture and Development Policies Working Together*. - Organization for Economic Co-operation and Development publication, Paris, France, pp. 167.
- PRESSMAN E., PEET M.M., PHARR D.M., 2002 - *The effect of heat stress on tomato pollen characteristics is associated with changes in carbohydrate concentration in the developing anthers*. - Annals of Botany, 90(5): 631-636.
- R DEVELOPMENT CORE TEAM, 2017 - *R: A Language and Environment for Statistical Computing*. - R Foundation for Statistical Computing, Vienna.
- RENNENBERG H., LORETO F., POLLE A., BRILLI F., FARES S., BENIWAL R., GESSLER A.J.P.B., 2006 - *Physiological responses of forest trees to heat and drought*. - Plant Biol., 8(5): 556-571.
- ROSENZWEIG C., PARRY M.L., 1994 - *Potential impact of climate change on world food supply*. - Nature, 367(6459): 133.
- ROUDIER P., SULTAN B., QUIRION P., BERG A., 2011 - *The impact of future climate change on West African crop yields: What does the recent literature say?* - Global Environmental Change, 21(3): 1073-1083.
- SATO S., PEET M., THOMAS J., 2000 - *Physiological factors limit fruit set of tomato (Lycopersicon esculentum Mill.) under chronic, mild heat stress*. - Plant, Cell & Environ., 23(7): 719-726.
- SIVAKUMAR R., SRIVIDHYA S., 2016 - *Impact of Drought on Flowering, Yield and Quality Parameters in Diverse Genotypes of Tomato*. - Adv. Hort. Sci., 30(1): 3-11.
- STROBEL J., 1970 - *Walter and Tropic-new tomato varieties for Florida growers*. - Proceedings of the Florida State Horticultural Society, 1969, 82: 121-124.
- SYLLA M.B., ELGUINDI N., GIORGI F., WISSER D., 2016 - *Projected robust shift of climate zones over West Africa in response to anthropogenic climate change for the late 21st century*. - Climatic Change, 134(1-2): 241-253.
- UCANR, 2011 - *USDA color chart for Tomato (Solanum lycopersicum)*. - University of California Agriculture and National Resources Repository <https://ucanr.edu/repository/view.cfm?article=83755%20&groupid=9>
- UNITED NATIONS, 2018 - *World Population Prospects 2017*. United Nations Population Division Publication: Data Booklet. New York, USA.
- WAY D.A., OREN R., 2010 - *Differential responses to changes in growth temperature between trees from different functional groups and biomes: a review and synthesis of data*. - Tree Physiology, 30(6): 669-688.
- WICKHAM H., 2016 - *Ggplot 2: Elegant graphics for data analysis*. - Springer-Verlag, New York, USA.
- XIMÉNEZ-EMBÚN M.G., ORTEGO F., CASTAÑERA P., 2016 - *Drought-stressed tomato plants trigger bottom-up effects on the invasive Tetranychus evansi*. - PloS One, 11(1): e0145275.
- ZHOU R., YU X., OTTOSEN C.O., ROSENQVIST E., ZHAO L., WANG Y., YU W., ZHAO T., WU Z., 2017 - *Drought stress had a predominant effect over heat stress on three tomato cultivars subjected to combined stress*. BMC Plant Biology, 17(1), 24.