Can intraspecific variation in an herbivorous mite alter responses to drought-stressed host plant? A common garden experiment in the context of climate change

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Abstract

The effects of drought stress on plants and phytophagous arthropods are topics currently extensively investigated in the context of climate change. Dryness not only impacts cultivated plants but also their parasites, which in some cases are favoured by drought. It represents a major challenge that agriculture is facing in a perspective of intensification of drought. Direct effects of drought on herbivorous arthropods typically produce bigger offspring and faster development but attractiveness can also occur. However, how much responses to abiotic factors differ among populations of a species remains poorly documented. The impact of drought-stressed plants on key life-history parameters is here investigated for a major agricultural pest, the two spotted spider mite, *Tetranychus urticae*, depending on the climatic conditions of the localities at origin. Sampled localities represent a rather wide range of core climate conditions across the mite's native distribution area with contrasting climatic profiles, ranging from wet temperate to cool Atlantic localities to medium to dry hot Mediterranean localities. Plant drought stress effects on mites was estimated by measuring four life history traits: development time, fecundity, sex-ratio and emigration rate in a common garden experiment made of two modalities: well-watered and drought-stressed bean plants. Mites feeding on drought-stressed plants displayed shorter developmental time and attempted to leave leaf patches less often, and young females were more fecund. The mites originating from wet temperate to cool Atlantic localities respond more strongly to drought than mites originating from medium to dry hot Mediterranean localities, suggesting local adaptation of *T. urticae* populations to various aridity values and indicates that mite feeding behaviour is shaped by the climatic conditions they faced in the area of origin.

Keyword

Acari; *Tetranychus urticae*; Europe; Mediterranean; local adaptation; common garden experiment; life-history traits

Introduction

"A Quarter of Humanity Faces Looming Water Crises", that was the title of an article in The New York Times of August 6th, 2019 (Sengupta and Cain, 2019). It is a fact that drought is a major challenge around the World, with 17 countries facing extreme water shortages. One of the major consequences of water shortage, in addition to its impact on human survival and health, is the impact it has on agriculture. Many cities in the global South (Mitlin et al. 2019) face water shortages, which is leading to conflicts between immediate human needs and agriculture. Agricultural production currently represents 70% of the overall water consumption worldwide (OECD, https://www.oecd.org/agriculture/topics/water-and-agriculture/) and projections for 2050 indicate water use in agriculture will increase. Low water availability not only impacts cultivated plants but also their parasites, which in some cases are favoured by drought (Showler, 2013). Thus, both water availability and pests are major agricultural challenges that are increasing because of global change and the resulting intensification of drought.

Understanding the effects of drought and more precisely drought stress on plants and phytophagous organisms is important to supporting future agricultural production. Chaves et al. (2003) reviewed how drought affects plants physiology and Showler (2013) and Hummel et al. (2010) documented changes in the amino-acids and free sugar balances in drought-stressed plants. The impact of drought on plant-associated fauna has been documented at the population level. For example, Dale & Frank (2017) observed that fitness of scale insects increased on drought-stressed urban maple trees relative to well-watered trees. Effects of drought stress on herbivorous arthropods organisms has been also quantified experimentally. For example, drought stress in beans increased oviposition by the bug *Orius insidiosus* (Seagrave et al., 2011) and drought stress in the grass *Holcus lanatus* increased offspring and rates of emergence of the moth *Spodoptera littoralis* increasing their fitness overall relative to well-watered plants (Walter et al. 2012). Field and laboratory observations of spider mites have revealed diverse and sometimes divergent results. Drought stress of soybeans led to faster development and thus increased density of the spider mite *Tetranychus turkestani* (Nikolova et al. 2014). This pattern was also observed in *Tetranychus urticae* and *Oligonychus pratensis* on maize (Chandler et al. 1979), and in a mixed mite population (75% of *Tetranychus pacificus* and 25% of *Panonychus citri*) on almond (Youngman & Barnes, 1986; Youngman et al., 1988). Gillman et al. (1999) observed that the damage caused by *T. urticae* increased on drought stressed buddleia plants. Ximénez-Embun et al. (2016, 2017a, 2017b) observed a global increase of performance of three important tomato mite pests, *Tetranychus evansi*, *T, urticae* and *Aculops lycopersici,* reared on

drought-stressed tomato plants, especially for tomato-adapted strains in the case of *T. urticae*. A non-linear response with an increase of density and fecundity of *t*his mite was reported at an intermediate level of drought, and a linear increase of development rate at a severe drought stress regime (English-Loeb, 1989). In contrast, the opposite pattern was reported by Oloumi-Sadeghi et al. (1988) who observed a decrease of *T. urticae* abundance on drought-stressed soybean and by Sadras et al. (1998) for *T. urticae* on cotton.

The degree to which different populations of a phytophagous arthropods differ in responses to abiotic factors remains poorly documented. However, adaptation and phenotypic plasticity are regarded as main way that organisms respond to changing environments (Bowman et al. 2018). For example, Kelley et al. (2011) reported a latitudinal and temperature-linked gradient increasing maximum thermal tolerance of the crab *Carcinus maenas* populations from coldest to warmest localities Among the tetranychids mites, common garden experiments revealed a latitudinal gradient of life history traits (fecundity, development time, sex-ratio and dispersal) from Western European core distribution of *T. urticae* to the northernmost part of the distribution area (Van Petegem et al. 2016). Diapause as a means of cold avoidance is another trait that varies according to the climate the mite experiences. For example, Koveos et al. (1993) reported a gradient of diapause duration linked to latitude and altitude in *T. urticae* where Japanese alpine populations displayed similar traits than the most northern mites indicating the importance of temperature on regulation of this trait. Similarly, Takafuji et al. (1991) also in *T. urticae* and Suwa & Gotoh (2006) in *Tetranychus puerariсola*, observed a South-North gradient in the diapause induction of these two species along the Japanese archipelago.

Thus, intraspecific variation is common in many organisms. Drought stress also varies historically in different geographic origins, and is becoming more common in some regions due to climate change Here, we explore how drought stress in host plants affects different populations of an herbivorous mite that is a major plant pest, the two spotted spider mite, *T. urticae*. This work focuses on if and how responses depend on the geographic origin of the mites.

Material and methods

The effect of plant drought stress on mites was estimated by measuring four life history traits in two common garden experiments, each using well-watered and drought-stressed bean plants. We measured development time of females (experiment I) and fecundity, leaving rates and sex ratio of progeny (experiment II). *Tetranychus urticae* is an arrhenotokous mite, and sex ratio represents a way to respond to changing environments (Crozier, 1985).

1 Mite material

Origin of mites. *Tetranychus urticae* populations (green and red forms - Auger et al. 2013) originating from 12 different locations in Europe were chosen to provide diversity in our experiments (Table 1, Figure 1). Among the localities sampled, Greece, Cyprus and to a lesser extent Spain and Italy correspond to places with dry hot summers while France and United-Kingdom correspond to wet hot summer to medium summer.

Table 1: Characteristics of the populations of *Tetranychus urticae* used in the common garden experiments.

Mite population	Country	Locality	Latitude (DD)	Longitude (DD)	Mite body color	Host plant name
IT-I	Italy	Lerici	44.086	9.889	Red	*Convolvulus arvensis*
SP-I	Spain	Palafolls	41.671	2.758	Red	*Phaseolus vulgaris*
CY-I	Cyprus	Paralimni	35.050	33.990	Red	*Convolvulus arvensis*
CY-II	Cyprus	Kouklia	34.693	32.578	Green	*Convolvulus arvensis*
CY-III	Cyprus	Kouklia	34.693	32.578	Green	*Malva sp*
GR-I	Greece	Karystos	38.027	24.404	Green	*Malva sp*
GR-II	Greece	Karystos	38.027	24.404	Green	*Xanthium italicum*
UK-I	U-K	East-Mailing	51.285	0.448	Green	*Urtica dioica*
FR-IV	France	Cappy	49.928	2.783	Green	*Solanum tuberosum*
FR-II	France	Burnhaupt	47.741	7.142	Red	*Urtica dioica*
FR-III	France	Guewenheim	47.756	7.091	Green	*Urtica dioica*
FR-I	France	Livron	43.227	-0.139	Red	*Urtica dioica*
FR-V	France	Salies	43.464	-0.916	Green	*Urtica dioica*

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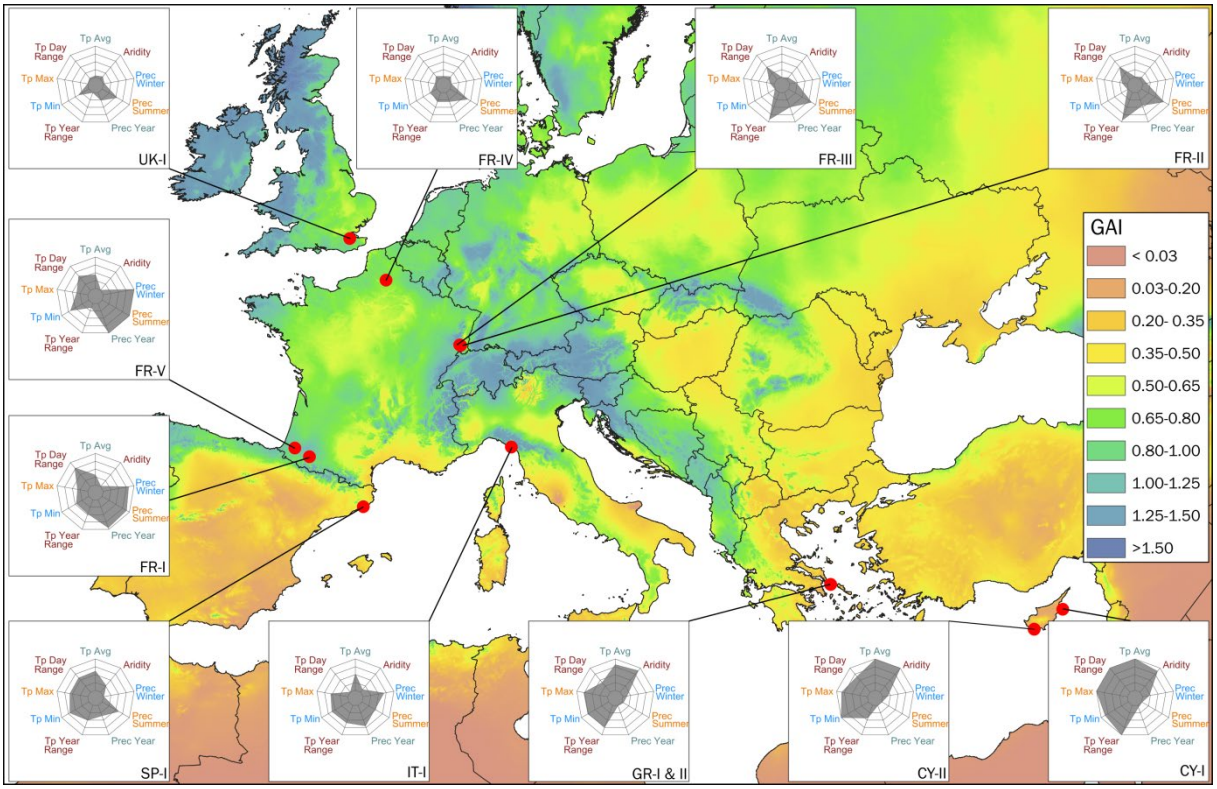

Figure 1. Map of the localities sampled. The background colour is scaled on Global Aridity Index (Trabucco & Zomer, 2019). The radar charts display the values of some important climatic variables: (from top, clockwise) annual temperature average (Tp Avg), 1/global aridity index (Aridity), precipitations of the coldest quarter (Prec Winter), precipitations of the warmest quarter (Prec Summer), total year precipitations (Prec Year), temperature annual range (Tp Year Range), minimal temperature of the coldest month (Tp Min), maximal temperature of the warmest month (Tp Max), mean diurnal range (Tp Day Range).

Mite rearing. Mite stock populations were maintained separately on detached bean leaves (*Phaseolus vulgaris* cv Contender) placed on moist cotton blanket in double-bottom plastic boxes (13.5 x 9.5 x 5 cm) with water reservoir and maintained in growth chambers at 21 ± 1 °C, 60 ± 10 % RH with a photoperiod of L/D 16/8 h. Each population was maintained for at least six generations before being used in the experiments. In experiment I, adult females of various ages were transferred directly to bean plants (see the experimental design description below and Fig.2A.). In experiment II (see experimental design and Fig. 2B), to have adult females of known age and to avoid possible variation in feeding history on fecundity we transferred females reared on detached leaves to drought-stressed or well-watered beans seedlings (according to the experimental treatment) and left to oviposit for 24 h. These females were subsequently removed and laid eggs were allowed to develop to adult. This produced known age adult females were then used in experiment II.

2 Plant material

Plant production. French bean (*Phaseolus vulgaris* cv. Contender) plants were grown from seeds in 2 L pots (diameter: 15 cm, height: 17 cm) (CEP, HR 17YPP) filled with 815 g (R.H. about 30%, measured with a soil moisture sensor HH150 (Delta-T Devices Ltd, Cambridge, UK)) of peat mix (Huminsubstrat N2, Neuhaus®, Klasmann-Deilmann, Geeste, Germany). Two sets of pots were differentiated according to the watering regime: well-watered plants (high water regime) were watered to saturation every day and drought-stressed plants (low water regime) were watered only once at seeding time with 200 ml of water. Pots were first kept in a regulated greenhouse with additional light when necessary (25 ± 7 °C / 40 ± 30 % RH) for ten days after sowing.

Ten days after sowing, bean seedlings (two expanded seed leaves) were transferred to a climatic chamber with diurnal (25 ± 0.5 °C) and nocturnal (23 ± 0.5 °C) temperatures and using a light cycle of L/D 16/8 h. Plants were watered differentially according to treatment in the climatic chambers as described below. Light was provided by agro red and blue LED lamps (Philipps Green Power LED). Relative humidity was not regulated but limited using an air dehumidifier (Rexair 2500T, Rexair, 95330 Domont, France) and was 50 ± 20 % RH.

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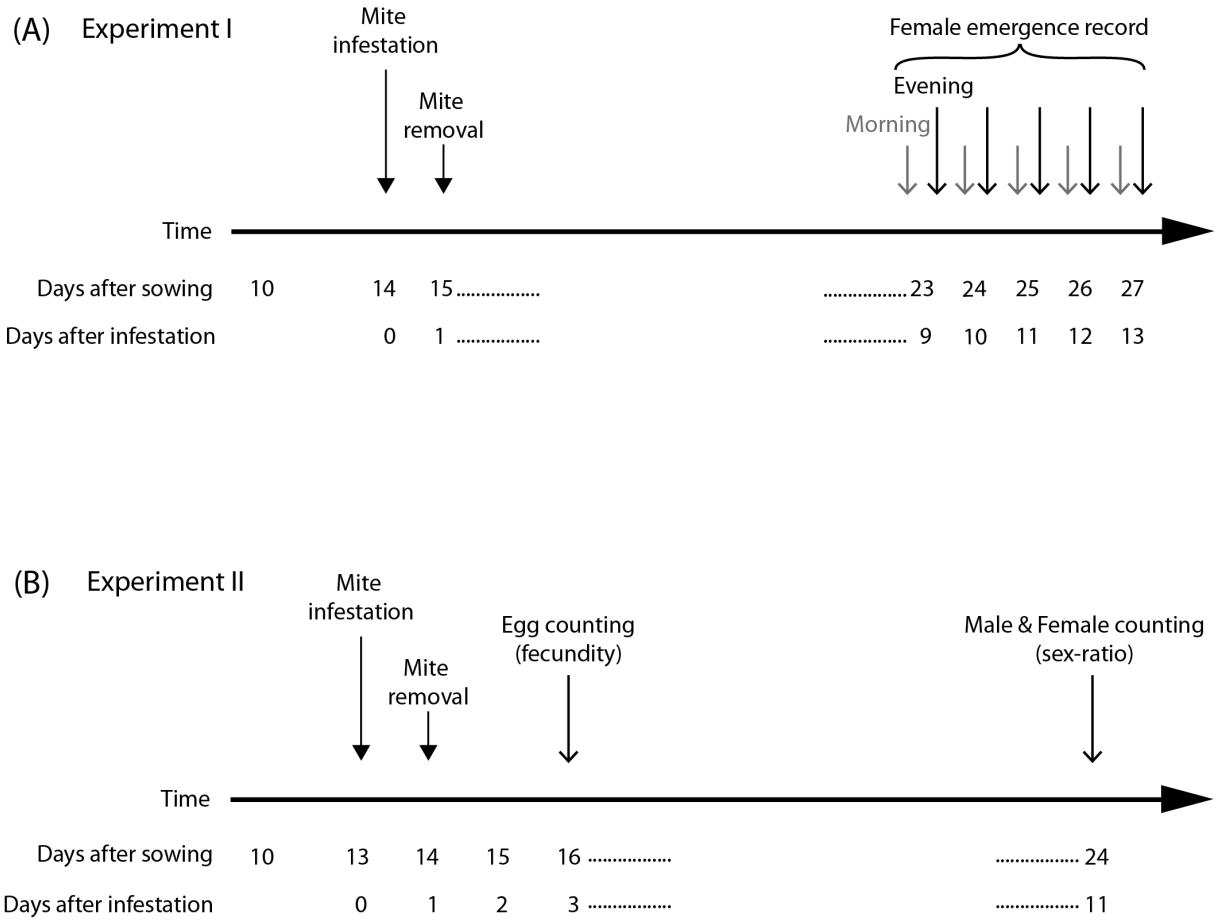

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170 Figure 2. Assessment of development time in female mites in Experiment I (A); assessment of fecundity

171 and sex ratio in Experiment II (B).

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Drought stress maintenance and assessment. After transferring bean seedlings from the greenhouse to the climatic chamber, these continued to be exposed to two different water regimes: either well-watered or drought-stressed regime. These two modalities corresponded to soil moisture maintained above 45% and between 10-8% (8% is over the wilting point), respectively. Plant watering was carried out in two ways depending on the experiment: (1) in experiment I, all water regimes were ensured using an automatically regulated drip irrigation system. Soil water content (RH) was measured using 5 moisture sensors (SM150 with GP2 Data Logger, Delta-T Devices Ltd, Cambridge, UK) in each watering treatment and linked to DeltaLINK 3.1.1 PC software (Delta-T Devices Ltd, Cambridge, UK) for setting up and downloading data from a GP2 station. In the well-watered treatment, when the average soil moisture dropped to 45%, each plant was automatically watered for 30 seconds (delivering 17 ml of water) by a drip. In the drought-stressed treatment, watering was activated (same duration and amount of water per watering event) when soil moisture dropped to 8% (see Supplementary Figure 1 as an example); (2) in the experiment II, plants were watered manually. For the well-watered regime, beans daily received 100 ml of water. In the drought-stressed regime, they received once 20 ml of water when transferred to the climatic chamber (10 days after sowing) with no water delivered until 17 days after sowing; from when plants were daily watered with 20 ml of water.

Water stress level of plants was assessed several times during the experiments by measuring the following parameters: a) the leaf stomatal conductance (experiments I, II) reported to be a reliable drought indicator (Verslues et al., 2006), was assessed on 10 plants per water regime for each mite population tested using a leaf porometer (SC-1 Leaf Porometer, Decagon Devices, Inc., Pullman, WA, USA). For young seedlings, from 10 to 19 days after sowing, the sensor was placed head in the upper third of the seed leaf (the part closest to the petiole of the leaf), on the side of the leaf. For older seedlings, from 21 days after sowing and later, measurements were taken in the first trifoliate leaf, placing the sensor head on the side of the central leaflet; b) the soil moisture (experiment II) was assessed using a soil moisture sensor (HH150, Delta-T Devices Ltd, Cambridge, UK) and by weighing the pot (seedling, pit mix and pot) using a balance (KSR1 Proline, Darty Ptc©, UK).

3 Experimental design

Due to restricted space available, each population was assayed separately. All the experiments were conducted in a climate room with diurnal (25 ± 1 °C) and nocturnal (23 ± 1 °C) temperatures and using a light cycle of L/D 16/8 h. Relative humidity was maintained at 50 ± 20 % RH using a dehumidifier (Rexair 2500T, Rexair, 95330 Domont, France).

Experiment I (Figure 2A)

Experiment I was designed to estimate the development time of mites. Well-watered and drought-stressed plants corresponding to 2 expanded simple leaves (cotyledons) stage, were randomly arranged in the climatic chamber and then infested with mites when steady stress conditions were reached in plants assigned to the drought-stressed treatment (Supplementary Figure S1). As shown in Figure S2, water-stress of bean seedlings was assessed at seven time-points throughout the experience from 11 to 27 days after sowing, by using 10 bean plants per watering regime.

For each population tested, 14 days after sowing plants were infested with females of unknown age (old females were excluded) from stock culture by gently transferring with a fine camel hairbrush 10 females per plant (5 per each simple leaf) in a squared arena built on leaves upper surface (Figure 3). Each squared arena was delimited by four flexible PVC tape stripes (electrical insulation tape, Coteka, Chaulnes, France) of 50 x 7.5 mm forming an internal square about 18 cm^2 glued onto the leaf surface. To avoid mite losses, Vaseline (CAS 8009-03-8; Gifrer, Décines-Charpieu, France) mixed with 10% organic olive oil (Bio Classico, Carapelli Firenze SpA, Tavarnelle Val di Pesa, Firenze, Italy) was applied on the tape stripe to form a cord (that delimits a squared arena) that spider mites cannot cross. Females placed in these arenas were allowed to lay eggs for 24 hours and then removed (Figure 2A) using a Rena® vacuum. At this time, individuals were recorded as living, dead or drowned in the oily barrier. The mites found in the barrier were recorded to estimate attempts to leave the patch of leaf. Twelve to 15 replicates (12-15 plants) per water regime were performed for each mite population. From day 9 to 13 after infestation, newly emerged adult females were recorded and then removed twice a day, at 8 am and 4 pm (Figure 2A), using a stereomicroscope Leica EZ4 (Leica microsystems CMS GmbH, Wetzlar, Germany).

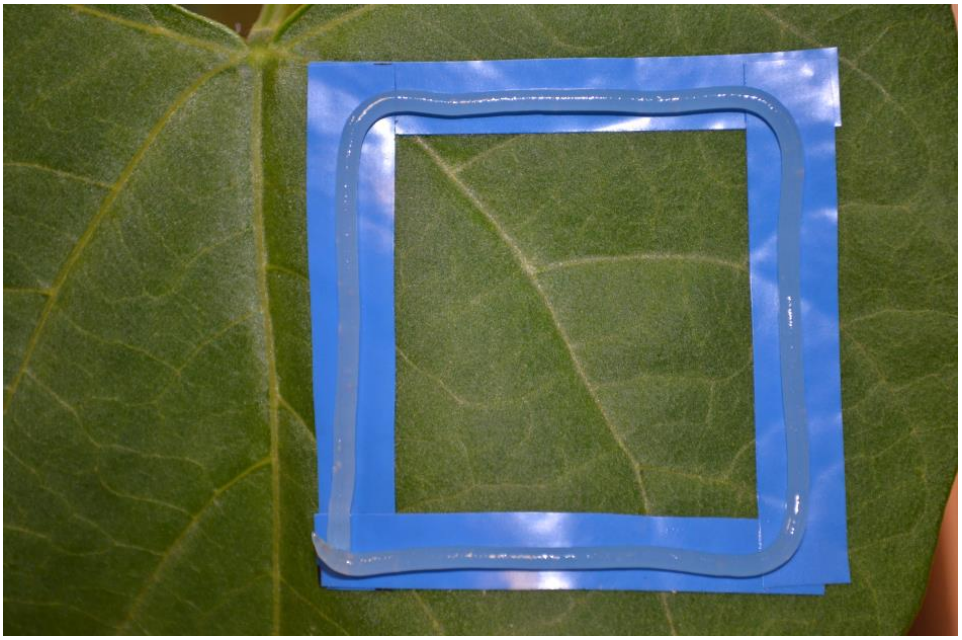

Figure 3. Mite confining arena built on bean leaf.

Experiment II (Figure 2B)

Experiment II was designed to assess the effect of plant drought stress on females' fecundity and on the sex ratio of their progeny. When drought stress conditions occurred in plants (Supplementary Figure 1) three days after their transfer in the climatic room (13 days after sowing), plants of both water regimes were infested with *T. urticae* females of specific ages collected from rearing plants. To simultaneously obtain females of known age in both watering modalities studied, the day of mite infestation of each treatment of rearing plants was calculated from the results of experiment I, resulting in simultaneous three-day-old females in both, well-watered and drought-stressed rearing plants. To ensure that the two watering modalities remained clearly distinct until the end of the experiment, water of bean seedlings stress was assessed as shown in Figures S3 and S4.

A first batch of plants was infested with three-day-old females and a second batch with nine-day-old females. Mites were reared on plant experiencing the same watering regime as the treatment they were transferred to. The procedures for plant infestation, mite confinement, and assessment of water status of plants were the same as those mentioned in experiment I, except water status assessment of plants which was also done by measuring the peat mix RH (%) and the weight of the pots on 10 replicates per watering treatment.

Females were allowed to lay eggs for 24 h and subsequently removed using a Rena® vacuum. At this time, individuals were recorded as living, dead or drowned in the oily barrier. The mites found in the barrier were recorded to estimate attempts to leave the patch of leaf. Female fecundity was assessed by counting eggs two days after females were removed from arena with the aid of a stereomicroscope Leica® EZ4 (Leica Microsystems, Weltzar, Germany). The eggs were kept on plants until hatching and offspring allowed to development to adulthood. The sex-ratio of newly emerged adult mites was then assessed 11 days after mite infestation.

4 Climate data and method of analysis

Climate data were retrieved from WolrdClim (Fick & Hijmans, 2017) and CGIAR (Trabuco & Zomer, 2019). We used monthly values of temperatures (minimum, maximum and average) to construct Gaussen climatograms. The Bioclimatic variables gather a set of 19 synthetic variables describing the climate. The Global Aridity Index (GAI) developed to quantify the precipitation availability over atmospheric demand (Trabuco & Zomer, 2019), was also used here. This is a synthetic variable expressing the moisture availability for potential growth of reference vegetation.

The 19 Bioclimatic variables plus the Global Aridity Index were analysed via a principal component analysis followed by a hierarchical clustering on principle components to obtain a pattern of the climates encountered in the 12 mite sampling locations.

5 Data analysis

All data analyses were conducted using R 3.5 (R Core Team, 2018). Principal component analysis (PCA) and hierarchical clustering on principle components (HCPC) using Euclidian distances and Ward's clustering method were computed with the library FactoMineR (Lê et al., 2008). Graphics were produced using the libraries ggplot2 (Wickham, 2016) and factoextra (Kassambara & Mundt, 2019).

The development time of mites was calculated by using a logit regression (library MASS, Venables & Ripley, 2002) to determine the time of 50% of emergence of adults. For each population, an ANOVA analysis (Chi^2 model) was used to test the effect of watering regime on logistic regression representing the development time.

Differences in fecundity, leaving rate and sex ratio between mites from drought-stressed and well-watered plants were evaluated with *t*-tests for each population. Because escape rate (expressed as number of escaped females per plant / number of females deposited per plant) and sex-ratio (expressed as number of female per plant/ (number of females per plant + number of males per plant) are both limited from 0 to 1, they were respectively transformed to [arcsin(√(1-x))] and [arcsin(√x)] before analysis.

Our estimate of development time is a population-level estimate, and thus there is only one value per population and plant watering regime. Similarly, there is only one difference value in fecundity, leaving rate and sex-ratio per population and watering regimes (the same plant cannot be drought-stressed and non-stressed).

ANOVAs were conducted separately to test significance (1) of stress factors; (2) between populations for each trait and (3) between age of females (3 and 9 days old). When the ANOVA analyses between watering regimes were significant, correlations were tested for the difference between water regimes and each of the 20 climatic variables (19 Bioclimatic variables + Global Aridity Index). In the same way, correlations were tested for non-stressed or drought-stressed traits' plant data when the ANOVAS analyses between populations were significant.

Results

1 Climatic characteristics of the mite sampled locations

The sampled locations represent a quite wide range of climatic conditions encountered in Europe where *T. urticae* has been recorded (Migeon et al. 2019) and where the mite can develop (Litskas et al. 2019). The Global Aridity Index ranges from 0.2 in Kouklia (CY-II, Cyprus) to 1.13 in Salies-de-Béarn (FR-V, France), 0.2 being the threshold of the arid classification (Trabuco & Zomer, 2019). Other Cyprus and Greece locations sampled correspond to semi-arid classification (Global Aridity Index < 0.5), Spain locality to dry sub-humid (Global Aridity Index < 0.65) and Italy, France and United Kingdom to the humid classification (Global Aridity Index > 0.65). Among the humid and sub-humid locations sampled, important differences are to be noted: the French FR-I and FR-V locations display a very humid climate (Global Aridity Index > 1), and maximal summer temperature > 24 °C, whereas the United Kingdom and FR-II locations are less humid (Global Aridity Index < 1) and have colder summer (maximal summer temperature < 21 °C). Spain and Italy localities are characterized by hot summers (> 27 °C) with a drier tendency for the Spanish locality.

The analysis of Gaussen climatograms (Figure S5) reveals that Cyprus localities have 7 months of hydric deficit, Greece locality 6 months, Spain and Italy 1 month. All values are summarized in Figure 1.

According to the PCA analysis on sampled localities, completed by the HCPC based on the climate values (Figure 4), the first three axes gather 90% of the total variance and were retained for following analysis and clustering. The first axis opposed the arid and hot Mediterranean cluster (+) to the oceanic-continental wet and temperate cluster (-) localities. The second axis opposed the wet winter Pays Basque cluster (+) to the drier winter Channel and Alsace (-) localities, whereas the third axis discriminated the continental Alsace cluster (+) of the more oceanic Channel cluster (-) localities.

The Bioclimatic variables BIO02, BIO03, BIO04, BIO07 (annual and daily temperature ranges), BIO08 (temperature of the wettest quarter) contributed less (cos^2) to the first two axes as a result of the choice of the sampled localities, maximizing Global Aridity Index extent.

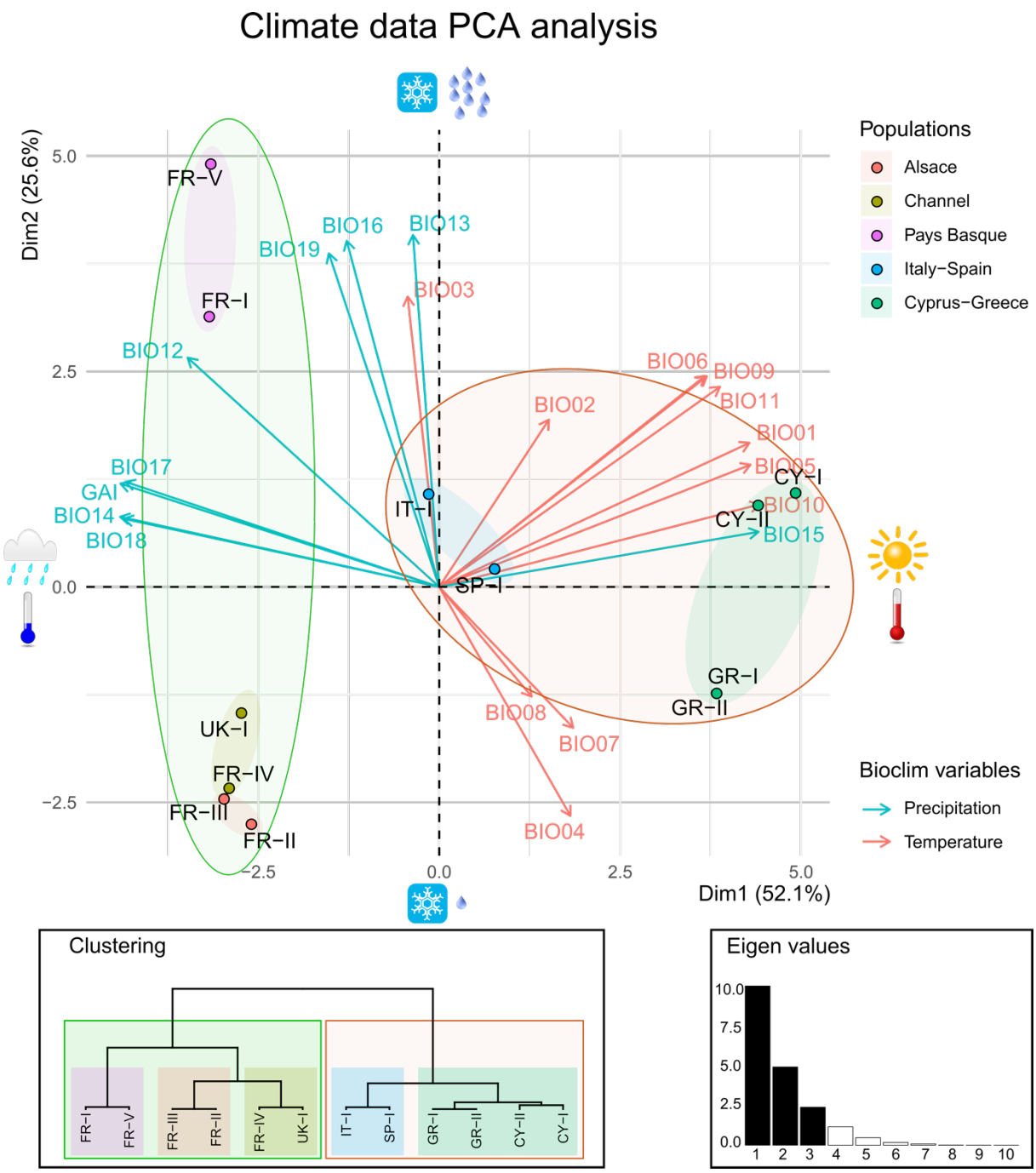

Figure 4. PCA analysis on the 20 climatic variables analysed (19 Bioclim + Global Aridity Index, see Supplementary Table S1 for complete description). The Eigen values and hierarchical clustering are reported inside the cartridges.

2 Life History traits analyses

2.1 Development time

Mites from all populations developed faster when reared on drought-stressed plants (Table 2 and Figure 5). The reduction in development time from the egg to adult ranged from 0.54 day (GR-II) to 1.35 day (FR-II).

Table 2. Development duration for each population of *Tetranychus urticae* on non stressed and drought stressed plants. Logit values of the 50% adult emergence +/- CI (in days).

Population	Non-stressed (NS)	Stressed (S)	Difference (S-NS)	F value	Df	*P*-value	Variation direction
CY-I	10.15 ± 0.02	9.22 ± 0.02	-0.93	3574	8	<0.001***	↘
CY-II	9.97 ± 0.03	9.16 ± 0.02	-0.81	2050	8	<0.001***	↘
FR-I	9.92 ± 0.02	8.61 ± 0.02	-1.31	3311	8	<0.001***	↘
FR-II	9.84 ± 0.02	8.49 ± 0.01	-1.35	3818	8	<0.001***	↘
FR-III	9.94 ± 0.02	9.08 ± 0.01	-0.86	2648	8	<0.001***	↘
FR-IV	9.97 ± 0.02	9.31 ± 0.02	-0.66	3803	8	<0.001***	↘
FR-V	10.60 ± 0.02	9.38 ± 0.02	-1.23	2586	8	<0.001***	↘
GR-I	10.00 ± 0.02	9.21 ± 0.02	-0.79	3276	8	<0.001***	↘
GR-II	9.82 ± 0.02	9.28 ± 0.02	-0.54	4947	8	<0.001***	↘
IT-I	10.05 ± 0.03	9.22 ± 0.02	-0.84	2355	8	<0.001***	↘
SP-I	9.77 ± 0.02	9.14 ± 0.02	-0.63	4239	8	<0.001***	↘
UK-I	9.84 ± 0.02	8.97 ± 0.01	-0.87	3847	8	<0.001***	↘
Mean	9.99	9.09	-0.90				

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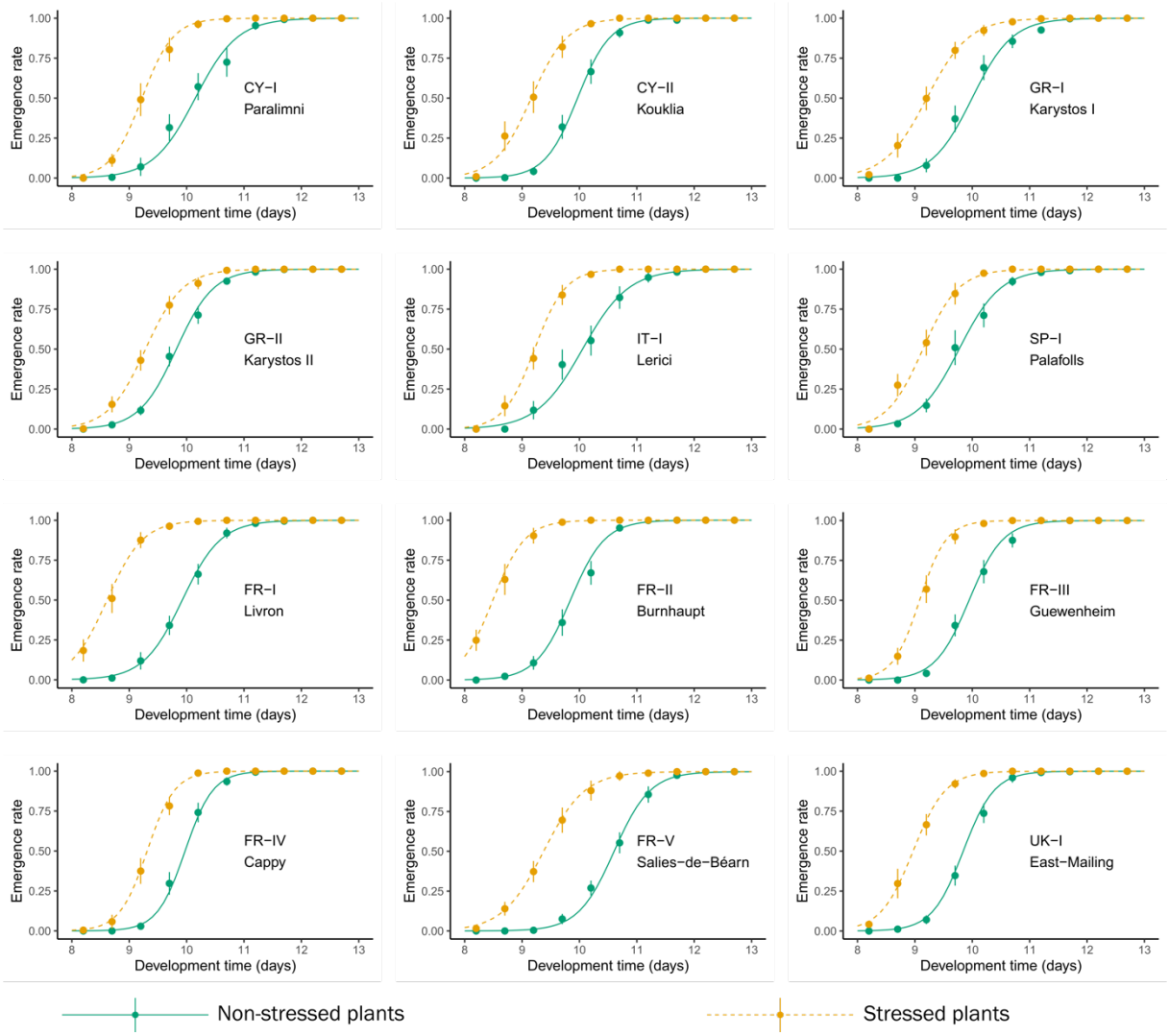

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353 Figure 5. Development time from egg to adult of the twelve populations of *Tetranychus urticae*
354 reared on drought-stressed and non-stressed plants. Values correspond to mean emergence rate
355 of adults and error bar to standard error at each observation point. Curves represent the logit
356 regression.

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359 ANOVA conducted on development time data showed highly significant variation between the water
360 regimes ($P < 0.001$) but not between populations (Table 3). Thus we further only tested the
361 correlations between the differences of development time and the climatic variables of the locations.
362 We observed a positive correlation between the reduction in development time and Global Aridity
363 Index (see Table 4). The development time was shorter on drought-stressed plants and the reduction
364 increased for the mites originated from locations with high summer humidity (high Global Aridity
365 Index). In addition, a significant correlation was also observed for five others climatic variables (see
366 Table 4 and Supplementary Table 1). All but one of the climatic variables (BIO19, Winter
367 Precipitations) refer to summer hydric local conditions that may be responsible for plant water
368 stress, which is in line with the correlation obtained with the Global Aridity Index. Despite the fact
369 that BIO19 was also correlated to others rainfall variables, the variable is not relevant for French,
370 English and to a lesser extent, Spanish and Italian two spotted spider mite populations. While mites
371 from these origins do experience a winter diapause, they are not subject to variations for theses
372 climatic parameters during winter.
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Table 3. ANOVA on each life history trait.

Life history trait		df	Sum. of sq.	F value	*P-value*
Development duration	Stress factor	1	4.86	140.389	**< 0.001 *** **
	Population	11	0.98	2.574	0.066
	Residuals	11	0.38		
Fecundity of 3-day-old females	Stress factor	1	5.72	9.058	**0.012 ***
	Population	11	34.75	5.000	**0.006 ****
	Residuals	11	6.95		
Fecundity of 9-day-old females	Stress factor	1	0.60	1.586	0.234
	Population	11	55.38	13.416	**< 0.001 *** **
	Residuals	11	4.13		
Fecundity on non-stressed Plants	Age	1	41.87	52.074	**< 0.001 *** **
	Population	11	37.46	4.235	**0.012 ***
	Residuals	11	8.84		
Fecundity on drought stressed plants	Age	1	65.47	53.479	**< 0.001 *** **
	Population	11	41.44	3.077	**0.038 ***
	Residuals	11	13.47		
Progeny sex ratio of 3-day-old-females	Stress factor	1	0.001	1.805	0.206
	Population	11	0.093	10.450	**< 0.001 *** **
	Residuals	11	0.009		
Progeny sex ratio of 9-day-old-females	Stress factor	1	0.007	1.995	0.186
	Population	11	0.152	3.818	**0.018 ***
	Residuals	11	0.040		
Progeny sex-ratio on non-stressed plants	Age	1	0.226	65.152	**< 0.001 *** **
	Population	11	0.099	2.599	0.064
	Residuals	11	0.038		
Progeny sex-ratio on drought stressed plants	Age	1	0.273	69.85	**< 0.001 *** **
	Population	11	0.114	2.65	0.061
	Residuals	11	0.043		
Leaving rate of 3-day-old females	Stress factor	1	0.034	6.351	**0.029 ***
	Population	11	0.119	1.995	0.134
	Residuals	11	0.060		
Leaving rate of 9-day-old females	Stress factor	1	0.092	10.975	**0.007 ****
	Population	11	0.317	3.464	**0.025 ***
	Residuals	11	0.092		
Leaving rate of 9-day-old females on non-stressed plants	Age	1	0.076	6.769	**0.025 ***
	Population	11	0.264	2.138	0.112
	Residuals	11	0.123		

Leaving rate of 9-day-old females on drought-stressed plants	Age	1	0.025	3.336	0.095
	Population	11	0.117	1.406	0.291
	Residuals	11	0.083		

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Table 4. Correlations between difference in development time between the two water regimes and climatic variables. Only significant values are reported.

Climatic variable	R^2	*P*-value
GAI Global Aridity Index	0.386	0.031
BIO12 Annual Precipitations	0.427	0.021
BIO14 Precipitations Driest Month	0.391	0.03
BIO17 Precipitations Driest season	0.356	0.041
BIO18 Summer Precipitations	0.338	0.048
BIO19 Winter Precipitations	0.363	0.038

378

379

380 ## 2.2 Fecundity

381 Life history traits variation in mite populations in response to host plant water regimes is summarised

382 in Figure 6.

383

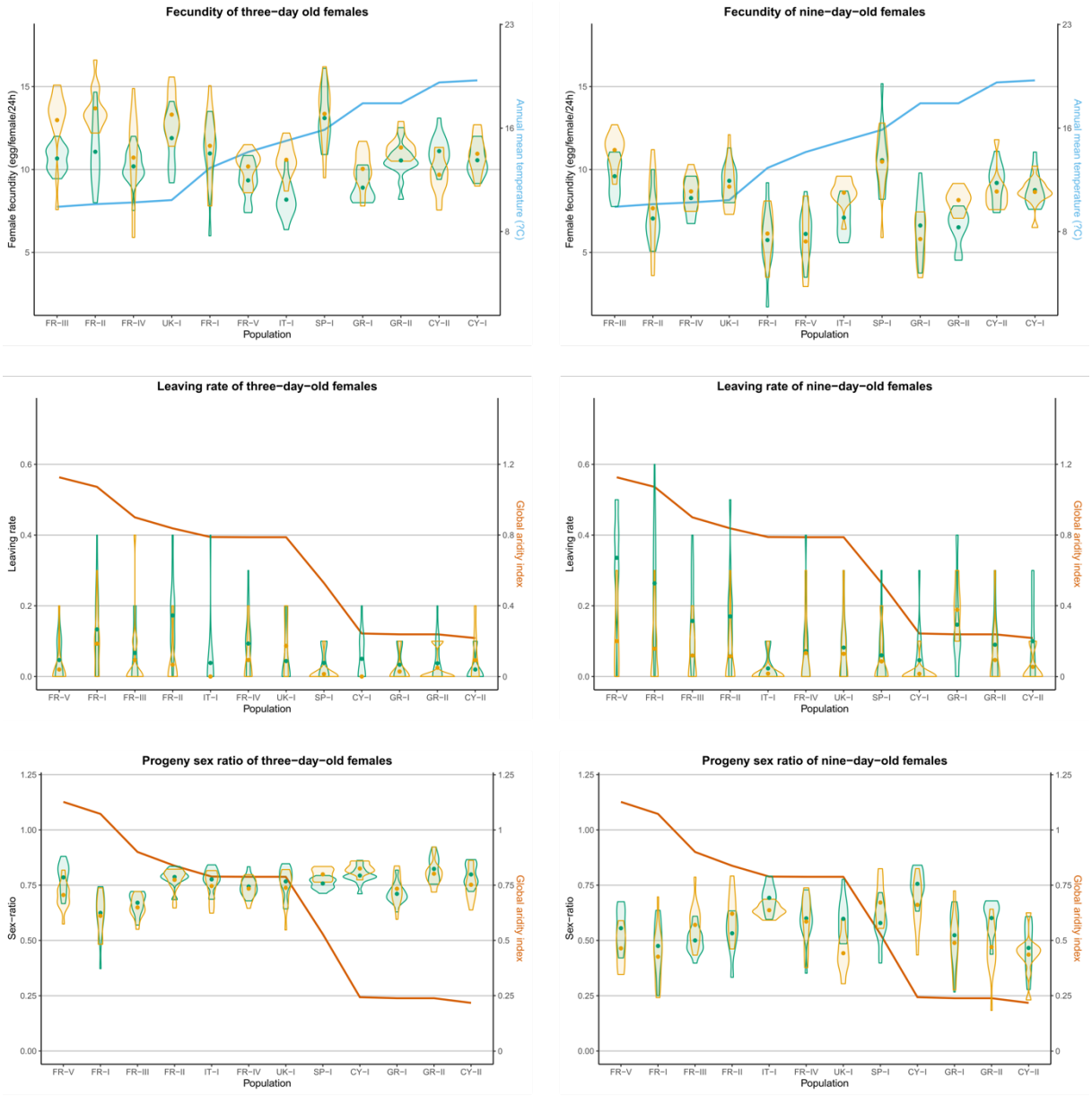

Figure 6. Life history trait variation among the 12 populations of *Tetranychus urticae* studied, in response to plant water stress regime. For each of the traits, populations are ordered by the climatic variable selected as a synthesis of the link between the trait and the climate: Annual Mean Temperature (blue line) for fecundity and Global Aridity Index (brown line) for progeny sex-ratio and leaving rate.

2.2.1 Three-day-old females

For all but one population (CY-II), we observed an increase in the fecundity of females reared on drought-stressed plants (Table 5) and it was significant for seven populations: FR-I, FR-III, FR-V, GR-I, GR-II, IT-I and UK-I. The two ANOVA analyses performed with differences in fecundities observed between water regimes and between mite populations, were significant (Table 3). Three sets of correlations were subsequently tested with the climatic variables on sampling locations and the differences of fecundity of three-day-old females, the values of fecundity three-day-old females reared on drought-stressed plants and the values of fecundity three-day-old females reared on non-stressed plants. Significant correlations were observed for fecundity differences of three-day-old females between water regimes and for fecundity of three-day-old females reared on drought-stressed plants. By contrast, none of the correlations were significant for fecundity of three-day-old females reared on non-stressed plants. Three climatic variables (BIO01, BIO06 and BIO11) showing significant correlations are the same for both (differences between water regimes and drought stressed plants) and are related to temperature, especially winter temperatures (see Table 6) with an increase in fecundity and with the difference of fecundity between the two water regimes for the locations with colder temperatures (Figure 6).

In summary, the fecundity of three-day-old females increased (Table 5) for 8 out of the 12 mite populations studied, showing significant greater values on drought-stressed plants. The increase was higher for mites from locations with cold winter and low annual mean temperatures (Figure 6).

Table 5. Fecundity of the females for each population of T*etranychus urticae* on non-stressed and drought-stressed plants.

Fecundity of 3-day-old female fecundity (egg/female/day)

Population	Non-stressed (NS)	Stressed (S)	Diffrence (S-NS)	F value	Df	*P*-value	Variation direction
CY-I	10.56 ± 0.25	10.95 ± 0.32	0.39	-1.004	24	0.325	↗
CY-II	11.11 ± 0.26	9.68 ± 0.32	-1.43	3.859	28	<0.001***	↘
FR-I	10.97 ± 0.56	11.43 ± 0.61	0.46	-0.616	27	0.543	↗
FR-II	11.07 ± 0.59	13.69 ± 0.34	2.62	-4.155	24	<0.001***	↗
FR-III	10.67 ± 0.21	12.98 ± 0.58	2.31	-4.204	28	<0.001***	↗
FR-IV	10.19 ± 0.3	10.72 ± 0.73	0.53	-0.744	28	0.463	↗
FR-V	9.34 ± 0.31	10.18 ± 0.26	0.84	-2.346	28	0.026 *	↗
GR-I	8.90 ± 0.24	10.04 ± 0.32	1.13	-3.171	27	0.004 **	↗
GR-II	10.55 ± 0.29	11.33 ± 0.19	0.78	-2.592	30	0.015 *	↗
IT-I	8.18 ± 0.3	10.58 ± 0.27	2.40	-6.142	24	<0.001***	↗
SP-I	13.10 ± 0.46	13.36 ± 0.52	0.26	-0.388	25	0.701	↗
UK-I	11.89 ± 0.42	13.31 ± 0.36	1.42	-2.907	29	0.007 **	↗
Mean	10.54	11.52	0.98				

Fecundity of 9-day-old female fecundity (egg/female/day)

Population	Non-stressed (NS)	Stressed (S)	Diffrence (S-NS)	F value	Df	*P*-value	Variation direction
CY-I	8.76 ± 0.27	8.65 ± 0.24	-0.11	0.305	24	0.763	↘
CY-II	9.19 ± 0.29	8.67 ± 0.35	-0.52	1.147	24	0.262	↘
FR-I	5.74 ± 0.58	6.13 ± 0.38	0.39	-0.584	23	0.565	↗
FR-II	7.05 ± 0.45	7.66 ± 0.61	0.61	-0.75	22	0.461	↗
FR-III	9.59 ± 0.29	11.18 ± 0.25	1.58	-4.107	27	<0.001***	↗
FR-IV	8.28 ± 0.26	8.68 ± 0.32	0.40	-0.982	21	0.337	↗
FR-V	6.11 ± 0.37	5.66 ± 0.78	-0.45	0.599	19	0.556	↘
GR-I	6.62 ± 0.44	5.80 ± 0.47	-0.82	1.212	22	0.238	↘
GR-II	6.51 ± 0.34	8.15 ± 0.17	1.64	-4.842	23	<0.001***	↗
IT-I	7.10 ± 0.28	8.60 ± 0.25	1.51	-3.974	23	<0.001***	↗
SP-I	10.56 ± 0.48	10.47 ± 0.47	-0.09	0.127	27	0.900	↘
UK-I	9.32 ± 0.30	8.96 ± 0.37	-0.35	0.712	23	0.484	↘
Mean	7.90	8.22	0.32				

416

Table 6. Correlations between the fecundity of 3-day-old females: (1) difference between water regimes and (2) drought-stressed plants, and climatic variables. Only significant values are reported.

	Difference between water regimes		Drought-stressed plants	
Climatic variable	R^2	*P*-value	R^2	*P*-value
BIO01 Annual Mean Temp.	0.361	0.039	0.355	0.041
BIO03 Isothermality	0.427	0.021	-	-
BIO06 Min Temp. Coldest Month	0.484	0.012	0.416	0.024
BIO09 Mean Temp. Driest Quarter	-	-	0.373	0.035
BIO11 Mean Temp. Coldest Quarter	0.49	0.011	0.391	0.03

417

418

419 ### *2.2.2 Nine-day-old females*

420 We observed a significant increase (Table 5) of fecundity of females reared on drought-stressed
421 plants for three populations (FR-III, GR-II and IT-I). Only the ANOVA analysis performed between
422 populations show significant differences. Two sets of correlations were subsequently tested between
423 the climatic variables on sampling locations and the fecundity of nine-day-old females reared on non-
424 stressed plants and on drought-stressed plants. Only the BIO19 (Winter Precipitations) variable was
425 significant with non-stressed plants.

426

427 ### *2.2.3 Comparison between three- and nine-day-old fecundity*

428 ANOVA analysis performed between fecundity of the two different age females (three-day-old and
429 nine-day-old) were significant (Table 3). The nine-day-old females laid fewer eggs than the three-day-
430 old females, for both non-stressed and drought-stressed plants. We also observed a correlation
431 between females reared on well-watered plants (three-day-old and nine-day-old, r^2=0.395, p=0.029).

432 ## 2.3 Leaving rate

433 ### *2.3.1 Three-day-old females*

434 Although ten of the twelve populations studied showed a decrease in the leaving rate of females on
435 drought-stressed plants (Table 7), results were significant for only two of them (CY-I and FR-II). The
436 ANOVA analysis on differences in leaving rate of three-day-old females calculated between plant
437 water regimes was also significant (Table 3) and the average mite leaving rate was found to be
438 approximately twice lower on drought-stressed plants than on non-stressed ones. Subsequently, one
439 set of correlations was tested between the differences of leaving rate of three-day-old females and
440 the climatic variables. Only the correlation with the climatic variable BIO07 (Annual Temperature
441 Range) was significant.

442

443 ### *2.3.2 Nine-day-old females*

444 The leaving rate of nine-day-old females was generally higher for mites exposed to non-stressed
445 plants. From the twelve populations studied, eleven showed an increase in the leaving rate on non-
446 stressed plants (Table 7), and four of them (FR-I, FR-II, FR-III, FR-V) were significant. The two ANOVA
447 analyses performed, one on differences calculated between plant water regimes and a second
448 between populations were significant (Table 3). On average, the leaving rate was twice lower on
449 drought-stressed plants than on non-stressed ones. Subsequently, three sets of correlations were

tested with the climatic variables and the differences calculated between plant water regimes of the leaving rate of nine-day-old females, the values of the leaving rate of nine-day-old females reared on non-stressed plants and the values of the leaving rate of nine-day-old females reared on drought-stressed plants. Significant correlations (Table 8) with climatic variables were observed for differences between plant water regimes and for drought-stressed plants, while none of the tests involving non-stressed plants were significant. Each of climatic variables BIO12, BIO14, BIO17, BIO18 and BIO19 were correlated with the differences between water regimes and also with the leaving rate on non-stressed plants. These represent precipitations variables and all but one (BIO19) denote to summer precipitation or dryness. Global Aridity Index and BIO16 were also correlated with the differences calculated between water regimes.

As observed for the development time pattern, mites originating from the four most humid localities (FR-I, FR-II, FR-III, and FR-V) showed higher differences between the two water regimes and in line with this, the climatic variables related to precipitation and dryness were linked to the correlations with differences in the two water regimes.

2.3.3 Comparison between three and nine-day-old females

ANOVA analysis between female mites from the two age groups showed significant differences for mites reared on non-stressed plants only (Table 3). The leaving rate of nine-day-old females was twice that of the three-day-old females.

Table 7. Leaving rate of females for each population of T*etranychus urticae* on non-stressed and drought stressed plants.

Leaving rate of 3-day-old females (number of females attempted to leave/number totat of females)

Population	Non-stressed (NS)	Stressed (S)	Diffrence (S-NS)	t on arcsin(sqrt(y))	Df	*P*-value	Variation direction
CY-I	0.05 ± 0.017	0 ± 0	-0.050	-2.825	24	0.009 **	↘
CY-II	0.02 ± 0.011	0.046 ± 0.019	0.026	1.021	28	0.316	↗
FR-I	0.133 ± 0.032	0.093 ± 0.025	-0.040	-0.693	27	0.494	↘
FR-II	0.173 ± 0.033	0.033 ± 0.019	-0.139	-4.541	24	<0.001***	↘
FR-III	0.067 ± 0.021	0.047 ± 0.027	-0.020	-0.915	28	0.368	↘
FR-IV	0.093 ± 0.023	0.047 ± 0.019	-0.047	-1.76	28	0.089	↘
FR-V	0.047 ± 0.017	0.02 ± 0.014	-0.027	-1.462	28	0.155	↘
GR-I	0.033 ± 0.013	0.014 ± 0.010	-0.019	-1.185	27	0.246	↘
GR-II	0.037 ± 0.015	0.025 ± 0.011	-0.012	-0.519	30	0.608	↘
IT-I	0.038 ± 0.031	0 ± 0	-0.038	-1.375	24	0.182	↘
SP-I	0.038 ± 0.014	0.007 ± 0.007	-0.031	-2.031	25	0.053	↘
UK-I	0.044 ± 0.018	0.087 ± 0.024	0.043	1.386	29	0.176	↗
Mean	0.064	0.035	-0.030				

Leaving rate of 9-day-old females (escaped females/number totat of females)

Population	Non-stressed (NS)	Stressed (S)	Diffrence (S-NS)	t on arcsin(sqrt(y))	Df	*P*-value	Variation direction
CY-I	0.046 ± 0.024	0.008 ± 0.008	-0.038	-1.572	24	0.129	↘
CY-II	0.1 ± 0.032	0.027 ± 0.014	-0.073	-1.536	24	0.138	↘
FR-I	0.264 ± 0.053	0.079 ± 0.026	-0.185	-3.322	23	0.003 **	↘
FR-II	0.17 ± 0.047	0.057 ± 0.025	-0.113	-2.473	22	0.021 *	↘
FR-III	0.157 ± 0.033	0.059 ± 0.019	-0.098	-2.724	27	0.011 *	↘
FR-IV	0.071 ± 0.03	0.067 ± 0.037	-0.005	-0.226	21	0.823	↘
FR-V	0.336 ± 0.037	0.1 ± 0.044	-0.236	-3.558	19	0.002 **	↘
GR-I	0.147 ± 0.034	0.189 ± 0.026	0.042	1.281	22	0.214	↗
GR-II	0.09 ± 0.031	0.047 ± 0.022	-0.043	-1.316	23	0.201	↘
IT-I	0.023 ± 0.012	0.008 ± 0.008	-0.015	-0.984	23	0.336	↘
SP-I	0.06 ± 0.024	0.043 ± 0.02	-0.017	-0.585	27	0.563	↘
UK-I	0.082 ± 0.03	0.064 ± 0.025	-0.018	-0.528	23	0.603	↘
Mean	0.129	0.062	-0.067				

Table 8. Correlations between leaving rate of 9-day-old females: (1) differences between water regimes and (2) non-stressed plants, and climatic variables. Only significant values are reported.

	Difference between water regimes		Non-stressed plants	
Climatic variable	R^2	*P*-value	R^2	*P*-value
BIO12 Annual Precipitation	0.492	0.011	0.346	0.044
BIO14 Precipitation of Driest Month	0.44	0.019	0.429	0.021
BIO16 Precipitation of Wettest Quarter	0.395	0.029	-	-
BIO17 Precipitation of Driest Quarter	0.414	0.024	0.351	0.042
BIO18 Precipitation of Warmest Quarter	0.404	0.026	0.341	0.046
BIO19 Precipitation of Coldest Quarter	0.438	0.019	0.336	0.048
GAI Global Aridity Index	0.403	0.027	-	-

2.4 Progeny sex-ratio

2. 4.1 Three-day-old females

Sex-ratio progeny showed significant differences between water regimes in four populations (Table 9). However, two of them corresponded to an increase (CY-II and FR-V) and two others (CY-I and SP-I) to a decrease of male proportion. ANOVA analysis between populations showed significant differences in this life trait (Table 3) but ANOVA analysis between drought regimes was not significant. Two sets of correlations were then tested between the climatic variables and the sex-ratio values of the progeny of three-day-old females reared on non-stressed plants and on drought-stressed plants. A significant correlation between the climatic variables and the sex ratio values was only found for the progeny of females reared on stressed-plants. These variables were Global Aridity Index and BIO12, BIO14, BIO17, BIO18. All of them denote precipitation regimes, in particular summer precipitation and dryness. As a result, the females originating from drier locations and reared on drought-stressed plants produced more females than the females originating from wet locations.

2.4.2 Nine-day-old females

A significant increase (Table 9) of male proportion was observed in five populations (CY-I, FR-V, GR-II, IT-I, UK-I) but a decrease in three others (FR-II, FR-III, SP-I). As for three-day-old females only the ANOVA analysis performed between populations showed significant differences in the value of progeny sex ratio. Subsequently, two correlations were tested between climatic variables and the sex-ratio values of nine-day-old female progeny reared on non-stressed plants and on drought-stressed plants. None of the tested correlations were significant.

2.4.3 Comparison between three and nine-day-old females

ANOVA comparing progeny sex ratio between the two different age females (three-day-old and nine-day-old) age showed significant differences for both, non-stressed and drought-stressed plants regimes (Table 3). For the two water regimes the sex-ratio of nine-day-old female progeny was lower, i.e. more males were produced by old females than by young females.

Table 9. Progeny sex-ratio for each population of T*etranychus urticae* on non-stressed and drought stressed plants.

Progeny sex-ratio of 3-day-old females (number of females/(number of males +females))

Population	Non-stressed (NS)	Stressed (S)	Diffrence (S-NS)	t on arcsin(sqrt(y))	Df	*P*-value	Variation direction
CY-I	0.794 ± 0.010	0.825 ± 0.007	0.032	-2.523	24	0.019 *	↗
CY-II	0.799 ± 0.012	0.752 ± 0.017	-0.047	2.139	28	0.041 *	↘
FR-I	0.624 ± 0.025	0.611 ± 0.025	-0.013	0.368	27	0.716	↘
FR-II	0.787 ± 0.012	0.774 ± 0.013	-0.013	0.686	24	0.499	↘
FR-III	0.671 ± 0.012	0.649 ± 0.012	-0.021	1.26	28	0.218	↘
FR-IV	0.744 ± 0.010	0.735 ± 0.011	-0.009	0.616	28	0.543	↘
FR-V	0.785 ± 0.017	0.706 ± 0.016	-0.080	3.504	28	0.002 **	↘
GR-I	0.711 ± 0.011	0.734 ± 0.018	0.023	-1.156	27	0.257	↗
GR-II	0.824 ± 0.014	0.802 ± 0.014	-0.022	1.081	30	0.289	↘
IT-I	0.777 ± 0.013	0.746 ± 0.018	-0.030	1.362	24	0.186	↘
SP-I	0.758 ± 0.007	0.799 ± 0.007	0.041	-4.301	25	<0.001***	↗
UK-I	0.767 ± 0.016	0.738 ± 0.019	-0.029	1.185	29	0.246	↘
Mean	0.753	0.739	-0.014				

Progeny sex-ratio of 9-day-old females (number of females/(number of males +females))

Population	Non-stressed (NS)	Stressed (S)	Diffrence (S-NS)	t on arcsin(sqrt(y))	Df	*P*-value	Variation direction
CY-I	0.756 ± 0.017	0.661 ± 0.030	-0.095	2.759	24	0.011 *	↘
CY-II	0.466 ± 0.028	0.436 ± 0.029	-0.030	0.729	24	0.473	↘
FR-I	0.475 ± 0.029	0.426 ± 0.032	-0.049	1.023	23	0.317	↘
FR-II	0.532 ± 0.028	0.621 ± 0.028	0.088	-2.179	22	0.040 *	↗
FR-III	0.500 ± 0.015	0.570 ± 0.023	0.070	-2.481	27	0.012 *	↗
FR-IV	0.600 ± 0.025	0.586 ± 0.040	-0.014	0.305	21	0.763	↘
FR-V	0.555 ± 0.023	0.464 ± 0.033	-0.091	2.283	19	0.034 *	↘
GR-I	0.524 ± 0.029	0.489 ± 0.043	-0.035	0.677	22	0.506	↘
GR-II	0.601 ± 0.024	0.470 ± 0.030	-0.131	3.134	23	0.005 **	↘
IT-I	0.693 ± 0.017	0.637 ± 0.008	-0.056	2.871	23	0.009 **	↘
SP-I	0.579 ± 0.022	0.671 ± 0.024	0.092	-2.823	27	0.009 **	↗
UK-I	0.598 ± 0.027	0.442 ± 0.023	-0.155	4.333	23	<0.001***	↘
Mean	0.573	0.539	-0.034				

Discussion

How much the climate in the geographical area of origin of organisms conditions their response to drought stress is a central question in the context of climate change. This is the focus of the present study which explores responses of a phytophagous mite, the two spotted spider mite, challenged to feed on drought-stressed plants. In this study, we reveal that three main factors linked to the increase of mite populations reared on drought-stressed plants act together in relation to the climatic variables of the location of origin of mite populations: (1) a shortening of development time, (2) an increase of fecundity and (3) a decrease of females' emigration, resulting in longer staying on the plant leaves.

The shortening of development time for all the studied populations is in line with Nikolova et al. (2014) who characterised the population increase of a closely related mite species, *Tetranychus turkestani*, as a result of development time shortening on drought-stressed plants. To be notice is that mites collected from different origins did not respond significantly different for the development time parameter when reared on well-watered plants, suggesting that mite development time is an intrinsic parameter of the species which mainly depends on the host-plants species and the temperature. Temperature is a well-known factor governing development time of ectotherms (Logan et al., 1976). While Van Petegem et al. (2016) founded a relationship between development time and latitude (which in their study corresponds to a thermal gradient), variation in development time was mainly resulting of a development shortening in the northern edge of the mite's distribution. The absence of relationship of development time observed on well-watered plants and any of the climatic variables in our study is in accordance with their results as attention was done to collect our two spotted spider mite populations from localities with contrasting climatic profiles in a quite wide range of core climate conditions distribution (Litskas et al., 2019) in which the mite can be observed across its native distribution area (Navajas et al., 1998).

The increase of fecundity of mites reared on drought-stressed plants has already been reported by Chandler et al. (1979), Youngman & Barnes (1986), and Youngman et al. (1988). Physiological changes that occur in drought-stressed plants may also induce shifts in plant-feeding mites. For example, development time may decrease and fecundity can increase, as found by Ximénez-Embun et al. (2017a) and Santamaria et al. (2018) for *T. urticae* and also for another plant mite, *A. lycopersici* (Ximénez-Embun et al. 2017b). These shifts in mite life history are likely linked to increased concentration of essential amino acids and free sugars in tomato plants as it was observed by the

same authors, which improved the nutritional value of drought-stressed tomato plants. The increase of fecundity observed here is more modest than seen in Ximenez-Embun et al. (2017a). Differences between the two studies might be due to differences in methods used. For example, we measured fecundity as the number of eggs laid over a 24 h period, while Ximenez-Embun et al. (2017a) measured fecundity as "eggs laid and mobile forms" over a longer period which resulted in a combination of increased fecundity and decreased mite emigration when females were placed on drought-stressed whole plants.

On drought-stressed plants, the decrease of development time and the increase of fecundity of young females are concomitant. Nevertheless, the higher fecundity of young female is not counterbalanced by the lower fecundity of nine-day-old females. These results are not in accordance with Youngman et al. (1988) with *T. pacificus* on almond trees. They observed a shift in peak fecundity, the increase of the first ten days on drought-stressed plant was counterbalanced by a decrease after ten days. Nevertheless, our experimental design did not allow us to observe such a shift with females older than 9-day-old females. When mites were placed on well-watered tomatoes plants, Alzate et al. (2017) described a quadratic relationship between fecundity and longevity, suggesting an optimal balance between these two traits. Our experiments highlight this relationship between fecundity of young and older females and reinforce Alzate et al. (2017) hypothesis of optimal balance. Thus, fecundity appears as an intrinsic population trait according to the correlations observed between three-day-old and nine-day-old females reared on well-watered plants. These results are also in line with Van Petegem et al. (2016) who reported variation in lifetime fecundity of mites for populations originated from the mite's core distribution varying in a scale from 20 to 110 eggs per female and not linked to latitude or temperature. Fecundity, dispersal and sex-ratio are often linked by complex relationships (Van Petegem et al. 2016) and the quality of the environment which in turn can shape the nutritional quality and the appetence of the host plants, also impacts these relationships. The hypothesis tends to be supported in the literature: for example, Wrensch and Young (1983) observed an increase in the proportion of females on plants of poor nutritional value that was linked to a decrease of fecundity and Yano and Takafuji (2002), using an artificial selection experiment of low and high dispersal strains, observed an increase of diapause incidence and a decrease of general performance, especially in non-appetent plants for highly dispersal strains.

Our study reveals changes in life-history traits of mites when exposed to feed on drought-stressed plants, with a shortened development time and an increased fecundity along with a decrease of mite dispersal. Importantly, not all mites tested responded equally but changes varied depending on the climate conditions experienced in their area of origin. Mite responses while complex, can be, at least

partially, explained by the climatic conditions in the sampled locations. Since all the females coming from the different localities were reared under identical conditions in a common garden experiment, it is reasonable to accept that observed variation resulted from genetic differentiation in the tested populations. Mites originating from wet to cool localities (Alsace and Pays Basque) had seldom experience of drought-stressed host plants while mites from Cyprus and Greece had to face harsh climate and dryness half of the year. Previous studies (Chen et al., 2020) highlighted that genetic variation for two closely related species *Tetranychus truncatus* and *Tetranychus puerariсola*, were associated with climatic parameters, mainly temperature and precipitation across China. For both species, genotype association was stronger with precipitation parameters together with the neuropeptide receptor NPR-9 gene adjacent genomic region. The NPR-9 affects foraging behaviour and nutrient storage (Bendena et al., 2015) and as a consequence development time and fecundity. Literature tends then to support that local adaptation to diverse levels of aridity could shape mite responses allowing them to adjust feeding behaviour in accordance with native local climatic conditions and nutritional quality of the host plants.

Under a climate change scenario, it is expected that mites will experience harsher drought episodes with environmental conditions leading to the selection of drought-adapted mites. In agricultural, intensification of damage in humid areas during the first years of drought (see Legrand et al., 2000 for an example) will probably be limited by physiological costs but progressively lead to adaptation as suggested by the mite responses in the driest areas of this study. These are important issues to be taking into account for future strategies of pest management.

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Data

Data and statistical analysis are available here

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