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DEVELOPMENT OF A MEXICAN CORN LANDRACE, NORTHERN CONICAL, UNDER TEMPERATURE AND RAINFALL CONDITIONS PREDICTED BY THE MIDDLE OF THIS CENTURY: AN EXPERIMENTAL FIELD APPROACH

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Abstract

Background: Corn is the most important crop in Mexico, but it can be affected by climate change. Small farmers from arid and semiarid ecosystems mainly use rainfed native landraces with short productive cycles (less than 90 days), which are adapted to elevated temperatures and intense drought. Among these landraces we can find the Norther Conical corn.

Hypothesis: As Northern Conical seems to be adapted to arid agroecosystems, we hypothesize that this corn landrace can tolerate the mid-century climate change conditions.

Studied species: *Zea mays* subsp. *mays* (Poaceae), Northern Conical landrace.

Study site and dates: An abandoned agricultural field in San Luis Potosí, central Mexico, between August and October 2022.

Methods: In a field experiment, corn seeds were sowed under the conditions of higher temperature and lower rainfall predicted by the middle of this century (period 2041-2060), as well as under the current climate. Emergence and survival of plants were regularly monitored, and their functional responses were measured by the end of the experiment.

Results: Northern Conical plants performed better (in terms of emergence, survival, growth rates, and photosynthetic performance) under higher temperature and lower rainfall, as compared with those developed under the current climate.

Conclusions: Our results suggest that the Northern Conical corn landrace may tolerate the increases in aridity expected in the short term. However, simulations under contrasting environmental and ontogenetical conditions are needed.

Keywords: aridity, chlorophyll fluorescence, drought, growth rate, survival rate, warming.

Resumen

Antecedentes: El maíz es el cultivo más importante en México, pero puede ser afectado negativamente por el cambio climático. Los pequeños agricultores de ecosistemas áridos y semiáridos principalmente emplean razas nativas de temporal con ciclos productivos cortos (menos de 90 días), que están adaptadas a temperaturas elevadas y sequías intensas. Entre estas variedades se encuentra el maíz Cónico Norteño.

Hipótesis: Como el Cónico Norteño parece estar adaptado a los agroecosistemas áridos, hipotetizamos que esta raza de maíz puede tolerar las condiciones del cambio climático de mediados de siglo.

Especie estudiada: *Zea mays* subsp. *mays* (Poaceae), raza Cónico Norteño.

Sitio y fechas de estudio: Un campo agrícola abandonado en San Luis Potosí, México central, entre agosto y octubre de 2022.

Métodos: En un experimento de campo, se sembraron semillas de maíz bajo las condiciones de mayor temperatura y menor precipitación pronosticadas para mediados de este siglo (período 2041-2060), así como bajo el clima actual. Se monitoreó regularmente la emergencia y supervivencia de las plantas, y se midieron sus respuestas funcionales al final del experimento.

Resultados: Las plantas de Cónico Norteño se desempeñaron mejor (en términos de emergencia, supervivencia, tasas de crecimiento y desempeño fotosintético) bajo condiciones de mayor temperatura y menor precipitación, en comparación con las desarrolladas bajo el clima actual.

Conclusiones: Nuestros resultados sugieren que la raza de maíz Cónico Norteño puede tolerar los aumentos de aridez esperados en el corto plazo. Sin embargo, todavía se necesita realizar simulaciones en condiciones ambientales y ontogenéticas contrastantes.

Palabras clave: aridez, calentamiento, fluorescencia de clorofila, sequía, tasa de crecimiento, tasa de supervivencia.

The corn, *Zea mays* subsp. *mays* (Poaceae), was domesticated in Mexico about 8,000-6,000 years ago (Matsuoka *et al*. 2002, Kato-Yamakake *et al*. 2009) and this crop currently constitutes a key food resource for the population of this country (Callen 1965, Tracy 1999). Between six and eight million hectares of corn are annually sowed in Mexico, where up to 80 % of them are rainfed crops and just a few farmers use assisted irrigation (Reyes-Santiago *et al*. 2022). Rainfed corn is the economic pillar of more than 2.6 million of small Mexican farmers that maintain this traditional agricultural practice on surfaces below five hectares (Damián-Huato *et al*. 2014). The main factors constraining the productivity of rainfed corn in this country include the nutritional poverty of soils, invasive weeds that compete with its early life-cycle stages, and diseases caused by viruses, bacteria, fungi and insects (Bennett *et al*. 2012). Although corn has C_4 photosynthetic metabolism and this confer it tolerance to moderate water deficits (Lopes *et al*. 2011), the increasing warming and drought due to climate change are also treating the viability of this crop (Murray-Tortarolo *et al*. 2018, Murray-Tortarolo 2021).

The latest general circulation models of the World Climate Research Programme (CMIP6 models) predict that global mean temperature can increase up to 5 °C by the end of this century and this, in turn, will reduce rainfall in several countries (Cook *et al*. 2020, Murray-Tortarolo 2021). These enhanced aridity conditions can negatively affect most rainfed crops, as higher temperatures and lower rainfall would promote mortality of plants and reduce their growth (Mendelsohn 2009, DaMatta *et al*. 2010, Olesen *et al*. 2011, Wang *et al*. 2018). These effects, however, have been mainly assessed with genetically improved crop varieties (hybrids or transgenics) that have less genetic variability than their wild ancestors and, consequently, they have less tolerance to climate variability (Jarvis *et al*. 2008).

Although improved corn varieties were introduced in Mexico during the last century, most small farmers of this country still preferring to cultivate some of the 59 native landraces (Sanchez *et al*. 2000). The concept of "landrace" refers to corn varieties that share morphological, functional and genetic traits due to common cultivation histories (Kato-Yamakake *et al*. 2009). Mexican corn landraces are the product of biocultural practices applied since pre-Columbian times, as farmers reserve part of the seeds harvested at each productive cycle for sowing them in the next one and this, together with the influence of local environmental factors, promoted a combination of natural and artificial selection processes that resulted in corn varieties adapted to a wide range of climatic conditions (Vielle-Calzada & Padilla 2009, Caldu-Primo *et al*. 2017).

Rainfed corn landraces from Mexico are classified according to the length of their productive cycles. There are long-cycle landraces (more than 200 days between sowing and harvesting), intermediate-cycle landraces (120-130 days between sowing and harvesting) and short-cycle landraces (less than 90 days between sowing and harvesting), where the length of the productive cycle relates with the duration of the rainfall season at the region where they originate from (Ruiz-Corral *et al*. 2013, Castillo-Nonato 2016). In drylands of Mexico, farmers use short-cycle landraces because they quickly develop with short rainfall seasons (Eagles & Lothrop 1994, Kato-Yamakake *et al*. 2009). Thus, it can be proposed that short-cycle corn landraces could tolerate the temperature and drought conditions expected with the advance of climate change.

We tested this proposal assessing the responses of Northern Conical corn plants (*Cónico Norteño*, in Spanish) developed under the current climate and under conditions of higher temperature and lower rainfall. This short-cycle corn landrace derives from Conical of the Central Plateau (*Cónico de la Mesa Central*, in Spanish), which has higher water requirements (Wellhausen *et al*. 1951, Sanchez *et al*. 2000). Because the Northern Conical is more tolerant to drought than its ancestor, and because it reaches maturity within three months with less than 400 mm during the rainy season, it is cultivated in arid and semiarid ecosystems of central and northern Mexico (Wellhausen *et al*. 1951, Ruiz-Corral *et al*. 2013). Therefore, we hypothesized that the higher temperatures and lower rainfall expected in the future should not substantially affect the development of this corn landrace. As previous studies indicated that the early life-cycle stages of corn are more sensitive to climatic changes than adult plants (Li *et al*. 2014, Xue *et al*. 2021, Diédhiou *et al*. 2022), we focused on young individuals only (*i.e.,* preadults ~60 days old). For this, we performed a field experiment sowing corn seeds under the current and mid-century conditions temperature and rainfall, and measured the emergence of the coleoptile, survival and growth of individuals, and their photosynthetic responses (chlorophyll fluorescence).

Materials and methods

Study site. The experiment to evaluate the effects of climate change on the development of Northern Conical plants was conducted in an agricultural field abandoned more than 70 years ago, which was converted in an urban park protected by the municipality of the City of San Luis Potosí, State of San Luis Potosí, central Mexico (22° 8' 57'' N, 101° 2' 44'' W, 1,904 m). We chose this site because its climate is arid-temperate, concurring with the conditions of most sites where Northern Conical is cultivated. Mean winter temperature is below 12 °C and mean summer temperature oscillates between 18 and 20 °C. A marked rainy season starts between June and July, and it last until in September or October, depending on the year (Medina-García *et al*. 2005). Vegetation in the study site is secondary xeric scrub, mainly composed by native and exotic grasses with scattered bushes.

Origin of corn seeds and productive cycle. The seeds of Northern Conical required for the experiment (Figure 1) were provided by small farmers from the municipality of Mexquitic de Carmona, located 15 km northwest of the study site (22° 15' 57'' N, 101° 6' 47'' O). The identity of this landrace was corroborated using the taxonomic descriptions provided by Wellhausen *et al*. (1951). In the agroecosystems of this region, Northern Conical is sowed between June and August, and crops are harvested between September and November. Sowing months vary because there is between-year variability in the starting of the rainy season, and local farmers always attempt developing the crops during the wettest quarter of the year. In our case, the seeds were harvested in the productive cycle of 2021 and were sowed in August 2022 because the rainy season was delayed on that year.

Climate change estimations for the field experiment. To simulate climate change conditions in the field, it is required to determine how much temperature and rainfall will change at the selected experimental site (Badano *et al.* 2019, Guerra-Coss *et al.* 2021). Considering this principle, we focused on the mean temperature and mean accumulated rainfall during wettest quarter of the year, as this is the period on which rainfed corn landraces, such as Northern Conical, are developed (Eagles & Lothrop 1994, Ruiz-Corral *et al.* 2013). We used the climatological normals of these two variables (averages over the last 30 years) for approximating to their near-to-present values, while their mid-century values were obtained from predictions of CMIP6 models (2041-2060).

Because there are no weather stations in the study site, we used the records of the three nearest stations of the National Meteorological service of Mexico to estimate normal temperature and normal rainfall during the wettest quarter of the year. These stations are located 7 km around the study site (station codes 24,111, 24,069 and 24,070, consulted at smn.conagua.gob.mx on 12 May 2022), which estimated that near-to-present mean air temperature in this period of year is 19.57 °C (± 0.46 95 % CI), while mean accumulated rainfall is 210.23 mm (± 19.73 95 % IC).

Future values of these variables were obtained at the geographic coordinates of the study site using the CMIP6 geoclimatic layers of WorldClim at a spatial resolution of 2.5 arcmin (20 km^2/pixel, downloaded from www.worldclim.org on 19 January 2022). However, as there are more than 100 CMIP6 models with different equilibrium climate sensitivity (ECS), their predictions about the future climate vary (Knutti *et al*. 2017). To include this variability, we selected three CMIP6 models largely differing in ECS - CanESM5, a model with elevated ECS (5.6 °C), MIROC6, a model with intermediate ECS (2.6 °C), and INM-CM4-8, a model low ECS (1.8 °C) - and visualized them in a geographic information system (Quantum GIS 3.22, available at qgis.org) to extract the values of temperature and rainfall during the wettest quarter of the year at the geographic coordinates of the study site. These values were averaged among CMIP6 models to integrate them in a single prediction. All these predictions were performed considering the four main shared socioeconomic pathways, which are associated with increasing radiative forcing levels (2.6, 4.5, 7.0 and 8.5 W/m^2), *i.e.,* the highest the radiative forcing, the largest the climatic changes (Riahi *et al*. 2017).

The differences between near-to-present and future climate indicated that, during the wettest quarter of the year, mean air temperature at the study site will increase between 0.6 and 1.8 °C, while the mean accumulated rainfall will decrease between 5.03 and 5.82 % (Table 1). These differences suggest that aridity will increase in our experimental site by the middle of this century, and we used them as reference to perform climate change simulations in the field.

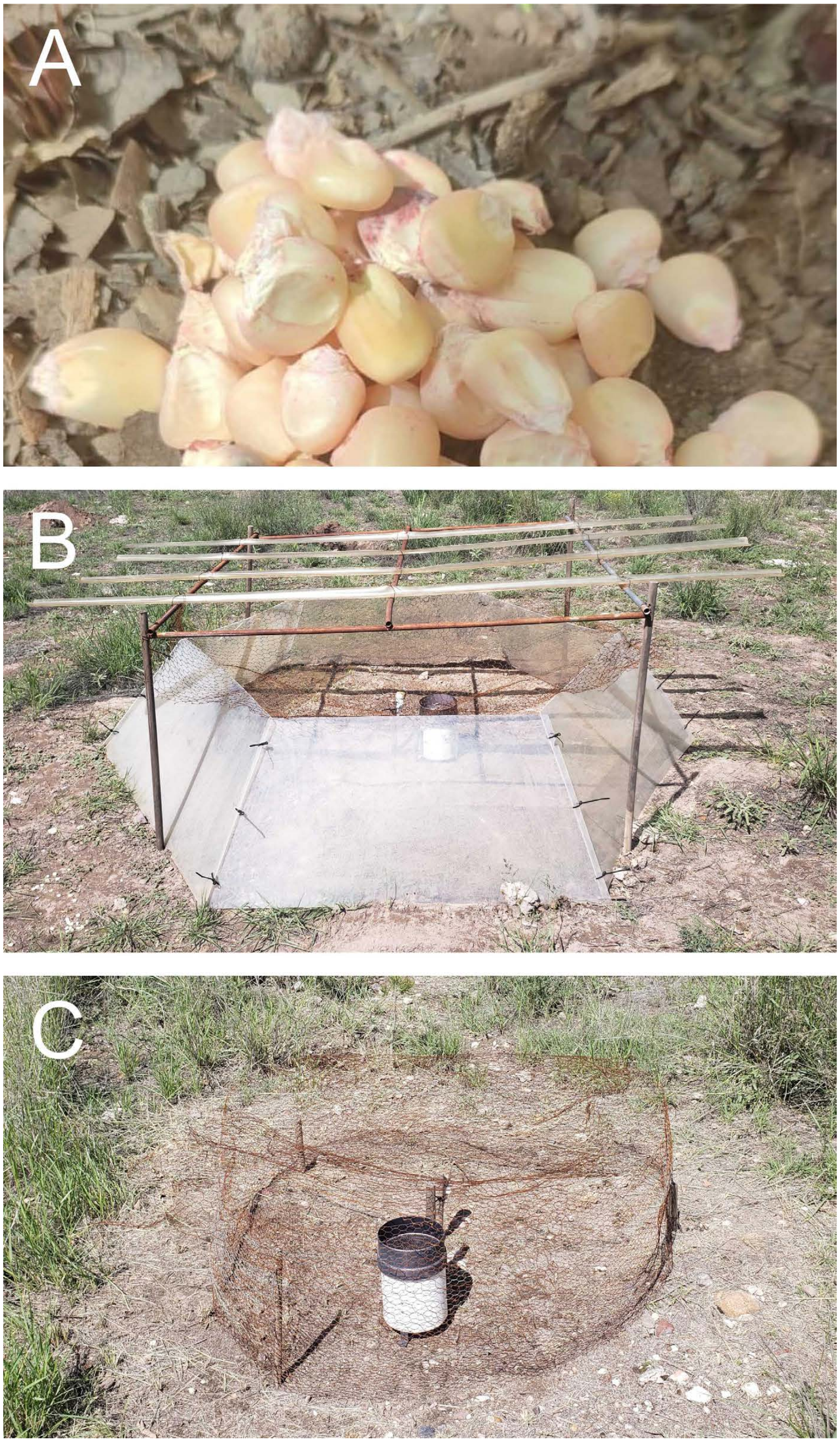

Figure 1. Seeds of the Norther Conical corn landrace (A) provided by small farmers from Mezquitic de Carmona, State of San Luis Potosí, Mexico. The figure also shows the experimental plots mounted in the field. In the climate change simulation plots (B) temperature was increased with open-top chambers and rainfall was reduced with rainout shelters. The control plots (C) were fenced with wire mesh only. The devices within plots are the automatized sensors of temperature, air relative humidity and rainfall.

Table 1. Mean air temperature and accumulated rainfall in the wettest quarter of the year predicted by the middle of this century (2041-2060) at the geographic coordinates of the study site by the three CMIP6 models considered in this study (CanESM5, MIORC6 e INM-CM4-8) at different levels of radiative forcing (2.6, 4.5, 7.0 y 8.5 W/m^2). The table also shows the averages (±95 % CI) among the three CMIP6 models for each radiative forcing level and the difference between these values those recorded under the current climate (+ = increase; - = decrease).

Climatological variable	**Radiative forcing**	**CMIP6 model**			**Average**	**Difference**
		CanESM5	**MIORC6**	**INM-CM4-8**		
Mean air temperature (°C)	2.6 W/m^2	20.83	20.73	20.60	20.72 ± 0.13	+0.60
	4.5 W/m^2	21.93	21.90	21.00	21.61 ± 0.60	+1.49
	7.0 W/m^2	22.28	20.95	21.30	21.51 ± 0.78	+1.39
	8.5 W/m^2	22.53	22.07	21.40	22.00 ± 0.64	+1.88
Accumulated rainfall (mm)	2.6 W/m^2	225.00	188.00	186.00	199.67 ±24.85	-5.03%
	4.5 W/m^2	227.00	183.00	187.00	199.00 ±27.53	-5.34%
	7.0 W/m^2	224.00	187.00	183.00	198.00 ±25.58	-5.82%
	8.5 W/m^2	224.00	184.00	190.00	199.33 ±24.41	-5.18%

Experimental design. To perform the climate change experiment, we randomly selected 20 points in the study site on August 08, 2022, always maintaining a minimum distance of 5 m among them to prevent interferences. Vegetation was fully removed within a radius of 3 m around each point and, later, the soil was tilled with shovels to make 10-cm depth furrows. The half of these points was randomly assigned to controls that remained under the current climatic conditions, while the other half of the points was assigned to climate change simulations where we increased temperature and reduced rainfall.

In the climate change simulation plots (hereafter, CCS plots), the temperature levels expected by the middle of this century were simulated with the hexagonal open-top chambers proposed by Marion *et al*. (1997). These structures were built with six trapezoidal sheets of transparent acrylic (3-mm thick, 134 cm at the base, 50 cm at the top) that resulted in 50 cm tall chambers, with diameters of 2.0 m at the base and 1.5 m at the open-top (Figure 1). The operative principle of these structures relies in increasing the accumulation of heat by reducing air circulation within the chambers (Hollister & Webber 2000, Aronson & McNulty 2009). Indeed, previous experiments conducted in this region demonstrated these chambers increase air temperature between 1.1 and 2.0 °C, as compared with the external environment (Aragón-Gastélum *et al*. 2014, Guerra-Coss *et al*. 2021), which concurs with the temperature levels predicted by CMIP6 models at the experimental site (Table 1). To reduce precipitation to the levels predicted by climate change models, open-top chambers of CCS plots were covered with a modified version of the rainout shelters proposed by Yahdjian & Sala (2002). Our rainout shelters consisted in U-shaped channels of transparent polycarbonate (1.5 mm thick, 10 cm wide, 3 m long), equidistantly arranged on metallic frames (2.5 × 2.5 m) and supported on wood poles, with an inclination of 10º between sides to allow rainfall drainage outside the target area. The amount of rainfall intercepted by these shelters depends upon the number of channels they have, and previous studies showed that rainout shelter equipped five channels reduce precipitation by 8-12 % (Pérez-Ruiz *et al*. 2018, Badano & Sánchez-Montes de Oca 2022, Sandoval-Martínez *et al*. 2022). As these values surpass the rainfall decreases expected at the study site by the middle of this century (Table 1), our rainout shelters were equipped with four U-shaped channels only (Figure 1). Regarding this climate change simulation methodology, it is important to note that open-top chambers and rainout shelters are designed to approach temperature and rainfall to the values that these variables would reach on an average year during the period 2041-2060, while these structures do not allow simulating the increasing interannual variability in temperature and rainfall that is also expected to occur in the future (de Elía *et al*. 2013). Finally, open-top chambers were covered with wire mesh (13 mm openness) to prevent the access of seed predators, while the experimental controls that remained under the current climate were just fenced with wire mesh (Figure 1).

To determine whether open-top chambers and rainout shelters properly simulated the mean climate change conditions expected by the middle of this century, we measured microclimatic variables in controls and CCS plots. For this, we installed automatized sensors of air temperature and air relative humidity (HOBO U23-Pro-V2, Onset Computer Corporation, USA) at the center of all experimental units, which were supported on wooden stakes 20 cm above the ground. These sensors were programmed to measure both variables every hour during the entire experiment. We also randomly selected five plots of each climate treatment and installed automatized rain gauges (HOBO S-RGB-M002, Onset Computer Corporation, USA) at the center of each of them, which were programed to measure precipitation at each rainfall event. Rain gauges were fixed with metallic stakes and their water-receiving funnels were located 20 cm above the ground. In all experimental units, we also measured the volumetric water content of the soil every three days using a time domain reflectometer (TDR Field Scout 300, Spectrum Technologies, USA). At each monitoring date, these soil moisture measurements were performed on six random points within each experimental unit and the values recorded by the device were averaged.

Plant response variables. On August 10, 2022, we sowed 25 seeds of Northern Conical corn in the furrows traced within each experimental plot. Seeds were sowed maintaining a linear distance of 10 cm between them to simulate the sowing density reported by the farmers that provided the seeds. Sowing positions were marked with small, numbered wooden stakes. The emergence of the coleoptile and the survival of plants were monitored every three days until October 09, 2022 (60 days). The experiment was stopped on that date because the aerial shoots of most plants were near to be as tall as the walls of the open-top chambers, which would have invalidated the effects of warming.

On day 61 after seed sowing, immediately after finishing the monitoring of the emergence and survival of plants, we used a portable fluorometer (Y-II-meter, Opti-Sciences, USA) to measure chlorophyll fluorescence on the leaves of the individuals that survived until that date. These measurements were taken at four moments of the day (04:00, 09:00, 14:00 h and 19:00 h) on five randomly selected plants within each experimental plot. In those experimental units where less than five plants survived until the end of the experiment, these measurements were performed on all available individuals. Measurements at the predawn (04:00 h) were used to estimate the maximum quantum yield of photosystem II (F_v/F_m) because this variable must be estimated on dark-adapted leaves. These values were estimated as $F_v/F_m = (F_m - F_0)/F_m$, where F_0 is the fluorescence emitted by dark-adapted leaves when they are exposed to a low-intensity pulse of actinic light (~50 μmol photons m^{-2} s^{-1}), while F_m is the maximum fluorescence emitted by these leaves when a saturating pulse of actinic light is applied (~2,500 μmol photons m^{-2} s^{-1}). Measurements on sun-exposed leaves (09:00, 14:00 h and 19:00 h) were used to estimate the effective quantum yield of photosystem II (ϕ_{PSII}) as $\phi_{PSII} = (F'_m - F_s)/F'_m$, where F_s is the basal fluorescence emitted by leaves under steady-state illumination (*i.e.*, environmental light) and F'_m is the maximum fluorescence emitted by leaves when a saturating pulse of actinic light (~2,500 μmol photons m^{-2} s^{-1}) is superimposed to the environmental illumination. Overall, F_v/F_m and ϕ_{PSII} decrease as the environmental conditions that allow plants to grow become harsher (Maxwell & Johnson 2000, Adams & Demmig-Adams 2004).

Because plants can also dissipate excesses of light energy as heat through the xanthophyll cycle, we also estimated the non-photochemical quenching of chlorophyll fluorescence (*NPQ*) as $NPQ = F'_m/F_m$ (Adams *et al.* 2008). Additionally, as our fluorometer measure the photosynthetic photon flux density (*PPFD*) in the surroundings of leaves, we computed the electron transport rate in the thylakoid membranes of chloroplasts (*ETR*) as $ETR = PPFD \times \phi_{PSII} \times 0.84 \times 0.5$, where 0.84 and 0.5 are constants that indicate the fraction of light harvested by photosystems II and I, respectively. Overall, increasing values of *NPQ* and decreasing values of *ETR* indicate that plants are exposed to suboptimal growing conditions (Baker & Oxborough 2004). As additional variables, we measured foliar temperature and air temperature in the surroundings of leaves to corroborate that the effects of open-top chambers were transferred to plants (*i.e.,* the values of these variables should be higher within CCS plots than in controls).

Plants on which chlorophyll fluorescence was measured were harvested. For this, we carefully excavated around them to collect stems (including leaves) and root systems. During this process, we revised that the root systems of plants from CCS plots were located within these experimental units, so as they would not have escaped from the effects of open-top chambers and rainout shelters. Harvested plants were placed in individual paper bags and taken to the laboratory, where they were rinsed with water for removing dust particles. Afterwards, we separated the stem and the root of each plant, and placed these structures in paper bags to dry them in a forced air oven at 60 °C. Plant structures were weighed every 24 h in an analytical balance with precision 0.01 mg (Cubis model, Sartorius, Germany) until their biomass (dry weight) remained constant. We later computed the ratio between the biomass of these structures and the age of plants (days elapsed between the emerge of the coleoptile and plant harvesting) to estimate the growth rates of shoots, roots and the whole plant (whole plant biomass = shoot biomass + root biomass). These data were also used to compute the root:shoot ratio of each plant because individuals exposed to drought conditions commonly prioritize the development of root systems over the development of shoots to increase water uptake (Jackson *et al*. 1999).

Statistical analyses. Data of air temperature and air relative humidity gathered by each automatized sensor were averaged on three-day intervals, while rainfall data gathered by each rain gauge were accumulated over these time intervals. This information was compared across time between climate treatments (controls and CCS plots) using one-way ANOVAs of repeated measures. Nevertheless, as these statistical tests do not admit groups with zero variance (Zar 2010), those periods in which no rainfall was recorded were excluded from the analyses. The same analyses were used to compare the volumetric water content of the soil between climate treatments but, in this case, we directly used the values recorded every three days in the experimental units.

Data recorded on plants during the experiment were used to compute their cumulative emergence and survival rates every three days with the Kaplan-Meier method (Kaplan & Meier 1958). To estimate plant emergence rates, we assigned values of zero (0) to all seeds at the beginning of the experiment and turned them into values of one (1) on the date in which the emergence of the coleoptile was observed. Estimations of survival rates only included seeds that gave rise to plants, which received values of one (1) at the beginning of the experiment that were turned into values of zero (0) on the date in which the individuals died. Plant emergence and survival rates were compared across time between climate treatments using pairwise Gehan-Wilcoxon tests (Kleinbaum & Klein 2005).

With the measurements performed with the fluorometer, we firstly compared *PPFD* between climate treatments to establish whether open-top chambers and/or rainout shelters interfered with the entrance of sunlight within CCS plots. We proceeded in this way because, if plant within CCS plots were subjected to different light levels than those from controls, then the variables estimated from chlorophyll fluorescence would not be comparable between climate treatments. For this, we used a one-way ANOVA of repeated measures where the different moments of the day were considered repeated observations. After that, we used the same analysis to compare the values of F_v/F_m, Φ_{PSII}, *NPQ*, *ETR*, foliar temperature and temperature in the surroundings of leaves between climate treatments. Growth rates of shoots, roots and whole plants, as well as root:shoot ratios, were compared between climate treatments with Student *t*-tests.

Results

Climate change simulation. Considering the entire experimental period (60 days), average air temperature in CCS plots was 20.48 °C (± 0.24 95 % CI), while in controls it was 19.03 °C (± 0.30 95 % CI). Significant differences were found between these values ($F_{(1,18)} = 54.417$, $P < 0.001$) and open-top chambers increased air temperature by 1.45 °C, as compared to controls. This approaches to the warming levels predicted by CMIP6 models at radiative forcings between 4.5 and 7.0 W/m^2 (Table 1). However, air temperature varied along the experiment ($F_{(19,342)} = 54.417$, $P < 0.001$) and that interactive effects between time and climate treatments were found ($F_{(19,342)} = 6.317$, $P < 0.001$). These effects were due to larger differences in temperature between controls and CCS plots during the hottest periods of the experiment (Figure 2A).

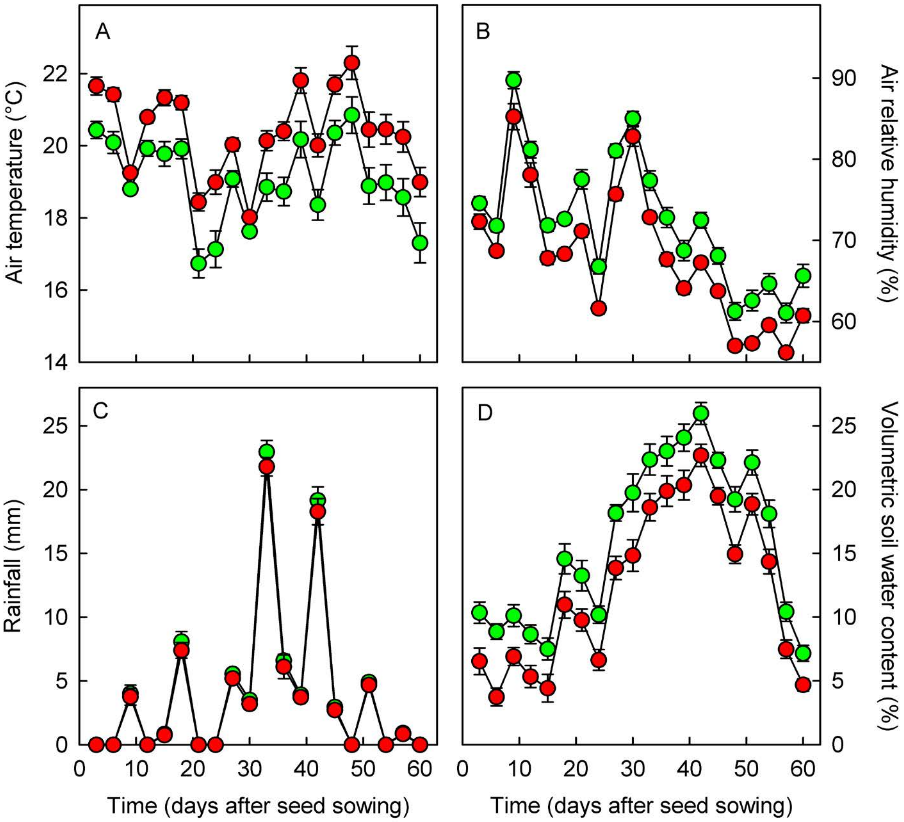

Figure 2. Air temperature (A), rainfall (B) and volumetric soil water content (C) recorded on three-day periods (averages ± 95 % CI) in controls (green symbols) and climate change simulation plots (red symbols) of the field experiment.

Air relative humidity during the experiment averaged 72.34 % (± 0.84 95 % CI) in the controls and 69.91 % (± 0.84 95 % CI) in CCS plots, and significant differences were found between these climate treatments ($F_{(1,18)}$ = 84.274, $P < 0.001$). This indicates that air relative humidity was 4.43 % lower in CCS plots than in controls. The values of this variable also varied across time ($F_{(19,342)}$ = 1011.967, $P < 0.001$), mostly because they increased on dates in which air temperature decreased in controls and CCS plots (Figure 2B). There were also significant interactive effects between climate treatments and time ($F_{(19,342)}$ = 4.361, $P < 0.001$), as larger differences in air relative humidity between controls and CCS plots occurred on dates with lower air temperatures (Figure 3B).

Accumulated rainfall differed between climate treatments ($F_{(1,8)}$ = 18.102, P = 0.003). This variable averaged 78.48 mm in CCS plots (± 1.46 95 % CI) and 83.72 in controls (± 1.92 95 % CI), indicating that rainout shelters reduced rainfall by 6.3 %. It is important to note that this difference between climate treatments is higher than that predicted by CMIP6 models, irrespective of the radiative forcing level (Table 1). Although rainfall values varied over time ($F_{(11,88)}$ = 1094.702, $P < 0.001$), no interactive effects between this factor and climate treatments were found ($F_{(11,88)}$ = 0.645, P = 0.785), which indicates that rainfall differences between CCS plots and controls were similar during the entire experiment (Figure 2C).

The volumetric water content of the soil averaged 12.22 % in CCS plots (± 0.47 95 % CI) and 15.81 % in controls (± 0.64 95 % CI), and significant differences were found between climate treatments ($F_{(1,18)}$ = 78.812, $P < 0.001$). These values also varied over time ($F_{(19,342)}$ = 518.312, $P < 0.001$), increasing in periods with higher rainfall. Nevertheless, no interactive effects between time and climate treatments were found ($F_{(19,342)}$ = 1.446, P = 0.103), and this indicates that differences in soil moisture between controls and CCS plots were approximately constant during the experiment (Figure 2D).

Responses of Northern Conical plants to higher temperature and drought. Plant emergence rates of Northern Conical estimated through time quickly increased during the first 12 days of the experiment and later stabilized around 80 % in CCS plots and around 56 % in the controls (Figure 3A). These values significantly differed between climate treatments (Gehan-Wilcoxon statistic = 8.388, d.f. = 1, $P < 0.001$), indicating that seeds sowed on CCS plots gave rise to plants faster than those sowed in controls.

Plant survival rates also differed between climate treatments (Gehan-Wilcoxon statistic = 26.11, d.f. = 1, $P < 0.001$). Survival rates in CCS plots decreased abruptly from 100 % to less than 80 % during the first 18 days of the experiment but, after this period, these values decreased slower until reaching a final a value of 70 % by the end of the experiment (Figure 3B). In the controls, instead, there was a slower decrease in plant survival rates during the first 18 days of the experiment (100 to 96 %), but these values later decreased sharply until day 36 after the sowing of seeds, when plant survival was less than 30 % (Figure 3B). After this period, plant survival rates in the controls decreased more gradually until reaching a final value of 22 % by the end of the experiment (Figure 3B).

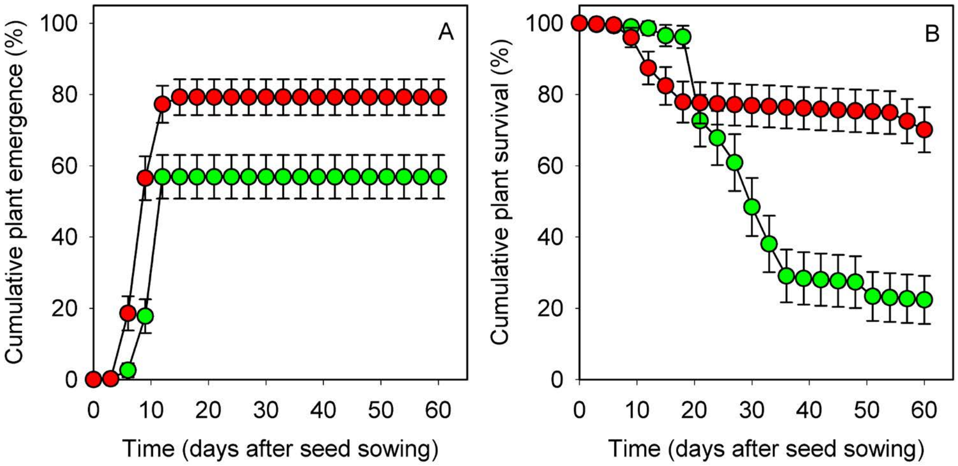

Figure 3. Rates (± 95 % CI) of plant emergence (A) and plant survival (B) estimated through the time for the Norther Conical corn landrace in controls (green symbols) and climate change simulation plots (red symbols) of the field experiment.

Although *PPDF* values varied across the moments of the day in which this variable was measured, no differences between climate treatments were found (Table 2). This indicates that neither open-top chamber nor rainout shelters interfered with the passing of light inwards CCS plots when chlorophyll fluorescence measures were performed (Figure 4A). All other variables measured with the portable fluorometer significantly differed between climate treatments and varied over time, and interactive effects between these two factors were also found (Table 2). Both foliar temperature (Figure 4B) and temperature in the surroundings of leaves (Figure 4C) were higher in CCS plots than in controls, indicating that the warming effects induced with open-top chambers were effectively transferred to plants.

The maximum quantum yield of photosystem II (F_v/F_m), measured on dark-adapted leaves (04:00 h), was higher in plants from CCS plots than in those developed in controls (Figure 4D). In plants exposed to sunlight, the effective quantum yield of photosystem II (ϕ_{PSII}) was higher in CCS plots than in controls but, in both climate treatments, these values decreased as *PPDF* increased from 09:00 to 14:00 h (Figure 4D). Values of ϕ_{PSII} increased once again in the sunset (19:00 h), but this was the moment of the day in which the largest difference between climate treatments was recorded (Figure 4D). Non-photochemical quenching of chlorophyll fluorescence (*NPQ*; Figure 4E) and electron transport rate in the thylakoid membranes of chloroplasts (*ETR*; Figure 4F) increased with *PPDF* from 09:00 to 14:00 h, for later decreasing in the sunset (19:00 h). Although the statistical analyses indicated that the values of these two variables were higher in CCS plots than in controls, the differences in *NPQ* and *ETR* between climate treatments were only evident at 14:00 h, when corn plants were exposed to the highest level of solar radiation.

Table 2. Results of the ANOVAs of repeated measures comparing environmental and plant variables measured with the portable fluorometer in controls and CCS plots. These variables include photosynthetic photon flux density (*PPFD*), maximum and effective quantum yield of photosystem II (F_v/F_m y ϕ_{PSII}), non-photochemical quenching of chlorophyll fluorescence (*NPQ*), the electron transport rate through the thylakoid membranes of chloroplasts (*ETR*), foliar temperature (*FT*°) and air temperature in the surroundings of leaves (*ET*°). The table shows the sources of variation included in these analyses and the corresponding statistics (α critical value = 0.05 in all cases).

Variable	Variation source	Statistics
PPDF	Climate treatments	$F_{(1,79)} = 0.453$, $P = 0.503$
	Time	$F_{(3,237)} = 14{,}414.460$, P < 0.001
	Interaction between factors	$F_{(3,237)} = 0.116$, $P = 0.891$
F_v/F_m y ϕ_{PSII}	Climate treatments	$F_{(1,79)} = 131.439$, $P < 0.001$
	Time	$F_{(3,237)} = 358.479$, $P < 0.001$
	Interaction between factors	$F_{(3,237)} = 22.620$, $P < 0.001$
NPQ	Climate treatments	$F_{(1,79)} = 125.904$, $P < 0.001$
	Time	$F_{(3,237)} = 164.281$, $P < 0.001$
	Interaction between factors	$F_{(3,237)} = 78.236$, $P < 0.001$
ETR	Climate treatments	$F_{(1,79)} = 100.361$, $P < 0.001$
	Time	$F_{(3,237)} = 1{,}117.461$, $P < 0.001$
	Interaction between factors	$F_{(3,237)} = 81.287$, $P < 0.001$
FT°	Climate treatments	$F_{(1,79)} = 56.440$, $P < 0.001$
	Time	$F_{(3,237)} = 924.655$, $P < 0.001$
	Interaction between factors	$F_{(3,237)} = 3.238$, $P = 0.023$
ET°	Climate treatments	$F_{(1,79)} = 138.292$, $P < 0.001$
	Time	$F_{(3,237)} = 2{,}551.355$, $P < 0.001$
	Interaction between factors	$F_{(3,237)} = 3.794$, $P = 0.011$

Growth rates of shoots, roots and whole plants were significantly higher in CCS plots than in controls (Figure 5), which indicates that the induction of climate change conditions promoted the development of young plants of Northern Conical corn. The root:shoot ratio, on the other hand, was smaller in CCS plots than in controls (Table 3), indicating that Northern Conical plants would prioritize the development of aerial structures over the development of roots when they are subjected to higher temperature and drought.

Discussion

Climate change simulation. Mean air temperature in our control treatment was close to the normal temperature estimated for the study site in the wettest quarter of the year. This suggests that mean temperature during the experiment was similar to that historically recorded during the productive cycles of rainfed crops in the study region. The implementation of open-top chambers in the study site increased air temperature to the mid-century levels expected during the wettest quarter of the year at radiative forcing levels between 4.5 and 7.0 W/m^2 (~1.45 °C higher than the current temperature), and the temperature measurements conducted on corn leaves with the fluorometer indicated that these warming effects were transferred to plants within CCS plots.

Relative air humidity, on the other hand, must be interpreted as the ratio between the amount of water vapor contained in an air volume at a given temperature and the maximum amount of water vapor that such air volume can contain. Therefore, if absolute air moisture is similar across a landscape, relative humidity decreases in warmer habitats (e.g., deforested sites) and increases in cooler habitats (*e.g.,* beneath forest canopies) (Pierrehumbert *et al*. 2008). Although the

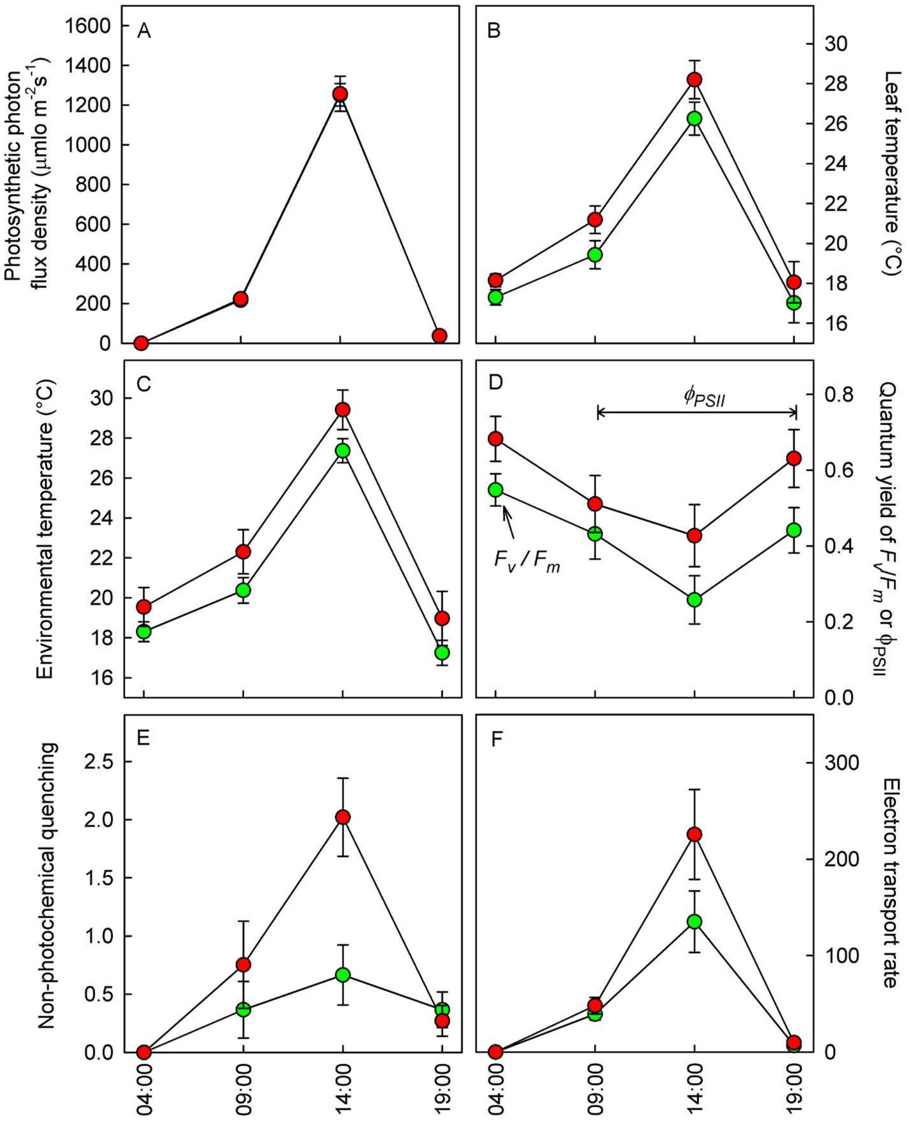

Figure 4. Average values (± 95 % CI) of variables measured with the portable fluorometer in controls (green symbols) and climate change simulation plots (red symbols) of the field experiment. These variables include photosynthetic photon flux density on Norther Conical leaves (A), leaf temperature (B), environmental temperature (C), maximum quantum yield of photosystem II (F_v/F_m) measured on dark-adapted leaves and effective quantum yield of photosystem II (ϕ_{PSII}) measured in plants exposed to sunlight (D), non-photochemical quenching of chlorophyll fluorescence (E) and electron transport rate in the thylakoid membranes of chloroplasts (F).

general circulation models that are currently available do not provide predictions for changes in relative humidity due to increasing warming, its dependence on air temperature may explain why these values were lower in CCS plots than in the experimental controls, and this may also explain why these values decreased during the warmer periods of the experiment.

Rainfall in the controls of the experiment was 60 % lower than the climatological normal estimated for the study site during the wettest quarter of the year. On this issue, it is important to note that the region in which the experiment was developed is highly vulnerable to intense drought events because of elevated interannual variability in rainfall -precipitation in dry years might be between fourfold and tenfold lower than in wet years (Ortega-Gaucin *et al*. 2018, Rocha-Escalante *et al*. 2022). Thus, it seems that our experiment was conducted in an extremely dry year, where the implementation of rainout shelters in CCS plots reduced mean rainfall to levels that were below those predicted by CMIP6 models by the middle of this century.

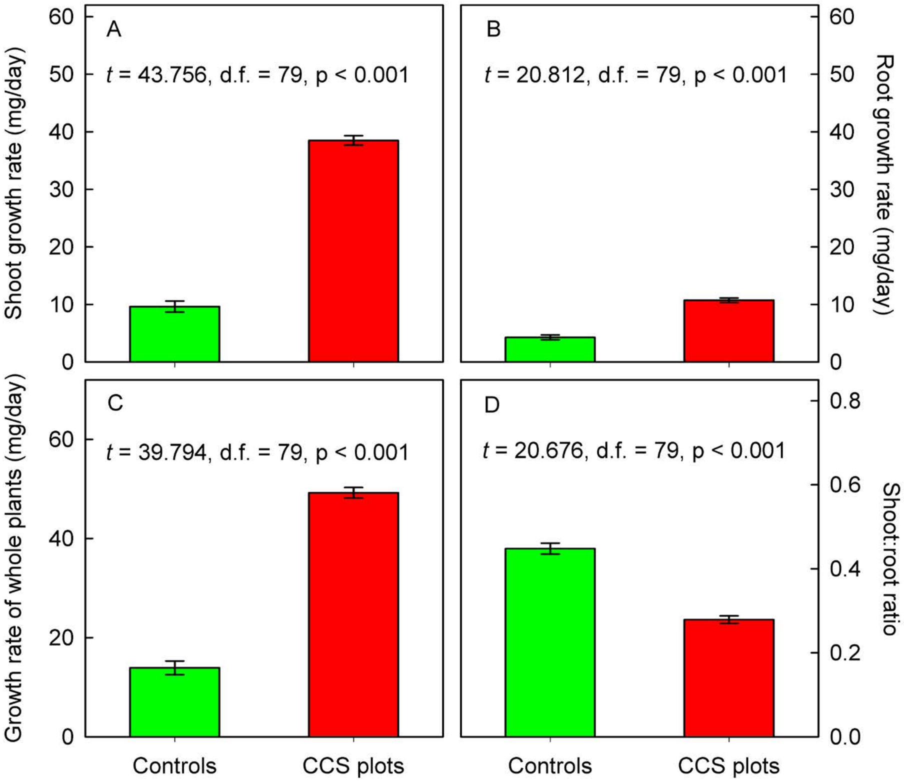

Figure 5. Average growth rates (mg/day ± 95 % CI) of shoots (A), roots (B) and whole plants (C), as well as root:shoot ratios (D), of Norther Conical plants in controls and climate change simulation plots (CCS plots, in the figures). Values within the panels are the results of the Student t-test comparing these values between climate treatments (α critical value = 0.05 in all cases).

The lower volumetric soil water contents recorded in CCS plots, as compared to values from controls, were probably due to combined effects of open-top chambers and rainout shelters. This suggestion relies in the increased soil water evaporation that higher temperatures may have caused in these experimental units which, together with the decreased soil water recharge due to rainfall reduction, would have resulted in lower soil moisture (Parlange *et al.* 1998). In this way, these results confirm that corn plants developed in CCS plots were exposed to more intense aridity conditions than those occurring under the current climate.

Although open-top chambers and rainout shelters are useful to simulate climate change conditions in the field, our experimental design has several limitations. For instance, we used these structures for increasing temperature and reducing rainfall to the levels expected on an average year during the period 2041-2060, but this approach does not allow assessing the effects of the elevated between-year variation that these two variables exhibit in arid and semiarid ecosystems of Mexico (Ortega-Gaucin *et al.* 2018, Rocha-Escalante *et al.* 2022). Thus, as interannual variability in temperature and rainfall is expected to increase across North America due to the advance of climate change (de Elía *et al.* 2013), a single year of experimentation, as our case, is not enough to fully assess the potential effects of increasing warming and drought on the development of plants, either wilds species or rainfed crops. Copping this limitation requires performing experiments over several consecutive years, as this would allow accounting for the temporal variation in temperature and rainfall occurring under the current climate, while the inclusion of open-top chambers and rainout shelters in these experiments would allow simulating the future interannual variability (Hollister & Webber 2000). Alternatively, open-top chambers and rainout shelters can be modified for generating different warming and drought levels in a single year, which could allow including the putative effects of interannual variability in temperature and rainfall. Previous experiences indicate warming within open-top chambers can be enhanced adding small acrylic sheets in their upper section because this reduces air circulation within them, while drilling small holes at the base of chambers reduce heat accumulation due to increased inner ventilation (Guerra-Coss *et al*. 2021). Different rainfall levels, on the other hand, can be regulated just increasing or decreasing the number of channels of rainout shelters (Badano *et al*. 2019).

Another important limitation of this study is its local scope. Because our experiment was conducted in a single site, it did not account for the variability in temperature and rainfall regimes that occur across the different agroecosystems in which Norther Conical corn is cultivated in Mexico, which can be as important as the temporal variability in these climatic variables (Carter *et al*. 2018). Thus, besides considering the temporal variability in temperature and rainfall, future research addressed to assess how climate change could affect plants should also consider the spatial variability in climate. To deal with this limitation of our study, the experiments with open-top chambers and rainout shelters can be conducted on sites deferring in temperature and rainfall within the target region.

Responses of Northern Conical plants to higher temperature and drought. Contrary to our expectations, Northern Conical plants displayed higher emergence, survival and growth rates in the experimental units where temperature and drought were enhanced. Studies conducted with the main commercial corn varieties from North and South America, Africa and Europe indicated that the optimal temperature range for seed germination is between 26 and 29 °C (Riley 1981, Xue *et al*. 2021), while temperatures between 27 and 32 °C promote the growth of stems, roots and leaves (Sánchez *et al*. 2014, Waqas *et al*. 2021). As far as we are aware, no studies have analyzed the optimal temperatures for germination and development of Mexican corn landraces but, in our case, mean temperature in both climate treatments was below the optimal thresholds reported for commercial varieties. Thus, the faster emergence of corn plants in CCS plots could be due to the warming effects of open top chambers, and these higher temperatures may have also prompted the growth of the aerial shoots and root systems. This probably gave rise to more vigorous individuals, less susceptible to environmental vicissitudes (Ellis 1992), that had higher survival chances than those from controls. Although these findings would indicate positive effects of warming on the early development of Norther Conical plants, it must be highlighted that our results are preliminary and more extensive and detailed experiments are still needed to determine how varying temperatures influence its germination, survival and growth. Further, because corn is a key food resource for the Mexican population (Reyes-Santiago *et al*. 2022), studies of this type should include other native landraces of this crop.

Even when temperature enhancements may be responsible of the higher emergence, survival and growth rates of Norther Conical plants in CCS plots, it is hard to explain why this occurred under the reduced rainfall conditions induced in these experimental units. These results are counterintuitive because, although its C_4 photosynthetic metabolism may confer to corn some drought tolerance (Lopes *et al*. 2011), water is the most critical resource for plants in the drylands where the Norther Conical landrace is cultivated (Snyder & Tartowski 2006, Ruiz-Corral *et al*. 2013, Rane *et al*. 2022). Indeed, the lower root:shoot ratio of individuals from CCS plots opposites to the responses that most plant species display under drought conditions (Jackson *et al*. 1999). The greater development of shoots and roots that plants from CCS plots displayed, as compared with control plants, might explain this unexpected result. This is because, even when roots of plants developed within CCS plots were about twice larger than those of plants developed in controls, their shoots were fourfold bigger, and these differences were transferred to the root:shoot ratios. Further, the larger root systems of plants from CCS plots may have increased the uptake of water and soil nutrients. This probably contributed to mitigate the drought effects induced with rainout shelters, while the resulting plants were bigger than those from controls. Nevertheless, these results must be taken with caution because we focused on manipulating temperature and rainfall only, while we were unable to assess the effects of other factors that can influence plant growth. For instance, we did not measure the soil properties in the points assigned to the experimental units before staring the experiment trial and after finishing it. In consequence, we are not aware if the microclimatic manipulations induced with open-top chambers and rainout shelters altered substrate texture, availability of nutrients and/or water retention capability of soil, among other physicochemical soil properties that can affect crop development (Brevik 2013, Chen *et al*. 2020).

The higher survival and growth rates of Northern Conical plants in CCS plots may be also linked with a series of functional responses they displayed when subjected to warming and enhanced drought. In most terrestrial plants, the maximum quantum yield of photosystem II (F_v/F_m) approaches to 0.8 when the environmental stress is negligible. This value indicates that plant photosystems are close to their maximum capacity to process light energy, while lower F_v/F_m values indicate that external stress factors damaged their photosynthetic apparatus (Adams & Demmig-Adams 2004). In our case, although F_v/F_m ratios of plants from CCS plots were below 0.8, these values were closer to 0.8 than those of control plants. Because Northern Conical corn seem to have elevated drought tolerance (Wellhausen *et al*. 1951, Ruiz-Corral *et al*. 2013), the rainfall reductions induced in CCS plots probably have low relevance for explaining these results, as precipitation in these experimental units was slightly lower than that recorded in controls. Instead, the higher F_v/F_m ratios recorded in CCS plots may be due to a series of physiological responses that these plants triggered when exposed to higher temperatures, which allowed them maintaining higher integrity of photosystems in periods of elevated environmental stress. This does not necessarily mean, however, that the advance of climate change will enhance the photosynthetic performance of Northern Conical plants. Addressing this issue would require specifically assessing the physiological responses of Northern Conical in face of different levels of temperature and water stress, as this would provide more accurate insights about their photosynthetic responses under climate change conditions.

The putative lower damage to photosystems of plants from CCS plots may explain their higher effective quantum yields (ϕ_{PSII}) and electron transport rates during daylight hours. These two processes are critical for carbon assimilation because they are involved in the synthesis of the energy molecules (ATP and NADPH) required in the Calvin cycle (Baker & Oxborough 2004, Cavendar-Bares & Bazzaz 2004). Thus, it is feasible to propose that Northern Conical plants form CCS plots had higher photosynthetic rates than those from controls. However, in both controls and CCS plots, ϕ_{PSII} and *ETR* decreased at 14:00 h, when the highest foliar and environmental temperatures were recorded. This was probably due to the midday depression in carbon assimilation, as most plant species partially close their stomata during the hottest moment of the day to reduce water loss by transpiration, but this also reduces gas exchange (Xu & Shen 2005). Besides reducing the photosynthetic rate, a large fraction of photosystems reaction centers are disabled to reduce the flow of electrons in the thylakoid membrane, and hence prevent the accumulation of reactive oxygen species (*e.g.,* singlet oxygen, superoxide and hydrogen peroxide) that could damage the photosynthetic apparatus (Foyer & Hanke 2022). These processes linked to the midday depression in carbon assimilation occur in plants with both C_3 and C_4 photosynthetic metabolism (Xu & Shen 2005), but it is commonly less severe in C_4 plants because they are more tolerant to drought and warming (Wu *et al*. 2022, Mares-Guerrero *et al*. 2024). In our case, even during the hottest moment of the day (14:00 h), ϕ_{PSII} and *ETR* of plants were higher in CCS plots than in controls, suggesting that individuals subjected to warming and drought had higher photosynthetic rates. Further, in both climate treatments, the putative disabling of photosystems after the midday depression was reversible because ϕ_{PSII} increased towards the sunset (19:00 h), but these recoveries in photosynthetic capability were more notable in plants from CCS plots than in those from controls. On this issue, it could be argued that open-top chambers and rainout shelters could interfere with the entry of light within CCS plots and, consequently, alter the photosynthetic processes of plants. However, the *PPDF* values measured with the fluorometer indicated that these effects are negligible, and this concurs with the results of several experiments that used identical structures to simulate climate change in the field (Badano *et al.* 2019, Badano & Sánchez-Montes de Oca 2022, Sandoval-Martínez *et al*. 2022). These results then suggest that moderate increases in temperature might stimulate the photosynthetic performance of Norther Conical corn but, regardless of these apparently positive responses, these findings must be taken with caution. This is because our results come from a spatially and temporally limited experiment, while more extensive and detailed field trials are required to verify them.

As compared to corn plants developed under the current climate, those that grew within CCS plots also displayed higher capability for dissipating excesses of light energy as heat through the xanthophyl cycle. Indeed, the non-photochemical quenching of chlorophyll fluorescence (*NPQ*) during the moment of maximum solar radiation were eightfold higher in plants from CCS plots than in those from controls. Together with the results obtained for ϕ_{PSII}

and *ETR*, these findings suggest that neither plants from controls nor CCS plots use all the light they harvest to generate energetic molecules for carbon assimilation in the Calvin cycle (ATP and NADPH), as a large fraction of that energy seems to be dissipated as fluorescence or heat. Further, the elevated *NPQ* recorded in plants from CCS plots allows proposing that they were more efficient than those from controls for dissipating excesses of light energy through the xanthophyl cycle. Although the chlorophyll fluorescence variables that we measured on these plants do not allow determining why this occurred, studies conducted with other plant species suggest that the expression of genes associated with the synthesis of violaxanthin de-epoxidase (which catalyzes the conversion of violaxanthin to antheraxanthin, and then to zeaxanthin, in plants subjected to elevated light levels) and zeaxanthin epoxidase (which catalyzes the reverse reactions when light levels are not saturating) are partially regulated by changes in temperature and water availability (North *et al*. 2005, Du *et al*. 2009, Dobra *et al*. 2010). In the case of Northern Conical plants, however, more studies are required for determining if they display such a differential gene expression when exposed to higher temperature and drought.

Overall, our study suggests that the Northern Conical corn landrace could tolerate the increasing temperature and drought expected across Mexico in the near term. Although these findings could be of interest for agronomists and agroecologists, we strongly recommend considering the experimental limitations of our study. This is because open top-chambers and rainout shelters may induce undesirable physicochemical changes besides simulating warming and drought conditions. For instance, as open-top chambers reduce wind speed to induce warming (Marion *et al*. 1997), the air boundary layer around plant leaves may be thicker within CCS plots than in controls and, because this affects CO_2 exchange with the environment, these structures may mask the true effects of climate change on photosynthesis and other physiological processes (Yu *et al*. 2003). Future experiments of this type must also take into account that open-top chambers and rainout shelters might alter soil properties that influence plant growth, such as texture and nutrient availability. Additionally, as we just focused on the vegetative development of young Northern Conical individuals, it would be important determining if adult plants exhibit similar responses, and this would require modifying the open-top chambers to make them as taller as adult corn plants or, alternatively, using other warming methods. Finally, future simulation experiments should consider the whole suite of climatic spatial-temporal variability within the distribution range of native corn landraces, allowing to predict agronomic, ecological and physiological traits of maize, therefore promoting strategies for agricultural adaptation towards the new climatic regimes.

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