UNIVERSIDAD AUTÓNOMA DE SAN LUIS POTOSÍ

FACULTAD DE CIENCIAS QUÍMICAS, INGENIERÍA Y MEDICINA

PROGRAMA MULTIDISCIPLINARIO DE POSGRADO EN CIENCIAS AMBIENTALES

TESIS QUE PARA OBTENER EL GRADO DE

DOCTOR EN CIENCIAS AMBIENTALES

PHYSIOLOGY, METABOLOMIC PROFILES, AND YIELD OF NATIVE GENOTYPES OF MAIZE (*ZEA MAYS* L.) AND THEIR *MILPA* SYSTEMS (MAIZE+BEAN+SQUASH) FROM SAN LUIS POTOSÍ, MEXICO, UNDER RELATED EFFECTS OF CLIMATE CHANGE

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IDRISSA DIÉDHIOU

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Abstract

Maize (*Zea mays* L.) is the most important crop in Mexico and is grown in a wide range of habitats, from sea level to more than 3000 m a.s.l., and from tropical, humid surroundings to semi-desert conditions. Maize is also intercropped with other crops, principally bean (*Phaseolus* spp. or *Vigna unguiculata* (L) Walp), and squash (C*ucurbita* spp.), and this crop production system, called the *milpa*, is practiced on a large scale by Mexican smallholders. However, warmer temperatures and predicted as a result of climate change will have an impact on maize and *milpa* system.

In this context, the aim of this study was to determine the physiology, metabolomic profiles, grain yield, and photosynthetic capacity response of creole (native) genotypes of maize from three agroclimatic regions of San Luis Potosí (SLP), Mexico, and their intercropping system (*milpa*) under the related effect of climate change.

For that, five specific objectives were considered: 1) to evaluate the germination and initial growth of creole genotypes of maize coming from different agroclimatic regions at different temperatures and levels of stress under laboratory conditions; 2) to provide a reference for research on the antistress mechanism of maize with a special focus on Mexican native maize, loading for strategies and future perspectives for the protection of native maize for its importance to Mexican smallholders "*campesinos*" and the negative impact of the related effect of climate change on the crop; 3) to determine the metabolomic profiles of native maize seedlings from warm-dry, temperate, and hot and humid climates of the state of SLP grown in controlled environments related to some effects of climate change (temperature increase and water deficit stress) by gas chromatography/mass spectrometry (GC/MS) techniques; 4) to evaluate the emergence, initial growth and photosynthetic parameters of native maize genotypes from different climates or agro-ecological zones under induced passive heat; 5) to determine the effect of an increase in temperature on physiology, photosynthetic capacity, and grain yield responses of three *milpa* systems from different climates from SLP.

Considering our hypothesis was: when native genotypes of maize and his intercropping system (*milpa*) suited to specific local conditions are subjected to relevant effects of climate change, their metabolomics profiles, germination, emergence, initial growth and development, grain yield, and photosynthetic parameters respond differently depending on their origin.

Native genotypes of maize (and their intercropped bean and squash) from the three agroclimatic regions of the state of SLP, called *Altiplano* (warm-dry), *Media* (template) and *Huasteca* (hot and humid), were used.

In the laboratory conditions, the germination and initial growth, and the metabolomic profile of maize genotype seedlings (corresponding to stage V2 (visible the neck of the second leaf)) were evaluated at different temperatures and water potentials.

With the use of OTC in the field, the emergence of young maize plants (corresponding to the growth stage between V9 and V12) and their growth parameters and photosynthetic capacity were evaluated. OTC was developed to evaluate the complete cycle of *milpas* (maize+bean+squash) genotypes from the three agro-ecological regions. It is important to note that a literature review of the metabolomic profiles of maize plants under abiotic stress has been proposed with a special focus on Mexican native maize.

The germination and initial growth of creole genotypes of maize coming from different agroclimatic regions were drastically affected by the increase of temperature and water deficit.

Untargeted metabolic profiling using gas chromatography/mass spectrometry in combination with multivariate data analysis provided molecular differentiation of the native genotypes of maize from warm-dry (*Altiplano*), template (*Media*), and hot and humid (*Huasteca*) environments.

The emergence of the seedlings and the photochemical quenching of the maize young plants genotypes were affected negatively by the increase in air temperature. Plant growth benefited from the increase in temperature and accelerated.

The growth and development of maize, bean, and squash in the *milpa* systems increased under the effect of induced heating. In addition, the *milpas* of the *Huasteca* (warmer region) were the least affected by induced passive heat. Instead, the warming reduced the grain yield parameters of the crops; the squash was the most affected, while the bean was the least.

Induced warming altered chlorophyll fluorescence and gas exchange parameters differently for each crop. However, in the early stage (45 days after the emergence), the maximum efficiency of photosystem II (Fv/Fm) and the non-photochemical quenching (qN) of bean and maize were reduced, while in the reproductive stage (75 days after the emergence), they were Fv/Fm, qN, and photochemical quenching (qP) for maize; the stomatal conductance and transpiration rate of the squash plants improved under the effect of warming.

The results allow us to establish the following:

The maize genotypes of the region with the highest mean annual temperature and precipitation (*Huasteca*) were the most affected in germination and initial growth [laboratory conditions and early stages (field conditions of young plants)]. This is associated with adaptations to local conditions of their genetic material with fewer stress conditions compared to the *Altiplano* and *Media* materials, regions of unfavorable conditions associated

with abiotic stresses due to the combination of temperatures with wide variations and lower precipitation.

The metabolomic profiles of the maize genotypes grown under related effects of climate change obtained through this research represent useful reference information to evaluate possible ways to counteract abiotic stresses (water deficit and heat stress) in native maize genotypes. In addition, important metabolites were identified in the different native genotypes of maize under heat, water deficit stress, and the combination of these factors. However, the review of the state of the art indicates that the metabolic profile of native Mexican maize has not been well studied and may be the key to understanding how to deal with the negative effect of climate change on this crop.

The results of the experiment of the *milpa* system in full growth and development cycle indicate that the warming considerably delayed the parameters of grain yield of the crops. Despite this, the *milpa* from the *Huasteca* was the least affected by the induced warming, the fruit yield of the squash was the most affected, and the bean grain the least.

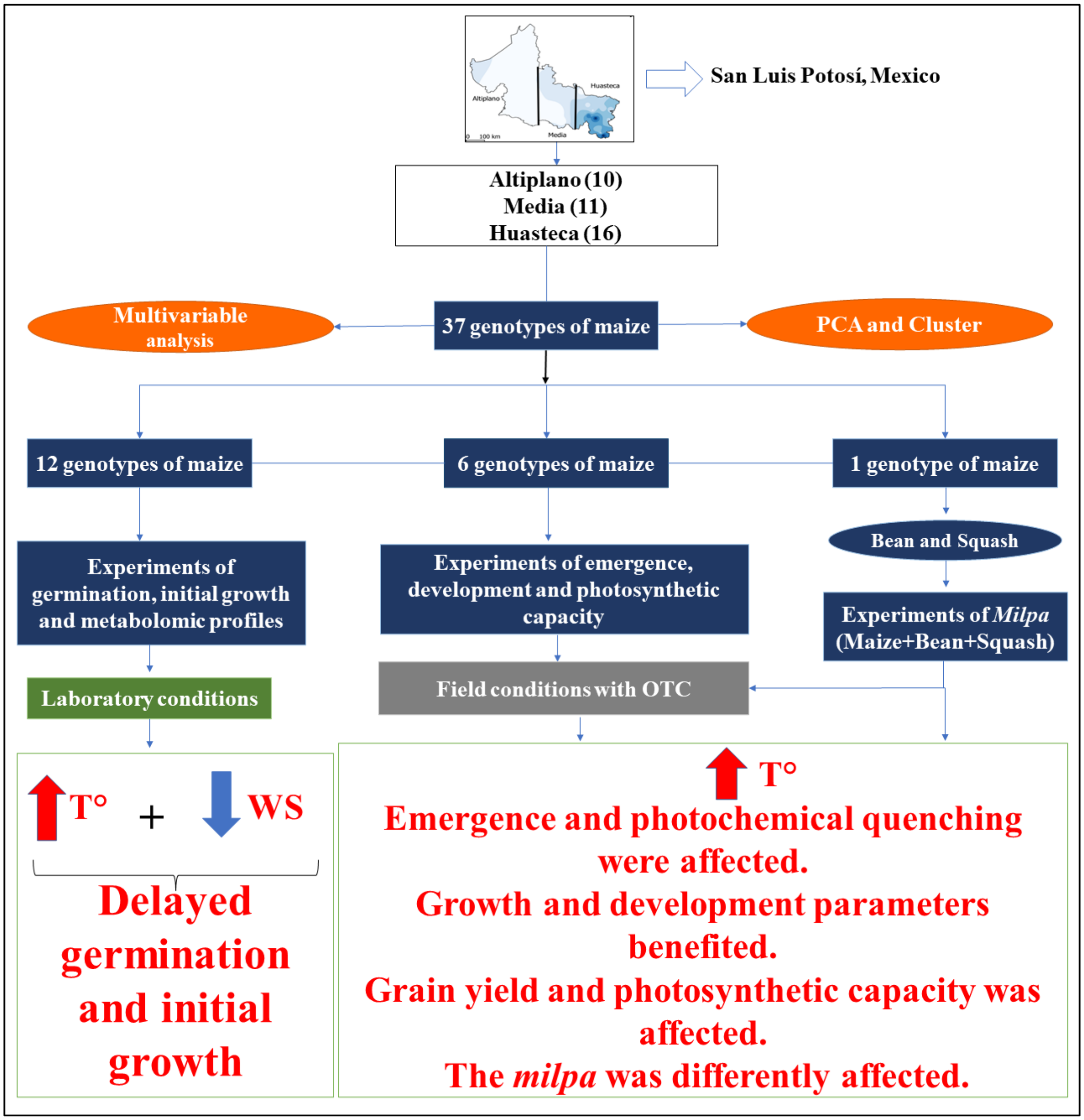
The induced warming affected the chlorophyll fluorescence and gas exchange differently for each crop. However, in the early stage (45 days after emergence), Fv/Fm and qN were reduced for bean and maize, while in the reproductive stage (75 days after emergence), they were Fv/Fm, qP, and qN for maize; stomatal conductance and squash transpiration rate improved under the effect of induced warming.

We concluded that maize genotypes can be affected differently by the increase in temperature due to climate change and that their tolerance represents an opportunity for improvement of production systems. Likewise, the increase in temperature has adverse effects on the physiology of the crops that make up the milpa system; it accelerates growth but reduces grain yield, although each crop (maize, bean and squash) has differentiated responses.

The graphical abstract resume the methodology and results of this research.

Keywords: abiotic stress, heat, water deficit stress, omics, climate.

Graphical abstract



T°: temperature, WS: water stress; OTC: Open top chamber; PCA: Principal component analysis.

Resumen

El maíz (*Zea mays* L.) es el cultivo más importante de México, se cultiva en climas diversos y se intercala con otros cultivos, principalmente frijol (*Phaseolus* spp. o *Vigna unguiculata* (L) Walp) y calabaza (C*ucurbita* spp.). Sin embargo, es muy probable que el aumento de las temperaturas y el déficit de agua, previstas como resultado del cambio climático, tengan un fuerte impacto en el maíz y en su sistema milpa.

El objetivo general de esta investigación fue determinar los parámetros fisiológicos, metabolómicos, fotosintéticos y de rendimiento de genotipos criollos (nativos) de maíz procedentes de tres regiones agroclimáticas de San Luis Potosí (SLP), México, y su sistema de intercalación (milpa) bajo los efectos relacionados con cambio climático.

Para ello, se consideraron cinco objetivos específicos: 1) evaluar la germinación y el crecimiento inicial de genotipos criollos de maíz procedentes de diferentes regiones agroclimáticas a diferentes temperaturas y niveles de estrés hídrico en condiciones de laboratorio; 2) proporcionar una referencia para la investigación sobre el mecanismo antiestrés del maíz con un enfoque especial en el maíz nativo mexicano, generando estrategias y futuras perspectivas para la protección del maíz nativo por su importancia para los campesinos mexicanos y el impacto negativo del cambio climático en el cultivo; 3) determinar los perfiles metabolómicos de plántulas de maíz nativas de climas cálido-seco, templado y cálido y húmedo del estado de SLP cultivadas en ambientes controlados relacionados con efectos del cambio climático (aumento de temperatura y déficit de humedad) por técnicas de cromatografía de gases/espectrometría de masas (CG/EM); 4) evaluar la emergencia, crecimiento y parámetros fotosintéticos de plantas jóvenes de genotipos de maíz nativos procedentes de diferentes climas bajo efecto del calentamiento pasivo inducido; 5) determinar el efecto de un aumento de la temperatura en los parámetros fisiológicos, fotosintéticos y de rendimiento de tres sistemas de milpa procedentes de diferentes climas del estado de SLP.

Nuestra hipótesis fue que los genotipos nativos de maíz y su sistema de intercalación (milpa), adaptados a condiciones locales específicas, responderán en dependencia de las características climáticas de sus orígenes a efectos relacionados con el cambio climático, lo que se evidenciará en sus perfiles metabolómicos, germinación, emergencia, crecimiento inicial, rendimiento de grano y parámetros fotosintéticos.

Se evaluaron genotipos de maíz (y sus cultivos intercalados, frijol y calabaza) procedentes de tres regiones agroecológicas del estado de SLP llamadas Altiplano (cálido-seco), Media (templado) y Huasteca (cálido y húmedo).

En laboratorio se evaluó la germinación y crecimiento inicial y el perfil metabolómico de genotipos de maíz (correspondiente a la etapa V2 (visible el cuello de la segunda hoja)) en diferentes temperaturas y potenciales de agua.

Con el uso de OTC, en campo, se evaluaron la emergencia de plantas jóvenes de maíz (correspondiente a la etapa de crecimiento entre V9 y V12) y sus parámetros de crecimiento y fotosintéticos. Se desarrollaron OTC para evaluar el ciclo completo de milpas constituidas por genotipos de maíz, frijol y calabaza procedentes de las tres regiones agroecológicas señaladas. Además, se elaboró una revisión del estado del conocimiento de los perfiles metabolómicos de las plántulas de maíz bajo estreses abióticos (altas temperaturas, déficit de agua y la combinación de ambos) con especial atención al maíz nativo mexicano.

La germinación y el crecimiento inicial de genotipos criollos (nativos) de maíz provenientes de diferentes regiones agroclimáticas fueron drásticamente afectados por el aumento de la temperatura y por el déficit hídrico, siendo los cultivares de Huasteca los más afectados y los de Media y Altiplano los menos afectados.

El perfil metabólico no modificado, mediante cromatografía de gases/espectrometría de masas, en combinación con el análisis de datos multivariables, proporcionaron una diferenciación molecular de los genotipos nativos de maíz de ambientes cálido-seco (Altiplano), templado (Media) y cálido-húmedo (Huasteca).

La emergencia de las plantas jóvenes de los genotipos de maíz fue afectada negativamente por el aumento de la temperatura y también alteró la disipación fotoquímica. El crecimiento de las plantas jóvenes de genotipos de maíz se benefició del aumento de la temperatura y se aceleró.

El crecimiento y el desarrollo del maíz, el frijol y la calabaza en los sistemas milpa aumentó bajo el efecto del calentamiento inducido. Además, las milpas de la Huasteca (región más cálida) fueron las menos afectadas por el calor pasivo inducido. En cambio, el calentamiento redujo los parámetros de rendimiento de granos de los cultivos, con mayor medida en la calabaza y en menor medida el frijol.

El calentamiento inducido alteró los parámetros de fluorescencia de la clorofila y de intercambio de gases de manera diferente para cada cultivo. Sin embargo, en la etapa temprana (45 días después de la emergencia), se redujeron la eficiencia máxima del fotosistema II (Fv/Fm) y la disipación no fotoquímica (qN) del frijol y maíz, mientras que en la etapa reproductiva (75 días después de la emergencia), fueron Fv/Fm, qN, y la disipación fotoquímica (qP) para el maíz; la conductancia estomática y la tasa de transpiración de las plantas de calabaza mejoraron bajo el efecto del calentamiento.

Los resultados permiten establecer lo siguiente.

Los genotipos de maíz de la región con mayor temperatura media anual y precipitación (Huasteca) fueron los más afectados en la germinación y crecimiento inicial [condiciones de laboratorio y etapa temprana (condiciones de campo de plantas jóvenes)] y esto se asocia a las adaptaciones a las condiciones locales de su material genético con menos condiciones de estrés en comparación con los materiales del Altiplano y Media, regiones de condiciones desfavorables asociadas a tensiones abióticas debidas a la combinación de temperaturas con variaciones amplias y precipitaciones inferiores.

Los perfiles de metabolitos de los genotipos bajo los efectos relacionados con cambio climático obtenidos con esta investigación representan información de referencia útil para evaluar las posibles formas de contrarrestar los estreses abióticos (déficit de humedad y calor) en genotipos nativos de maíz. Además, se identificaron importantes metabolitos en los diferentes genotipos nativos de maíz bajo calor, estrés hídrico y la combinación de estos factores. No obstante, la revisión del estado del arte indica que el perfil metabolómico del maíz nativo mexicano no ha sido bien estudiado y puede ser la clave para entender cómo enfrentar el efecto negativo del cambio climático en este cultivo.

Los resultados del experimento del sistema milpa en ciclo completo de crecimiento y desarrollo señalan que el calentamiento retrasó considerablemente los parámetros de rendimiento de granos de los cultivos. Pese a ello, la milpa procedente de la Huasteca fue la menos afectada por el calentamiento inducido, el rendimiento de frutos de la calabaza fue el más afectado y el de grano del frijol el menos afectado.

El calentamiento inducido afectó la fluorescencia de la clorofila y el intercambio de gases de manera diferente para cada cultivo. Sin embargo, en la etapa temprana (45 días después de la emergencia), se redujeron Fv/Fm y qN para frijol y maíz, mientras que en la etapa reproductiva (75 días después de la emergencia), fueron Fv/Fm, qP, y qN para el maíz; la conductancia estomática y la tasa de transpiración de calabaza mejoraron bajo el efecto del calentamiento inducido.

Se concluye que los genotipos de maíz pueden ser afectados de manera diferencial por el aumento de temperatura debido al cambio climático y que su tolerancia representa oportunidades de mejoramiento de los sistemas de producción. Asimismo, el aumento de temperatura tiene efectos adversos en la fisiología de los cultivos que componen el sistema milpa, acelera el crecimiento, pero reduce el rendimiento de granos, aunque cada cultivo (maíz, frijol o calabaza) tienen respuestas diferenciadas.

El “graphical abstract” resume la metodología y los resultados de esta investigación.

Palabras claves: estrés abiótico, calor, déficit de agua, ciencia ómica, clima.

Introduction

Maize (*Zea mays* L.) is among the most commonly cultivated grain crops and also an important part of livestock and poultry industry across the world (Tanumihardjo et al., 2020). In Mexico and Central America, where it is a staple food, the crop is especially important. Maize was domesticated for first time in South West Mexico between 6,000 and 10,000 years ago, and it is currently one of the most diversified crop species on the planet (Piperno et al., 2009). Maize is grown in a wide range of habitats in Mexico, from sea level to more than 3000 meters above sea level, and from tropical humid surroundings to semi-desert conditions. Over 2.5 million Mexican farmers cultivate roughly 8 million hectares of land each year, with over 75% of the seed stored from past harvests. Maize landraces or natives genotypes comprise at least one half of the seed cultivated each year in Mexico (Eakin et al., 2014; Zhao et al., 2006).

According to Goritschnig (2020), maize is one of the most widely cultivated crops in the world, produced on almost 200 million hectares in practically all countries of the world. Maize has traditionally been intercropped with numerous other species in Mesoamerica (from southern Mexico to Costa Rica), its center of origin and diversity, in what is known as the "*milpa*" or "three sisters" system. Maize is usually intercropped with common beans (*Phaseolus* spp.) and squashes in the milpa (*Cucurbita* spp.) (Benz, 2001; Hart, 2008; Kistler et al., 2018). Farmers across Mesoamerica are still growing maize in *milpa* systems in a variety of agro-ecosystems, from desert and semiarid zones to temperate highlands and tropical lowlands. Maize can be intercropped with a variety of plants, including faba beans (*Vicia faba*), peppers (*Capsicum* spp.), tomato (*Solanum lycopersicum*), potato (*Solanum tuberosum*), and amaranth (*Amaranthus* spp.), as well as wild leafy species utilized for food or medicinal uses (de Tapia et al., 2014). Climate, soil type, topography, natural vegetation, traditional knowledge, culture, and diets all play a role in the degree of variance in milpa systems (Lopez-Ridaura et al., 2021). *Milpa* cultivated under somewhat regulated settings have been demonstrated to be an efficient conventional cropping system in studies of overall production. Niche complementarity, competition, and facilitation among species all contribute to overall effectiveness in *milpa* systems (Ebel et al., 2017; Pleasant and Burt, 2010; Vandermeer, 1989).

Climate change is one of the most pressing issues facing the globe today. Significant fluctuations in the average values of meteorological parameters such as precipitation and temperature, for which averages have been estimated over a lengthy period, are defined as extreme weather (Malhi et al., 2021; Maunder, 2012). According to Mendelsohn (2008); agriculture is the most vulnerable sector to climate change due to its enormous size and susceptibility to weather variables, resulting in massive economic consequences. Changes in climatic events such as temperature and rainfall have a substantial impact on crop productivity. Temperature rises and precipitation changes have different effects depending on the crop, location, and magnitude of change in the factors. The rising temperatures reduces grain yield, while rising precipitation is likely to offset or reduce the impact of rising temperatures (Adams et al., 1998).

Effect of climate change on maize germination, emergence and initial growth

In Mexico, climate change can cause an increment of the average annual temperature from 1 to 4°C and changes in the average yearly precipitation from 0.4 to 1.4 times during the present century, in function of the scenario of the population growth (Allen et al., 2014). Climate change is a change in the state of the climate that can be identified (e.g. using statistical tests) by changes in the mean and/or the variability of its properties and that persists for an extended period, typically decades or longer. It refers to any change in climate over time, whether due to natural variability or as a result of human activity (Stocker, 2014).

Temperature and water supply are critical drivers for seed (initiation, break) and germination. Hence, global climate change is altering these environmental cues and will preclude, delay, or enhance the regeneration of seeds, as already documented in some cases. Along with compromised seedling emergence and vigor, shifts in germination phenology will influence population dynamics, and thus, species composition and diversity of communities (Walck et al., 2011). A scenario of rising temperatures, declining rainfall, increase in extreme weather events, and shifting pest and disease patterns will lead to more short-term crop failures and long-term production declines (Chauhan et al., 2014; Kang and Banga, 2013). The increase in temperature and the intensification of due to the consequence of climate change have brought negative effects in ecophysiological processes such as germination and establishment of seedlings (Aragón-Gastélum et al., 2017; Walck et al., 2011). Recent evidence shows that maize is relatively more sensitive to high temperature and water deficit stress during sensitive stages of gametogenesis, flowering, and early grain filling stages of crop development (Prasad et al., 2019). Water deficit stress reduced the rate of seed germination in maize crops (Anjorin et al., 2017); heat stress slows maize growth; germination and seedling emergence are particularly vulnerable (Farooq et al., 2009). In addition, in maize development, the seedling stage is widely regarded as the most vulnerable to water deficit stress (Li et al., 2015).

For seed germination and seedling establishment to physiological maturity, the right planting date is critical. Heat stress during germination is linked to a lower plant stand and density, as well as an impeded emergency (Buriro et al., 2011). Fluctuations in mean daily temperature (either it is maximum or minimum) disturb seed germination ability (Bewley and Black, 2013). The main cause of low plant yield owing to poor germination is high-temperature stress. According to Essemine et al. (2010); Joshi et al. (2007) and Nejad et al. (2017) the effects of high temperatures on several developmental stages, particularly seedling emergence in different crop genotypes and seedling establishing stages, rapid growth periods are all critical stress periods in maize. It has been demonstrated that when stress is applied to a maize plant, not only is the leaf area lowered, but also the growth rate and the emergence of each leaf is delayed.

Maize metabolomics under abiotic stress (heat and water deficit stress)

Genetic variability of maize is a resource for the world's population, and can be the basis for achieving food sovereignty in Mexico, especially to face the related effect of climate change (Preciado Ortiz and Montes Hernandez, 2011) . This due to in México, there are 59-64 local varieties which are fundamental for future genetic improvement efforts that could generate new, environmentally resilient varieties. However, maize is highly sensitive to environmental deficiencies such as the availability of water, salinity, which combined with the perceived temperature as stress represent limitations of the environment for this crop (Cramer et al., 2011; Kato et al., 2009).

Maize yield is frequently limited when suffered from the individual or the combined abiotic stresses and is expected to get worst in future climates. Increases in frequency and magnitude of water deficit stress and heat stresses are the prime abiotic constraints that cause considerable adverse effects on maize production (Hatfield et al., 2011; Lesk et al., 2016; Liu et al., 2020b; Liu et al., 2020c; van der Velde et al., 2010). As the climate continues to change drastically, it may be more difficult to obtain enough yields. Therefore, the continuing challenges of environmental stresses such as water deficit stress, extreme temperatures, frost and heavy metal pollution must be taken into account to increase maize production and to do sustainable maize production systems (Feng et al., 2020).

The water deficit response of maize from metabolomics methods have been studied in seeds, leaves and roots where most of the proteins detected are assigned to energy and carbohydrate metabolic processes (Benevenuto et al., 2017). In the xylem sap of maize, Alvarez et al. (2008) found changes in the hormone abscisic acid and cytokinin, also the presence of high concentrations of the aromatic cytokinin 6-benzylaminopurine, and several phenylpropanoid compounds as coumaric, caffeic and ferulic acids. In maize hybrid, Witt et al. (2012) found an increase in metabolite levels under water deficit stress, including changes in amino acids, sugars, sugar alcohols, and intermediates of the tricarboxylic acid (TCA) cycle. Also, water deficit stress induced an accumulation of simple sugars and polyunsaturated fatty acids and a decrease in amines, polyamines, dipeptides, sphingolipid, sterol, phenylpropanoid and dipeptide metabolites. In kernels of maize, water deficit stress resulted in the greater accumulation of reactive oxygen species (ROS) (Yang et al., 2018).

For heat stress, protein processing in endoplasmic reticulum pathways plays a central role. Elevated respiration, reduced photosynthetic rates, altered timing of the circadian clock, induction of protein unfolding, aggregation and degradation, loss of membrane integrity and acceleration of senescence are one of the consequences of heat stress effect on maize. When maize is exposed to high temperatures, the genes related to protein processing in endoplasmic reticulum pathway was significantly enriched, which mainly induce heat shock proteins expression. Those heat shock proteins were targets genes of heat stress responsive transcription factors, which participate in regulation when heat stress occurs (Hemantaranjan et al., 2014; Qian et al., 2019).

Plants respond to stress with a wide range of modifications that cause to changes at the morphological, cellular, physiological, biochemical, and molecular levels (Aprile et al., 2013; Lopes and Reynolds, 2010). Overall, protein phosphorylation plays a critical role in regulating many biological functions, including stress responses by signal transduction. Phosphorylation and dephosphorylation can switch many regulatory proteins and enzymes on and off, thus control a wide range of cellular processes and signal relays (Yang et al., 2010). On the other hand, (Hu et al., 2015) reported five kinases and three phosphatases under heat stress, three kinases and two phosphatases under water deficit stress, and three kinases and three phosphatases under combined heat and water deficit stress.

Maize the most important crop in Mexico: intercropping system (*milpa*) and climate change

The importance of maize in Mexico is summarized with the following expression in Spanish "*Sin Maíz, no hay país*" translated as "without maize, there is no country" mentioned by (Cuellar, 2010; Esteva and Marielle, 2003; Florescano, 1986; Hellin et al., 2013; Richard, 2012; Wallenius and Concheiro Bórquez, 2016). Mexico is the country with the greatest genetic diversity of maize in the world and is a genuine global reference for this grain. Since its domestication about 10,000 years ago in the middle of the Neovolcanic Axis, this grassland has an extraordinary cultural and productive value that constitutes an enormous responsibility, in the historical, geographical and in the field of research, to achieve better results and yields by taking care of soil and water and ensuring sustainable systems to ensure food capacity in general, and to achieve, in particular, self-sufficiency standards.

In México, the expected climate change, according to climate change scenarios will cause an increase of the temperature trends up to 2.0°C at mid-century (Qin et al., 2014). However according to a recent study in United States, Central America and the Caribbean, the mean annual temperature and precipitation with biases between −0.93 and 1.27 °C and −37.90 to 58.45%, respectively, for most of the region. In addition the annual precipitations will decrease by 10-40% over Central America and the Caribbean, especially over the monsoon region (Almazroui et al., 2021). The global climate will experience continued warming caused by past anthropogenic emissions as well as from additional future anthropogenic emissions and México is one of the area which will likely become drier (Maliva, 2021; Ramirez-Cabral et al., 2017).

The negative impact of the related effects of climate change on maize in México has been studied (Aguirre-Liguori et al., 2019; Dendooven et al., 2012; Díaz-Álvarez et al., 2020;

Diédhiou et al., 2021; Donatti et al., 2019; Eakin, 2000; Mercer et al., 2012; Ramirez-Cabral et al., 2017; Smale et al., 2001). Heat and water deficit stress have been also related to the effects of climate change in Mexico and will affect negatively maize germination (Castro-Nava et al., 2012; Reddy and Kakani, 2007), seedlings (Lizárraga-Paulín et al., 2011), growth and reproduction (Alam et al., 2017; Castro-Nava et al., 2012) and grain yield (Green et al., 2020; Ramirez-Cabral et al., 2017). A reduction in grain yield from 55 to 75% were reported under water deficit stress, also combined water deficit and heat stress significantly reduced the average number of days to anthesis and plant height of Mexican maize(Cairns et al., 2013). However, taking into account the potential of the Mexican territory with various climates in states such as SLP, the related effects of climate change have not been well studied, from maize germination to grain yield and his intercropped system.

Mexican farmers cultivate maize on rainfed fields on plots smaller than 5 ha, some of these farmers still grow their crop in a traditional system called "*Milpa*" in which several species or crops as bean (*Phaseolus vulgaris* L. and *Vigna unguiculata* (L) Walp.) and squash (*Cucurbita* spp) grow simultaneously (Heindorf et al., 2019; Mercer et al., 2012; Pérez-Hernández et al., 2021a). Indigenous peoples in Mesoamerica, particularly in the humid and temperate mountains, continue to rely on this system for subsistence (Boege, 2008; Toledo and Barrera-Bassols, 2008).

According to Kahneman (2011); Rogé et al. (2013) and Wilken (1990) smallholders adapt to climate variability through continuous crop management adaptation based on their personal experience and historical background. Their adaptive capacity is determined by a complex interaction of socioeconomic, cultural, and political factors, existing infrastructure, and climate change experience (Adger et al., 2009). For example, for centuries, *milpa* farming has been a sustainable and reliable source of food and livelihood for Maya *milpa* communities in southern Belize as farmers allow areas to regenerate to a mosaic of forest succession stages and crop diversity (Altieri and Toledo, 2011; Benıtez et al., 2014; Ford and Nigh, 2016).

However, due to climatic changes (i.e., droughts and water deficit, flooding, hurricanes, and temperature increases), forest loss, pests and crop diseases, soil degradation, as well as social factors such as poverty, population growth, land tenure, marginalization, and other factors, milpa farming or farmers has become less reliable and sustainable in the last 50 years. In addition, milpa farmers depend upon the ecosystem for their basic needs, whole communities are impacted from system change; thus, there are implications for community food and livelihood insecurity from climate change impacts (Drexler, 2020, 2021; Lozada, 2014). The impacts of climate change are expected to threaten the sustainability of social, economic, and ecological systems in the world. These farmers are the ones preserving maize diversity *in situ* and it should be made possible for them to attain enough yields from native maize varieties or genotypes. For that, it is important to better understand the mechanisms of maize under abiotic stress with the use of the new era omics sciences such as metabolomics with have good advantages to bring researchers news perspectives to face the negative effects of climate change on Mexican native maize and his intercropping system called *milpa*.

Justification

It is proposed that the temperature values in S.L.P. will increase from 0.75 to 1.00°C in the short term (2010-2040) and from 2.75 to 3.00°C in the long term (2070-2100) (Medellín-Milan et al., 2006; Ávalos Lozano et al., 2017). Also, the variation in the quantity of rain received in a month through the successive years is very big. Siller et al. (2009) and Jiménez and Mendoza (2019) have also indicated the presence of water deficit stress in the state of SLP. It is probable that such an increase in temperature promotes, or associate with a decrease in the quantity of rain, will impact in the availability of water in soil and it will generate modifications like changes in the agricultural calendar, phenological alterations, and decrease of yields. For example, it has been documented in Sinaloa in crop production of maize, bean (*Phaseolus vulgaris*), potato (*Solanum tuberosum*), red tomato (*Solanum lycopersicum*) among other affected by climatic variations (Ojeda-Bustamante et al., 2011). In the state of S.L.P. nearly 14,000 ha of maize are cultivated annually, of which a high proportion, around 80%, is cultivated under dry farming conditions also called rainfed agriculture (SIAP, 2017). Hence, the production of maize depends on the tolerance from the adapted genotypes of maize to variable and extreme conditions due to the climate characteristics. This fact can mean the existence of highly adaptable creole genotypes of maize to adverse environmental conditions, what means an opportunity of use of such phylogenetic resources. Most of the areas cultivated with *milpa* systems in Mexico and in S.L.P. in particular are facing critical conditions related to the effect of climate change, such as an increase in temperature.

The study of the results of creole genotypes of maize coming from different agroclimatic regions can help to determine and understand how the species of maize adapt to environmental conditions they face during their development and establishment, which is necessary to predict some of the effects related to climate change (Dávila et al., 2013). Also, the abundance of the breed and/or creole genotypes of maize and their adaptations to diverse environmental conditions could represent alternatives to cultivate in scenarios that are poised to occur due to effects related to climate change.

Furthermore, the use of plant metabolomics can further provide information on the response of maize and other crop species to abiotic stress. Also taking account that in México maize is the most important crop with several races. The progress of metabolomics research on maize responses to abiotic stresses such as heat, water deficit, and combined heat/water deficit stress can help to understand how each genotype and/or race of maize responds under stress conditions.

In addition, the need to understand the mechanism of defense of plants with the use of metabolomics as a newly developed discipline in which it is intended to address the unbiased study of all metabolites present in a tissue, organ or organism at a particular point in its development or under particular environmental conditions, thus enabling the assessment of the contribution of genetic and/or environmental factors to the modification of metabolism (Fiehn, 2001).

Hypothesis

When native genotypes of maize and his intercropping system (*milpa*) suited to specific local conditions are subjected to relevant effects of climate change, their metabolomics profiles, germination, emergence, initial growth and development, grain yield, and photosynthetic parameters respond differently according to their region of origin.

General Objective

To determine the physiological, metabolomic profiles, grain yield, and photosynthetic parameters of native genotypes of maize from three agroclimatic regions of San Luis Potosí and their intercropping system (*milpa*) under the related effect of climate change.

Specific objectives

1. To evaluate the germination and initial growth of creole genotypes of maize coming from different agroclimatic regions at different temperatures and levels of water deficit stress under laboratory conditions.

2. To provide a reference for research on the antistress mechanism of maize with a special focus on Mexican native maize, loading for strategies and future perspectives for the protection of native maize for its importance to Mexican smallholders "*campesinos*" and the negative impact of the related effect of climate change on the crop.

3. To determine the metabolomic profiles of native maize seedlings from warm-dry, temperate, and hot and humid climates of the state of San Luis Potosí (Mexico) grown in controlled environments related to some effects of climate change (temperature increase and water deficit stress) by gas chromatography/mass spectrometry (GC/MS) techniques.

4. To evaluate the emergence, initial growth and photosynthetic parameters of native maize genotypes coming from different climates and/or agro-ecological zones to the effect of induced passive heat.

5. To determine the effect of an increase in temperature on physiology, photosynthetic, and grain yield of three *milpa* systems from different climates of SLP.

Thesis structure

This thesis is divided into six chapters. Firstly, the state of San Luis Potosí (Mexico) was divided into three agro-ecological regions named *Altiplano* (warm-dry), *Media* (template) and *Huasteca* (hot and humid) climates. In each region, collected crops were used to determine our objectives. In Chapter I, germination and initial growth of maize native genotypes were experimented under heat and water deficit stress related to the effects of climate change in the state. The second chapter is a review of the literature on the metabolomics of maize plants under heat and water deficit stress, which is also an important focus for Mexico's most important crop under climate change. In Chapter III, the metabolomics of maize genotypes grown under the related effects of climate change were determined. In Chapter IV, the effect of induced passive heat on maize seedlings' growth, and photosynthetical capacity was related. In Chapter V, an experimental model with the use of an open top chamber in a management system of maize intercropped with bean and squash was stated, and from an early stage to grain yield, the physiological, photosynthetic, and yield parameters of the *milpa* system were determined under a warming effect. Finally, Chapter VI was exclusively dedicated to build a solid discussion, recommendations, constraints and future prospects of the study.

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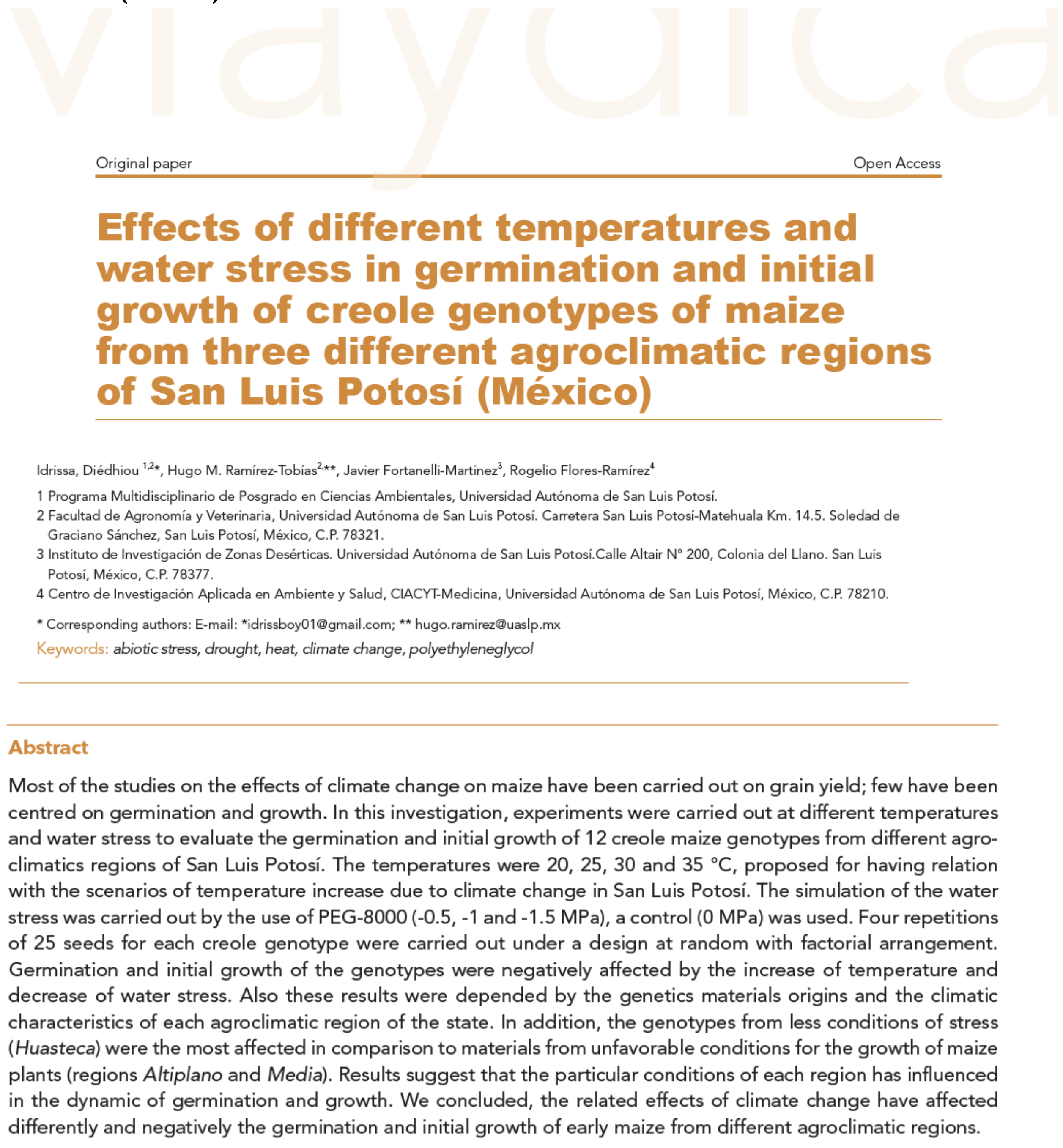
Chapter I: Effects of different temperatures and water stress on germination and initial growth of creole genotypes of maize from three different agroclimatic regions of San Luis Potosí (México)



Original paper Open Access

Effects of different temperatures and water stress in germination and initial growth of creole genotypes of maize from three different agroclimatic regions of San Luis Potosí (México)

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Keywords: *abiotic stress, drought, heat, climate change, polyethyleneglycol*

Abstract

Most of the studies on the effects of climate change on maize have been carried out on grain yield; few have been centred on germination and growth. In this investigation, experiments were carried out at different temperatures and water stress to evaluate the germination and initial growth of 12 creole maize genotypes from different agro-climatics regions of San Luis Potosí. The temperatures were 20, 25, 30 and 35 °C, proposed for having relation with the scenarios of temperature increase due to climate change in San Luis Potosí. The simulation of the water stress was carried out by the use of PEG-8000 (-0.5, -1 and -1.5 MPa), a control (0 MPa) was used. Four repetitions of 25 seeds for each creole genotype were carried out under a design at random with factorial arrangement. Germination and initial growth of the genotypes were negatively affected by the increase of temperature and decrease of water stress. Also these results were depended by the genetics materials origins and the climatic characteristics of each agroclimatic region of the state. In addition, the genotypes from less conditions of stress (*Huasteca*) were the most affected in comparison to materials from unfavorable conditions for the growth of maize plants (regions *Altiplano* and *Media*). Results suggest that the particular conditions of each region has influenced in the dynamic of germination and growth. We concluded, the related effects of climate change have affected differently and negatively the germination and initial growth of early maize from different agroclimatic regions.

Introduction

In Mexico, climate change can cause an increment of the average annual temperature from 1 to 4 °C and changes in the average yearly precipitation from 0.4 to 1.4 times during the present century, in function of the scenario of the population growth (IPCC, 2007). Climate change is a modification in the state of the climate that can be identified (e.g. using statistical tests) by changes in the mean and/or the variability of its properties and that persists for an extended period, typically decades or longer. It refers to any change in climate over time, whether due to natural variability or as a result of human activity (IPCC, 2013).

Temperature and water supply are critical drivers for seed (initiation, break) and germination. Hence, global climate change is altering these environmental cues and will preclude, delay, or enhance regeneration from seeds, as already documented in some cases. Along with compromised seedling emergence and vigour, shifts in germination phenology will influence population dynamics, and thus, species composition and diversity of communities (Walck *et al.*, 2011a). A scenario of rising temperatures, declining rainfall, increase in extreme weather conditions, and shifting pest and disease patterns will lead to more short-term crop failures and long-term production declines (Kang and Banga 2013; Chauhan *et al.* 2014). The increase in temperature and the intensification of droughts due to the consequence of climate change have brought negative effects in ecophysiological processes such as germination and establishment of seedlings (Walck *et al.*, 2011b; Aragon-Gastelumet *et al.*, 2017). Recent evidence shows that maize (*Zea mays* L.) is relatively more sensitive to high temperature and drought stress during sensitive stages of gametogenesis, flowering, and early grain filling stages of crop development (Prasad *et al.*, 2020).

Maize is the most important cereal cultivated in Mexico (FAO, 2018; García-Lara and Serna-Saldivar, 2019), and Mexico is considered the center of origin and domestication of maize and one of the most important centers in its diversity (Matsuoka *et al.*, 2002). The genetic variability of the maize constitutes a wealth for the population and it can be the base to achieve the domestic alimentary sovereignty, especially in the face of the changes in climate (Preciado Ortiz and Montes Hernandez, 2011). According to Cabrera *et al.* (2002), yields, like it has been documented in Sinaloa in crop production of maize, bean (*Phaseolus vulgaris*), potato (*Solanum tuberosum*), red tomato (*Solanum lycopersicum*) among others (Ojeda-Bustamante *et al.*, 2011). In the state of S.L.P. nearly 14,000 ha of maize are cultivated annually, of which a high proportion, around 80%, is cultivated under dry conditions (SIAP, 2017). Hence, the production of maize depends in great measure of the tolerance from the adapted genotypes of maize to conditions variables and many extreme times from the climate. This fact can mean the existence of highly adaptable creole genotypes of maize to adverse environmental conditions, what means an opportunity of use of such phylogenetic resources.

The study of the results of creole genotypes of maize cultivation and that use depends mainly on the type of agriculture; however, in the regions with typical rural agriculture 80 to 100% of the farmers use creole seed fundamentally for its production. However, their production is generally limited for a series of factors like drought, plagues and diseases among others that represent economic losses particularly for smallholder farmers (Bergvinson, 2004).

The state of San Luis Potosi (S.L.P.) has been considered as a potential source of genetic variation in maize. Fourteen variants of maize have been documented in a study (Ávila-Perches *et al.*, 2010a). The high abundanceof the maize variants in the state can be due to wide diversity of the surroundings, in way similar to what happens in the Mexican territory. This way, it is possible to recognize different agroecological regions, from the warm and humid climatic conditions to the dry and hot or temperate ones (INEGI, 2012). Nevertheless, it is probable that the abundance of the maize variants in the state are much bigger that consigned by Ávila-Perches *et al.* (2010b) because just in three towns of the *Huasteca*, a region that represent a fraction of the whole territory of S.L.P., 11 different variants were registered (Heindorf*et al.*, 2019).

It is proposed that the temperature values in S.L.P. will increase for a short-term scenario (2010-2040) and long term (2070-2100) (Medellín-Milan *et al.*, 2006; Ávalos Lozano *et al.*, 2017a). Also, the variation in the quantity of rain received in a month through the successive years is very big. Algara Siller *et al.* (2009) and Espinoza Jiménez & Gómez Mendoza (2019a) have also indicated the presence of drought in the state of S.L.P. It is probable that such an increase in temperature promotes, or associate with a decrease in the quantity of rain, will impact in the availability of water in soil and it will generate modifications like changes in the agricultural calendar, phenological alterations, and decrease of ne and understand how the species of maize adapt to environmental conditions they face during their development and establishment, which is necessary to predict some of the effects related to climate change in the abundance and distribution of species (Dávila *et al.*, 2013). Also, the abundance of the breed and/or creole genotypes of maize and their adaptations to diverse environmental conditions could represent alternatives to cultivate in scenarios that are poised to occur due to effects of climate change. The objective of this work was to evaluate the germination and initial growth of creole genotypes of maize coming from different agroclimaticregions at different temperatures and water stress (drought) under laboratory conditions. The above-mentioned, with the hypothesis that germination and initial growth of creole genotypes adapted to specific local conditions respond differently and in dependence of their origins when exposed to related effects of climate change.

Material and methods

Selection of creole genotypes of maize

The materials evaluated were collected in the state of S.L.P., in which, with basis on the mean annual of temperature and precipitation; three areas were identified whose average temperature and precipitation are around 14.5, 18.5 and 22.5 °C; 400, 700 and 1200 mm respectively (Noyola-Medrano *et al.*, 2009a). Such areas were denominated *Altiplano*, *Media* and *Huasteca* respectively, and some features are described (Figure 1 and Table 1). A total of 37 distributed samples were obtained in the following way: 10 from the region of *Altiplano*, 11 from *Media* and 16 from *Huasteca*.

The collected samples were assessed as established by Carballo & Benitez (2003). This way a total of 14 variables were described: longitude (cm), diameter (mm) and conicity of cob, number of rows per cob, number

Table 1. Denomination of evaluated genotypes, climatic characteristics and futures scenarios of temperature based on the mean annual temperatures (M.A.T.) of the three regions from the state of San Luis Potosí, México.

Genotypes	Region	Predominate climate based on modifications of the Köppen climate classification system and M.A.T.	Future mean annual temperature (M.A.T.) in short term (2010-2040) (M.A.T. + 0.75-1 °C)	Future mean annual temperature (M.A.T.) in long term (2070-2100 M.A.T. + 2.75-3.0 °C))
A3	*Altiplano*	BS1kw(e)gw" BSohw(e) gw"14.5 °C	15.25-15.5 °C	17.25-17.5 °C
A4				
A8				
A9				
A10				
M2	*Media*	Cb(w2)(w)(I') 18.5 °C	19.25-19.5 °C	21.25-21.5 °C
M4				
M11				
H4	*Huasteca*	(A)Cam(f)(e)w" Am(e)gw" 22.5 °C	23.25-23.5 °C	25.25-25.5 °C
H9				
H10				
H11				

References: García, 2004.IPCC, 2013b; Ávalos Lozano *et al.*, 2017b.

of grains per row, row arrangement, color and grain type, dry weight of 100 seeds (g), volume (mL) of 100 seeds in 50 mL, longitude (mm); thickness (mm) and wide (mm) of grain, phenological term (months). On the previous data were added,data on thermal and rainfall conditions facilitated by the producer. Such information was systematized with the following scale: low, regular and high.

With the objective of containing the samples in conglomerates (clusters) with high grade of internal homogeneity and external heterogeneity among the samples (Sanjinez and Julca, 2019), and to select representative samples from the all collected, a multivariate analysis was carried out to form groups. For

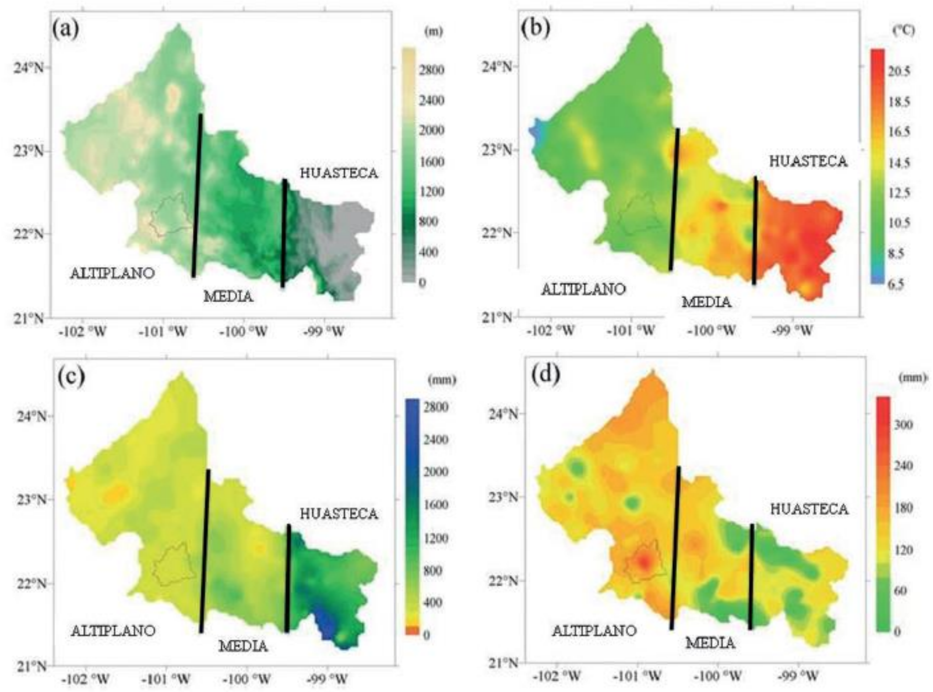


Figure 1. Horizontal distribution of (a) field elevation, (b) annual mean temperature, (c) annual mean precipitation, (d) annual mean evaporation of the three agroclimatics regions of the state of San Luis Potosí. Adapted from Noyola-Medrano et al. (2009b).

processing the statistical software Statistical Analysis System (SAS) 9 was used.The resulting groups of the cluster analysis used in this investigation were: white maize's of 5 months of life cycle (genotypes A3, A4 and A8), white maize of 3 months (genotype A9) and purple maize (genotype A10) of 4 months of the region of *Altiplano*; white maize of 4 months (genotype M2), purple maize of 3 months (genotype M4) and black maize of 3 months (genotype M11) of the region of *Media*, white maize's of 4 and 3 months (genotypes H4 and H11 respectively) and yellow maize's of 3 months (genotypes H9 and H10) of the region of *Huasteca*.

(Wescor, Logan, UT, USA). Samples of the solutions were taken approximately 2 mL and were placed in plastic trays in circular way 40 mm of diameter by 12 mm deep. The measurements obtained allowed to verify the levels of the wanted potentials.

Experimental Design

The experiment included a total of 192 treatments that resulted to a factorial arrangement of 4 x 4 x 12, with four repetitions. The temperature factor with four levels (20, 25, 30 and 35 °C), water stress with four levels (0, -0.5, -1 and -1.5 MPa) and the last factor represented by the 12 creole genotypes. Each experimental unit

Treatments of temperature and simulation of water stress

Germination experiments were conducted in controlled conditions of constant temperature (20, 25, 30 and 35 °C) and water potential [0 (control), -0.5, -1.0, and -1.5 MPa]. The temperatures were proposed for having relationship with scenarios of increase temperature due to effects of climate change (Figure 1 and Table 1). The conditions of soil humidity were determined at different levels of water potential since a very big variation in the quantity of rain received in a month through the successive years is expected (Espinoza-Jimenez and Gómez-Mendoza, 2019b).

The simulation of water deficit in the substrates was carried out with polyethyleneglycol 8000 (PEG-8000) as solution, with the purpose of simulating variations in the availability of soil humidity (Villalobos and Peláez, 2001; Huang *et al.*, 2018). This solution was used because it has been documented that it doesn't present toxicity on seeds (Khalil *et al.*, 2001). A control was also used with water potential of 0 MPa from deionized water.

To know the quantity of necessary PEG-8000 to obtain the potential water desired, the formula proposed by Burlyn (1983) was used:

$$\mathrm{PEG} = \frac{4- (5.16\,\varphi\, T - 560\,\varphi + 16)^{0.5}}{(2.58T - 280)}$$

Where:

PEG: Kg of PEG per liter of deionized water

φ: Required water potential in bars (1 bar= 0.1 MPa)

T: Temperature of prepared solution

The three water potentials (-0.5, -1 and -1.5 MPa) were obtained by mixing deionized water and 145, 290 and 400 g L^{-1} of PEG-8000 respectively. Water potential of each solution was measured in psychometric chambers consisted of 25 seeds for creole genotype and the experimental units were distributed at random in a design of complete blocks.

Before sowing, the seeds were disinfected submerging them during 3 min in a solution of commercial chlorine (hypochlorite of sodium to 10%) (Viloria and Méndez Natera, 2011) and were then washed with abundant water to eliminate the excess of chlorine. Later on, the seeds were placed on filter paper, previously humidified with the solution of corresponding PEG, inside a plastic tray of 14 cm of long, 18 cm of wide and 8 cm of height. At once, the seeds were placed under predefined temperatures inside a chamber for plant growth at a neuter photoperiod of 12 hours light with the different levels of water potential.

Germination variables

Percentage of germination (PG)

A germinated seed is considered as one which has a root length of more than or equal to 2 mm. PG was calculated using the following formula (Scott *et al.*, 1983):

$$PG = \frac{(\text{Number of germinated seeds})}{(\text{Number of seeds sowed})} \times 100$$

It was determined at 15 days after sowing, instead of the seven days indicated by the International Seed Testing Association (ISTA) methodology. Other investigators have evaluated the germination of maize at 12 days (Laynez-Garsaballet *al.*, 2007a), at 13, 14 and 15 days (Zagal-Tranquilino *et al.*, 2015), and at 16 days (Badr *et al.*, 2020).

Mean germination time (MGT)

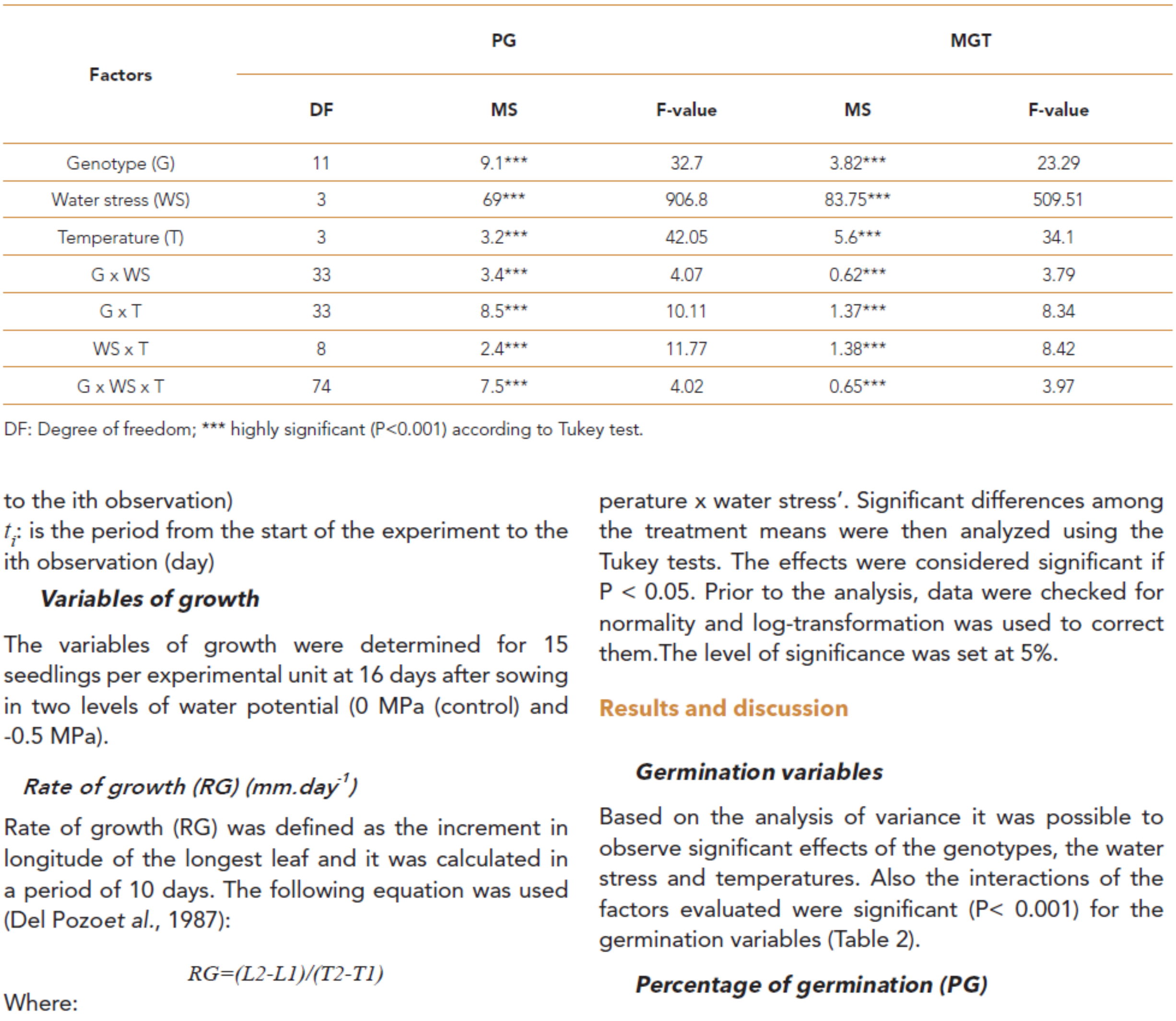
It was determined according to the formula (Labouriau, 1983) at 15 days after sowing:

$$MGT= (\Sigma n_i t_i)/\Sigma n_i$$

Where:

n_i: is the number of seeds germinated at day i (not the accumulated number, but the number corresponding

Table 2. Mean squares (MS) from the analysis of variance of the percentage of germination (PG) and the mean germination time (MGT) of creole genotypes of maize from the state of San Luis Potosi at 15 days after sowing.



Factors		PG		MGT	
	DF	MS	F-value	MS	F-value
Genotype (G)	11	9.1***	32.7	3.82***	23.29
Water stress (WS)	3	69***	906.8	83.75***	509.51
Temperature (T)	3	3.2***	42.05	5.6***	34.1
G x WS	33	3.4***	4.07	0.62***	3.79
G x T	33	8.5***	10.11	1.37***	8.34
WS x T	8	2.4***	11.77	1.38***	8.42
G x WS x T	74	7.5***	4.02	0.65***	3.97

DF: Degree of freedom; *** highly significant (P<0.001) according to Tukey test.

to the ith observation)

t_i: is the period from the start of the experiment to the ith observation (day)

Variables of growth

The variables of growth were determined for 15 seedlings per experimental unit at 16 days after sowing in two levels of water potential (0 MPa (control) and -0.5 MPa).

Rate of growth (RG) (mm.day^{-1})

Rate of growth (RG) was defined as the increment in longitude of the longest leaf and it was calculated in a period of 10 days. The following equation was used (Del Pozoet *al*., 1987):

$$RG=(L2-L1)/(T2-T1)$$

Where:

perature x water stress'. Significant differences among the treatment means were then analyzed using the Tukey tests. The effects were considered significant if P < 0.05. Prior to the analysis, data were checked for normality and log-transformation was used to correct them.The level of significance was set at 5%.

Results and discussion

Germination variables

Based on the analysis of variance it was possible to observe significant effects of the genotypes, the water stress and temperatures. Also the interactions of the factors evaluated were significant (P< 0.001) for the germination variables (Table 2).

Percentage of germination (PG)

L1 and *L2* are the longitudes of the seedlings at 5 and 15 days respectively while *T1* and *T2* are the previously mentioned times.

Root length (RL) (cm)

Root length (RL) was determined with a rule graduated in cm starting from the root of major longitude.

Dry weight of shoots (DWS) and root (DWR) (g)

The samples were weighed, then dried off in stove at 70°C during 72 hours (Laynez-Garsaball *et al.*, 2007b) and weighed in an analytic balance (Ohaus Compass™).

Statistical analysis

The data were submitted to an analysis of variance, using the procedure PROC GLM of the program Statistical Analysis System (SAS, 2003). The model consists of three fixed factors,'genotypes', 'temperatures' and 'water stress' and their interaction 'genotype x tem-

The percentages of germination (PG) tend to reduce as water potential decreased; however, diminishing of PG varied depending on the creole genotypes and the temperatures (Table 2). At 0 MPa, the PG of genotypes from *Huasteca* was more affected by temperature variation than those from *Altiplano* and *Media*. The best germination percentages, with values highest than 96%, were registered in principally in genotypes from *Altiplano* and *Media*, even if genotypes A4 and A10 registered a reduced PG at 25 °C and 35 °C. The PG of the genotypes from *Huasteca* resulted highly reduced by variation of temperature in H4, H10 and H11 but in different way. In H4, 20-30 °C temperatures averaged a PG of 87% but it dropped to 13% at 35 °C, in H10 a gradual reduction of PG from 100% to 5% was registered along temperature increased. The PG of H11 was less than the half of all other genotypes (Figure 2a).

The temperatures promoted differentials reactions of PG in the water potential of -0.5 MPa. The genotypes

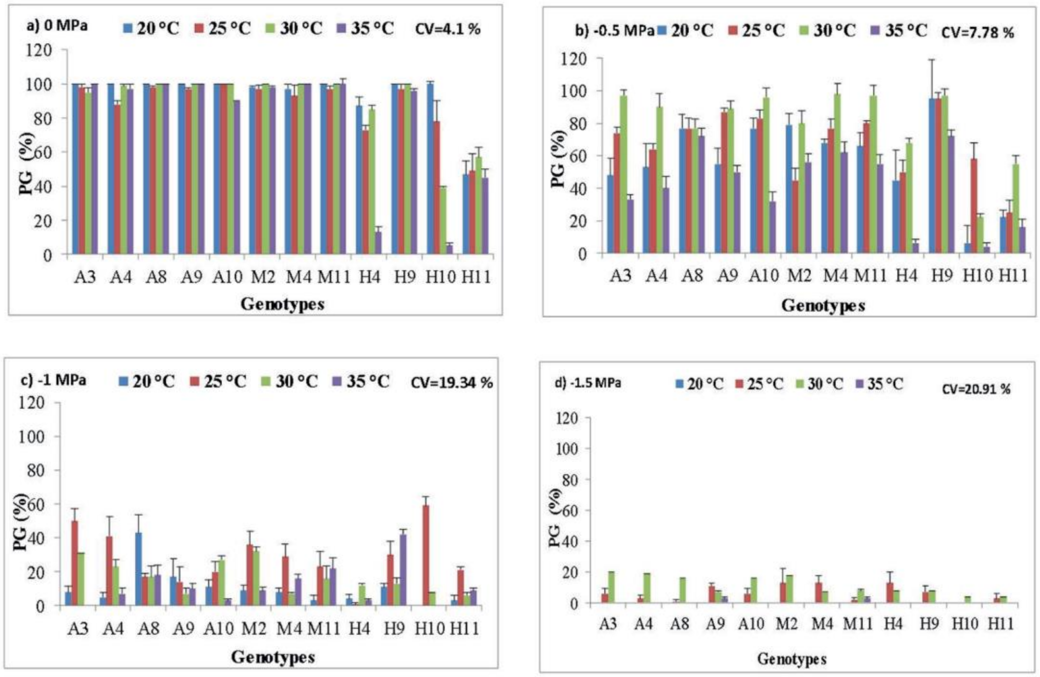


Figure 2. Effect of different water potentials (0, -0.5, -1 and -1.5 MPa) and temperatures (20, 25, 30 and 35 °C) in the percentage of germination (PG) of creole genotypes of maize from different regions of the state of San Luis Potosi. A: *Altiplano*, M: *Media*, H: *Huasteca*. The vertical bars indicate the standard error (n=4).

from *Altiplano*, *media* and H9 presented the highest PG at 25 and 30 °C. At 35 °C, the same genotypes reduced up to more than 50% their PG. The PG of the genotypes from *Huasteca* resulted highly influenced by variation of temperature in H4, H10 and H11. H4 and H11 registered an increment of PG between 20 and 30 °C but drastically reduced at 35 °C until 6% and 16% respectively. However H10 registered an average of 10.6% at 20, 25 and 35 °C while at 25 °C had the best PG with 58% (Figure 2b).

At -1 MPa, the PG of the creole genotypes of the *Media* was highly affected by the temperature factor while for those from *Altiplano* and *Huasteca* responded differently for temperature variation. In the same way, the creole genotypes from the *Media* registered the best PG at 25 °C with an average of 29% however those values decreased at the maximum temperature (35 °C) until 18%. For those from the *Altiplano* A3 and A4 registered the best values at 25 °C with an average of 46% while for the creole A8, A9 and A10 the best PG varied for each temperature. In addition the creole genotypes of the *Huasteca* were the most affected, specifically H4 and H11. However H9 and H10 responded differently by the variation of temperature. For that H9 registered best PG at 25 and 35 °C with 30 and 42% respectively (Figure 2c).

In a more extreme water stress (-1.5 MPa), germination was registered in all materials only at 30 °C although it was not more than 20%. At 25 °C, all of the materials germinated although all below 15%. At 20 °C none of the genotypes germinated. At 35 °C, only the creole genotypes A9 and M11 registered a PG value of 3%, all the other materials did not register any germination (Figure 2d).

The germination response of creole genotypes of maize seeds was significantly affected by drought stress induced by PEG solutions and temperature. These findings extend those of Queiroz *et al.* (2019a) and Pawar *et al.* (2020), confirming that a water potential in a negative gradient tends to reduce the PG of maize seeds. In addition, the results noted in our study were related to temperature and creole genotypes. This study therefore indicates that creole genotypes from different regions responded differently for temperature; results were more accentuated at -1 and -1.5 MPa. Ramírez-Tobias *et al.* (2014) found that the germination of Agave species seeds decreased on dependence of species by up to 50% when water potential drops to -1.5 MPa. For the extreme stress (-1.5 MPa) at 20 °C, the maize creole genotypes did not germinate. Fancelli and Dourado-Neto (2000) stated that the temperature suitable for the germination of maize varies between 25 and 30 °C. Sans& Santana (2005) reported germination of maize may not occur at temperatures higher than 40 °C or near to 10 °C. Also, Borba *et al.* (1995) and dos Santos *et al.* (2019) reported that temperatures above 35 °C cause a significant decline in germination percentage of maize.

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Heat and water stress response in early maize 7

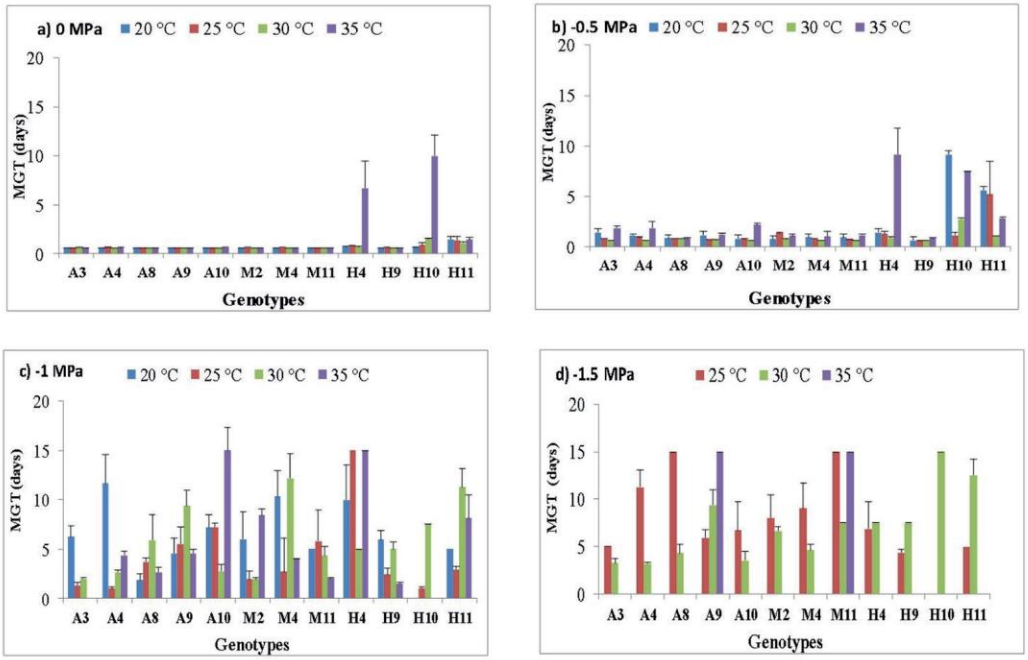


Figure 3. Effect of different water potentials (0, -0.5, -1 and -1.5 MPa) and temperatures (20, 25, 30 and 35 °C) in the mean germination time (MGT) of the creole genotypes of maize from different regions of the state of San Luis Potosi. A: *Altiplano*; M: *Media*, H: *Huasteca*. MGT at 20 ºC in d) did not exist because the creole genotypes did not germinate at this temperature and water potential (-1.5 MPa). Vertical bars show the standard error (n=4).

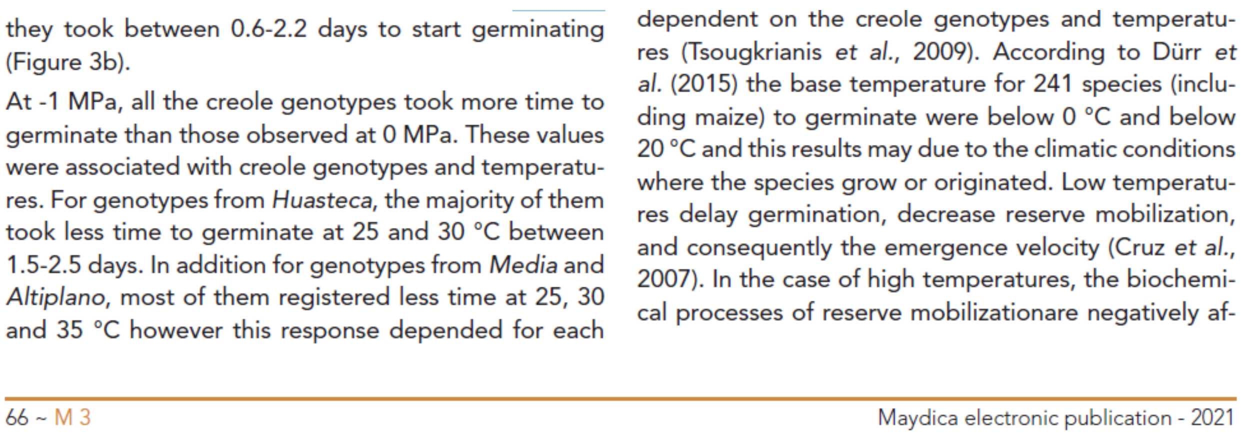
Mean germination time (MGT)

The number of days for seeds to germinate increased when the water potential decreased; however, increment of the number of days for seed to germinate varied depending on the genotypes and temperatures. The genotypes from *Huasteca*, specifically H4 and H9, took more time to germinate at 35 °C and 0 MPa. In addition, all the others creole genotypes from *Altiplano* and *Media* took between 0.6 to 1.5 days to start germinating independently for the temperature (Figure 3a).

At water potential -0.5 MPa, the MGT varied by the creole genotypes and temperatures as in 0MPa. In the same way, the most affected creole genotypes were from *Huasteca* but at 20, 25 and 35 °C. The maximum time to start germination was between 9.2-5.2 days. However the genotypes from *Altiplano* and *Media* responded equals no matter the temperature. Besides, genotype and took between 1.9-4.3 and 1.3-4.6 days respectively (Figure 3c).

At -1.5 MPa, the MGT varied depending creole genotypes and temperatures. Also they took more time to germinate in comparison to 0, -0.5 and -1 MPa. The genotypes did not germinate at 20 °C. In addition, all the genotypes from *Altiplano* and *Media* took less time to start germination at 30 °C with an average of 5-6 days while genotypes from *Huasteca* registered the less MGT at 25 °C with an average of 5 days (Figure 3d).

Our results reveal more negative is the water potential, longer it takes for the creole genotypes to germinate. This variable is important since it explains the time it takes for seeds to germinate after being embedded and thus take advantage of the short periods of rain, especially in arid and semi-arid areas (De la Barrera and Nobel, 2003). The results confirmed that the MGT



they took between 0.6-2.2 days to start germinating (Figure 3b).

At -1 MPa, all the creole genotypes took more time to germinate than those observed at 0 MPa. These values were associated with creole genotypes and temperatures. For genotypes from *Huasteca*, the majority of them took less time to germinate at 25 and 30 °C between 1.5-2.5 days. In addition for genotypes from *Media* and *Altiplano*, most of them registered less time at 25, 30 and 35 °C however this response depended for each dependent on the creole genotypes and temperatures (Tsougkrianis *et al.*, 2009). According to Dürr *et al.* (2015) the base temperature for 241 species (including maize) to germinate were below 0 °C and below 20 °C and this results may due to the climatic conditions where the species grow or originated. Low temperatures delay germination, decrease reserve mobilization, and consequently the emergence velocity (Cruz *et al.*, 2007). In the case of high temperatures, the biochemical processes of reserve mobilizationare negatively af-

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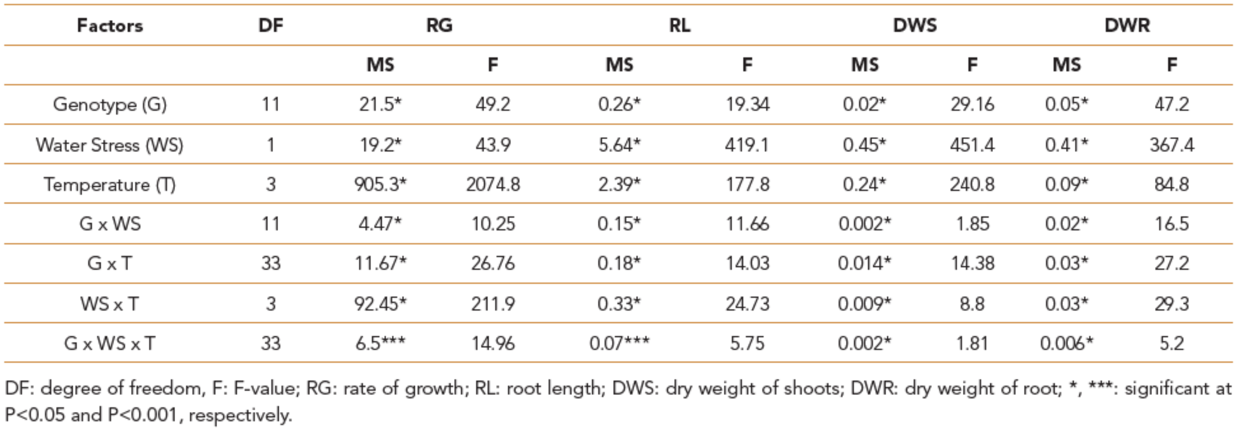
Table 3. Means squares (MS) from the analysis of variance of the growth variables of the creole genotypes of maize from the state of San Luis Potosi at 16 days after germination.



Factors	DF	RG		RL		DWS		DWR	
		MS	F	MS	F	MS	F	MS	F
Genotype (G)	11	21.5*	49.2	0.26*	19.34	0.02*	29.16	0.05*	47.2
Water Stress (WS)	1	19.2*	43.9	5.64*	419.1	0.45*	451.4	0.41*	367.4
Temperature (T)	3	905.3*	2074.8	2.39*	177.8	0.24*	240.8	0.09*	84.8
G x WS	11	4.47*	10.25	0.15*	11.66	0.002*	1.85	0.02*	16.5
G x T	33	11.67*	26.76	0.18*	14.03	0.014*	14.38	0.03*	27.2
WS x T	3	92.45*	211.9	0.33*	24.73	0.009*	8.8	0.03*	29.3
G x WS x T	33	6.5***	14.96	0.07***	5.75	0.002*	1.81	0.006*	5.2

DF: degree of freedom, F: F-value; RG: rate of growth; RL: root length; DWS: dry weight of shoots; DWR: dry weight of root; *, ***: significant at $P<0.05$ and $P<0.001$, respectively.

fected, due to low water availability. In addition, it may alter the constitution of cell membranes, affecting metabolic processes, especially cellular respiration (Taiz & Zeiger, 2004). For the factor water stress, Campos *et al.* (2020) recorded in succulents (*Agave lechuguilla* Torr. And *Agave salmiana* Otto ex Salm-Dyck) the time to reach maximum germination increases at more negative water potential. For corn germination in water stress conditions, the germination speed index expressed in seeds.day^{-1} decreases as the water potential decreases (Khatami *et al.* 2015; Santos *et al.,* 2016).

Variables of growth

The results of the analysis of variance showed significant effects (P < 0.05) for the main effects of creole genotypes, water potential levels and temperature, as well as significant interactions, for the variables evaluated. The significant interaction between the main effects of the factors (genotypes, water stress and temperature) indicates that genotypes have a distinct response when exposed to different drought levels and temperature (Table 3).

Rate of growth (RG)

High variation of the RG was registered among combination of temperatures, genotypes and water potential; however, tendencies due to reduction of water potential and temperature change were observed. Reduction of water potential promotes different patterns of RG values as temperature changed and a reduction of average RG. The RG of creole genotypes was drastically reduced with the decrease of water potential level from 0 to -0.5 MPa, in average of 30% respect to that obtained at 0 MPa. Maximum values of rate of growth (RG) were observed at 20 and 30 °C for all of the genotypes at 0 MPa and for genotypes from *Media* and *Huasteca* at -0.5 MPa. However, on genotypes from *Altiplano*, the maximum RG values only occurred at 30 °C. These maximum RG values doubled those registered at 25 and 35 °C (Figure 4). Then the seedlings growth velocity depended on the temperature and the origin of the genotypes.

According to Espinosa *et al.* (2015) the first process affected by the effect of water deficit is growth, which

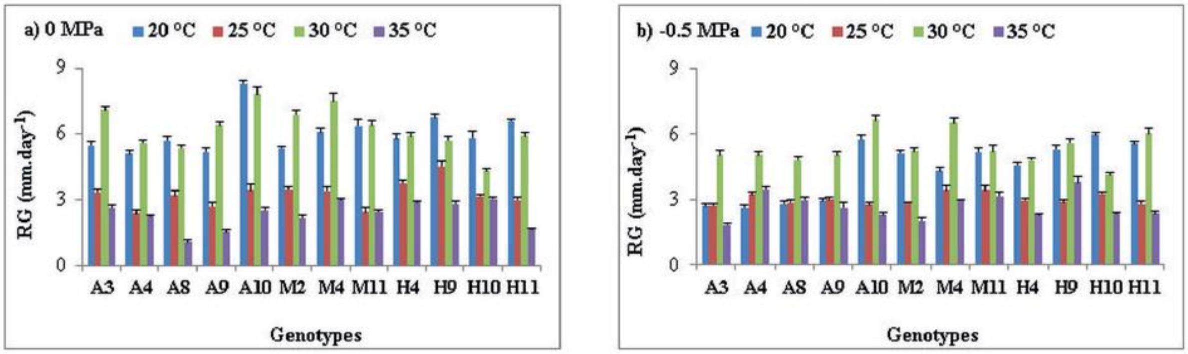


Figure 4. Effect of different water potentials (0 and -0.5 MPa) and temperatures (20, 25, 30 and 35 °C) on the rate growth (RG) of creole genotypes of maize from different regions of the state of San Luis Potosí. A: *Altiplano*; M: *Media*, H: *Huasteca*. Vertical bars indicate the standard error (n= 15).

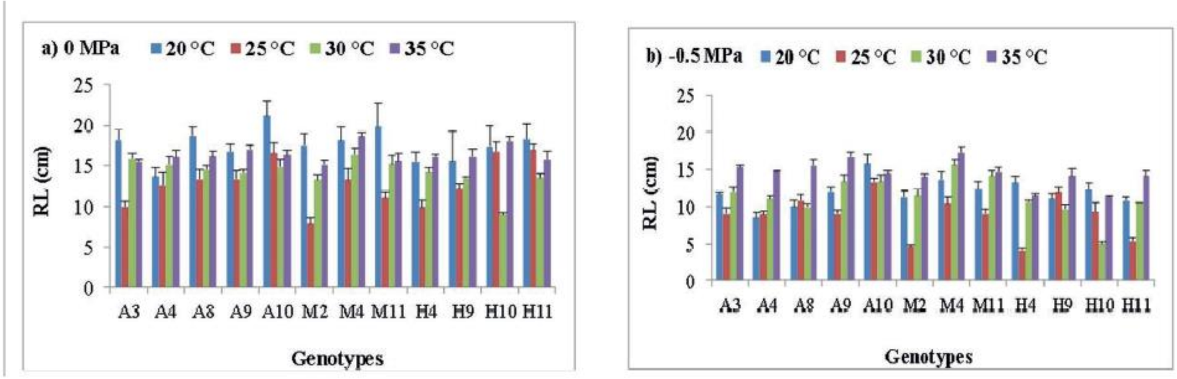


Figure 5. Effect of different water potentials (0 and -0.5 MPa) and temperatures (20, 25, 30 and 35 °C) on the root length (RL) of creole genotypes of maize from different regions of the state of San Luis Potosí. A: *Altiplano*; M: *Media*, H: *Huasteca*. Vertical bars indicate the standard error (n= 15).

begins with the germination, which comprises the imbibition, metabolism and growth start phases of the structures found in the embryo. Heat stress (27-35 °C during 14 days for maize (Virdi, 2016)) can induce irreversible damage to crop growth and yield (Fahad *et al.*, 2017). It was found that a combination of drought and heat stress had a significant detriment effect on the growth in two contrasting maize landraces (Castro-Nava *et al.*, 2014). Seedlings that emerge more quickly have higher time to develop compared to those that germinate later, and may have increased in seedling length (Queiroz *et al.*, 2019b). Our results agree with this seedling growth dynamic because less growth was registered in germinated seedlings under water stress and high temperature (35 °C). Also at 25 °C the creole genotypes reduced their RG no matter the water potential and this effect can be associated to the temperatures that they are adapted during the initial growth contrary to the recommended temperature for corn growth as indicated Sun *et al.* (2017).

Root length (RL)

The root length of the maize genotypes was significantly affected by the combination of different temperatures and drought stress. That response presented differences depending on precedence of the creole genotypes. All the creole genotypes registered their maximum values of RL at 20 and 35 °C, but a fall of 21% at 25 and 30 °C in 0 MPa (Figure 5a). The minimum values of RL were observed in genotypes from *Altiplano* and *Media* in the two water potentials at 25 °C however for some genotypes from *Huasteca* the minimum RL moved at 30 °C. Reduction of water potential from 0 to -0.5 MPa decreased average RL to 35%. At -0.5 MPa, the RL at 20 °C tended to go down respect to 0 MPa (Figure 5b).

Trachsel *et al.* (2010) found that high temperature reduced RL of tropical maize seedlings. Similarly, Seiler *et al.* (1998) showed that increasing the root-zone temperature for sunflowers in growth pouches from 25 to 35 °C largely reduced length of the primary and lateral roots as well as the number of lateral roots. An increase in root-zone temperature from 22 to 38 °C for wheat grown hydroponically reduced the overall root length by 40

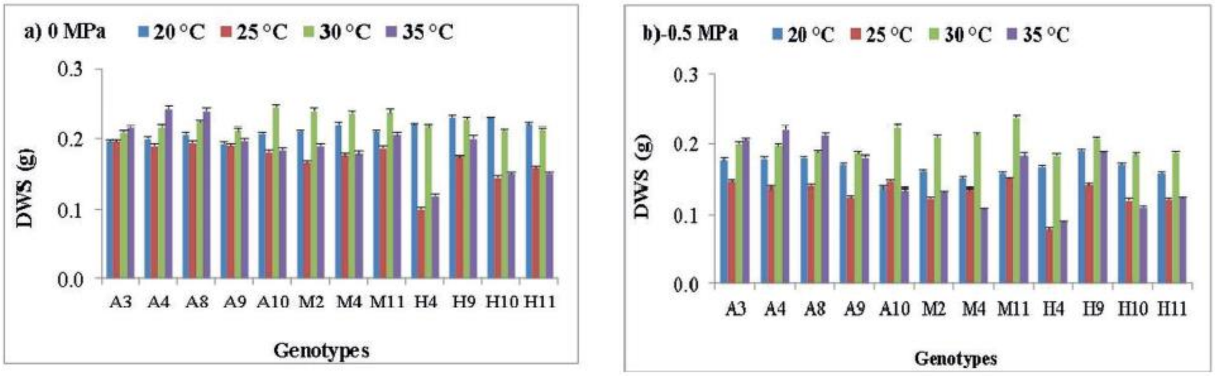


Figure 6. Effect of different water potentials (0 and -0.5 MPa) and temperatures (20, 25, 30 and 35 °C) on dry weight of shoots (DWS) of creole genotypes of maize from different regions of the state of San Luis Potosí. A: *Altiplano*; M: *Media*, H: *Huasteca*. Vertical bars indicate the standard error (n= 15).

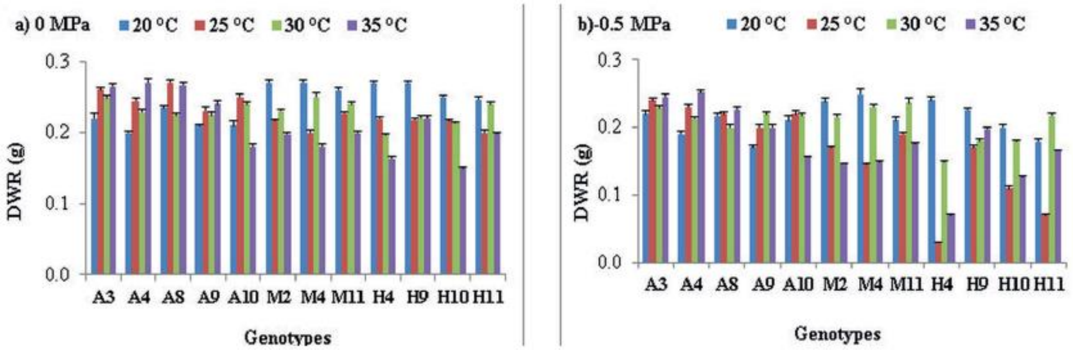


Figure 7. Effect of different water potentials (0 and -0.5 MPa) and temperatures (20, 25, 30 and 35 °C) on dry weight of roots (DWR) of creole genotypes of maize from different regions of the state of San Luis Potosí. A: *Altiplano*; M: *Media*, H: *Huasteca*. Vertical bars indicate the standard error (n= 15).

to 60% depending on the level of tolerance of the evaluated genotypes (Tahir *et al.*, 2008). Radhouane (2007) recorded a significant decrease in root length at -2 MPa with a reduction of more than 88% from Tunisian autochthonous pearl millet (*Pennisetum glaucum* (L.) R. Br.). Ren *et al.* (2020) showed that growth variables (root length, seedling, fresh weights of the root and aerial part decreased significantly under saline stress conditions in corn. Our results did not agree with this seedling growth dynamic where, in the combination of the abiotic factors, more growth of the RL was registered in germinated seedlings under water stress and at higher temperature (35 °C) in most of the genotypes. These results explain that genotypes with more roots at seedling stage subsequently developed stronger root system for the combination of the abiotic factors (high temperature and water stress), produced more biomass and had higher values for most characters determining seed yield (Bocev, 1963). However they decreased their RL in respect to control conditions.

Dry weight of shoots and roots

The DWS under control water potential (0 MPa) showed different responses of the genotypes for each temperature and agroclimatic region. In most of the genotypes from *Altiplano*, it was observed that the maximum values were found at 30 and 35 °C while 20 °C normally had low DWS (in average 80% respect to maximum values). A10 response was different, the temperatures 25 and 35 °C were not the ideal for his growth because it was significantly affected and their DWS decreased. Seedlings from *Media* and *Huasteca* registered their best DWS at 20 and 30 °C and their minimum ones at 25 and 35 °C; minimums were22% and 32% reduced respect to the maximum values (Figure 6a).

The DWS of the genotypes was reduced with the decrease ofwater potential level but responses varied with genotypes. The genotypes from *Altiplano* (A3, A4, A8 and A9) registered their maximum values at 30 and 35 °C while A10 only at 30 °C. A3, A4, A8 and A9 reduced drastically their DWS at 25 °C under water stress where they lost until 30% in comparison to 0 MPa. All the genotypes from *Media* obtained their maximum values at 30 °C, with 36% respect to those at 20, 25 and 35 °C. The genotypes from *Huasteca* registered their maximum values of DWS at 20 and 30 °C with 33% more weight for those found at 25 and 35 °C (Figure 6b).

As temperature increased, a slighted and discontinuous trend of DWR to increase was perceived in most of genotypes from *Altiplano* while in genotypes from *Media* and *Huasteca* the tendency was opposite and the water potential variation changed the trend (Figure 7). At 0MPa, most of the genotypes from *Altiplano* (A3, A4, A8 and A9) obtained their maximum values at 25 and 35 °C with 15% more to those registered at 20 and 30 °C. Also, genotypes from *Media* and *Huasteca* registered their best values at 20 °C but it was observed a decrease of 33% of their values with the increase of temperature (Figure 7a).

At -0.5 MPa, a reduction of the DWR occurred respect to 0 MPa. The genotypes from *Altiplano* delayed at least 10% of the weight at -0.5 MPa. Genotypes from *Media* were the most affected in the combination of 25 and 35 °C with -0.5 MPa. All the genotypes from *Media* significantly decreased their DWR and delayed at least 15% respect to 20 and 30 °C. Genotypes from *Huasteca* responded differently for each temperature at -0.5 MPa, they registered the maximum weight at 20°C but decreased up to 35% of their weight respect to 25, 30 and 35 °C. For *Huasteca* genotypes, the increase of the temperature reduced the DWR on H4 and H10 but increased on H9 and an absence of tendency was registered on H11 (Figure 7b).

In our investigation, the combination of each temperature (20, 25, 30 and 35 °C) with -0.5 MPa decreased the dry weights of the shoots and roots in most of the creole genotypes except in some from *Altiplano* (A3 and A10 at 20 °C, A9 and M11 at 30 °C). Ashagre *et al.* (2014) found different results in the evaluation of highland maize cultivars under moisture stress at germination and seedling growth stages, they registered statistically higher values with the use of PEG-6000 (60, 120 and 180 mg. L^{-1}) for the variables shoot and root dry weight. Farsiani & Ghobadi (2009), Khayatnezhad *et al.* (2010), Bibi *et al.* (2012), Radic *et al.* (2019), reported that drought drastically affected the fresh and dry weights of seedlings and roots in cultivars of sorghum, wheat, corn and sunflowers. These results agree with ours in the combination 20, 25 °C and water stress levels. However not in temperatures 30 and 35 °C; where creole genotypes A9 (at 30 °C), A8 and A9 (at 35 °C) were statistically equals. Toscano *et al.* (2017) recorded similar results in three sunflower cultivars at different water potentials (0, -0.15, -0.3, -0.45 and -0.65 MPa) at 20 °C. They found a significant decrease in root length, seedling length, fresh and dry seedling weights at the most negative water potential. Significant losses of germination and accumulation of dry matter were reported when using potentials of -0.5 MPa in creole of corn and beans (Aguilar-Benítez *et al.*, 2014).

In most of the evaluated variables, the creole genotypes from *Huasteca* were the most affected and that results can be related to the particular conditions different to *Altiplano* and *Media* where they were collected. The region of *Huasteca* is the one with higher mean annual temperature and rainfall in comparison to *Altiplano* and *Media* (Figure 1); then their genetics materials are already adapted to no stress conditions. Then, these results can be associated to their local conditions where they grow with less stress in respect to those from the others regions of the state (Jiang *et al.*, 1999). In addition, according to Mercer *et al.* (2008), maize landraces from tropical temperate conditions do not tolerate warmer climates due to local adaptation. In the state of San Luis Potosí, the sowing date of maize corresponds to the dates from May 15 to July 10 for *Altiplano*, May 15 to July 15 for *Media* while for the king account rainfall, photoperiod and the most significantly temperature of their local adaptations or origins. These results have important implications for thinking about the effect of climate change adaptation of maize in the country because they indicated the way to take for contrasting the negative effects of climate change taking account the local conditions. Most notably, this is the first study to our knowledge to investigate effects of the increase of temperature and drought in creole genotypes of maize in San Luis Potosí taking account the three agroclimatics regions.

With the combination of the heat and water stress, the results obtained were null or below 20% for PG. The MGT was delayed by the lower osmotic potential and the different temperature while for the growth variables most of them decreased under water stress conditions and depended to temperatures. However at high temperature and water stress (35 °C/-0.5 MPa) the results decreased compared at 20, 25 and 30 °C.

Additionally, it has been documented that the effects of climate change will affect the grain yield of corn crops (Mina *et al.*, 2012; Guerrero-Jiménez, 2016; Yang *et al.*, 2017; Amouzou *et al.*, 2019; Martins *et al.*, 2019; Chen & Pang, 2020; Ureta *et al.*, 2020); in this work, some of the effects related to climate change (drought and high temperatures) drastically affected the germination and initial growth of creole genotypes of maize from the state of S.L.P. under laboratory conditions. Then in this work, it has documented how the increase of temperature and the decrease of precipitation will affect negatively the germination and initial growth of creole genotypes from different agroclimatic regions. Besides the local particular conditions of each agroclimatic region has influenced the dynamic of germination and growth of the creole genotypes. Also, the materials were selected based on successful results from different environments, with different levels of water and thermal stress. Therefore, materials from less stressed

Huasteca it is from May 15 to 31 of July. On those dates, less monthly evapotranspiration, more cloudiness, more monthly average temperature and therefore more intensity in terms of the amount of water received in 24 hours in the *Huasteca* were recorded compared to the two others agroclimatics regions of the state. These environmental characteristics explain some of the responses obtained from the creole genotypes.

Similarly, maize is planted throughout Mexico, from very warm and humid climates at sea level to temperate and dry in the central plateau (equivalent to *Altiplano*). Distinct races and or genotypes of maize have been associated with particular environmental conditions since they were first classified (Wellhaussen *et al.*, 1952). Corral *et al.* (2008) classified Mexican maize ta-

areas (in this case *Huasteca*) will be less resilient to the related effect of climate change.

Conclusions

The germination and initial growth of creole genotypes of maize coming from different agroclimatic regions were drastically affected by the increase of temperature and drought. The creole genotypes from the region with more high mean annual temperature and precipitation (*Huasteca*) were the most affected and this is associated to the local conditions adaptations of their genetic material with less conditions of stress in comparison to the materials from *Altiplano* and *Media*, regions of unfavorable conditions are associated with stress for the combination of less mean annual temperature and precipitation. The creole genotypes from *Altiplano* and *Media* can represent an important phylogenetic potential to counteract negative effects of the increase of temperature and drought in the state of S.L.P for being the less affected in laboratory conditions and coming from unfavorable conditions for the development of maize plants.

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farmers who proportionated seeds and information.

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Chapter II: Metabolomics in maize plant under abiotic stress (heat and water deficit): a review

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Abstract

Changing climatic scenarios affect plant growth and consequences are more malicious in water deficit stress, heat and combined heat and water deficit conditions. Maize is one of the crops most important in worldwide and the most important in México which is the center of domestication of this crop. In this review, the importance of maize in Mexico was targeted, technologies applied for the metabolomic study, the metabolomic profile in single stress of heat, water deficit and their combination heat and water deficit were also summarized. A special issue was done for the Mexican native maize. We discuss the status of metabolomics profiles in maize in response to abiotic stresses such as water deficit, heat, and their combination, analyze the challenges and opportunities. Furthermore, the notable metabolites detected in response to different stresses are summarized to provide a reference for applications of metabolomics in Mexican maize research. We conclude that the metabolomics profile of Mexican native maize has not been well studied and can be the key to understand how to face the negative effects of climate change for smallholders.

Keywords: Mexico, native maize, climate change, metabolites, NMR, GC-MS, abiotic stress.

Introduction

Maize (*Zea mays* L.) originated in the highlands of Mexico approximately 8700 years ago and is one of the most commonly grown cereal crops worldwide, followed by wheat and rice. Is one of the four most important crops in the world and the most important in Mexico due to its cultural, socio-economic influence, culinary attribute and its primary role in food security among others. Also maize is Mexico's staple food crop, thus, decrements in national production would strongly compromise food security in the country without forgetting that Mexico is the center of origin and diversity of this crop (Gong et al., 2014; Hellin et al., 2014; Hermann et al., 2009; Li et al., 2011; Mauricio et al., 2011; Mercer and Perales, 2010; Msowoya et al., 2016; Thornton, 2003).

Genetic variability of maize is a resource for the world’s population, and can be the basis for achieving food sovereignty in Mexico, especially to face the related effect of climate change (Preciado Ortiz and Montes Hernandez). This due to in México, there are 59-64 local varieties which are fundamental for future genetic improvement efforts that could generate new, environmentally resilient varieties. However, maize is highly sensitive to environmental deficiencies such as the availability of water, salinity, which combined with the perceived temperature as stress represent limitations of the environment for this crop (Cramer et al., 2011; Kato et al., 2009).

Maize yield is frequently limited when suffered from the individual or the combined abiotic stresses in future climates. Increases in frequency and magnitude of water deficit and heat stresses are the prime abiotic constraints that cause considerable adverse effects on maize production (Hatfield et al., 2011; Lesk et al., 2016; Liu et al., 2020b; Liu et al., 2020c; van der Velde et al., 2010). As the climate continues to change drastically, it may be more difficult to obtain enough yields. Therefore, the continuing challenges of environmental stresses such as water deficit, extreme temperatures, frost and heavy metal pollution must be taken into account to increase maize production (Feng et al., 2020).

Abiotic stress is one of the most challenging of all major constraints on crop production and is directly related to changes in various cellular metabolic pathways(Chebrolu et al., 2016; Clarke et al., 2013; Maharajan et al., 2021; Zulfiqar et al., 2020). Maize production is often affected by abiotic stress, for example a recent study predicted that the temperature increase and changes in precipitations related to the effect of climate change will have negative impact on Mexican maize yield (Ureta et al., 2020). According to Manavalan et al. (2009) studying plant traits related to abiotic stress is difficult and complicated because under field conditions, crops are often subjected to multiple stresses that can cause various plants responses that may be additive, synergistic or antagonistic (Meena et al., 2017; Prasch and Sonnewald, 2015; Zhang et al., 2012).

Plants recurrently survive up with the rapid variations and adversity of environmental conditions because of their intrinsic metabolic capabilities (Manova and Gruszka, 2015; Rawat et al., 2020; Sheth and Thaker, 2014; Wiszniewska, 2021). Variations in the outside environment could put the plant metabolism out of homeostasis (Hatami et al., 2021; Lan et al., 2011), and generate necessity for the plant to harbor some advanced genetic and metabolic mechanisms within its cellular system (Apel and Hirt, 2004; Gill and Tuteja, 2010). Plants possess an array of protective mechanisms acquired during the course of evolution to combat adverse environmental circumstances (Crandall et al., 2020; Fraire-Velázquez et al., 2011; Yolcu et al., 2016). Such mechanisms cause metabolic reprogramming in the cells to assist routine biophysico-chemical processes irrespective of the external situations. That mean plants respond to abiotic stresses and adaptation processes at the molecular, cellular, physiological and biochemical levels (Kitazaki et al., 2018; Massad et al., 2012; Wang et al., 2018). For example according to Yamaguchi-Shinozaki and Shinozaki (2006) at molecular level; plants respond to stress through changes in gene expression, protein abundance, and accumulation of metabolites. In this sense, proteomics, ionomics, transcriptomics and metabolomics are extensively used to reveal these responses (Nguyen et al., 2020; Obata and Fernie, 2012; Sanchez et al., 2008; Singh et al., 2016; Wei et al., 2021).

In the particular case of maize crop, their metabolomics response to abiotic stress were studied in different conditions as heat (Christensen et al., 2021; Dong et al., 2021; Qi et al., 2017; Sivaram et al., 2019), water stress (Benešová et al., 2012; Benevenuto et al., 2017; Hu et al., 2011; Hu et al., 2012; Huang et al., 2012; Naveed et al., 2014), combined heat and drought (Georgii et al., 2017; Gong et al., 2014; Obata et al., 2015). For example, drought affects many processes involved in plant growth and development, including antioxidant capabilities, osmotic adjustment, photosynthetic rate reduction and abscisic acid accumulation. These processes are controlled by many proteins(Desoky et al., 2021).

The drought response of maize from metabolomics methods have been studied in seeds, leaves and roots where most of the proteins detected are assigned to energy and carbohydrate metabolic processes (Benevenuto et al., 2017). In the xylem sap of maize, Alvarez et al. (2008) found changes in the hormone abscisic acid and cytokinin, also the presence of high concentrations of the aromatic cytokinin 6-benzylaminopurine, and several phenylpropanoid compounds as coumaric, caffeic and ferulic acids. In maize hybrid, Witt et al. (2012) found an increase in metabolite levels under drought stress, including changes in amino acids, sugars, sugar alcohols, and intermediates of the tricarboxylic acid (TCA) cycle. Also induced an accumulation of simple sugars and polyunsaturated fatty acids and a decrease in amines, polyamines, dipeptides, sphingolipid, sterol, phenylpropanoid and dipeptide metabolites. In

Kernels of maize, drought stress resulted in the greater accumulation of reactive oxygen species (ROS) and aflatoxin (Yang et al., 2018).

For heat stress, protein processing in endoplasmic reticulum pathways plays a central role. Elevated respiration, reduced photosynthetic rates, altered timing of the circadian clock, induction of protein unfolding, aggregation and degradation, loss of membrane integrity and acceleration of senescence are one of the consequences of heat stress effect on maize. When maize exposed to high temperature, the genes related to protein processing in endoplasmic reticulum pathway was significantly enriched, which mainly induce heat shock proteins expression. Those heat shock proteins were targets genes of heat stress responsive transcription factors, which participate in regulation when heat stress occurs (Hemantaranjan et al., 2014; Qian et al., 2019).

Combined heat and stress resulted in only a few significantly affected metabolites in the leaves of field grown in maize plants, of which most were shared responses under the single heat and stresses (Obata et al., 2015). According to Lawas et al. (2018) there are two major reactions of plants to combined heat and drought stress: the massive induction of heat shock proteins and the sugar starvation phenotype. In addition, proteomic analysis indicates that few common proteins are observed responding to single and multiple high temperature events (Hu et al., 2010; Yang et al., 2010). Then according to (Vile et al., 2012) & (Suzuki et al., 2014), the simultaneous occurrence of several stress results in highly complex responses of plants; extrapolated the response to combined stresses is largely controlled by different, and sometimes opposing, signaling pathways that may interact with and inhibit each other.

Plants respond to stress with a wide range of modifications that cause to changes at the morphological, cellular, physiological, biochemical, and molecular levels (Aprile et al., 2013; Lopes and Reynolds, 2010). Overall, protein phosphorylation plays a critical role in regulating many biological functions, including stress responses by signal transduction. Phosphorylation and dephosphorylation can switch many regulatory proteins and enzymes on and off, thus control a wide range of cellular processes and signal relays (Yang et al., 2010). On the other hand, (Hu et al., 2015) reported five kinases and three phosphatases under heat stress, three kinases and two phosphatases under drought stress, and three kinases and three phosphatases under combined heat and water deficit stress.

To determine those metabolites in plants and maize in particular, several methods are used in this era of omics science. Those technologies used in metabolomics are liquid chromatography coupled with single-stage mass spectrometry (LC-MS) (Ciborowski et al., 2012; Lozovaya et al., 2006; Raji et al., 2013) or tandem mass spectrometry (LC-MS/MS)(Cho et al., 2009; Guo et al., 2013), gas chromatography coupled to mass spectrometry (GC-MS) (Emwas et al., 2015a; Emwas et al., 2015b; Richter et al., 2015; Sivaram et al., 2019), high or ultrahigh performance liquid chromatography coupled to UV or fluorescent detection (HPLC/UPLC)(Al-Talla et al., 2011; Rodríguez-Aguilar et al., 2020;

Zheng et al., 2010), and nuclear magnetic resonance (NMR) spectroscopy (Kim et al., 2013; Zhang et al., 2008). Each analytical platform has its own advantages and disadvantages. The choice of the platform depends primarily on the focus of the study as well as on the nature of samples. However, the selection of a given platform or platforms is also often determined by the cost, its accessibility, and the available expertise(Emwas et al., 2019; Emwas, 2015). For example, with the development of new chromatography and mass spectrometry technologies, increasing numbers of plant metabolomics studies have occurred (Putri et al., 2013).

Then, the use of plant metabolomics methods to study these metabolites can further provide information on the response of maize and other crop species to abiotic stress. Also taking accoung that in México maize is the most important crop with several races. In this review, we summarized the progress of metabolomics research on maize responses to abiotic stresses such as heat, drought and the combined heat/drought stress. In addition, we related the advantages and disadvantages of most of the technologies used to determine the metabolites in maize crop. The aim is to provide a reference for research on the antistress mechanism of maize with a special focus on Mexican native maize, loading for strategies and futures perspectives for the protection of native maize for his importance in Mexicans smallholders "*campesinos*" and the negative impact of the related effect of climate change on the crop. Also, understanding the effects of climate change on maize growth and yield in Mexico is important for a national and international perspective.

Maize: the most important crop in México and climate change

The importance of maize in Mexico is summarized with the following expression in Spanish "*Sin Maíz, no hay país*" translated as "without maize, there is no country" mentioned by (Cuellar, 2010; Esteva and Marielle, 2003; Florescano, 1986; Hellin et al., 2013; Richard, 2012; Wallenius and Concheiro Bórquez, 2016). Mexico is the country with the greatest genetic diversity of maize in the world and is a genuine global reference for this grain. Since its domestication about 10,000 years ago in the middle of the Neovolcanic Axis, this grassland has an extraordinary cultural and productive value that constitutes an enormous responsibility, in the historical, geographical and in the field of research, to achieve better results and yields by taking care of soil and water and ensuring sustainable systems to ensure food capacity in general, and to achieve, in particular, self-sufficiency standards (https://repository.cimmyt.org/handle/10883/20330?show=full).

A recent study reported by Pelcastre et al. 2021 demonstrated this importance also with an analysis of the perspectives on native maize conservation in Mexico from a public program. Then, maize is the most important crop cultivated, being central to the diets of both urban and rural consumers, particularly the poor. It occupies the largest planted area in the country devoted to any crop and involves cultivation by a large number of smallholders (Mercado and Manuel). According to Cabrera et al., 2002, 76.5% of the Mexican farmers use native seeds for its cultivation and that use depends mainly on the type of agriculture; however, in the regions with typical rural agriculture 80 to 100% of the farmers use native seed fundamentally for its production. However, their production is generally limited for a series of factors like drought, plagues and diseases among others like the related effects of climate change that represent economic losses particularly for smallholder farmers (Bergvinson, 2004).

In México, the expected climate change, according to climate change scenarios will cause an increase of the global temperature trends up to 2.0°C at mid-century (Qin et al., 2014). However according to a recent study in United States, Central America and the Caribbean, the mean annual temperature and precipitation with biases between −0.93 and 1.27 °C and −37.90 to 58.45%, respectively, for most of the region. In addition the annual precipitations will decrease by 10-40%% over Central America and the Caribbean, especially over the monsoon region (Almazroui et al., 2021). The global climate will experience continued warming caused by past anthropogenic emissions as well as from additional future anthropogenic emissions and México is one of the area which will likely become drier (Maliva, 2021; Ramirez-Cabral et al., 2017).

The negative impact of the related effects of climate change on maize in México has been largely studied (Aguirre-Liguori et al., 2019; Dendooven et al., 2012; Díaz-Álvarez et al., 2020; Diédhiou et al., 2021; Donatti et al., 2019; Eakin, 2000; Mercer et al., 2012; Ramirez-Cabral et al., 2017; Smale et al., 2001). Heat and drought stress have been also related to the effects of climate change in Mexico and will affect negatively maize germination (Castro-Nava et al., 2012; Reddy and Kakani, 2007), seedlings (Lizárraga-Paulín et al., 2011), growth and reproduction (Alam et al., 2017; Castro-Nava et al., 2012) and grain yield (Green et al., 2020; Ramirez-Cabral et al., 2017). A reduction in grain yield from 55 to 75% were reported under drought stress, also combined drought and heat stress significantly reduced the average number of days to anthesis and plant height of Mexican maize(Cairns et al., 2013).

Previous investigations that have studied the impacts of climate change on maize in Mexico have focused on shifts in the suitability of geographic areas by projecting the plants climate threshold or have focused on the impact of changes in climatic variables on specific native races or varieties (Conde et al., 1998; Mercer and Perales, 2010; Monterroso rivas et al., 2011; Ureta et al., 2012). For example, all Mexican races of maize and their wild relatives were projected under different climate change scenarios with the objective to evaluate the potential impacts in their geographic distribution. It was found that the potential distribution area of most races was negatively impacted by climate change (Ureta et al., 2012).

Mexican farmers cultivated maize on rainfed fields on plots smaller than 5 ha, some of these farmers still grow their crop in a traditional system called "*Milpa*" in which several species or crop as bean (*Phaseolus vulgaris* L.), squash (*Cucurbita spp*) grown simultaneously (Heindorf et al., 2019; Mercer et al., 2012; Pérez-Hernández et al., 2021a). These farmers are the ones preserving maize diversity *in situ* and it should be made possible for them to attain enough yields from native maize varieties or genotypes. For that, it is important to better understand the mechanisms of maize under abiotic stress with the use of the new era omics sciences such as metabolomics with have good advantages to bring researchers news perspectives to face the negative effects of climate change on Mexican native maize.

Technology applied for the study of metabolomics in maize

The first metabolite profiling publications and research originated from the Baylor College of Medicine in the early 1970s where Devaux et al. 1971; Horning and Horning 1970; 1971a; and Horning and Horning 1971b) illustrated their concept trough the multicomponent analyses of steroids, acids, and neutral and acidic urinary drug metabolites using GC/MS. They are also credited with coining the term ‘‘metabolite profiling’’ to refer to qualitative and quantitative analyses of complex mixtures of physiological origin (Sumner et al., 2003).(Lei and Huang, 2017) reported that it aims to analyze qualitatively and quantitatively all metabolites within biological samples and that research processes to determine the metabolomics of samples, including the collection of samples, the removal, separation and detection of metabolites and the analysis of data require the retention of metabolite information as much as possible. However, it should be noted that due to the complex composition of metabolites, there is currently no way to detect all metabolites simultaneously (Lu et al., 2013; Rochfort, 2005).

Metabolites are generally classified into primary and secondary metabolites. The primary metabolites are indispensable for the growth and development of a plant and secondary metabolites are not essential for growth and development but are necessary for a plant to survive under stress conditions by maintaining a delicate balance with the environment. Primary metabolites are highly conserved in their structures and abundances but secondary metabolites differ widely across plant kingdoms (Guerriero et al., 2018; Rama and Vinutha, 2019; Scossa et al., 2016). Then metabolomics could contribute significantly to the study of stress biology in plants by identifying different compounds, such as by-products of stress metabolism, stress signal transduction molecules or molecules that are part of the acclimation response of plants (Shulaev et al., 2008).

In maize, studies have been done to study the metabolomics profile of the crop under abiotic stress such as heat (Sivaram et al., 2019; Sun et al., 2016b), (Dubery et al., 2020; Liu and Qin, 2021; Sun et al., 2016a) and multiple stress (LI et al., 2021; Sun et al., 2015) with various technologies (Deng et al., 2020; Fu et al., 2021; Janistyn, 1983; Li et al., 2019; Obata et al., 2015; Riedelsheimer et al., 2013; Wen et al., 2014; Wen et al., 2015). Nuclear magnetic resonance (NMR) and gas chromatography-mass spectroscopy (GC-MS) are the two noteworthy analytical tools for investigations of metabolites however other technologies such as combining Fourier transform-ion cyclotron resonance mass-spectrometry, capillary electrophoresis-mass spectrometry and pressurized liquid extraction, liquid chromatography tandem mass spectrometry (LC-MS/MS), high or ultrahigh performance liquid chromatography coupled to UV or fluorescent detection (HPLC/UPLC) have been used to determine the metabolomics profile in maize (Leite et al., 2020; Leon et al., 2009; Sharanya et al., 2020; Tang et al., 2013).

NMR has become one of the main analytical techniques used in metabolomics. Also, in the present, LC-MS and GC-MS are increasingly popular in metabolomics studies for maize. The crucial advantage of these latest technologies is that they have been long used for metabolite profiling, so that stable protocols for machine configuration and maintenance, chromatogram evaluation and interpretation already exists (Fernie, 2004; Halket et al., 2005; Herrero et al., 2012; Li et al., 2020a; Lioupi et al., 2020; Lisec et al., 2006). Other advantages are related to the short run time and relatively low running costs for GC-MS. However, their use is limited for thermally stable volatile compounds, making the analysis of high molecular weight compounds difficult. Furthermore, it facilitates the identification and robust quantification of a few hundred metabolites in plant samples such as sugars, sugar alcohols, amino acids, organic acids and polyamines, resulting in fairly complete coverage of the central pathways of primary metabolism (Rama and Vinutha, 2019).

Rogachev and Aharoni (2011) indicated that LC-MS does not require prior sample treatment or separation of components in the liquid phase and therefore has no limitation due to the volatilization of compounds. Therefore, LC has the potential to analyze a wide variety of metabolites in plants. The technique becomes increasingly powerful due to the recent development of the UPLC which has higher resolution, sensitivity and performance than the High Performance Conventional Liquid Chromatography (HPLC). These technologies can be combined with other techniques to identify a wide variety of metabolites even when they have high molecular mass, high polarity and low thermo stability (Rama and Vinutha, 2019). Those types of MS including quadrupole (Q), TOF, qTOF, triple quadrupole (QqQ), ion trap (IT), quadrupole trap (LTQ)-Fourier transformed ionic cyclotron resonance etc. are used depending on sensitivity, mass resolution and range dynamics required (Allwood and Goodacre, 2010; Lei et al., 2011).

Some of the advantages and disadvantages of the two most widely used technologies from the evaluation, preparation and reuse of the sample until the numbers of detectable metabolites for the determination of metabolites in maize are summarized below (Table 1).

Table 1. Advantages and disadvantages of the two most widely used technologies from the evaluation, preparation and reuse of the sample until the numbers of detectable metabolites for the determination of metabolites in maize are summarized below.

Parameters	NMR	MS
Evaluation of the sample	It enables relatively rapid measurement using ^{1}D ^{1}H-NMR spectroscopy, where all metabolites detectable at a concentration level can be observed in a measurement.	Different ionization methods are required to maximize the number of metabolites to be detected.
Preparation of the sample	Minimal preparation required and usually the sample is transferred to an NMR tube and a solvent is added also can be automated.	More wear, requires chromatography and gas sample derivatization.
Reuse of the sample	It is non-destructive and therefore several analyses can be performed on the same sample. Additionally, the sample can be recovered and stored for a long time.	It is a destructive technique; therefore, the sample cannot be recovered. However, it only needs a small amount of sample.
numbers of detectable metabolites	Depending on spectral resolution, generally less than 200 metabolites can be detected and identified in a single measurement.	It is possible to detect thousands of metabolites and identify hundreds of them.

It should be added that in maize more work has been done with genetically modified maize and hybrid maize to determine their metabolomic profiles under different conditions and with various methodologies (Blondel et al., 2016; Tang et al., 2017; Zhang et al., 2020). However, in terms of native maize, in this present not much work has been done to determine their metabolomic profiles in our knowledge but there exist works with compare the wild maize *Teosinte* with existing maize breeds. Morphological and metabolomic changes from wild to domesticated maize where it was reported an increment of flavonoids and decrement of amino acids as metabolomic changes for maize crop (Xu et al., 2019).

Maize's metabolomic profile response to water stress deficit

In Mexico around 80% of all maize cultivated is grown under rainfed conditions, where the possibilities for alleviating water stress are limited (Aquino et al., 2001; Ribaut and Ragot, 2007). In addition, predictions through climate models point to increased frequency and severity of drought in the near future (Change, 2007). For this reason, considerable efforts have been made to understand the response of plants to stress. Studies have revealed an important role of metabolism and its regulation as much as that of photosynthesis and accumulation of osmolytes in the response to stress (Verslues and Juenger, 2011).

Sun et al. (2016a) found an accumulation of different metabolites to successive drought and re-watering cycles in two inbred lines of maize. The metabolites identified were glucose, fructose, malate, proline, aspartate, asparagine and threonine significantly different in the metabolomic profile of the two inbred lines under normal conditions. As compatible solutes, amino acids, sugars, and complex carbohydrates are known to be accumulated at high levels under stress, possibly to maintain cell turgor, stabilize proteins and cell membranes, and restore redox balance(Rodziewicz et al., 2014; Witt et al., 2012). For example, in maize cv. FR697; changes were found in the hormones abscisic acid (ABA) and cytokinin, and presence of high concentrations of the aromatic cytokinin 6-benzylaminopurine (BAP). Also, several phenyl propanoid compounds (coumaric, caffeic and ferulic acids) were reported in xylem sap. The concentrations of some of these phenylpropanoid compounds changed under drought conditions (Alvarez et al., 2008). A drought tolerant hybrid maize exhibited a significant increase in non-structural carbohydrates and aromatic amino acids during the mid and late stages of a drought treatment, respectively, and a reduction in tricarboxylic acid cycle intermediates relative to a susceptible genotype (Caldana et al., 2011).

Other studies showed the recovery of inbred maize plants after being subjected to drought stress, where the recovery time is related to the regulation of metabolism. For example, levels of compounds such as shikimate, succinate, fumarate, isoleucine, leucine, valine, tryptophan, tyrosine, proline, and choline were completely reversed after re-watering, but sterols, aldehyde group, terpenes, fatty acids, free fatty acids and polyunsaturated fatty acids were only partially restored and remain below control levels, particularly after a second watering. Also, several compounds, such as sucrose, glucose, fructose and inositol, are corrected in excess after re-watering. This finding suggests that different metabolic pathways of maize return to their normal state at different rates. One study showed that recovery from the metabolic processes initiated by irrigation during water stress is considerably complicated. It is likely that metabolic profile patterns are functionally related to each other (Oliver et al., 1998; Sun et al., 2016c).

With the use of MS in Mexican landraces seeds, identification of 18 anthocyanins was done with the objectives to obtain UV−vis spectral signatures and ionomic fingerprints from differently pigmented corn genotypes including a new purple maize variety called “Vitamaize”, a new hybrid that no transgenic. Similarly they found differences for the total concentration of anthocyanins (Peniche-Pavía and Tiessen, 2020). Also in three Mexican maize landraces were found that the transcript levels of photosynthesis associated with genes decreased under drought stress (Hayano-Kanashiro et al., 2009).

Metabolomics profile of maize response to heat stress

Most of the studies dealing with possible climate change effects on Mexican maize have detected negative impacts due to the increase of the temperature (Mercer and Perales, 2010; Ray et al., 2015; Ureta et al., 2016). Heat stress can be very detrimental for their development and consequently negatively impact yield. Flowering and grain filling stages are very heat sensitive in maize and sterility increases with higher temperatures. The optimum temperatures for most of its developmental phases range between 26 and 32 °C (Lobell et al., 2011; Sánchez et al., 2014). High temperature affects maize plants at all levels, ranging from molecular and cellular effects to whole plant growth. More importantly, tissue injuries caused by heat stress exposure of crop plants grown under field conditions are mostly irreversibles. Severe heat stress at vegetative developmental stages can cause significant decreases in photosynthetic area and reduction in metabolites production (Burke and Chen, 2006; Chen et al., 2010; Chen et al., 2012; Doğru, 2021; Jiang and Huang, 2001).

Han et al. (2009) and Peverelli and Rogers (2013) indicated that heat stress decreases the development phase and leads to small organs, also a lower perception of light due to a reduced and altered life cycle due to carbon assimilation and loss of yields in cereals. It can also affect germination and depending on the intensity of the stress can negatively affect photosynthesis, cell respiration, water relations and cell membrane stability, as well as hormone levels as both primary and secondary metabolites (Wahid et al., 2007).

Under heat stress conditions, the metabolomic profile of maize lines reveals the presence of succinate, myoinositol, xylitol, proline, putrescine, glycerol-3-P, beta algalacanin, fructose, malate, tricarboxylic acid, fumarate, GABA, octadecanoate, as the most accumulated in leaves (Obata et al., 2015; Sun et al., 2016c). While from the root part of maize hybrid, accumulation of glutathione and cysteine were the components with greater presence related to heat stress (Nieto-Sotelo and Ho, 1986). A recent work comparating the metabolomics profile of maizes (temperate and tropical) and its wild ancestor (*Teosinte*) targeted distinct sets of metabolites. Alkaloids, terpenoids, and lipids were specifically targeted in the divergence between *Teosinte* and tropical maize, while benzoxazinoids were specifically targeted in the divergence between tropical and temperate maize(Xu et al., 2019).

Metabolomics profile response of maize to the combination of heat and water deficit stress

The combination of drought and heat stress represents an excellent example of two different abiotic stress conditions that occur in the field simultaneously (Moffat, 2002; Shah and Paulsen, 2003). The maize grain yield loss caused by heat and drought stresses together could exceed 40% to 70%, with a possibility of 100% yield loss. Heat and drought stresses greatly affected the production and yield stability. The improving and understanding those abiotic stresses in maize has become one of the priorities for maize breeding (Chen et al., 2012; Lobell et al., 2011).

Metabolomic research on cereals has also recently begun and may, in the future, provide valuable information, for instance, on the sugar and amino acid metabolism in the vegetative and reproductive organs of cereals under various environmental conditions (Langridge et al., 2006). However, studies have been done to determine the metabolomics response of maize to the combined heat and stresses. For example, 10 hybrid maize lines were used under combined heat and drought stresses, to identify promising metabolite markers to be used as part of a stress-tolerant maize breeding program. Analysis of maize leaf metabolite profiles combined with traits associated with grain yields showed that glycine and serine, two amino acids important for photorespiration, and the sugar alcohol myo-inositol were accumulated under drought and combined drought and heat stress conditions. Moreover, statistical analysis revealed a significant correlation between glycine and myo-inositol contents and grain yields under drought and combined drought and heat stress. They also reported that the effect of drought stress was more influential than that of heat stress, and the tendency of metabolite accumulation under combined stress was closer to that under drought than heat stress (Obata et al., 2015; Sato et al., 2004).

The Table 2 identifies the most common metabolites in the combination of water and heat stress in maize crop and a summary of their possible functions obtained with the help from the website www.plantcyc.org.

Table 2. Most common metabolites in the combination of water and heat stress in maize crop and a summary of their possible functions

Most common metabolites	Biological role	References
Asparagine (Asn)	Pathways of biosynthesis, protein constituent and amino group donor.	(De la Torre et al., 2007; Miesak and Coruzzi, 2002)
Aspartic acid (Asp)	Photosynthetic carbon assimilation cycle in C4 plants.	(Alvarez et al., 2013)
Beta alanine	Osmoprotector in abiotic stress conditions.	(Hanson et al., 1991; Rathinasabapathi, 2000)
Fructose 2, 6-bisphosphate	Powerful allosteric regulator with simultaneous dual functions. It is a phosphofructose-1, 6-bisphosphatase activator and a fructose-1,6-bisphosphatase inhibitor, being key enzymes that limit the speed of glycolysis and gluconeogenesis, respectively.	(Pilkis et al., 1995)
Fumarate	It is involved in the glycoxylate cycle and the breakdown of fatty acids.	(Bologna et al., 2007; Karsten et al., 2003)
Glycerol-3-phosphate	Intervenes in oxidation and reduction reactions of NAD and NADH that must be balanced to continue with catabolism and anabolism.	(Shen et al., 2006)
Glycine betaine	It accumulates in high cytoplasmic concentrations in response to osmotic stress to act as an osmoprotector.	(Ji and Kaplowitz, 2003; Monobe et al., 2005)
Malate	Photosynthetic carbon assimilation cycle in C4 plants.	(Rothermel and Nelson, 1989)
Nicotinate	It is involved in the routes degradation and recovery of pyridine compounds. Depending on the species, the nucleotide cycle involves a number of steps that emphasize the flexibility of this pathway in response to environmental conditions.	(Ashihara et al., 2005)
Phosphate	It has a number of signaling functions, including regulation of	(Coelho et al., 2005)

	nuclear mRNA export, binding of clathrin assembly proteins AP2 and AP3, Clathrin cage assembly inhibition and inhibition of serine and threonine phosphatase proteins that regulate L-type Ca^{2+} channels.	
Putrescine	Its presence is related to water stress, oxidative and wounds. Evidence has suggested his presence in the biosynthesis of chloroplasts.	(Patel et al., 2017)
Pyroglutamate	It mitigates oxidative stress by degrading glutathione from extracellular space; it may also be involved in the transport of glutathione.	(Shachar-Hill et al., 1995)
Serine	It is involved in photorespiration. Under conditions of abiotic stress its supply is important to counteract for example high concentrations of salts, floods etc.	(Kim et al., 2002)
Succinate	It is involved in aerobic respiration and the generation of energy and reducing power and therefore, very related to trichloroacetic acid.	(Fernie, 2004)
Threonine	Its conversion involves two enzymes (homoserine kinase and theorin synthase) both catalyzed in chloroplast.	(Mas-Droux et al., 2006; Redfearn et al., 2005)

Prospects and challenges

Maize is one of the most important crops in the world and the most important in Mexico. Also being the center of domestication of maize, it is an international interest to protect maize in Mexico where almost 64 races have been reported. At the same time, the native maize is very important for Mexican smallholders "*campesinos*" because is the principal component of their agricultural system "*Milpa*". "*Milpa"* farmers carefully selected their own maize and other crops varieties for generations, resulting in a vast amount of heritage landrace diversity that is locally endemic and found nowhere else in the world (Novotny et al., 2021; Perales and Golicher, 2014; Perales et al., 2005; Wang et al., 2017). However in the present and future, the related effect of climate change such as drought, heat and combined heat and drought stress present in fields' production have been reported to bring negative impact for maize from the establishment until the yield (Hein et al., 2021; Muitire et al., 2021; Prasch and Sonnewald, 2015).

Taking account this case, a public policy from the Federal Government of Mexico have been reported with the name "*Programa de Conservación de Maíz Criollo"* (Program for the Conservation of Native Maize in Mexico; PROMAC) was rolled out in 52 natural protected areas and 22 priority regions for conservation, which are biodiversity hotspots with unique ecosystems and high numbers of endemic species, and they are considered to have great potential for successful conservation efforts. What is interesting about this case is how the Mexican government moved from the traditional strategy of priority species conservation to considering native maize as a priority species and incorporating it into this strategy but this strategy have been started just at 2009. However according to Pelcastre et al. (2021) the problem was that its design ignored what the experts determined to be the main threats to native maize. Furthermore, designing the program as a series of financial subsidies led to a significant rift between the conceptualizers and the implementers. In addition in the present, farmers are the most affected by the related effect of climate change and until now they are facing and adapting their crop or system to achieve their production. For example Ureta et al. (2012) reported a decrease in Mexican maize yield related to the effect of climate change.

To understand how plants face to the environmental conditions, metabolomic emerges as an emerging field in the post-genomic era dedicated to the global study of metabolites, their composition, and response to changes in the environment, in cells, tissues, or fluids (Varghese et al., 2011). However, due to the complex composition of metabolites, there is currently no way to detect all metabolites simultaneously (Lu et al., 2013). Different technologies are used to detect different types of metabolites. Analytical platforms GC-MS and NMR are the most used but recommended the use of multiplatform detection for different tissue samples, making full use of the advantages of different detection platforms (Feng et al., 2020).

The work of Obata et al. (2015) were done with ten maize lines from the International Maize and Wheat Improvement Center (CIMMYT-México) and really related the metabolomics profiles of maize from single stress (and heat), their combination and grain yields. This work was one of the most completed that reported metabolomics profile of maize in the country we found however we did not found a work with this kind of objective with Mexican maize even landraces. However it is important to note that, works were done in Mexican maize but with the objective of the detection of aflatoxin in the Mexican population such as women for health studies (de León-Martínez et al., 2019a; Diaz de Leon-Martinez et al., 2020; Rodríguez-Aguilar et al., 2020).

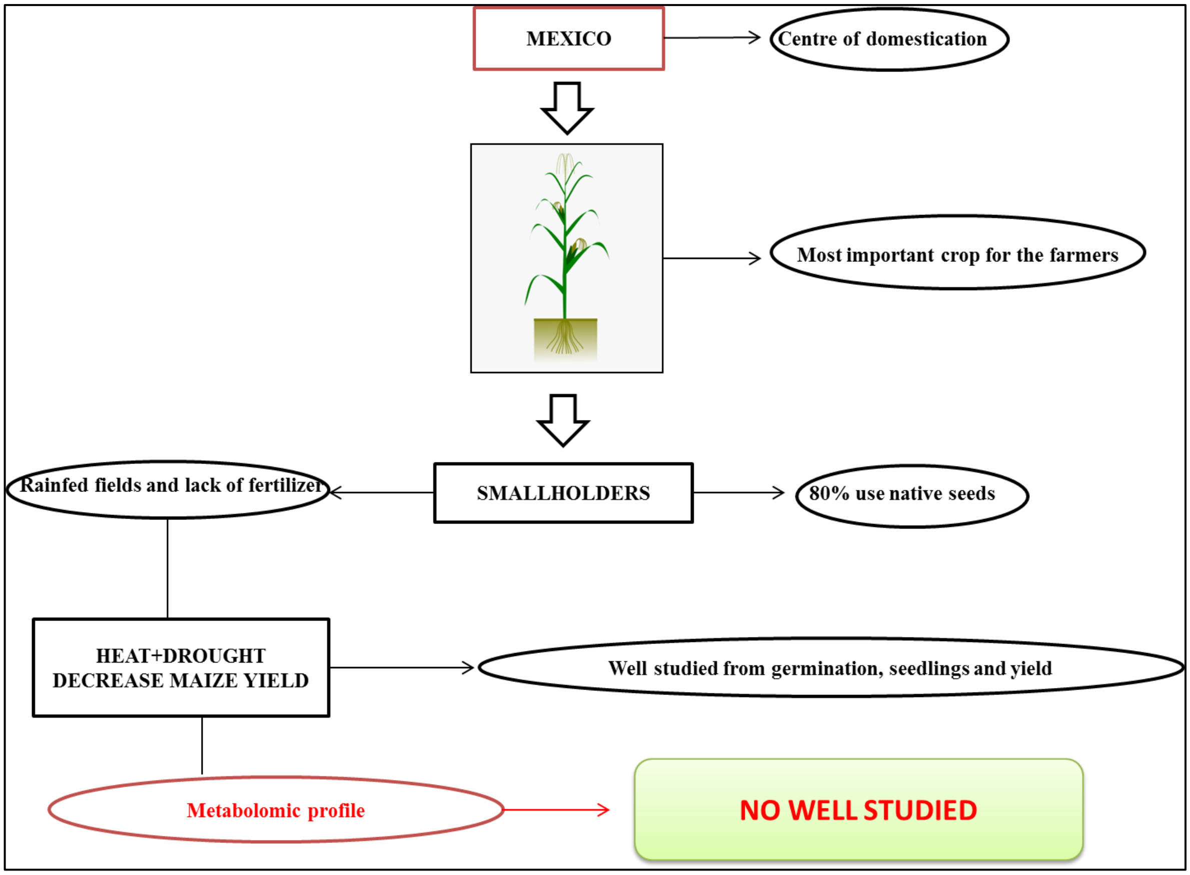

Fig. 1. Summarize of the actual research advances in Mexican native maize

Taking account the importance of native maize for smallholders and for the country, it will be really attractive to investigate about the profile metabolite of native maize and that will help to understand how some of them counterattack the limits of the environments then they face at fields production. It will be very important to add the post genomic era as one of the objective of the PROMAC to support Mexican government for the conservation of native maize. In the present, metabolomic profile in Mexican native maize have not yet well studied and most of the profile investigated was done on trans genetic, hybrid, wild ancestral maize. In addition, the response of maize to stress involves complex physiological and biochemical processes, and the molecular mechanism governing this response needs to be elucidated in depth via combinations of various analytical methods, such as metabolomics, proteomics, genomics, transcriptomics, and bioinformatics. The Figure 1. summarize the actual advances in native maize in the country where we conclude that the metabolomic profile of Mexican native maize have not been well studied and can be the key to understand how to face and how maize face the negative effect of climate change.

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Author contribution statement

ID was mainly responsible for conducting literature review, research and wrote the first draft of the manuscript. HMRT project leader, obtained the financial resources for the study execution, supervised the research project. Coordinated the research work and revised/edited the manuscript. JFM reviewed the manuscript and contributed to the final version of the manuscript. RFR reviewed the manuscript, revised and edited the final version of the manuscript.

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Data and material availability

All data generated or analyzed during this study are included in this article

Declarations Conflict of interest.

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Human and animal rights statement.

This article does not contain any studies with human or animal subjects.

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Chapter III: Metabolomic profiles of native genotypes of maize (*Zea mays* L.) seedlings from warm-dry, temperate, and hot and humid environments grown under related effects of climate change

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Abstract

Introduction Maize is the most important crop in Mexico and is grown in a range of climates. The increase in temperature and accentuation of water stress has resulted in negative effects on ecophysiological processes. Despite this, there is no report on the metabolomic profile of native genotypes of maize seedlings grown under the related effects of climate change.

Objective To determine the metabolomic profiles of 12 native maize genotypes seedlings from different climates grown under related conditions of climate change with the gas chromatography/mass spectrometry technique.
Method 25, 30, and 35°C were proposed because they were related to the temperature increase. The simulation of water stress was performed using PEG-8000 (-0.5, -1, and -1.5 MPa), a control (0 MPa) was used. Germination experiments were performed; after 16 days, the metabolomic profiles of each native genotype were determined.

Results Principal component analysis demonstrated variation depending on temperature and water stress. 15 major metabolites were discovered under heat stress. A clear separation between samples from different climates was observed. Secondary metabolites and their possible metabolic pathways found in the different treatments were shown. The results showed that the highest correlation coefficients were found in the combination of high temperatures and water stress.

Conclusions The results provide significant baseline information for assessing possible ways to counterattack abiotic stresses in native genotypes in the early stage of growth.

Keywords: Heat, water deficit, abiotic stress, secondary metabolites, multivariable analysis

Declarations The authors declare no conflict of interest.

Conflict of interest The authors declare no conflict of interest.

Human and animal rights This article does not contain any studies with animal performed by any of the authors.

Introduction

Climate change is a threat not only to this country but to the entire world, and its impact on maize (*Zea mays* L.) would be particularly severe in Mexico, which is its center of origin and diversification (Msowoya et al., 2016). Smallholder 'communities have made their genetic evolution possible, allowing their gradual adaptation to climatic variations.

A recent study reported by (Pelcastre et al., 2021) demonstrated the importance of this crop also with an analysis of the perspectives on native maize conservation in Mexico from a public program. Then, maize is the most important crop cultivated, being central to the diets of both urban and rural consumers, particularly the poor. It occupies the largest planted area in the country devoted to any crop and involves cultivation by a large number of smallholders (Bellon et al., 2021; Montgomery et al., 2021). According to Ibarrola-Rivas et al. (2020), 79% of the Mexican farmers o locally called "*campesinos*" use native seeds for its cultivation and that use depends on the type of agriculture. However, their production is often limited due to a variety of causes, such as water stress, plagues, and diseases, among others, as well as the connected effects of climate change, which constitute economic losses, particularly for smallholder farmers. (Donatti et al., 2019).

In Mexico, climate change can cause an increase in the average annual temperature from 1 to 4°C and decrease in the average annual precipitation from 0.4 to 1.4 times during this century (Allen et al., 2018; Change, 2007). The increase in temperature related to climate change and the accentuation of water stress have resulted in negative effects on ecophysiological processes such as germination and seedling establishment (Aragón-Gastélum et al., 2017; Walck et al., 2011). Taking into account that plant species are sensitive to temperature, water stress and their combination (heat and water stress) and suffer when these are low or very high with respect to the thresholds defined for each specie (Choudhary et al., 2020).

The genetic information contained in native or creole maize could be strategic for the future development of maize varieties, both creole/native and commercial hybrids, capable of adapting to the expected climate change scenarios in different parts of the world (Bellon et al., 2017; Mercer and Perales, 2010). This due to in México, there are 59-64 local varieties which are fundamental for future genetic improvement efforts that could generate new, environmentally resilient varieties. However, maize is highly sensitive to environmental deficiencies such as the availability of water, salinity, which combined with the perceived temperature as stress represent limitations of the environment for this crop (Cramer et al., 2011; Kato et al., 2009).

Maize yield is frequently limited when suffered from the individual or the combined abiotic stresses in future climates. Increases in frequency and magnitude of water stress and heat stresses are the prime abiotic constraints that cause considerable adverse effects on maize production (Hatfield et al., 2011; Lesk et al., 2016; Liu et al., 2020c; van der Velde et al., 2010). As the climate continues to change drastically, it may be more difficult to obtain enough yields. Therefore, the continuing challenges of environmental stresses such as water stress, extreme temperatures, frost and heavy metal pollution must be taken into account to increase maize production (Feng et al., 2020).

Abiotic stress is one of the most challenging of all major constraints on crop production and is directly related to changes in various cellular metabolic pathways (Chebrolu et al., 2016; Clarke et al., 2013). Maize production is often affected by abiotic stress, for example a recent study predicted that the temperature increase and changes in precipitations related to the effect of climate change will have negative impact on Mexican maize yield (Ureta et al., 2020). Research on plant traits related to abiotic stress is difficult and complicated because under field conditions, crops are often subjected to multiple stresses that can cause various plants responses that may be additive, synergistic or antagonistic (Meena et al., 2017; Prasch and Sonnewald, 2015; Zhang et al., 2012).

Plants recurrently survive up with the rapid variations and adversity of environmental conditions because of their intrinsic metabolic capabilities (Manova and Gruszka, 2015; Rawat et al., 2020; Wiszniewska, 2021). In the particular case of maize crop, their metabolomics response to abiotic stress were studied in different conditions as heat (Christensen et al., 2021; Dong et al., 2021; Qi et al., 2017; Sivaram et al., 2019), water stress (Benešová et al., 2012; Benevenuto et al., 2017; Hu et al., 2011; Hu et al., 2012; Huang et al., 2012; Naveed et al., 2014), combined heat and water stress (Georgii et al., 2017; Gong et al., 2014; Obata et al., 2015).

Hence, the need to understand the mechanism of defense of plants with the use of metabolomics as a newly developed discipline in which it is intended to address the unbiased study of all metabolites present in a tissue, organ or organism at a particular point in its development or under particular environmental conditions, thus enabling the assessment of the contribution of genetic and/or environmental factors to the modification of metabolism (Fiehn, 2001). In this sense, the objective of this study was to evaluate the metabolomic profiles of native maize seedlings from warm-dry, temperate and hot and humid climates of the state of San Luis Potosí, México grown in controlled environments related to some effects of climate change (temperature increase and water deficit) by Gas Chromatography/Mass Spectrometry (GC/MS) techniques. The above-mentioned, with the hypothesis that metabolomics profiles of native genotypes adapted to specific local conditions could be different and in dependence of their origins when exposed to related effects of climate change.

Material and methods

Study sites and their environmental factors

The state of San Luis Potosí (SLP) is characterized by having basically three important agro-ecological regions. 1) *Huasteca*: formed by the foothills of the "*Sierra Madre Oriental*", it has a territory of 10,676.5 km^2 and its altitude varies between 50 and 800 m asl. It has extensive fertile plains and represents a hot and humid climate. 2) *Media*: with elevations ranging from 883 to 2000 m asl, its territorial extension is 13,509 km^2, and it has a steppe and temperate climate, with average rainfall ranging from 500 to 700 mm per year; occasionally frost and hail occur at the start of the rainy season. 3) *Altiplano*: with a warm-dry climate, it is located in the state's northern and western sections. In this region, the average temperature fluctuates between 15 and 20°C and it has an average height of approximately 2,000 m asl, where early frost in October and late frost in May are common.

Selection of native genotypes of maize

The materials evaluated were collected in the state of SLP in Mexico., in which, with basis on the mean annual of temperature and precipitation; three areas were identified whose average temperature and precipitation are around 14.5, 18.5 and 22.5 °C; 400, 700 and 1200 mm respectively (Diédhiou et al., 2021; Noyola-Medrano et al., 2009). Such areas were denominated *Altiplano*, *Media* and *Huasteca* respectively, and some features are described (Table 1; supplementary data). A total of 37 distributed samples were obtained in the following way; 10 from the region of *Altiplano*, 11 from *Media* and 16 from *Huasteca*.

The collected samples were assessed as established by Carballo and Benítez (2003). This way a total of 14 variables were described: longitude (cm), diameter (mm) and conicity of cob, number of rows per cob, number of grains per row, row arrangement, color and grain type, dry weight of 100 seeds (g), volume (mL) of 100 seeds in 50mL, longitude (mm); thickness (mm) and wide (mm) of grain, phenological term (months). On the previous data were added, data on thermal and rainfall conditions facilitated by the producer. Such information was systematized on the following scale: low by the number one, regular by the number two, and high by the number three.

Statistical analysis of the native collected genotypes of maize

With the objective of containing the samples in conglomerates (clusters) with high grade of internal homogeneity and external heterogeneity among the samples and to select representative samples from the all collected, a multivariate analysis was carried out to form groups (Sanjinez and Otiniano, 2019).

Germination and growth conditions of native maize seedlings: treatments of temperature and simulation of water stress

Germination experiments were made in controlled conditions of constant temperature (25, 30 and 35°C) and water potential [0 (control), -0.5, -1.0, and -1.5MPa]. The temperatures were proposed for having relationship with scenarios of increase temperature due to effects of climate change (Table 1; supplementary data). The conditions of soil humidity were determined at different levels of water potential since a very big variation in the quantity of rain received in a month through the successive years is expected (Jiménez and Mendoza, 2019).

The simulation of water deficit in the substrates was carried out with polyethylene glycol 8000 (PEG-8000) as solution, with the purpose of simulating variations in the availability of soil humidity (Huang et al., 2018). This solution was used because it has been documented that it doesn't present toxicity on seeds and has used on maize seeds (Khalil et al., 2001). A control was also used with water potential of 0 MPa from deionized water.

To know the quantity of necessary PEG-8000 to obtain the potential water desired, the formula proposed by (Michel, 1983) was used:

$$\mathrm{PEG} = \frac{4 - (5.16\varphi\mathrm{T} - 560\varphi + 16)^{0.5}}{2.58\mathrm{T} - 280}$$

Where:

PEG: Kg of PEG per liter of deionized water

φ: Required water potential in bars (1 bar= 0.1MPa)

T: Temperature of prepared solution

The three water potentials (-0.5, -1 and -1.5MPa) were obtained by mixing deionized water and 145, 290 and 400g L^{-1} of PEG-8000 respectively (Diédhiou et al., 2021). Water potential of each solution was measured in a psychometric camera (WPA Dewpoint PotentiaMeter, Decagon Devices Inc.). Samples of the solutions were taken approximately and were placed in plastic trays in circular way 40mm of diameter by 12 mm deep. The measurements obtained allowed to verify the correct use of the wanted potentials.

Preparation of seedlings extracts and metabolomics analysis by gas chromatography coupled to mass spectrometry (GC-MS)

Seedlings germinated at different temperatures and water stress at 16 days after germination was used for metabolomics analysis. Therefore, plant extracts were used following the protocol used by our research team (de León-Martínez et al., 2019a; de León-Martínez et al., 2019b; Diaz de Leon-Martinez et al., 2020).

It was described below: 0.1 g of each seedling (stem) was weighed and cut into very small particles. They were then placed in glass vials and 8 mL of the hexane mixture was added: acetone (1:1) for each sample (well specified temperature and water stress level). Then each sample underwent sonication at a low temperature and one pulse every second for 1 minute. Each tube was then centrifuged at 3500 rpm for 5 minutes in order to settle the seedlings fragments at the bottom of the tube. Once centrifuged, the solvent was removed and placed in 15 mL tubes to be evaporated with nitrogen for 15 minutes at 28 °C, to remove the solvent. At the end of the solvent evaporation (acetone), the samples were concentrated at 1 mL, which was transferred to microvials.

The metabolomic analysis was carried out on a GC-MS (Agilent Technologies Model 5973inert) under the following conditions: oven settings were as follows: 60°C (2 min), 180°C (5°C / min), 200°C (2°C / min), 300°C (10°C / min), 310°C (10°C / min) 5 min, with a run time of 52 min. The injector temperature was 230°C in splitless mode. Helium was used as carrier gas at a linear rate of 1.0 ml/min. The mass spectrometer was run in SCAN mode (50-500 m/z) to identify compounds. Results were obtained and processed using Chemstation Software (Agilent).

Characterization of metabolomics profiles

The characterization of the compounds was carried out through the use of Agilent Technologies equipment (model 5973inert), which provided for each sample the compounds identified by peak number, retention time, percentage of area, name of the compound, Chemical Abstractyts Service (CAS) number. The following information made it possible to identify the metabolites and the Qual parameter. Taking into account that the Qual is the percentage that indicates the probability of a compound being detected by the GC-MS. For this research, each peak was identified with a Qual greater than or equal to 30.

Chemometric analysis

To evaluate the metabolomic profiles of the study, Principal Component Analysis (PCA) and Canonical Principal Coordinate Analysis (CAP) were performed. CAP was performed using the multivariate data cloud that best discriminated between groups (temperature and water stress level). CAP analysis Anderson and Willis (2003) was based on Euclidean distance matrices calculated from log(X + 1)-transformed normalized data of chromatographic peak area (62 compounds analyzed); differences between groups were calculated using 9999 permutations. The CAP procedure included cross-validation in order to leave out a procedure to predict group membership and thus obtain overall classification success rates. Using the leave out method in which a single observation is extracted from the training set, and then a CAP model is built with the rest of the set, finally the excluded observation is classified in the canonical space and the correct classification of the excluded observation is determined. This is performed for each of the observations in the data set and then the proportion of observations that were misclassified is calculated. The relationships of the analyzed compounds with the CAP axis were assessed by Spearman correlation. Statistical significance was determined using 5 and 1%. Multivariate analysis was performed using the Primer 7+ Permanova software package (v7.0.12 and v1.0.6; PRIMER-E Lt., Ivybridge, UK) and metabolite identification via the website https://plantcyc.org/; Plant Metabolic Network (PMN) which provides an extensive network of plant metabolic pathway databases containing curated information from computational literature and analysis on genes, enzymes, compounds, reactions and pathways involved in the primary and secondary metabolism of plants.

The PCA was obtained through the multivariate data cloud that was the best to discriminate between predefined groups (CC, CIN, and controls). PCA provides a summary of all the variables entering in the statistical analysis by finding correlations among the variables. Following correlation, it reduces the variables into a smaller number of principal components which is responsible for the possible variance in the observed variables. Finally, PCA expressed the whole data sets in a global and qualitative visual pattern, highlighting similarities and differences between and within the sample (Naz et al., 2014). Partial least squares discriminant analysis (PLS-DA) and variable importance in projection (VIP) were performed to identify the differential sensors among groups and to rank the sensor's response according to their importance in discriminating groups. PLS-DA is a supervised statistical method that uses multivariate regression techniques to extract, by a linear combination of independent variables, information to predict class belonging. It is used to improve separation between groups by rotating the PCA components to obtain a maximum separation.

All variables were transformed to a Euclidean distance dissimilarity matrix calculated from normalized (X- mean/standard deviation) and log(X + 1)-transformed data pre-processed from the 32-sensor ΔR data; the difference between groups was calculated using 9999 permutations (Rodríguez-Aguilar et al., 2021a; Rodríguez-Aguilar et al., 2021b). Canonical Analysis of Principal Coordinates (CAP) was then used to ordinate the matrices, and to further determine the level of misclassification between sampling regions the method of leave-one-out was applied to variables in canonical space (using a K-fold) to predict group associations and thus obtain the overall classification success rates, using a value of m= 3. Additionally, the CAP model was employed to predict the clustering of the new samples. The associations of the analysed sensors with the CAP axis were evaluated by Spearman correlation.

Results

Genetic materials

After the multivariable analysis of the 37 samples of maize collected in all the state of SLP, the resulting groups of the cluster analysis used in this investigation were: white maize's of 5 months of life cycle (genotypes A3, A4 and A8), white maize of 3 months (genotype A9) and purple maize (genotype A10) of 4 months of the region of *Altiplano* (warm-dry climate); white maize of 4 months (genotype M2), purple maize of 3 months (genotype M4) and black maize of 3 months (genotype M11) of the region of *Media* (temperate climate), white maize's of 4 and 3 months (genotypes H4 and H11 respectively) and yellow maize's of 3 months (genotypes H9 and H10) of the region of *Huasteca* (hot and humid climate). In addition, in Figure 1 characteristics and conditions of the seed samples collected were given for each environment by the smallholders.

Figure 1. Seed conditions for storage by the smallholders in the three environments of the state of San Luis Potosí (México). A: *Huasteca* (hot and humid climate); B: *Media* (temperate climate), and C: *Altiplano* (warm-dry climate).

Metabolomics profiles of native genotypes of maize seedlings under heat stress

For Metabolic fingerprinting, the GC–MS was used to identify metabolomic changes in maize seedlings under different temperatures. Figure 2 shows the Principal Components Analysis (PCA) of metabolites found depending on the abiotic factor temperature. A natural variation was observed between the metabolites by study groups, which was explained by approximately 13% and 7% of the components 2 and 1 respectively (Figure 2a). Similarly, the metabolites found formed three groups with a significant difference between the metabolites found at 30°C and 35°C while for the latter there is similarity with those found at 25°C. This result demonstrated good sample separation, and it was discovered that some of the high temperature samples (35°C) were grouped in the same area as the low temperature group used in this investigation (25°C), causing the two groups (25 and 35°C) to overlap while 30°C's separated into a single group (Figure 2b).

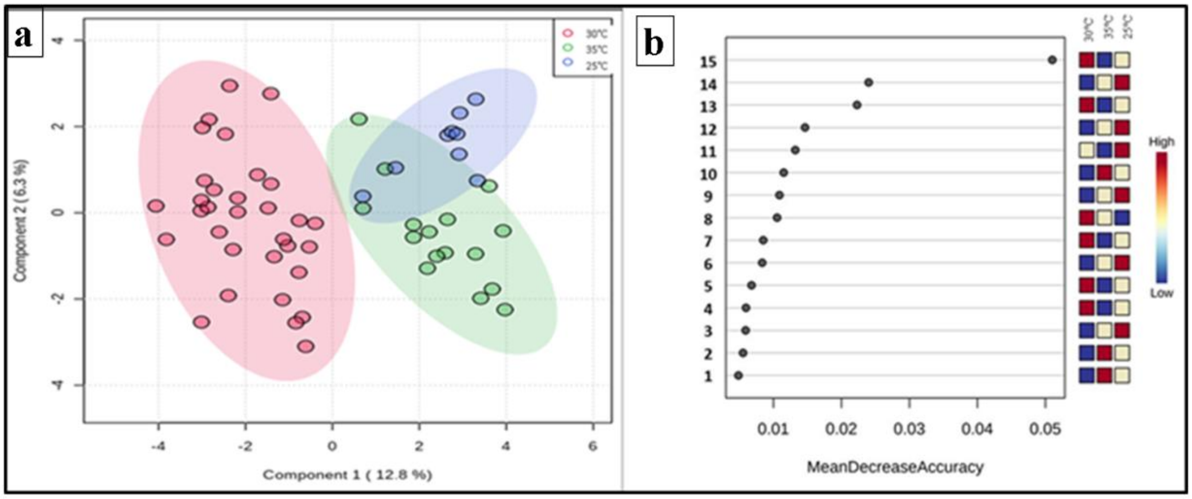
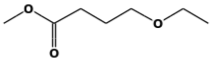
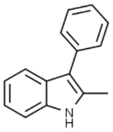
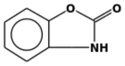
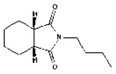
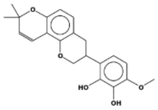
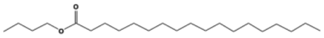
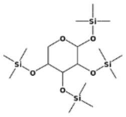
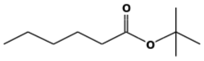
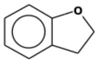
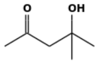
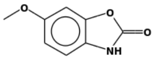
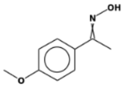
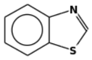
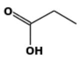


Figure 2. Partial Least Squares-Discriminant Analysis (PLS-DA). a) plot of component 1 vs. component 2; b) Plot of variable importance in projection.

There were a total of 15 major metabolites discovered, each of which manifested on a high and/or low scale depending on the temperature (Figure 2b). They were determined with the help of the Variable Importance of Projection (VIP). The VIP indicates the importance that a certain variable has in a model. As a result, the metabolite will be more important as the VIP increases. At 30°C, the metabolites propanoic acid, benzothiazole, oxime-, methoxy-phenyl, hexadecanoic acid, and beta.-D-ribopyranoside, methyl; octadecanoic acid; 4-cyclohexene and butanoic acid were high while 6-methoxy-2-benzoxazolinone; 2-pentanone-4; benzofuran, 2; 4-methoxybenze; heneicosane; 2 (3) H-benzoxazolone and 1H-indole-2,3 were low. At 35°C only 4-methoxybenze was high while propanoic acid; benzothiazole; hexadecanoic acid; beta.-D-ribopyranoside, methyl; octadecanoic acid; 4-cyclohexene y butanoic acid were reported low. In contrast, at 25°C, metabolites 6-methoxy-2-

benzoxazolinone; 2-pentanone-4; benzofuran, 2; heneicosane y 2 (3) H-benzoxazolone were reported high while only oxime-, methoxy-phenyl was low (Figure 2a and table 1).

Table 1. Fifteen most important metabolites identified and their chemical formula.

Number	Compounds	Chemical formula
1	Butanoic acid, 4-ethoxy-, methyl ester	
2	1H-Indole, 2-methyl-3-phenyl-	
3	2(3H)-Benzoxazolone	
4	Heneicosane	
5	4-Cyclohexene-1,2-dicarboximide, N-butyl	
6	4-Methoxybenzene-1,2-diol	
7	Octadecanoic acid, butyl ester	
8	beta.-D-Ribopyranoside, methyl	
9	Hexadecanoic acid, 1,1-dimethylethyl ester	
10	Benzofuran, 2,3-dihydro-	
11	2-Pentanone, 4-hydroxy-4-methyl-	
12	6-Methoxy-2-benzoxazolinone	
13	Oxime-, methoxy-phenyl	
14	Benzothiazole	
15	Propanoic acid	

After the PCA, a Canonical Analysis of Principal Coordinated (CAP) (Figure 3) was performed, which allowed to see the grouping of samples by temperature. Similarly, the formation of temperature groups was observed where samples evaluated at 30°C was most prominent, while the two other temperatures (25 and 35°C) continued to show similarities.

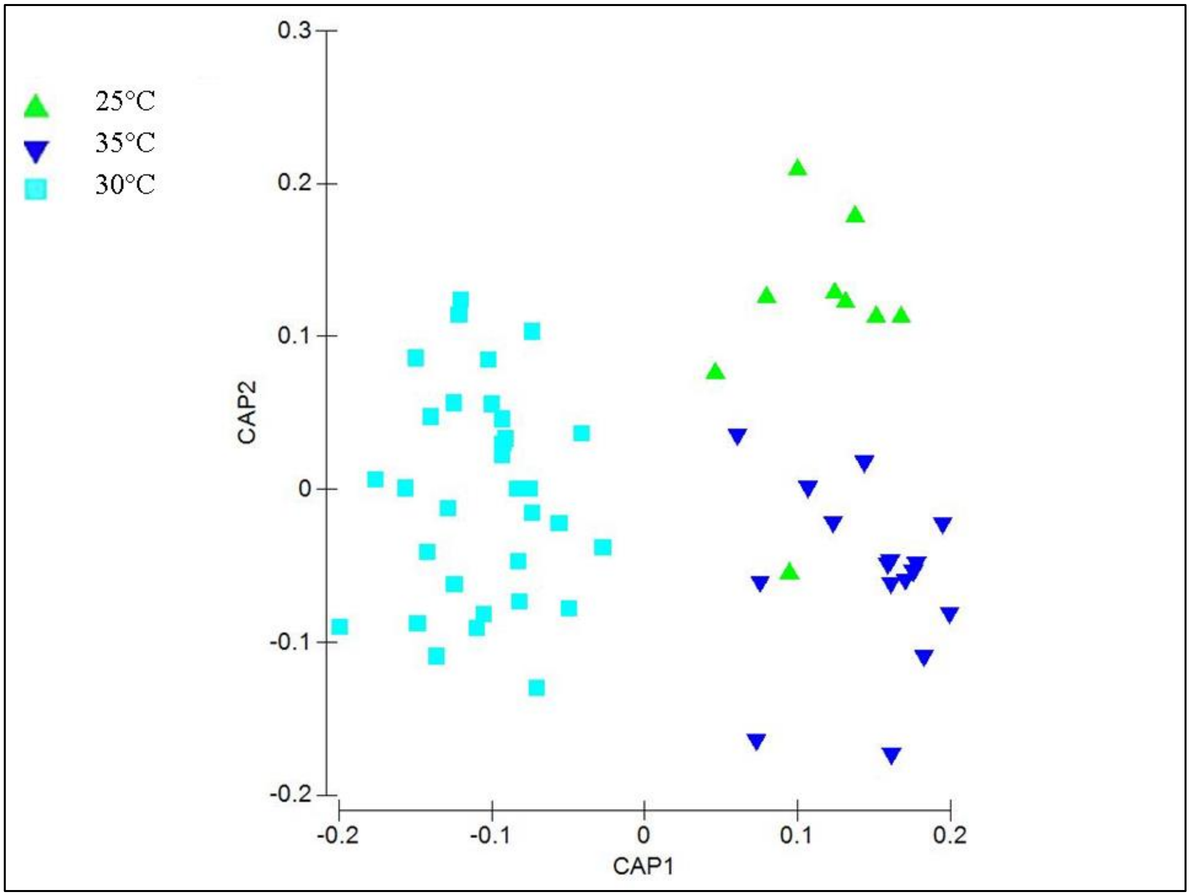


Figure 3. Canonical Analysis of Principal coordinated (CAP) of the seedlings of maize native genotypes from the three regions of the state of San Luis Potosí grown at different temperatures. VC: 25°C; T: 30°C and TC: 35°C. A: *Altiplano*; H: *Huasteca* and M: *Media*.

Metabolomics profiles of native genotypes of maize seedlings under water stress and heat stress

To further asses the relationship among the native maize genotypes from different climates, a heatmap as shown in Figure 5, was obtained after hierarchical cluster analysis of the metabolites profiles of the native maize seedlings. To find similarity between sample groups, this study utilized Euclidean distance in cluster analysis. In addition, the most intuitive and simple way to mathematically identify similarity between two objects, classes, or samples is the Euclidean distance measure (Uarrota et al., 2014).

So in native maize seedlings, two major clusters were identified. hexadecanoic acid, propanoic acid, octadecanoic acid, 4-cyclohexene-1-2, benzothiazole, 6-methyl, .beta.-D-ribopyran, 1H-indole, 2-methyl, butanoic acid, 4-ethyl, oxime-, methoxy-pn formed the first cluster. In the other hand, the second cluster was formed by heptacosane, 1,2-benzenedicarbone, 2-3, oxirane, 3-methyl, benzycynide, 2-3, dodecane, 2.5-dimethyl, 1H-indole-2,3-dione, silane, 1,4-phenyl, 2-pentanone, 4-hyd, heneicosane, benzofuran, 2,3-di, 4-methoxybenzene-1, 23H-benzoxazcione, 6-methoxy-2-benzox and mercaptophenyl.

In addition a closer look on the heatmap, revealed three classes formed by the different temperature. Similarly, 30°C formed the first group being the most abundant metabolites: hexadecanoic acid; propanoic acid; octadecanoic acid; 4-cyclohexene-1,2-; benzothiazole; beta.-D-ribopyrane; 1H-indole, 2-methyl; butanoic acid and oxime-methoxy; dianhydro. The second class was represented by 35°C, which was abundant: heptacosane; benzenedicarbo; oxirane, 3-methyl; benzylcynide and dodecane while at 25°C formed by the third and last class, the abundance of metabolites was marked by the following metabolites: silane, 1,4-phenyl; 2-pentanone, 4-hydroxy; heneicosane; benzofuran; 4-methoxybenzene; 23H-benzosaxclione; 6-methoxy-2-benzox and 4-mercaptophenol (Figure 4).

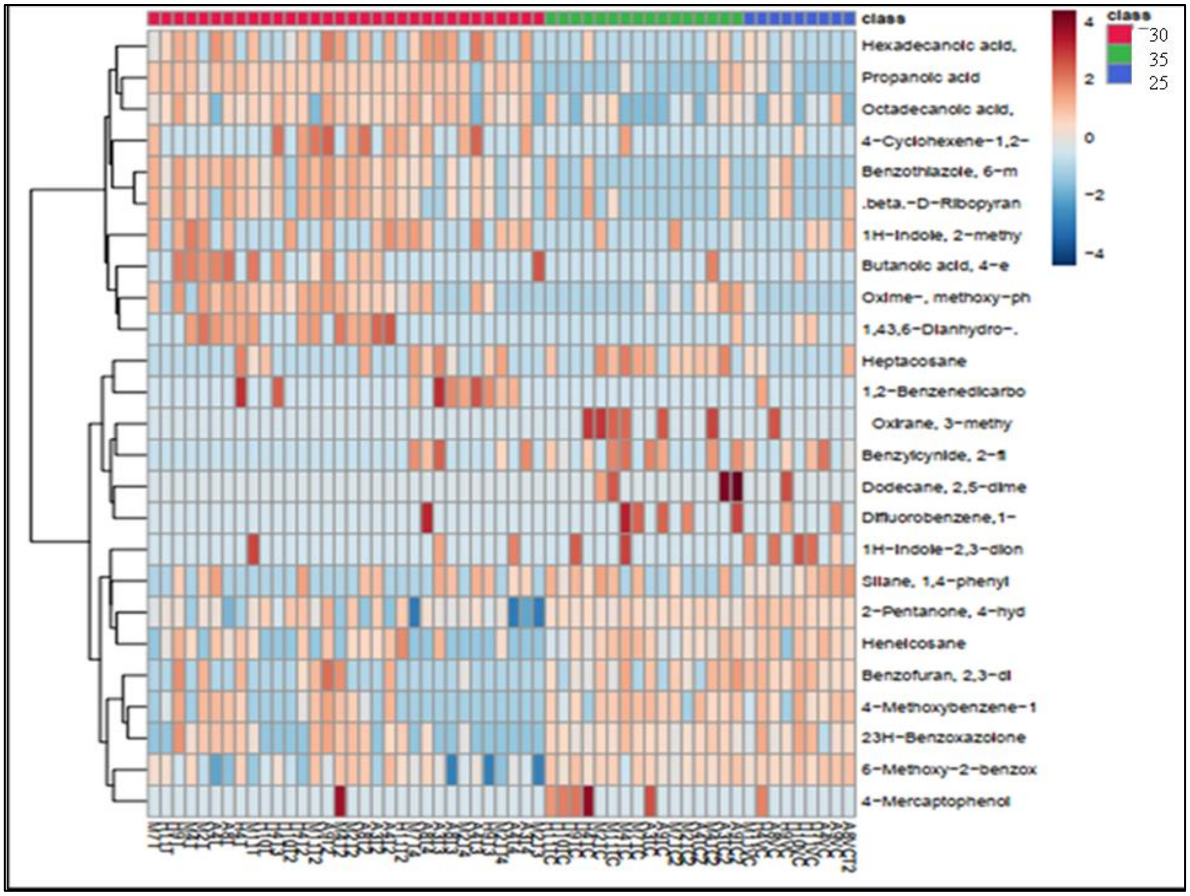


Figure 4. Clustering results are shown as a heat map (Distance measurement using Euclidean, and clustering allogaritme using Ward.D) of metabolic expression patterns for all samples studied at different temperatures (25; 30 and 35°C) and water stress level (T1: 0 MPa; T2:-0.5 MPa; T3: -1 MPa; T4:-1.5 MPa), A: *Altiplano*; H: *Huasteca*; M: *Media* and MPa: Mega Pascal.

A GC–MS was used to identify metabolomics changes in maize seedlings under different water stress at 30°C. Figure 5a shows the PCA of metabolites found at different level of water stress at this temperature. Similitude was found between water level T1 (0 MPa (control) and T2 (-0.5 MPa) while the others (T2 (-0.5 MPa) and T3 (-1.5 MPa)) formed another group with a significant difference between the two groups. This grouping corresponds to a metabolic difference between different environments caused by the combination of water and heat stress suffered by the seedlings in their initial growth conditions. In both cases, the metabolomic profiles allowed the discrimination of the samples, indicating that, although there are differences between different genotypes, the growth environment of the seedlings influences the metabolism.

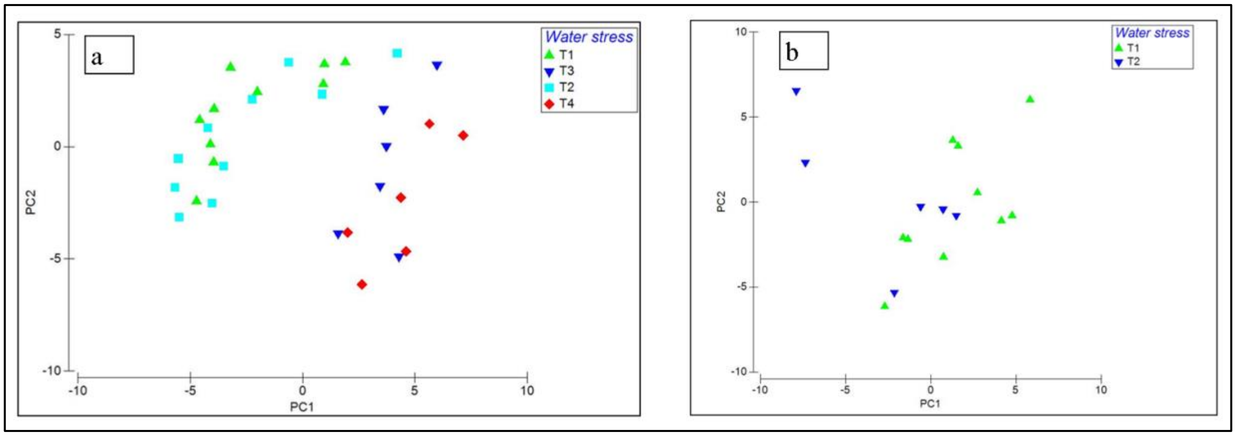


Figure 5. Principal components analyses of the metabolites found in native maize seedlings grown at 30°C (a); and 35°C (b) at different levels of water stress. T1: 0 MPa; T2:-0.5 MPa; T3: -1 MPa and T4: -1.5 MPa. MPa : Mega Pascal. ***In 5b; T3 and T4 did not appear because the native genotypes did not germinated at 35°C.***

On the other hand, at 35°C, germination was zero at -1 and -1.5 MPa; therefore, PCA was performed with the two levels of water stress (0 and -0.5 MPa). In this sense, in most of the samples, there was similarity in the metabolites found for the two water potentials. However, some of the samples from *Altiplano* (A3 and A9) were highlighted under conditions of water stress and/or temperature increase (35°C) (Figure 5b).

Secondary metabolites and their possible metabolic pathways found in the different treatments were shown. In this same sense, the most relevant correlation coefficients were highlighted for each CAP in each sample. The results showed that the highest correlation coefficients were found in the combination of high temperatures and water stress (Table 2; supplementary data). Thus, at 35°C/-0.5MPa; acetamide, N-[4-(trimethylsilyl) phenyl]- with 0.77 correlation coefficient reported in biosynthesis of free phenylropanoid acid. Phenylpropanoids serve as pigments, phytoalexins, phytoanticipines, UV protectors and signaling molecules between plant and microbes, can polymerize and perform cell wall stability functions, provide structures for evapotranspiration (lignin) and protect plants from water loss (cutin, suberin). Similarly the Bis (2-ethylhexyl) phthalate (r^2=0.71064) was very significant at 30°C/-1.5MPa (Table 2. Supplementary data).

Taking into account that at 35°C/-0.5MPa is an environment in which plants lose a lot of water due to rapid evapotranspiration; the presence of phenylpropanoids allows them to protect the seedlings from lack of water among others. On the other hand, the number of more representative metabolites increased depending on environmental conditions. The same phenomenon highlights the need for seedlings to develop conditions necessary to survive in these adverse conditions.

Discussion

Metabolomics profiles of native genotypes of maize seedlings under heat stress

This study demonstrates the great potential of determining the metabolomics footprint from CG-MS in the combination or not of abiotic factors (temperature and water stress) faced by seedlings in their future growth environment (Figure 2, 3, 4 and 5 and Table 2 (Supplementary data)). The results obtained in this study allow us to understand that the classification made using temperature suggests that, although the environment has an important influence on the composition of secondary metabolism, there is still a strong genetic component that determines (Arbona et al., 2014). According to Hasanuzzaman et al. (2013) the main consequence of the exposure of plants to high temperatures is the decrease of the carbon balance, as a result of the inactivation of the Rubisco4 and other crucial metabolites in the growth and adaptation of seedlings to thermal stress are sugars. In our work, thermal stress induced the production of secondary metabolites as was indicated by Wahid et al. (2007) who reported that phenols (flavonoids, anthocyanins, lignins, etc.) and carotenoids are the main compounds to be highlighted in these conditions of abiotic stress. In addition, under heat stress conditions, catabolism is stimulated and anabolism is inhibited; these changes promote survival and restore cellular homeostasis (Atkin and Tjoelker, 2003; Baena-González et al., 2007; Sung et al., 2003). Although there is no direct antecedent to the analysis of the complete metabolomics profile of the various organs of the native maize under different agronomic management environments, There are studies that report significant differences in the metabolic profiles of other crops such as soybeans (*Glycine max*) in their initial growth Zhang et al. (2016) who reported metabolomic profiles change in wild and cultivated soybean seedling leaves under salt stress. Also Kumar and Rai (2014) indicated that for wheat (*Triticum aestivum* L.), the heat stress induces an oxidative stress within the cell system, which is followed by an increase in the expression of proteins such as protein kinases, heat shock proteins, and antioxidant enzymes. In addition, they reported that, these stress proteins modulate the defense mechanisms of wheat by protecting the denaturation and aggregation of nascent proteins involved in various metabolic reactions. In the other hand, Sun et al. (2016b) reported metabolomic profiles and metabolite levels in the leaves of three maize inbred lines grown in different temperatures [18/10°C (low temperature); 25/15°C (optimal temperature) and 35/25°C (high temperature)] conditions where our results were similar to those found by them because they mentioned a functional and metabolic plasticity may play different roles in maize plant adaptation to temperature variations. For example, tropical plants are damaged when exposed to temperatures below 10 ºC (chilling injury) and most species begin to have problems between 30 and 40°C. Small temperature increases (from 30 to 35ºC) can damage the reproductive organs of many crops, including wheat (*Triticum aestivum* (L). Thell), maize (*Zea mays* L.), rice (*Oryza sativa* L.), peanuts (*Arachis hypogaea* L.) and tomatoes (*Solanum lycopersicum* L.). Our research is a pioneer in determining the metabolic profile of native maize from different environment of the state of

San Luis Potosí. In the same way, the metabolomic profiles helped in classifying the native maize genotypes based on thermal variability.

Metabolomics profiles of native genotypes of maize seedlings under water stress and heat stress

The combination of water stress and heat stress represents an excellent example of two different abiotic stress conditions that occur in the field simultaneously (Moffat, 2002; Shah and Paulsen, 2003). In our investigation, a heatmap (Figure 4) was used to determine the combination of the two abiotic factors (heat and water stress) in maize seedlings. We found different metabolites determined by a combination of water stress and heat stress. In the same way, in terms of metabolomic profiles, more compounds related to water stress such as soluble carbohydrates and proline were manifested. The latter is listed as one of the compatible solutes that accumulate in greater quantity in stressed environments compared to other amino acids. Results that agree with Herrera Flores et al. (2012) findings when comparing bean cultivation to different water potentials. Previous researchers Aslam et al. (2015); Klimešová et al. (2017); Lavinsky et al. (2016) have reported that in response to some type of stress (water stress, salinity or cold), non-vacuolated root tip cells accumulate high proline levels in the chloroplast stoma and cytoplasm, while other solutes (sugars, organic acids, potassium) are accumulated in the vacuole. For example, water stress affects many processes involved in plant growth and development, including antioxidant capabilities, osmotic adjustment, photosynthetic rate reduction and abscisic acid accumulation. These processes are controlled by many proteins (Ilyas et al., 2021; Rahman et al., 2021).

Metabolomic research on cereals has also provide valuable information, for instance, on the sugar and amino acid metabolism in the vegetative and reproductive organs of cereals under various environmental conditions (Comeau et al., 2010). For example, 10 hybrid maize lines were used under combined heat and water stress stresses, to identify promising metabolite markers to be used as part of a stress-tolerant maize breeding program. Analysis of maize leaf metabolite profiles combined with traits associated with grain yields showed that glycine and serine, two amino acids important for photorespiration, and the sugar alcohol myo-inositol were accumulated under water stress and combined water stress and heat stress conditions. Moreover, statistical analysis revealed a significant correlation between glycine and myo-inositol contents and grain yields under water stress and combined water stress and heat stress. They also reported that the effect of water deficit stress was more influential than that of heat stress, and the tendency of metabolite accumulation under combined stress was closer to that under water stress than heat stress (Obata et al., 2015; Sato et al., 2004). Also a recent study in *Populus simonii* (water stress-tolerant variety) and *Populus deltoides* (water stress-susceptible variety), it was demonstrated that carbohydrates, amino acids, lipids and energy were involved in the response of the two cultures to water stress. In the same vein, they added that the citric acid cycle was significantly inhibited to conserve energy, while multiple carbohydrates that act as osmolites and osmoprotectors were induced to alleviate the adverse effects of water stress. On the other hand, *P. simonii* underwent specific metabolic reprogramming that improved non-enzymatic antioxidants, coordinated the cellular carbon/nitrogen balance, and regulated wax biosynthesis (Jia et al., 2020).

In our investigation, the presence of phenylpropanoids under heat and water stress (35°C/-0.5 MPa) was notable and was related to the environment where the genotypes native of maize were grown. As indicated by Khlestkina (2013) who demonstrated that among secondary metabolites, phenolic compounds (e.g., flavonoids and phenylpropanoids) provide protection to plants against a range of biotic and abiotic stresses. This found collaborate with ours because of the combination of high temperature and the lack of water. However others authors associated the presence of phenylpropanoids with low stress temperature in maize seedlings (Mahmood et al., 2017). In the other hand the presence of phenylpropanoids was also associated to a single water stress in *Caragana korshinskii* plants (Liu et al. (2019)), in contrasting hybrid cultivars of maize (Liu et al. (2020a)) and in Jerusalem artichoke seedlings (*Helianthus tuberosus* L.) (Zhao et al., 2021). Also it was associated to heat stress as indicated by Dong and Lin (2021) who reported that phenylpropanoid metabolites are not dispensable, but are of vital importance for plant development and survival. It is important to note that previous studies have also reported that phenylpropanoids presence in plants is affected by growth and development, biotic and abiotic stresses (Batard et al., 1997; Bellés et al., 2008; Deng and Lu, 2017; Niinemets et al., 2013; Rastogi et al., 2019; Silva et al., 2012b; Solecka, 1997)

This study allowed to determine the metabolomic profiles of maize native genotypes seedlings from different environment of the state of San Luis Potosí and was able to identify differences related to the environment of origin (genetics) and the experimental conditions established in this work. Abiotic factors (increase in temperature and/or water stress and their combination) influenced both agronomic variables (Diédhiou et al. (2021)) and molecular characteristics. To the best of our knowledge, this study is a first in determining the metabolomic profiles in the early growth of native maize seedlings in Mexico, despite the fact that 80 to 100% of the country smallholders "*campesinos*" use native seeds for maize production. However, even if it was possible to determine the metabolomic profile of the native maize genotypes from different climates and to collaborate the differences between them from the two factors such as water stress, heat and their origin, we can say that our knowledge is limited because this first research was conducted in laboratory conditions where the factors are controlled differently from what really happens in the field where the maize genotypes face during their emergence and growth.

Conclusions

Untargeted metabolic profiling using Gas Chromatography/Mass Spectrometry (GC/MS) in combination with multivariate data analysis provided molecular differentiation of the native genotypes of maize from warm-dry, temperate, and hot and humid environments. As a result, we now have a better understanding of the molecular diversity of these maize genotypes. Important metabolites in the different native maize genotypes were identified under heat, water stress and their combination and the origins of each genotype. The metabolite profiles, which show the relative content of the metabolites of the genotypes under related effects of climate change, will be useful baseline information for assessing the possible ways to counterattack abiotic stresses (water stress and heat) in native genotypes of maize.

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Author contribution

HMRT project leader, obtained the financial resources for the study execution, supervised the research project. Coordinated the research work and revised/edited the manuscript. ID was mainly responsible for conducting fieldwork, research design, data analysis, and wrote the first draft of the manuscript. JFM reviewed the manuscript and contributed to the final version of the manuscript. RFR reviewed the manuscript, proportionated the statistical analysis, discussed the research results and revised/edited the final version of the manuscript.

Declarations The authors declare no conflict of interest.

Conflict of interest The authors declare no conflict of interest.

Human and animal rights This article does not contain any studies with animal performed by any of the authors.

Data availability statement

The metabolomics and the metadata reported in this paper were searched from the website https://plantcyc.org/; Plant Metabolic Network (PMN) which provides an extensive network of plant metabolic pathway databases containing curated information from computational literature and analysis on genes, enzymes, compounds, reactions and pathways involved in the primary and secondary metabolism of plants.

Supplementary data

Tab 1. Climatic characteristics and futures scenarios of temperature based on the mean annual temperatures (M.A.T.) of the three regions from the state of San Luis Potosí, México.

Genotypes	Region	Predominate climate based on modifications of the Köppen climate classification system and M.A.T.	Future mean annual temperature (M.A.T.) in short term (2010-2040) (M.A.T. + 0.75-1°C)	Future mean annual temperature (M.A.T.) in long term (2070-2100) M.A.T. + 2.75-3.0 °C)
A3		BS1kw(e)gw"	15.25-15.5°C	17.25-17.5°C
A4	*Altiplano*	BSohw(e)gw"		
A8		14.5°C		
A9				
A10				
M2		Cb(w2)(w)(I’)	19.25-19.5°C	21.25-21.5°C
M4	*Media*	18.5°C		
M11				
H4		(A)Cam(f)(e)w"	23.25-23.5°C	25.25-25.5°C
H9	*Huasteca*	Am(e)gw"		
H10		22.5°C		
H11				
References		García, 2004.	IPCC, 2013b; Ávalos Lozano et al., 2017b.	

Tab 2. Table 2. Secondary metabolites found and their coefficients of correlations (r^2) with the Canonical Principal Coordinate Analysis (CAP) coordinates of the seedlings of native genotypes of maize at different temperature and water stress.

Temperature (°C)	**Water Potential (MPa)**	**Metabolites with the highest representation**	**Coefficient of correlation (r^2)**	**Chemical formula**
25	**0**	.alpha.-D-Galactopyranoside, methyl 3,6-anhydro-	-0.38212	C7H12O5
		Oxime-, methoxy-phenyl	-0.30246	$C_8H_9NO_2$
		4-Methyl-2,5-dimethoxybenzaldehyde	0.39726	$C_{10}H_{12}O_3$
		2-Amino-4,5-dimethoxyacetophenone	0.40715	$C_{10}H_{13}NO_3$
		Benzylcynide, 2-fluoro-3,4-dimethoxy-	-0.38188	$C_{10}H_{10}FNO_2$
		Cyclotrisiloxane, hexamethyl-	0.39493	$C_6H_{18}O_3Si_3$
		Silane, 1,4-phenylenebis[trimethyl	0.42980	$C_{12}H_{22}Si_2$
		2-Hexanol, 2-methyl-	-0.31501	$C_7H_{16}O$
		2-Benzothiazolamine, N-ethyl-	0.31052	$C_9H_{10}N_2S$
		3-Fluoro-4-methoxyphenylacetonitrile	-0.45860	C_9H_8FNO
		Hexadecane, 2,6,10,14-tetramethyl-	-0.45828	$C_{20}H_{42}$
30	**0**	4-Methyl-2,5-dimethoxybenzaldehyde	0.40894	$C_{10}H_{12}O_3$
		Benzylcynide, 2-fluoro-3,4-dimethoxy-	0.38583	$C_{10}H_{10}FNO_2$
		Tetracosane	0.33843	$C_{24}H_{50}$
		Nonadecane	-0.36956	$C_{19}H_{40}$
		2-Cyclopenten-1-one, 2-hydroxy-	0.35378	$C_5H_6O_2$
		3-Fluoro-4-methoxyphenylacetonitrile	0.41404	C_9H_8FNO
		Benzenamine, 2,3,4,5,6-pentamethyl	0.39688	$C_{11}H_{17}N$
		1H-Indole, 2-methyl-3-phenyl-	0.43872	$C_{15}H_{13}N$
		Acetamide, N-[4-(trimethylsilyl)phenyl]-	0.42843	$C_{19}H_{25}N_5O_3Si$
		Hexadecane, 2,6,10,14-tetramethyl-	-0.38617	$C_{20}H_{42}$
		6-Methoxy-2-benzoxazolinone	-0.33795	$C_8H_7NO_3$
	-0.5	Diethyl Phthalate	0.45175	$C_{12}H_{14}O_4$
		Acetic acid, octadecyl ester	-0.39406	$C_{20}H_{40}O_2$
		Tetracosane	0.41271	$C_{24}H_{50}$
		Hexadecanoic acid, 1,1-dimethylethyl ester	-0.39760	$C_{20}H_{40}O_2$
		Bis(2-ethylhexyl) phthalate	-0.39601	$C_{24}H_{38}O_4$
		Silane, 1,4-phenylenebis[trimethyl	0.45142	$C_{12}H_{22}Si_2$
		2-Hexanol, 2-methyl-	-0.34571	$C_7H_{16}O$
		Hexadecane, 2,6,10,14-tetramethyl-	-0.46626	$C_{43}H_{88}O_2$
	-1	2-Pentanone, 4-hydroxy-4-methyl-	0.43987	$C_6H_{12}O_2$

		.alpha.-D-Galactopyranoside, methyl 3,6-anhydro-	0.46211	$C_6H_{12}O_2$
		Benzofuran, 2,3-dihydro-	0.33463	C_8H_8O
		4-Methoxybenzene-1,2-diol	0.4014	$C_7H_8O_3$
		2(3H)-Benzoxazolone	0.608	$C_7H_5NO_2$
		4-Ethylphenyl isothiocyanate	0.57911	C_9H_9NS
		4-Methyl-2,5-dimethoxybenzaldehyde	0.50779	$C_{10}H_{12}O_3$
		Benzylcynide, 2-fluoro-3,4-dimethoxy-	0.50076	$C_{10}H_{10}FNO_2$
		Heneicosane	0.52150	$C_{21}H_{44}$
		Acetic acid, octadecyl ester	0.49624	$C_{20}H_{40}O_2$
		Octadecanoic acid, butyl ester	-0.38235	$C_{22}H_{44}O_2$
		Cyclotrisiloxane, hexamethyl-	0.64019	$C_6H_{18}O_3Si_3$
		2-Hexanol, 2-methyl-	-0.47106	$C_{10}H_{20}O_3$
		Benzenamine, N,N-diethyl-4-methyl-	0.47077	$C_5H_6O_2$
		2-Cyclopenten-1-one, 2-hydroxy-	0.70189	$C_8H_{12}O_2$
		3-Fluoro-4-methoxyphenylacetonitrile	0.39963	C_9H_8FNO
		Hexadecane, 2,6,10,14-tetramethyl-	0.43791	$C_{20}H_{42}$
		Benzenamine, 2,3,4,5,6-pentamethyl	0.69026	$C_{11}H_{17}N$
		Silane, 1,4-phenylenebis[trimethyl	-0.52183	$C_{11}H_{17}N$
	-1.5	Propanoic acid	-0.54909	$C_3H_6O_2$
		2(3H)-Benzoxazolone	0.44911	$C_7H_5NO_2$
		4-Methyl-2,5-dimethoxybenzaldehyde	0.42194	$C_{10}H_{12}O_3$
		4-Ethylphenyl isothiocyanate	-0.60567	C_9H_9NS
		Heneicosane	-0.48311	$C_{21}H_{44}$
		Hexadecanoic acid, 1,1-dimethylethyl ester	0.44290	$C_{20}H_{40}O_2$
		Acetic acid, octadecyl ester	0.53707	$C_{20}H_{40}O_2$
		Tetracosane	0.47271	$C_{24}H_{50}$
		Bis(2-ethylhexyl) phthalate	0.71064	$C_{24}H_{38}O_4$
		2-Cyclopenten-1-one, 2-hydroxy-	0.65580	$C_5H_6O_2$
		3-Fluoro-4-methoxyphenylacetonitrile	0.80371	$C_5H_6O_2$
		4-Geranyloxy-3-hydroxy-5-methoxyphthalaldehyde	0.45391	$C_{19}H_{24}O_5$
		Phenol, 2,2'-methylenebis[6-(1,1-dimethylethyl)-4-ethyl-	-0.51754	$C_{25}H_{36}O_2$
		Diethyl Phthalate	0.39827	$C_{12}H_{14}O_4$
		4-Ethylphenyl isothiocyanate	-0.60567	C_9H_9NS
35	**0**	Propanoic acid	0.48093	$C_3H_6O_2$
		4-Ethylphenyl isothiocyanate	0.53379	C_9H_9NS
		6-Methoxy-2-benzoxazolinone	-0.35801	$C_8H_7NO_3$
		Heptacosane	-0.37651	$C_{27}H_{56}$
		2-Hexanol, 2-methyl-	0.68154	$C_7H_{16}O$

	Benzenamine, 2,3,4,5,6-pentamethyl	0.35289	$C_{11}H_{17}N$
-0.5	.alpha.-D-Galactopyranoside, methyl 3,6-anhydro-	0.39634	$C_{13}H_{22}O_8$
	4-Methyl-2,5-dimethoxybenzaldehyde	-0.30012	$C_{10}H_{12}O_3$
	Diethyl Phthalate	0.30867	$C_{12}H_{14}O_4$
	4-Ethylphenyl isothiocyanate	0.51770	$C_{17}H_{12}FNS$
	7,9-Di-tert-butyl-1-oxaspiro(4,5)deca-6,9-diene-2,8-dione	0.34210	$C_{17}H_{24}O_3$
	Tetracosane	0.49719	$C_{24}H_{50}$
	Bis(2-ethylhexyl) phthalate	0.48968	$C_{24}H_{38}O_4$
	2-Hexanol, 2-methyl-	0.44739	$C_7H_{16}O$
	1H-Indole, 2-methyl-3-phenyl-	0.39514	$C_{15}H_{13}N$
	Phenol, 2,2'-methylenebis[6-(1,1-dimethylethyl)-4-ethyl-	0.33985	$C_{25}H_{36}O_2$
	Acetamide, N-[4-(trimethylsilyl)phenyl]-	0.77090	$C_{11}H_{17}NOSi$
	Arsenous acid, tris(trimethylsilyl) ester	-0.30318	$C_9H_{27}AsO_3Si_3$

The chemical formulas were extracted from https://pubchem.ncbi.nlm.nih.gov/

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Chapter IV: Induced passive heating on the emergence, early growth and photochemical responses of seedlings of native maize (*Zea mays* L.) genotypes from warm-dry, temperate, and hot and humid climates

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Abstract

The majority of research on the effects of climate change on maize has concentrated on yield, with only a few studies focusing on seedling emergence and growth. Warmer temperatures predicted as a result of climate change will have an impact on seedlings emergence and growth. An experiment was carried out with induced passive heat with the objective of simulating the increase in temperature in emergence, initial growth and photosynthetical parameters of native genotypes of maize from three different agro-ecological zones (warm-dry, temperate, and hot and humid climates) of San Luis Potosí, México. Two different environments, Open Top Chambers (OTC) and control, were used as treatment and two genotypes for each agro-ecological zone were used. A total of 100 seeds were used in a random design with factorial arrangement for each genotype and environment (OTC and control). Abiotic variables (mean daily temperature, minimum and maximum daily temperature and the accumulated heat units) were determined and compared between the two environments and confirmed that the OTC increased temperatures and heat units. The percentage and velocity of seedling emergence and photochemical quenching (qP) were negatively affected by the effect of induced heat while the rate of growth of plants was accelareted and its plant height was increased. These results reveal dependence on the adaptation of the native genotypes. According to seedling emergence and growth, genotypes from less stress conditions (hot and humid (*Huasteca*)) were most affected while those from places with major variations in temperature condicions (warm-dry and temperate (*Altiplano* and *Media* respectively)) were not. We concluded the effect of induced heat diminish the seedling emergence and photochemical quenching while the growth benefited.

Keywords: Climate change; Heat; Open top chamber; Temperature; *Zea mays* seedling

Introduction

Mexico is the origin of maize (*Zea mays* L.), as well as one of the most important centers for its diversification. (Matsuoka et al., 2002). The crop has been Mesoamerica's primary staple for at least two millennia (Goodman and Galinat, 1988) and is at the heart of dynamic cultural features (Hernández Xolocotzi, 1985). People in Mexico and South America have been developing new maize varieties for ages, adapting them not just to local conditions but also to cultural and gastronomic needs (Figueroa et al., 2013). The state of San Luis Potosí (SLP) has also been considered as a potential source of maize genetic variability. In research conducted by Ávila-Perches et al. (2010), fourteen variants of maize were identified. The large abundance of maize varieties in the state could be attributed to a wide variety of ecosystems, comparable to what occurs throughout Mexican territory. This allows diverse agroecological regions to be distinguished, ranging from warm and humid climatic conditions to dry and hot or temperate ones. (INEGI, 2012). Furthermore, it is likely that the number of maize variants throughout the state is significantly more than that reported by Ávila-Perches et al. (2010), because 11 variants were identified in just three cities of the

Huasteca, a region that represents a fraction of the entire territory of SLP (Heindorf et al., 2019).

According to Collins et al. (2013), Houghton et al. (2001) and Qin (2014), scientific studies and observational data reveal that the global climate has been changing for the past 100 years. In the case of México, climate change could cause an increase in average annual temperature of 1 to 4°C during the current century, depending on population growth scenarios (Change, 2007). Temperature values in SLP are expected to rise from 0.75 to 1.00°C in the short term (2010-2040) and from 2.75 to 3.00°C in the long term (2070-2100) (Medellín-Milan et al., 2006; Ávalos Lozano et al., 2017).

Maize genetic diversity is a source of wealth for the population and can be used to achieve domestic alimentary sovereignty, particularly in the face of climatic change (Preciado Ortiz and Montes Hernandez). According to Cabrera et al. (2002), 76.5% of Mexican farmers cultivate creole or native seeds, with the type of agriculture having the greatest influence. In traditional rural agriculture areas, 80 to 100% of farmers use local or native seeds to grow their crops. However, due to a variety of circumstances, such as water stress, plague infections, and the effects of climate change, among others, their production is often limited, resulting in economic losses, particularly for smallholder farmers known as "*campesinos*" (Bergvinson, 2004).

One of the most vulnerable systems to climate change is the agriculture system. The quantity and quality of agroclimatic resources associated with food production have changed as a result of global climate change in time and space (Bocchiola et al., 2013; Pais et al., 2020). Scientific reports by Adeagbo et al. (2021); Chen and Pang (2020); Fei et al. (2020); Sato et al. (2020); Ureta et al. (2020) and Cao et al. (2019) have demonstrated that climate change and variability have a significant impact on maize production. Therefore, climate change poses a negative impact on maize yield and seedling emergence due to the increase in mean temperature as Tumbo et al. (2020) stated and according to Hatfield and Prueger (2015) increased temperatures have a greater effect on grain production than on vegetative growth. Furthermore, recent evidence suggests that maize is particularly susceptible to high temperatures during gametogenesis, flowering, and early grain filling stages of crop growth (Prasad et al., 2020). That means, the rise in temperature caused by climate change has had a deleterious impact on ecophysiological processes such as germination, seedling establishment, and agricultural production systems (Mercer et al., 2008; Pappo et al., 2021).

The state of SLP is located on the Mexican Central Plateau, between parallels 21°10' and 24°32' north latitude and 98°20' and 102°18' west longitude, according to the National Institute of Statistics and Geography (INEGI, 2012). It has an area of more than six million hectares, of which 918 thousand hectares are dedicated to agricultural production. The entity is characterized by having basically three important agro-ecological regions. 1) *Huasteca*: formed by the foothills of the "*Sierra Madre Oriental*", it has a territory of 10,676.5 km^2 and its altitude varies between 50 and 800 m asl. It has extensive fertile plains and represent a hot and humid climate. 2) *Media*: with elevations ranging from 883 to 2000 m asl, its territorial extension is 13,509 km^2, and it has a steppe and temperate climate, with average rainfall ranging from 500 to 700 mm per year; occasionally frost and hail occur at the start of the rainy season. 3) *Altiplano*: with a warm-dry climate, it is located in the state's northern and western sections. In this region, the average temperature fluctuates between 15 and 20°C and it has an average height of approximately 2,000 m asl, where early frost in October and late frost in May are common.

Annually, nearly 14,000 ha of maize are cultivated in the state of SLP, with a high proportion, around 80%, cultivated in no-control environments (SIAP, 2017). As a result, maize output is heavily reliant on the modified genotypes' resistance to environmental factors and multiple extremes in the climate. This discovery could indicate the existence of maize genotypes that are extremely resistant to extreme climatic conditions, implying the possibility of utilizing such phylogenetic resources.

The study of native maize genotypes from the diverse environments present in SLP can assist in discovering and understanding how maize species adapt to environmental conditions they confront during growth and establishment, which is required to anticipate some of the consequences of climate change on the abundance and distribution of species (Dávila et al., 2013). In addition, the abundance of maize breeds or native genotypes, as well as their adaptations to a variety of climatic situations, could provide alternatives to cultivation in scenarios that are likely to occur as a result of the related effects of climate change. Then, the aim of this investigation was to evaluate the emergence, initial growth and photosynthetical parameters of native maize genotypes coming from different climates and/or agro-ecological zones to the effect of induced passive heat. The above-mentioned, with the hypothesis that when native genotypes suited to specific local conditions are subjected to relevant effects of climate change, their emergence, initial growth, and photosynthetical parameters respond differently depending on their origin.

Material and Methods

Maize native genotype selection

The genotypes were collected in the state of SLP, where three agro-ecological zones were determined based on mean annual temperature and precipitation, with average temperatures and precipitation of 14.5, 18.5 and 22.5°C; 400, 700, and 1200 mm, respectively (Noyola-Medrano et al., 2009). These agro-ecological zones were given the names *Altiplano*, *Media*, and *Huasteca*, and their climates were classified as war-dry, temperate, and hot and humid, according to Garcia (2004) adaptations of the Köppen climatic classification system. In addition, Figure 1 and Table 1 describe some features. 37 genotype seed samples were obtained in the following order: 10 from *Altiplano*, 11 from the *Media*, and 16 from

Huasteca. The obtained samples were evaluated according to the standards established by Carballo and Benítez (2003). A total of 14 variables were described in this way: longitude (cm), diameter (mm) and conicity of cob, number of rows per cob, number of grains per row, row arrangement, color and grain type, dry weight of 100 seeds (g), volume (mL) of 100 seeds in 50 mL, longitude (mm); thickness (mm) and wide (mm) of grain, phenological term (months). The prior data was supplemented with the producer's data on temperature and rainfall. The following scale was used to organize the data: low, regular, and high (Diédhiou et al., 2021).

The resulting groups of the genotypes of maize used in this investigation had a grade of internal homogeneity and external heterogeneity and were representative of all the 37 collected samples of the state of San Luis Potosí. A multivariate analysis was carried out to form groups and the following genotypes were used: purple maize (genotype A10) and A11 from *Altiplano*; M4 and M11 from the region *Media* and H10 and H11 from the *Huasteca* zone. All the genotypes used in this investigation had the same phenological cycle (3 months).

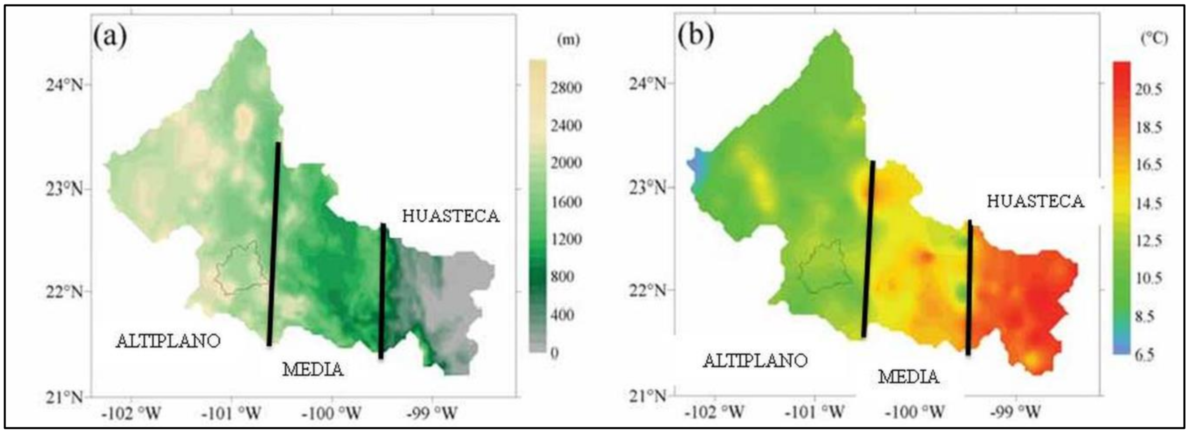

Figure 1. Horizontal distribution of (a) field elevation and (b) annual mean temperature in the three agro-ecological zones of San Luis Potosí (México). Adapted from Noyola-Medrano et al. (2009).

Table 1. Climatic characteristics and mean annual temperatures of the three differents climates of the state of San Luis Potosí, México.

Genotypes	Agroclimatic zone	Predominate climate based on modifications of the Köppen climate classification system	Mean annual temperature
A10		BS1kw(e)gw"	14.5°C
A11	*Altiplano*	BSohw(e)gw"	
M4		Cb(w2)(w)(I')	18.5°C
M11	*Media*		
H10		(A)Cam(f)(e)w"	22.5°C
H11	*Huasteca*	Am(e)gw"	
References		García, 2004.	(Noyola-Medrano et al., 2009)

Experimental establishment, design and agronomic practices

The experiment was established at the climate change research services of the Faculty of Agronomy and Veterinary Sciences of the Autonomous University of San Luis Potosí. The geographical coordinates of the locality are 100°01' 22" west and 22°12' 27" north latitude, at 1,883 m asl. All the maize genotypes were raised in a randomized block design with five replications in each environment. The investigation included a total of 30 treatments that resulted in a factorial arrangement of 2 x 3. The first factor was represented by the environment [passive induced heat with the use of Open Tops Chamber (OTC) and control], while the last one by the agro-ecological zone procedence of the genotypes of maize (*Altiplano*, *Media* and *Huasteca*). Each genotype had 10 seeds per experimental unit, and each plot included two experimental units with a total of 100 seeds for treatment.

Agronomic practices and plant protection measures (daily irrigation to prevent the effect of water stress and elimination of the undesirable plants) are accomplished throughout the crop growth period. Irrigation was done immediately after sowing.

Simulation of the induced passive heat

Open top chamber (OTC) structures were used to simulate the induced passive heat. These structures allow for passive heating and are a simple method for monitoring plant responses to warming in the field (Aragón-Gastélum et al., 2014; Aragón-Gastélum et al., 2017). The OTCs were constructed using UV-resistant transparent acrylic (3 mm thick; wavelength transmission 110 < 280 nm) in accordance with Mølgaard and Christensen (1997). The finished structures were 0.5 m tall, 1.5 m wide at the open top, and 2.08 m wide at the surface base. When compared to external ambient circumstances, this OTC design raises the air temperature by 1.9 to 5.0°C during the day (Aragón-Gastélum et al., 2014; Aragón-Gastélum et al., 2017; Musil et al., 2009; Nedunchezhiyan et al., 2020). Across the experiment, the magnitude with which OTCs altered the microclimate (air temperature) was regularly recorded both within and outside these structures.

Abiotic variables measurement

Temperatures were registered with data-loggers HOBO U23 (Onset Computer Corporation, MA, USA). Each OTC and control plot had one data logger mounted 10 cm above the ground in the center. The readings were scheduled to be taken every hour and averaged daily. These measurements were taken from October 11 to December 12, 2020, and the daily mean, minimum, and maximum air temperatures in each environment were calculated using the recorded data (OTCs and control). With the daily mean air temperature, the daily accumulated heat units were calculated with the residual classic method, which uses the following expression (Bierhuizen and Wagenvoort, 1974; Ruiz et al., 2002).

$$\text{Daily accumulated heat units} = \text{DMAT} - \text{Tb}$$

Where:

DMAT: Daily mean air temperature

Tb: 10°C base temperature for maize

In addition, the sums of the daily accumulated heat units during all the experiment were used to determine the Accumulated heat units or growing degree days (GDD) (Yousaf et al., 2020) for each environment and were compared between the two treatments.

Seedling emergence variables

Percentage of seedling emergence (%)

The percentage of seedling emergence was measured in five replications of 20 seeds each, for a total of 100 seeds evaluated from the first day after sowing to the 15th day. The percentage of seedling emergence calculates the number of seedlings that emerged for each genotype during the experiment. For that, the following formula was used:

$$\text{Percentage of seedling emergence (\%)} = \frac{\text{Number of emerged seedlings}}{\text{total of seeds sowed}} \times 100$$

Velocity of seedling emergence

The velocity of seedling emergence (emerged seedlings.day^{-1}) measured the number of seedlings emerged at the end of the evaluation of the percentage of seedling emergence. The following formula was used:

$$\text{Velocity of seedling emergence (emerged seedlings. day}^{-1}\text{)} = \frac{\text{Number of emerged seedlings}}{\text{15 (days after first emergence)}}$$

Seedling growth variables

Rate of growth

The rate of growth (RG, cm.day^{-1}) was calculated over a 10 days period and was defined as the increment in longitude of the seedlings measured from the base of the soil to the top of the longest leaf. The equation below was used Del Pozo et al. (1987):

$$\text{RG (cm. day}^{-1}\text{)} = \frac{\text{L2} - \text{L1}}{\text{T2} - \text{T1}}$$

Where:

The seedling longitudes at 5 and 15 days are L1 and L2, respectively, while T1 and T2 are the previously indicated times.

Plant height

Plant height was measured 35 days after the emergence of seedlings. A total of 20 seedlings for each genotype in different environment were selected and measured with a graduate ruler. Measurement was made from the soil to the top of the longest leaf.

Photosynthetic variables

The variables of chlorophyll fluorescence were evaluated on the third leaf of each plant. 25 plants were measured from every treatment. Measurements were performed between 12 and 14 pm, with a portable photosynthesis System (Li-cor LI6400XT).

The chlorophyll fluorescence parameters reported were: the effective efficiency of the PSII (ϕ_{PSII}), which was exposed to a distant red light for a few seconds to force electron migration between photosystem I (PSI) and photosystem II (PSII) (Buchanan et al., 2015). In addition, after applying a series of saturation pulses under increasing actinic irradiation, photochemical quenching (qP) was determined with saturated light pulses per 20 s (Kalaji et al., 2014). ϕPSII is the proportion of absorbed energy being used in photochemistry and qP indicates the proportion of PSII reaction centres that are open, and the larger qP value, the higher light energy conversion efficiency. Thus, whereas ϕPSII relates to achieved efficiency, qP gives information about the underlying processes which have altered efficiency (Maxwell and Johnson, 2000).

Statistical analysis

The data for the variables seedling emergence, growth, and chlorophyll fluorescence were analyzed using the GLM procedure of the program Statistical Analysis System (SAS, 2003). The model is characterized by two fixed factors, namely 'genotypes' and 'environment' as well as their interaction 'genotypes x environment'. The Tukey test was used to check for significant differences between the treatment means. If $P < 0.05$, the effects and interactions were considered significant. Data were examined for normality before being analyzed, and log-transformation was employed to correct them. The abiotic variables were analyzed using a repeated measure analysis of variance (ANOVA). They were compared between the OTC and control environments and summarized for each data-logger.

Results

Abiotic variables

During the experiment, the mean daily temperature (±estandar error) was 17.52±0.45°C inside OTC and 15.34±0.45°C in control. This variable significantly differed between the treatments ($F_{(4,69)}=16.42$, $P<0.0001$) and that means the structure of OTC increased the mean daily temperature during the experiment to 2.18°C (Figure 2a). On the other hand, the daily minimum temperature was 7.31±0.46°C inside the OTC and 3.49±0.47°C within control and significantly differed between the two environments ($F_{(4,69)}=18.65$, $P<0.0001$). The induced passive heat increased the minimum daily temperature to 3.82°C (Figure 2b). Daily maximum temperature was also affected by warming ($F_{(4,69)}= 21.82$, $P<0.0001$). The maximum value of this variable was registered in OTC, with a mean of 31.26±0.71°C, while it was 27.05±0.76°C in the control environment. The induced passive heat also increased the daily maximum temperature to 4.21°C (Figure 2c). The accumulated heat units was also affected by the induced heat passive ($F_{(4,69)}= 16.42$, $P<0.0001$). Then, the accumulated heat units recorded in OTC were statistically superior to the ones inside the control plots. The OTC treatment recorded 80.73 GDD (Growing Degree Days) more in comparison to the control treatment during the 62 days. That means the induced passive heat increased the accumulated heat units during all the experimentation (Figure 2d).

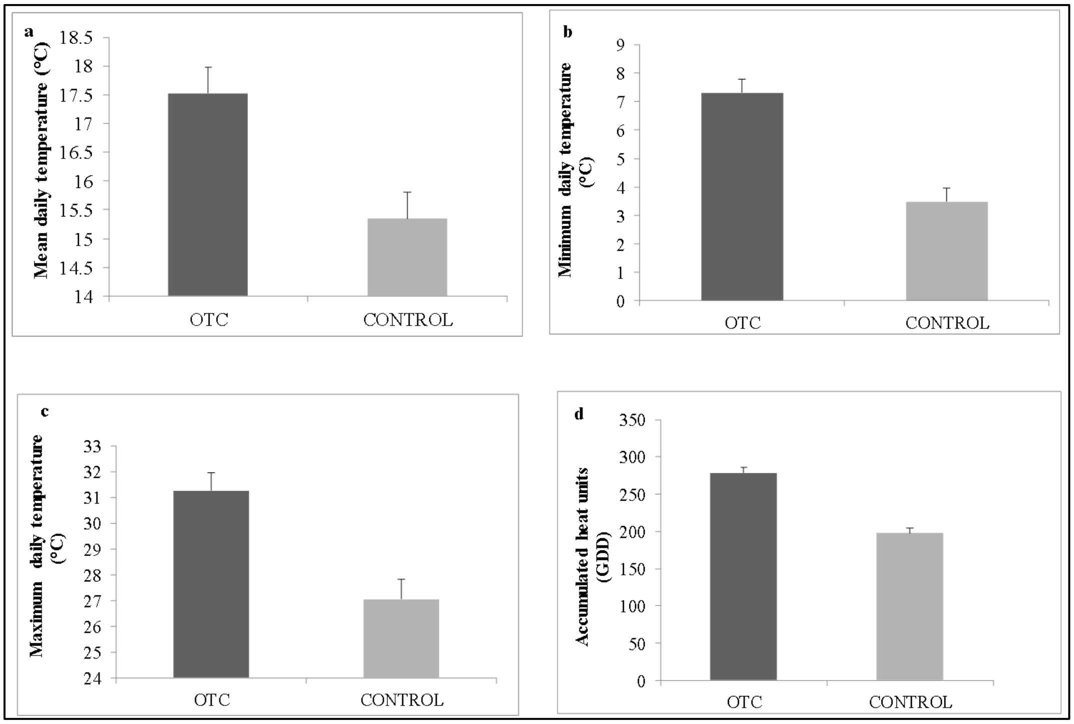

Figure 2. Average daily values of the registered temperatures and the accumulated heat units calculated during all the experiment. a) Mean daily temperature; b) Minimum daily temperature; c) Maximum daily temperature and d) Accumulated heat units in Open Top Chamber (OTC) and control treatments. Vertical bars indicate the standard error (n= 5).

Variables of seedling emergence

It was possible to observe significant effects of genotypes and the environment on the percentage of seedling emergence using analysis of variance. Only the factor genotype significantly affected the velocity of seedling emergence. The interactions G x E were not significant for any of the emergence variables (Table 2).

Table 2. Results of the analysis of variance of the emergence, growth and chlorophyll fluorescence variables of native genotypes of maize from the state of San Luis Potosí (Mexico).

Variables	**Seedlings emergence**				**Seedlings growth**				**Chlorophyll fluorescence**			
Factors	PE		VE		RG		PH		ϕPSII		qP	
	MS	F	MS	F	MS	F	MS	F	MS	F	MS	Fval
Genotype (G)	0.611	31.85***	1.58	186***	0.05	1.65ns	95.07	17.2***	0.0008	1.47ns	0.04	2.59ns
Environment (E)	0.01	1.02*	0.004	0.48ns	0.48	14.8**	403.59	73.1***	0.001	2.14ns	0.08	5.09*
G*E	0.01	0.9ns	0.01	1.28ns	0.14	4.49*	14.97	2.71*	0.0003	0.68ns	0.01	0.8ns
CV	7.51		15.13		20.5		14.63		1.58		10.18	

MS: Mean Square; F: Fvalue; PE: percentage of emergence; VE: velocity of emergence; RG; rate of growth; PH: plant height. ϕPSII: Effective efficiency of photosystem II; qP: Photochemical quenching; CV: Coefficient of variation; ns: no significant; *; **; ***: significant and highly significant at $P < 0.05$, 0.01 and 0.001 respectively.

Values of the percentage of seedling emergence and velocity of seedling emergence were different amongst genotypes. The genotypes from *Media* and *Altiplano* and one from *Huasteca* (H11) registered high values of percentage of emergence and velocity of emergence while the other one from *Huasteca* (H10) obtained the lowest values. The average of the percentage of seedling emergence of the genotypes with high values was up to 60%. However, M11 and A11 registered 90% of the percentage of seedling emergence. In addition, H10 registered the lowest values of percentage of emergence and velocity of emergence with (less than 5% and 0.1 emerged seedlings.day^{-1} respectively) (Figure 3A and 3C). The induced passive heat decreased the percentage of seedling emergence of the maize seedlings. The percentage of seedling emergence registered in control was statistically superior to that in OTC, with a mean of 68.16% and 65.20%, respectively (Figure 3B). The velocity of seedling emergence in OTC and in control was similar (Figure 3D).

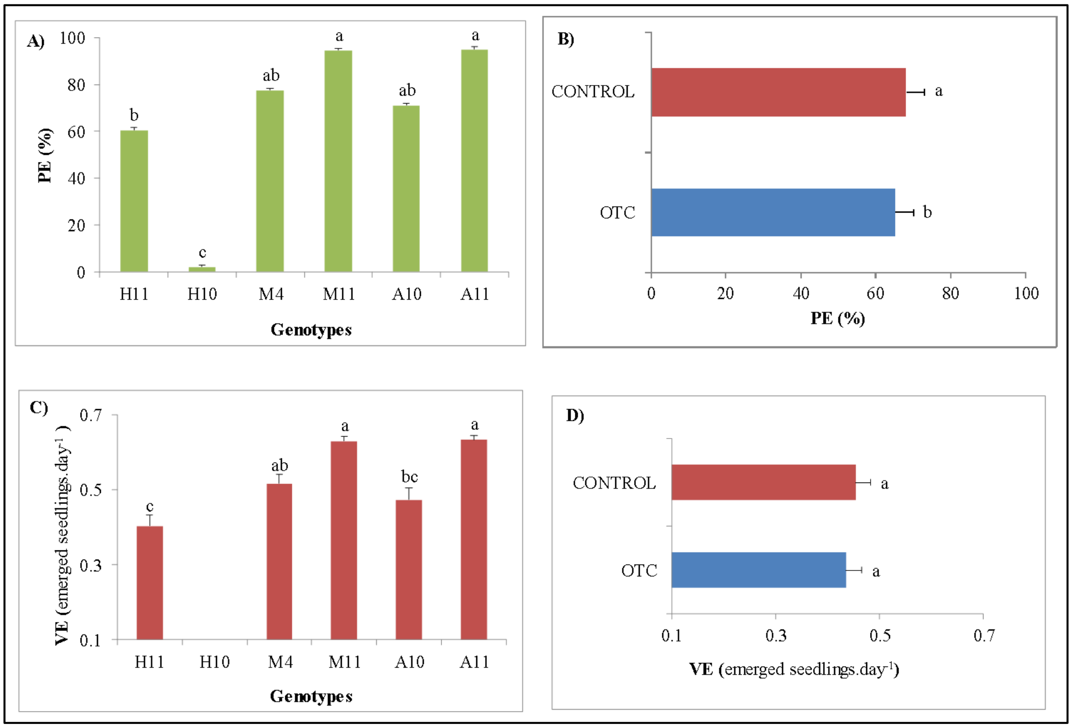

Figure 3. Effect of induced passive heating on the emergence variables of seedlings of native maize genotypes from three different agro-ecological zones of San Luis Potosí (México). H: *Huasteca*; M: *Media* and A: *Altiplano*. PE: percentage of seedlings emergence; VE: velocity of seedling emergence; OTC: Open Top Chamber. The letters a, b, c and d indicate significant differences according to the Tukey test ($P < 0.05$). VE H10 in C) did not appear because there PE was low and insufficiently emerged. Vertical bars indicate the standard error, (n= 20).

Variables of growth

Rate of growth and plant height were dissimilar in genotypes due to warming (Table 2). Majority of the genotypes indicated an increase in growth rate in OTC except A11 and H11, which registered no significant differences between the two treatments (OTC and control). The genotypes M4, M11 and A10 grew faster in OTCs; rates of growth of these genotypes were statistically superior to those found in control treatments. The mean of rate of growth ranged from 0.96 (M11) to 1.03 cm.day^{-1} (A10) in OTC conditions while in control it ranged from 0.76 (A10) to 0.87 (A11) cm.day^{-1} (Figure 4A). The highest values of plant height were recorded in OTC, except for H11. That means, the plant height of the maize genotypes was significantly affected positively by the passive induced heat. Significant differences were observed for plant height among the OTC and their mean ranged from 14.05 to 18.94 cm. In a control treatment, plant height ranged from 13.05 to 16.02 cm (Figure 4B). It should be noted that the genotypes from *Altiplano* and *Media* recorded the heighest values of the seedlings while the one from *Huasteca* recorded the lowest plant height and rate of growth in the two environments.

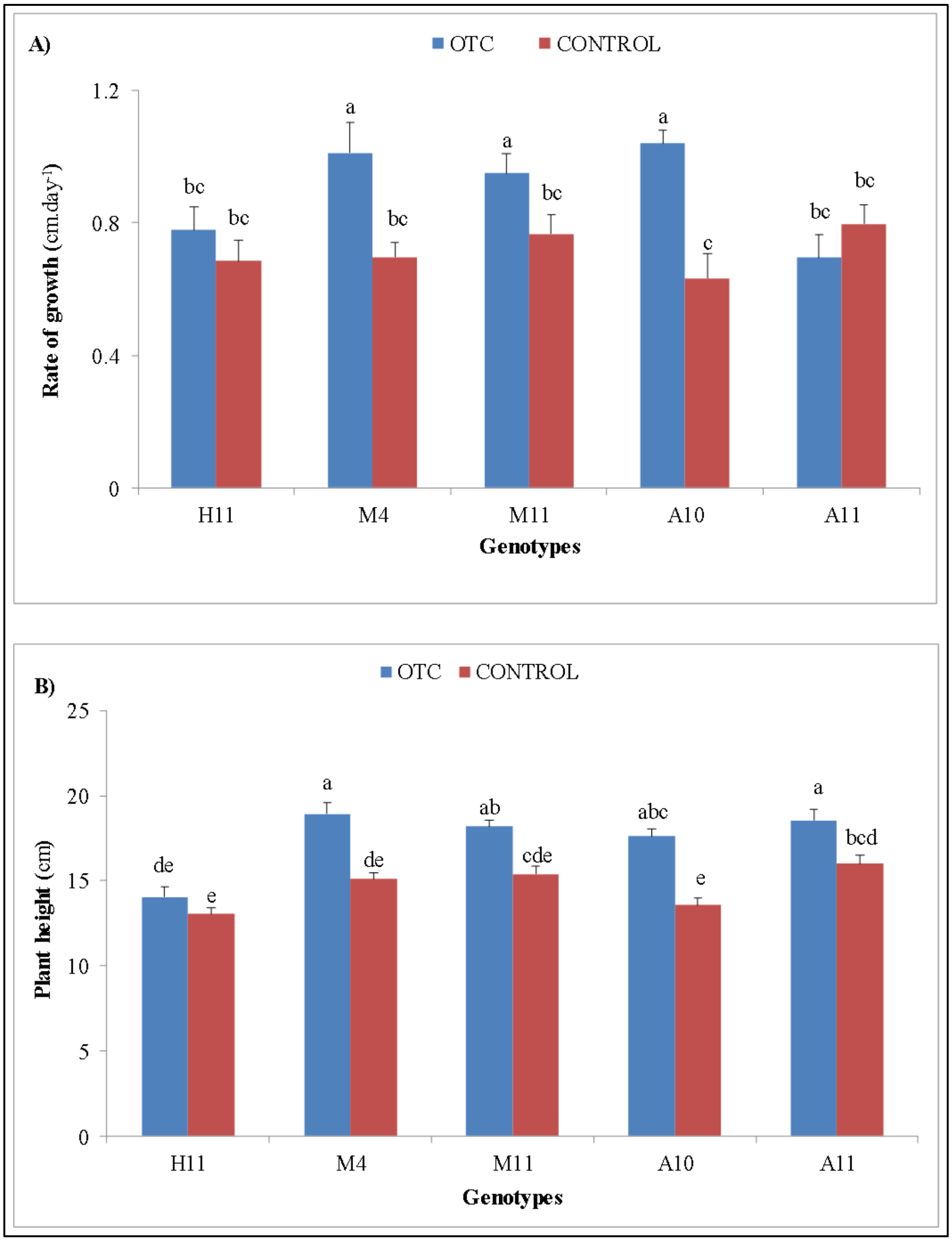

Figure 4. Effect of induced passive heating on variables of growth of native genotypes of maize from different agro-ecological zones of San Luis Potosí. A: *Altiplano*; M: *Media*, H: *Huasteca*. The letters a, b, c, d and e indicate significant differences according to the Tukey test (P < 0.05). H10 did not appear because they did not emerged sufficiently. Vertical bars indicate the standard error (n= 20).

Chlorophyll fluorescence variables

Photochemical quenching was reduced ($P < 0.05$) by the effect of warming into the OTC (Table 2; Figure 5). The mean of photochemical quenching recorded at control was significantly superior with 0.36 against 0.29 obtained in OTC (Figure 5). That mean the increase of temperature will affect negatively the photochemical quenching of the maize seedlings. The effective efficiency of photosystem II (ϕPSII) was not affected by simple effects and their interaction was not significant (Table 2).

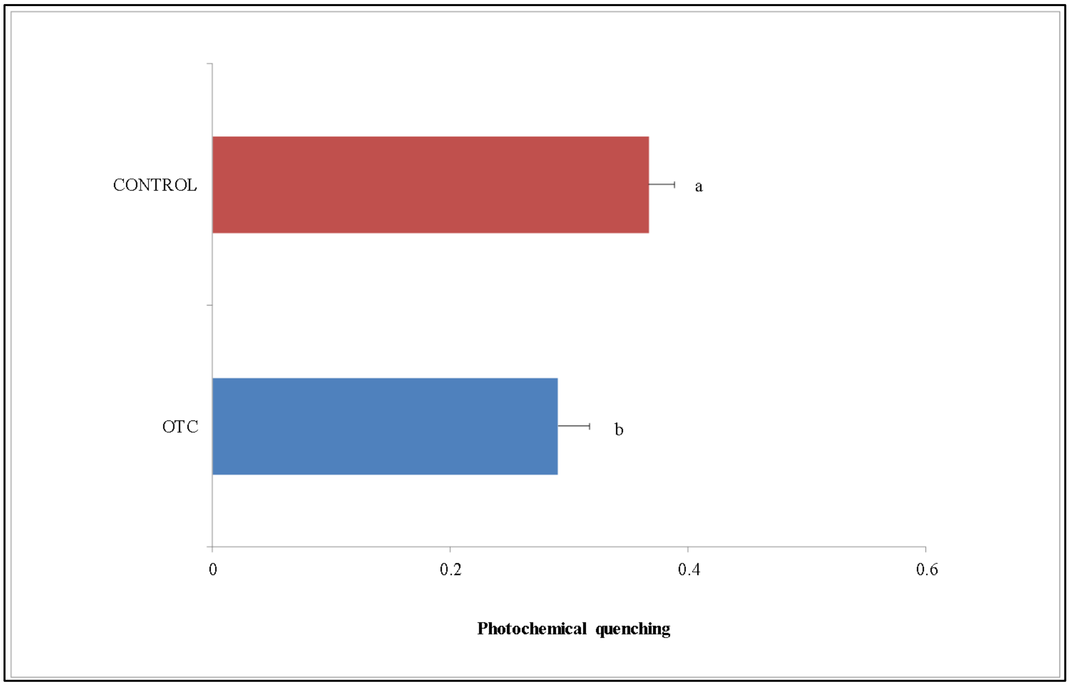

Figure 5. Effect of induced passive heating on photochemical quenching (qP) of native genotypes of maize from different agro-ecological zones of San Luis Potosí. OTC: Open top Chamber. The letters a and b indicate significant differences according to the Tukey test ($P < 0.05$). Vertical bars indicate the standard error, (n= 25).

Discussion

This is the first study to investigate the influence of increased air temperature (abiotic variable) under climate change scenarios on genotypes of native maize seedlings from distinct agro-ecological zones in the state of San Luis Potosí (México). The employment of OTC appears to have resulted in accurate temperature projections. Our warming methods resulted in a maximum increase of 2.41°C in the mean daily air temperature for OTC. This was within the expected 1–3°C increase in global warming by the late twenty-first century (Collins et al., 2013; Tejeda-Martínez et al., 2008). Moreover, because of more GDD found in OTC than in control (Figure 2d); the rate of growth and plant height were increased in comparision to maize grown in control. However Dan et al. (2020) stated that low temperatures (GDD<662°C, Mean Temperature<19.0°C, or maximum temperature<24.0°C) and high temperatures (GDD>641.4°C, or minimum temperature>21.5°C) decreased the rates of growth of maize. In our study, the emergence variables and photochemical quenching were affected for the accumulation of more heat units as reported by Amirjani (2012) on wheat seedlings (*Triticum aestivum* L.). According to Alvarado and Bradford (2002), heat units or thermal time model conforms to the timing of germination (in our case emergence). Ritchie and Nesmith (1991) applied this model to plants and animals and found that temperature has a different response function on leaf development rate than it does on growth rate. These results explain why the growth of maize genotypes in our investigation was high in OTC in comparison to the control environment. However, it is important to note that in our investigation, we did note evaluate the leaf development size of the native genotyes of maize.

The increase in the mean temperature affects the maize seedling emergence as was registered in our investigation (Figure 3B and D). That means the possible increase in mean temperature expected due to the related effects of climate change will negatively affect the seedling emergence of maize. Bocchiola et al. (2013) reported that an increase in temperature of 2-3°C will limit maize production. Surface air temperature increases reduced agricultural productivity in many crops (Southworth et al., 2000). Muhammad and Basıt (2019) mentioned that differences in seedling emergence of maize might be due to variation of mean monthly temperature and solar intensity and that variation could difficult for complete growth and developmental stages. As was indicated, an increase in temperature reduces the seedling emergence of maize plants and it was stated it also reduces production. Then warming due to climate change might affect maize crops from early development stages as seedling emergence. However, the findings by Li et al. (2014) did not corroborate with ours. They reported the increase in temperature provided better conditions for maize germination, emergence and grain filling.

Genotypes from *Altiplano* and *Media* were more tolerant to warming than the one from *Huasteca*. These results can be related to the different climatic conditions in the *Huasteca* region in comparison to those from *Altiplano* and *Media*. In comparison to the agro-ecological zones, *Altiplano* and *Media*, the zone *Huasteca* has the highest mean annual temperature and rainfall. (Figure 1 y Table 1) (Diédhiou et al., 2021). In addition, the

Huasteca zone had less monthly evapotranspiration, more cloudiness, a higher monthly average temperature, and thus a higher intensity in terms of the amount of water received in 24 hours (Campos-Aranda, 2018; Noyola-Medrano et al., 2009). Then the genetic material of genotypes from *Huasteca* is already adapted to less stressful conditions than that of genotypes from *Altiplano* and *Media* (Diédhiou et al., 2021; Jiang et al., 1999). Some of the responses obtained from the native maize genotypes can be attributed to environmental factors. Furthermore, according to Alonso-Blanco et al. (2003) and Schmuths et al. (2006), the rate of emergence of maize, wheat, bean, and rice seeds varies significantly, and this variation is determined by the interaction of the seed genotype with the specific environment of their origin.

Warming promoted high levels of growth in maize seedlings in our research, at least in majority of the studied genotypes. That mean the increase in temperature accelerated the rate of growth and the plant height of the seedlings. In addition, maximum plant heights of maize with the use of OTC were reported by Silva et al. (2012). However our results do not agree with what was mentioned by Argosubekti (2020) that stated negative results in the growth of plants especially when extreme temperatures coincide with the critical stage of plant growth. It should be noted that in our case, in the time that the experiment was conducted; the maximum daytime temperatures did not exceed 40°C. According to Hatfield and Prueger (2015), the rate of plant growth and development is largely influenced by temperature. In addition, Tollenaar et al. (1979) indicated that a temperature-based classification of maize is crucial since it is necessary in agriculture to identify the adaptation of genotypes to specific environments. On the other hand, is important to mention the geographical characteristics of the regions of origin of the genotypes, especially the ones from *Altiplano* and *Media* where the agricultural conditions are characterized by a lower rainfall quantity and a lot of heat during the planting periods of the maize crop in comparison to the one from *Huasteca* (Figure 1 and Table 1) (Diédhiou et al., 2021; Noyola-Medrano et al., 2009).

A simple effect for the photochemical quenching parameter due to the effect of the two environments (OTC and Control) was recorded. In this same sense, the photochemical quenching registered under control conditions were statistically higher than those in OTC. Our results agree with Xia et al. (2021) findings, that the qP of the two maize varieties decreased significantly under warming treatment. Schenone et al. (1994) indicated some differences in the measured of the physiological parameters of bean (*Phaseolus vulgaris* L.) due to the chambers effects which certainly caused by the physical structure of the OTC. In our investigation the photochemical quenching was affected by the passive induced heat. According to Silva et al. (2012) OTC can reduce up to 25% the photosynthetically active radiation and increase the air and leaf temperature. These results are consistent with ours, as there was a reduction of photochemical quenching and an increase in air temperature with respect to the control environment. Yüzbaşıoğlu et al. (2017) reported similar results to ours for maize seedlings grown in high temperatures, keeping in mind that 20/25°C is close to our mean diurnal temperature during the experiment. Also, our results were similar to other researchers such as Li et al. (2020) who found that an increase in temperature reduces photosynthesis in maize leaves. On the other hand, the effective efficiency of photosystem II (ϕPSII) was not affected by simple effects and their interaction was not significant (Table 2). That means the induced passive heat and the origins of the native genotypes had no influence on the ϕPSII and can be relacionated to the energy needed for photosynthesis and the age of the maize seedlings. In the same way, Guidi et al. (2019) reported that photoinhibition occurs when light energy exceeds the amount of energy used for photosynthesis, characterized by a decline in the ϕPSII. In addition, Sales et al. (2013) and Trujillo et al. (2013) reported that the photosynthetic apparatus depends on the severity and duration of the stress.

This study analyzed the effect of induced passive heat, or the increase of temperature, in native maize genotype seedlings from different agro-ecological zones of the State of San Luis Potosí. The influence of irrigation and extreme weather events on the seedlings were not taken into consideration because the smallhollders of the state do not use those practices in their fields. Huasteca genotypes were the most affected, and Mercer et al. (2008) found that tropical temperate maize landraces do not tolerate hot weather due to local adaptation. Since maize was originally categorized, different races and genotypes have been related to particular environmental conditions (Wellhausen et al., 1952). Mexican maize was classified by Ruiz Corral et al. (2008) based on rainfall, photoperiod, and, most importantly, temperature of local adaptations or origins. These findings have crucial implications for thinking about the effects of climate change adaptation on maize in the country in general, and the state of San Luis Potosí in particular, because they highlight a way to adopt to contrast the negative effects of climate change while taking local conditions into account. Most importantly, this is the first study to investigate effects of the induced passive heating in seedling emergence, initial growth and chlorophyll fluorescence of native seedling genotypes of maize taking account the three agro-ecological zones of the state of San Luis Potosí. Taking into account that Hernández et al. (2021) reported that a solid start to the plant cycle (seedling stage) is critical for achieving a good end performance and a high grain yield. However, high seedling performance alone is insufficient to ensure a good grain production at the conclusion of the cycle. It is important to note that, in the *Huasteca* agro-ecological zone, the temperature oscillation in one day and in the year is much lower than in the *Altiplano* and *Media*. So the *Altiplano* and *Media* genotypes are adapted to tolerate extreme temperatures (which explains their best results) while the *Huasteca* genotypes are adapted to high temperatures, but with less variation and better climatic conditions for plant growth.

Conclusions

Findings of the present study showed differential effects of warming on physiological attributes of native maize seedlings. The emergence of the seedlings and the photochemical quenching of the maize seedling genotypes were affected negatively by the increase in air temperature. The plant growth benefited from the increase in temperature and was accelerated. Also, the use of open top chambers generates increments of the air mean temperature, minimum and maximum daily temperatures and the accumulated heat units. The genotypes from the *Huasteca* region (hot and humid climate), which has a higher mean annual temperature, were the most affected, and this is linked to the local conditions of adaptation of their genetic material, which is less stressed than the materials from the *Altiplano* (warm-dry climate) and the *Media* (temperate climate), which have unfavorable conditions and stressful environments for maize plant growth.

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Author Contributions

Hugo Magdaleno Ramírez-Tobías project leader, obtained the financial resources for the study execution, supervised the research project. Coordinated the whole research work, designed the experimental work and revised/edited the manuscript. Idrissa Diédhiou was mainly responsible for conducting fieldwork, research design, data analysis, and wrote the first draft of the manuscript. Javier Fortanelli Martínez reviewed the manuscript and contributed to the final version of the manuscript. Rogelio Flores Ramírez reviewed the and contributed to the final version of the manuscript. Joel Flores reviewed the manuscript, discussed the research results and contributed to the final version of the manuscript.

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Chapter V: Photosynthetic capacity, growth, development and yield parameters of milpa (maize+bean+squash) from warm-dry, template and hot and humid climates under induced warming

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Main conclusion **Induced passive heat negatively affected *milpa* yield and photosynthetic capacity of maize and bean, while squash increased the photosynthetic capacity. The warming benefited plant growth and development.**

Abstract

Relay intercropping of *milpa* system is practiced on a large scale by Mexican smallholders. Warmer temperatures predicted as a result of climate change will have an impact on *milpa*. An experiment was carried out with induced passive heat with the objective of simulating the increase in temperature on physiological, photosynthetic, and yield parameters of *milpa* from different regions of San Luis Potosí, Mexico. Two different environments, Open top chambers (OTC) and control, were used as treatment and three *milpa*. A total of 12

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experimental units of 13.13 m^2 were used in the random design, with a factorial arrangement of 2 x 3 x 2. Abiotic variables (minimum, maximum, and mean daily temperatures, and accumulated heat units) were determined and compared between the two environments and confirmed that the OTC increased the abiotic variables. The growth and development parameters increased under the warming effect. Furthermore, the *milpa* from hot and humid climate was the least affected. In contrast, the warming considerably delayed yield parameters. The squash suffered the most, while the bean benefited the most. The warming affected the chlorophyll fluorescence and gas exchange differently for each crop. However, at an early stage, maximum photochemical efficiency (Fv/Fm) and non-photochemical quenching (qN) for bean and maize were reduced, while at a late stage they were Fv/Fm, photochemical quenching (qP), and qN for maize; stomatal conductance and transpiration rate of the squash were improved under the warming treatments. We concluded the effect of induced heat delayed yield and photosynthetic parameters while growth and development benefited.

Keywords: climate change, temperatures, heat stress, OTC, intercropping system.

Introduction

Milpa is an agro-ecosystem composed by maize (*Zea mays* L.), bean (*Phaseolus* spp. or *Vigna unguiculata* (L) Walp), squash (C*ucurbita* spp.) and other species that guarantees the foodways' of Mesoamerica (from central Mexico to the northern and western portions of Central America) (Zizumbo-Villarreal et al., 2012). Archaeobotanical and genetic-molecular studies show that maize and *Cucurbita argyrosperma* Hort. Ex L. H. Bayley were domesticated around 9,000 BP in western Mesoamerica (Matsuoka et al., 2002; Piperno et al., 2009; Ranere et al., 2009), as was *Phaseolus vulgaris* L. (Kwak et al., 2009), and being then possible that in this area they could have been integrated as an agro-ecosystem.

In Mexico, maize is the most important crop, as a large genetic diversity of the crop is reported. This country is also the center of domestication of *Zea mays*. Mexico's maize agro-ecosystems preserve not just germplasm, but also human knowledge and behavioural traditions that reflect the crop's long co-evolution with human communities (Bellon, 1991; Ureta et al., 2020). Various management strategies (such as maize intercropping and crops rotation) have evolved in very diverse situations, depending on the climatic, topographic, and biocultural aspects of a specific location (Weerarathne et al., 2017).

This ´*Milpa*´ system has a number of ecological benefits, including atmospheric nitrogen fixation by *Rhizobium* spp. in symbiosis with bean plants, weed control, soil moisture retention, and erosion protection from the squash. Maize, in turn, offers support for the bean plant as well as shade for the beans and squash. Maize also acts as a physical barrier against illness by preventing the spread of spores (Latati et al., 2016; Weerarathne et al., 2017). The *milpa* system, like many others around the world, is based on local technology and the longevity of the plants is dependent on rainfall and climatic conditions (Huffman, 2013; Palacios-Rojas et al., 2020).

Climate change can cause an increment of the average annual temperature from 1 to 4°C during the present century in Mexico, in function of the scenario of the population growth (Field and Barros, 2014; Letcher, 2021; Paglia and Parker, 2021; Stocker et al., 2013). Furthermore, is well is proposed that climate change is affecting food security of the crops grown under *milpa* system, due to altered environmental conditions such as temperature and an increased frequency of extreme climatic events, creating negative impacts on crop yields (Bergvinson, 2004).

Cropping strategies may help to offset the impact of climate change on food security, but few researches have looked at how temperature rises linked to climate change in agricultural practices affect the *milpa* system plant's physiological performance (Islam et al., 2016; Murray-Tortarolo et al., 2018). Such research is required for a better understanding of regional *milpa* system ecological and functional dynamics (Pérez-Hernández et al., 2021b). In addition, only a few research work has been done to characterize the physiological performance of plants under various agricultural management systems in the field (Farhad et al., 2018; Heydari and Pessarakli, 2010). Most of them focus their efforts on maize, forgetting the complexity of the system with the presence of the other crops (bean and squash).

There is therefore scope for a better understanding of the physiological response of the *milpa* system to the increase in temperatures related to the effects of climate change. The use of an Open top chamber (OTC) has been one of the most popular methods for simulating potential plant growth and development. The OTC structure has been used by Aragón-Gastélum et al. (2017); Aragón-Gastélum et al. (2014b); Alatalo et al. (2021) and Chang-Espino et al. (2021) to evaluate the effect of abiotic variables on plants. These studies are helpful in developing strategies for mitigating the negative effects of climate change on plant production in small-scale management systems, where food security is severely challenged by climate change (Nigh and Diemont, 2013).

In the state of San Luis Potosí (SLP) (Mexico), three agroclimatic regions are defined and in each region the smallholders are facing the increase in temperature and other problems related to the effect of climate change such as water stress. This way, it is possible to recognize different agroecological regions, from the warm and humid climatic conditions to the dry and hot or temperate ones. In each region, several native genotypes of maize have been reported and are used by the smallholders in their *milpa* systems (Diédhiou et al., 2021; Heindorf et al., 2021; Heindorf et al., 2019).

Most of the cultivated areas with *milpa* systems in Mexico, and in SLP in particular, are facing critical conditions related to the effect of climate change, such as an increase in temperature. Research as reported in this research may provide knowledge on how to contribute to this by investigating the effect of a rising temperature on the *milpa* systems. In addition, this investigation explores this effect using the *milpa* system existing in the state of SLP and evaluates the physiological response from the early to final stage of each crop in the system. Therefore, the aim of this study was to determine the effect of an increase in temperature on physiological, photosynthetic, and yield parameters of *milpa* systems from different climates of SLP. The above-mentioned, with the hypothesis that physiological, photosynthetic, and yield parameters of each *milpa* system and each crop within the system adapted to particular local conditions respond differently and in dependence of their origins' climate characteristics when exposed to an increase in temperature, which is related to the effect of climate change.

Materials and methods

The three *Milpa* system and their environments characteristics

The crops (maize, bean and squash) were collected in the state of SLP, where three agro-ecological zones were determined based on mean annual temperature and precipitation, with average temperatures and precipitation are 14.5, 18.5 and 22.5°C; 400, 700, and 1200 mm, respectively (Diédhiou et al., 2021; Noyola-Medrano et al., 2009). These agro-ecological zones were given the names *Altiplano*, *Media*, and *Huasteca*, and their climates were classified as warm-dry, temperate, and hot and humid, according to Garcia (2004) adaptations to the Köppen climatic classification system.

For the selection of the bean and squash, previous experiments (exclusively done with maize) in this study allowed us to choose specific farmers for each region. In this context, the farmers who proportionated the maize crops also proportionated the other crops (bean and squash).

In this sense, generous *Phaseolus vulgaris* bean were collected for farmers from the *Altiplano* and *Media*, while *Vigna unguiculata* (L) Walp bean was collected for farmers from *Huasteca*. It is the one used by the selected *Huasteca* farmers in their *milpa* system.

In addition, Figure 1 and Table 1 describe some features. Before this experiment, previous germination experiences were conducted (Diédhiou et al., 2021), and all the crops chosen in this study were 3 months old.

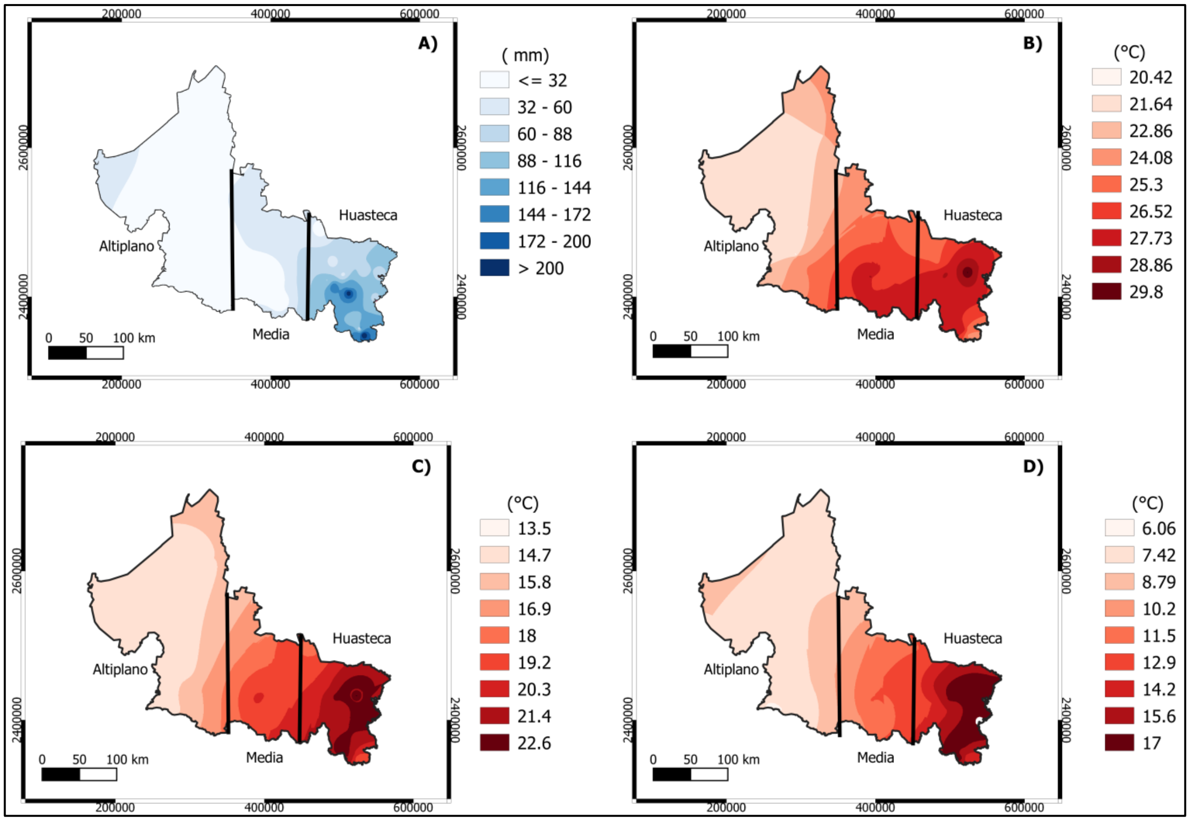

Fig 1. Monthly temperature and precipitation summaries for the state of San Luis Potosí in 2020. A) Precipitation; B) Maximum temperature; C) Mean temperature and D) Minimum temperature. The data was logged from https://smn.conagua.gob.mx/

Table 1. Climatic characteristics of the three regions of the state of San Luis Potosí, Mexico.

Milpa	**Region**	**Geographic coordinates of the points of collection**	**Predominate climate based on modifications of the Köppen climate classification system**	**Climate**
Maize+Bean+ Squash	*Altiplano*	2 062 m a.s.l. -101°7´W 22°16N	BS1kw(e)gw"	warm-dry
	Media	1 390 m a.s.l. -99°32´W 22°8´N	Cb(w2)(w)(I’)	template
	Huasteca	225 m a.s.l. -98°58´W 21°35´N	Am(e)gw"	hot and humid
Reference		García, 2004.		

Experimental establishment, design and agronomic practices

The investigation was carried out at the Faculty of Agronomy and Veterinary Medicine of the Autonomous University of San Luis Potosí. The geographical coordinates of the locality are 100° 01’ 22” west and 22° 12’ 27” north, at 1,883 m above sea level (m a.s.l.) The geographical area corresponds to the *Altiplano* agro-ecological zone of the state of San Luis Potosí and the climate characteristics are shown in Figure 1 and Table 1.

The experiment included a total of 12 plots of 13.13 m^2 (6 plots of Open Top Chamber (OTC) and 6 plots of control) that resulted in a factorial arrangement of 2 x 3 with two replications. The first factor was represented by the environment [passive induced heat with the use of the (OTC) and control], while the last one by the agro-ecological zone procedence of each *milpa* (*Altiplano*, *Media* and *Huasteca*). Prior to maize sowing, weeds were manually eliminated from the soil. Maize was sown by hand, placing four seeds in holes at 7 cm in depth along the rows in each environment. In all the treatments, maize was sown in June 2021, at an approximate density of 40,000 plants per ha. Bean and squash plants were intercropped with maize plants in a ratio of 2:1 in each block respectively, for a total of 8 plants of squash and 12 plants of bean in each block. The bean seeds and squash plants were sown and planted 30 days after the maize to avoid competition between seedlings (Pérez-Hernández et al., 2021b). Agronomic practices and plant protection measures (daily irrigation to prevent the effect of water stress and elimination of the undesirable plants) were accomplished throughout the crop~~s~~ growth period. Irrigation was done immediately after sowing

Simulation of the induced passive heat

Open top chamber (OTC) structures were used to simulate the induced passive heat. These structures allow for passive heating and are a simple method for monitoring plant responses to abiotic variables such as temperature increase in the field (Alatalo et al., 2021; Chang-Espino et al., 2021; Cossani and Sadras, 2021; Silva et al., 2012a). The finished structures were pentagonal at the surface base, with a perimeter of 10.8 m [(2.5 m x 4) + 0.8 m] and a height of 3 m (Figure 2). Each OTC was covered with a transparent natural tubular plastic. When compared to external ambient circumstances, this OTC design raises the air temperature. Across the experiment, the magnitude with which OTCs altered the microclimate (air temperature) was regularly recorded both within and outside these structures.

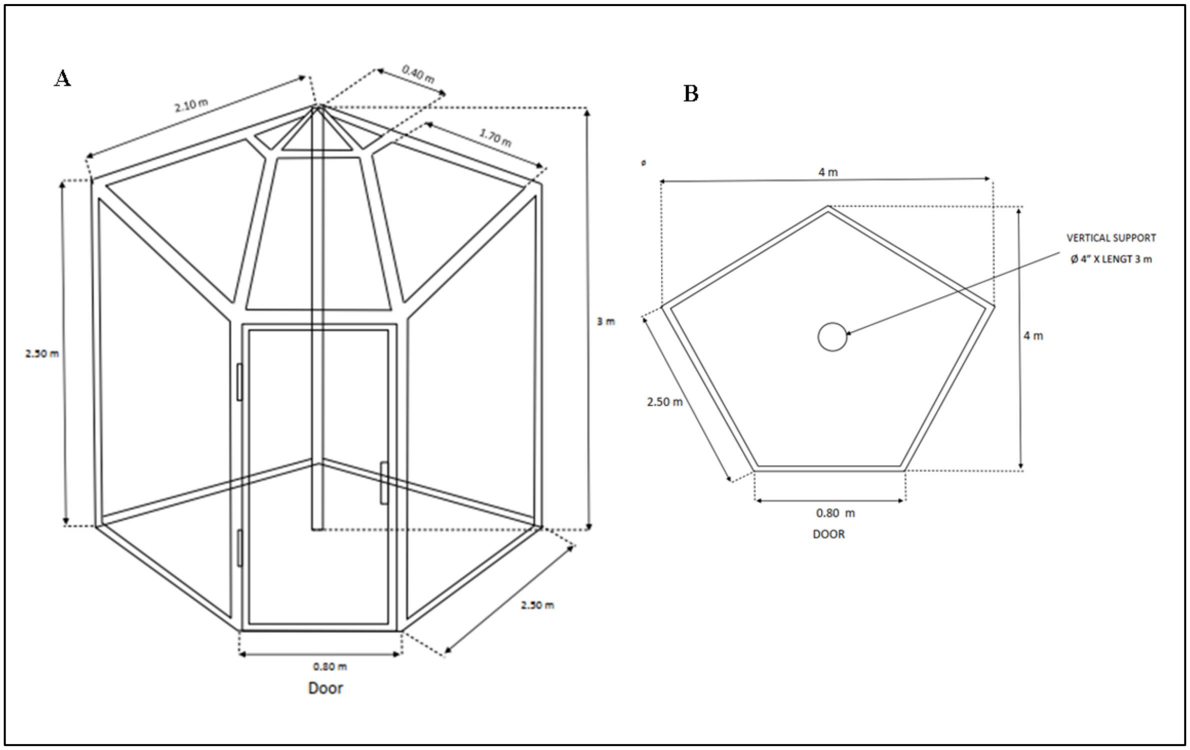

Fig 2. Dimensions and structural details of the open-top chambers (OTC) used to simulate the induced passive heat. A) Frontal view and B) basal view of the OTC.

Abiotic variables measurement

Temperatures were registered with data-loggers HOBO U23 (Onset Computer Corporation, MA, USA). In two selected OTC and control plots, two data loggers were mounted 15 cm and 150 cm above the ground in the center. These two positions allow us to monitor the air temperature in the relative space where the three crops are established. The readings were scheduled to be taken every hour and averaged daily. These measurements were taken from June 27 to November 12, 2021, and the daily mean, minimum, and maximum air temperatures in each environment were calculated using the recorded data. With the daily mean air temperature, the daily accumulated heat units were calculated with the residual classic method, which uses the following expression (Bierhuizen and Wagenvoort, 1974; Ruiz et al., 2002).

$$\text{Daily accumulated heat units} = \text{DMAT} - \text{Tb}$$

Where:

DMAT: Daily mean air temperature

Tb: base temperature

The daily accumulated heat units for maize were calculated with the data logged at 150 cm with a 10°C base temperature Hou et al. (2014); while for the crops (bean and squash) were calculated with the logged data at 15 cm with a base temperature of 8.3°C. In addition, the sums of the daily accumulated heat units during all the experiment were used to determine the accumulated heat units or growing degree days (GDD) (Yousaf et al., 2020) for each environment and were compared between the two treatments.

Physiological variables measurement

Physiological variables were determined for each crop in the intercropping system of the *milpa*. Table 2 summarizes the variables' measurement.

Table 2. Physiological variables and their description used to determine the effect of induced passive heat on *milpa* system from different climate of San Luis Potosí

Variables	Maize	Bean	Squash
Leaf number per plant	10 competitive plants were selected and counted the number of leaves in each plot.	5 competitive plants were selected and counted the number of leaves in each plot.	3 competitive plants were selected and counted the number of leaves in each plot.
Leaf length (cm)	10 leaves were selected just after the ear insertion.		
Width leaf (cm)	10 leaves were selected just after the ear insertion.		
Leaf area (cm^2)	Were calculated with data of the length and width.		
Rate of growth	10 competitive plants were selected and determined in a period of 135 days.	5 competitive plants were selected and determined in a period of 105 days.	3 competitive plants were selected and determined in a period of 105 days.
Height to ear insertion (m)	10 competitive plants were selected and determined in each plot.		
Stem thickness (mm)	10 competitive plants were selected and determined in each plot.	5 competitive plants were selected and determined in each plot.	3 competitive plants were selected and determined in each plot.
Plant height	10 competitive plants were selected and determined in each plot.	5 competitive plants were selected and determined in each plot.	3 competitive plants were selected and determined in each plot.
Days for female flowering per plot	In each plot, the female flowering in days to 50% silking.		

Days for male flowering per plot	In each plot, the male flowering in days to 50% anther extrusion.		
Number of flowers per plant		5 competitive plants were selected and counted the number of flowers in each plot.	3 competitive plants were selected and counted the number of flowers in each plot.
Chlorophyll fluorescence parameters	6 competitive plants in each were selected and measured from 13h to 16h in two moments.	3 competitive plants in each were selected and measured from 13h to 16h in two moments.	3 competitive plants in each were selected and measured from 13h to 16h in two moments.
Gas exchange parameters	6 competitive plants in each were selected and measured from 9h to 11h in two moments.	3 competitive plants in each were selected and measured from 9h to 11h in two moments.	3 competitive plants in each were selected and measured from 9h to 11h in two moments.

Plant growth and development measurement

Rate of growth, plant height, stem thickness, leaf length, width of leaf, leaf area, height to ear insertion, days to female and male flowering, number of flowers, and leaves were used to determine the growth and development dynamic of the crops in each plot.

The rate of growth (RG) was defined as the increment in longitude of the plants measured from the base of the soil to the top of the plant height. The RG for maize was determined from 30 days after first emergence to 170 days in m day^{-1}. For bean and squash, they were determined from 30 days after first emergence to 135 days in cm day^{-1}. The following formula was used:

The equation below was used Del Pozo et al. (1987):

$$\mathrm{RG} = \frac{\mathrm{PH2} - \mathrm{PH1}}{\mathrm{T2} - \mathrm{T1}}$$

Where: PH1 and PH2 are the plant height, T1 and T2 the previously indicated times.

Plant height was measured from the ground surface to the tip of the plant. Stem diameter (mm) was measured using the Vernier Caliper; it was measured at 10 cm above the ground level for each crop. Leaf characteristics (length and width) were evaluated in three leaves (one above and two below the leaf associated with the ear). The general equation was used to estimate individual leaf area of maize (Francis et al., 1969; Zhou et al., 2020): $Leaf\ area = L\ \times W\ \times A$ where L and W are the length and width, respectively, of the leaf. The height of the ear insertion was measured from the distance between the ground surface and the ear insertion of the selected maize. Male and female flowering were measured on each plot. Male flowering was recorded as the number of days from sowing to the first anther extrusion. Female flowering was the number of days from sowing to the first visible silk. The number of flowers and leaves per plant was estimated by counting the number of flowers and leaves on bean and squash plants; in the case of maize, only the number of leaves was determined.

Measurement of plant chlorophyll fluorescence parameters

On fully open leaves, chlorophyll fluorescence variables were measured using a portable photosynthesis system (LI-6400XT, LI-COR) fitted with a fluorescence chamber (LI-6400-XT). At predetermined intervals, minimal (Fo) and maximal (Fm) fluorescence were measured, followed by a 0.2 s weak modulated saturating light flash. Actinic light at 1600 mol m^{-2} s^{-1} was used to illuminate the leaf. It followed application of saturating light pulse for 0.8 s to record Fm. The actinic light was switched off and far-red light was applied to determine Fo. Total energy harvesting efficiency in the light, NPQ (alternative non photochemical quenching) and qN (non photochemical quenching), and electron transport rate (ETR) were calculated. The following equation was used to compute the photochemical quenching (qP) parameters, the proportion of open PSII, and the quantum yield of PSII (PhiPS2). The following equations was reported from Maxwell and Johnson (2000); Ramazan et al. (2021); Vargas-Ortiz et al. (2021):

$$\frac{Fv}{Fm} = \frac{Fm - Fo}{Fm}$$

$$qP = \frac{F'm - Fs}{F'm - F'o}$$

$$PhiPS2 = \frac{F'm - Fs}{F'm}$$

$$NPQ = \left(\frac{Fm}{F'm}\right) - 1$$

$$ETR = PhiPS2.PPFD.\alpha.\beta$$

Where:

Fv/Fm: Maximum efficiency of the Photosystem II (PSII)

Fo: Basal chlorophyll a fluorescence (in the dark) Minimal F (Fluorescence signal (zero subtracted))

F´o: Basal chlorophyll a fluorescence (after light-dark transition) Minimal F, light adapted

Fm: Maximum chlorophyll a fluorescence, dark adapted

F´m: Maximum chlorophyll a fluorescence, light adapted

Fs: Apparent chlorophyll a fluorescence in the light-adapted steady-state fluorescence

PPFD: Photosynthetic photon flux density

α denotes the leaf absorbance and β is the partitioning of absorbed quanta between photosystems I and II. Latter was assumed to be 0.5, indicating that equal distribution of excitation energy occurs between two photosystems, while the former is assumed as 0.86 (Tosens et al., 2012).

Plant gas exchange parameters measurement

The parameters of gas exchange were analysed in order to understand more about plant physiology and photosynthetic machinery of the crops from different climate under the effect of passive induced heat. Fully sun-exposed state was used for recording the leaf gas exchange parameters: CO_2 assimilation photosynthetic rate (µmol CO_2 m^{-2} s^{-1})), stomatal conductance (mmol H_2O m^{-2} s^{-1}), transpiration rates (mmol H_2O m^{-2} s^{-1}) and the intrinsic water use efficiency (iWUE (µmol CO_2 mol^{-1} H_2O) as the relationship between photosynthetic rate and transpiration (Cho et al., 2019; Estévez-Geffriaud et al., 2020). Also, with a LiCOR LI-6400XT system (LiCor, USA), the youngest fully developed leaves were used, and measurements were recorded from an intermediate leaf position on one side of the central nerve for maize genotypes Estévez-Geffriaud et al. (2020); while for bean and squash, competitive plants were selected and intermediate leaves were used for the measurements.

Prior to measurements of chlorophyll fluorescence and gas exchange parameters in light conditions, photosynthetic active radiation (PAR) was monitored near to plants with the PAR sensor of the LI-6400XT chamber Vargas-Ortiz et al. (2021); and values were estimated at 1500 µmol m^{-2} s^{-1} in control plots and 800 µmol m^{-2} s^{-1} in OTC plots for maize genotypes, while for bean and squash the values were 100 and 180 µmol m^{-2} s^{-1} respectively, due to the shade under maize plants. The level of PAR was provided for measuring leaves as actinic light (10% blue light and 90% red light) passed the LI-6400XT leaf chamber during assessment. Photosynthetic parameters were obtained directly (except iWUE) from the portable photosynthesis system LI 6400XT and its calculation was established on LI-6400XT instruction manual (LI-6400 T Instruction Manual, v6, LI-COR Bioscience, Inc.). The measurements were made at 45 and 75 days after the emergence of the crops, corresponding to the early stage and physiological maturity of the crops, respectively.

Yield variables and components plants

Different yield variables and components were determined for the three crops for each *milpa* system. For maize, cob diameter (mm), cob weight (g), cob length (cm), number of rows per cob, number of cobs per plant, number of grains per row, 100 grains weight per plot (g) and yield (t ha^{-1}) were registered. 10 cobs were used to determine the mentioned variables, while the number of cobs per plant was measured on 10 plants in each plot (See Table 2). However for bean and squash only the yield (t ha^{-1}) parameter was determined for each crop.

Statistical analysis

The data for the physiological (plants growth, development, and photosynthetic) and yield variables were analyzed using the GLM procedure of the program Statistical Analysis System (SAS, 2003). The model is characterized by two fixed factors, namely ‘genotypes’ and ‘environment’ as well as their interaction ‘genotypes x environment’ for each crop. The Tukey test was used to check for significant differences between the treatment means. If $P < 0.05$, the effects and interactions were considered significant. Data were examined for normality before being analyzed, and transformation was employed to correct them. The abiotic variables were analyzed using a repeated measure analysis of variance (ANOVA). They were compared between the OTC and control environments and summarized for each data-logger. Data shown are the means and standard error. Vertical bars signify standard error, and, on the top, different letters represent significant difference among the means according to Tukey’s test ($P < 0.05$). Correlations between abiotic variables and the physiological, photosynthetic and yield parameters were conducted in Paleontological Statistics Software package for education and data analysis (Past 4.0).

Results

Abiotic variables under OTC and control plots

Overall, the minimal, maximal, and mean daily temperatures all increased significantly in the OTC treatments, and a significant difference was also recorded for the accumulated heat units at the two evaluated positions (Figure 3).

During the experiment, at 15 cm above the soil, the minimal daily temperature (mean±error standard) was 10.68±0.37°C in the control plots and 12.17±0.3°C in the OTC plots. This variable significantly differed between the environments (Fvalue=2.29, CM=152.68 and P=0.0025) and that means the structure of OTC increased by an average of 1.49ºC the minimum daily temperature during the experiment. The maximum daily temperature was 35.26±0.31°C inside the OTC and 31.7±0.23°C within control and significantly differed between the two environments (Fvalue=82.05, CM=880.24 and P<0.0001) and the use of OTC increased up to 3.56°C in comparison to the control. The mean daily temperature was 21.20±0.22°C in control plots and 23±0.23°C in OTC plots. This variable significantly differed between the treatments (Fvalue=82.05, CM=880.24 and P<0.0001) and that means the structure of OTC increased the mean daily temperature during the experiment to 1.8°C. Then, the accumulated heat units recorded in OTC were statistically superior to the ones inside the control plots. The OTC recorded 350.36 GDD (Growing Degree Days) more in comparison to the control during the 139 days. That means the induced passive heat increased the accumulated heat units during all the experimentation (Figure 3A).

At 150 cm above the soil, the minimal daily temperature was 10.65±0.29°C in control and 11.87°C in OTC plots. The difference between the two conditions was significant (Fvalue= 7.82; CM=103.65 and P=0.005), indicating that the OTC raised the minimum daily temperature up to 1.22°C. The maximum daily temperature was 36.38±0.27°C inside the OTC and 30.30±0.22°C within control and significantly differed between the two environments (Fvalue=298.5, CM=2565.89 and P<0.0001) and the use of OTC increased up to 6.08°C in comparison to the control environment. The mean daily temperature was 20.48±0.17°C in the control plots and 24.13±0.19°C in the OTC plots. This variable showed significant differences between the environments (Fvalue=195.32, CM=925.25 and P<0.0001) showing that the OTC structure increased the mean daily temperature by 3.65°C during the experiment. A total of 1964.17±13.97 GDD was recorded in the OTC plots vs. 1459±10.37 GDD in the control plots during all the duration of the experiment. A significant difference was observed between the two environments (Fvalue=195.32, CM=925.25 and

P<0.0001). 504.18 GGD more was obtained in the OTC plots in comparison to the control plots (Figure 3B).

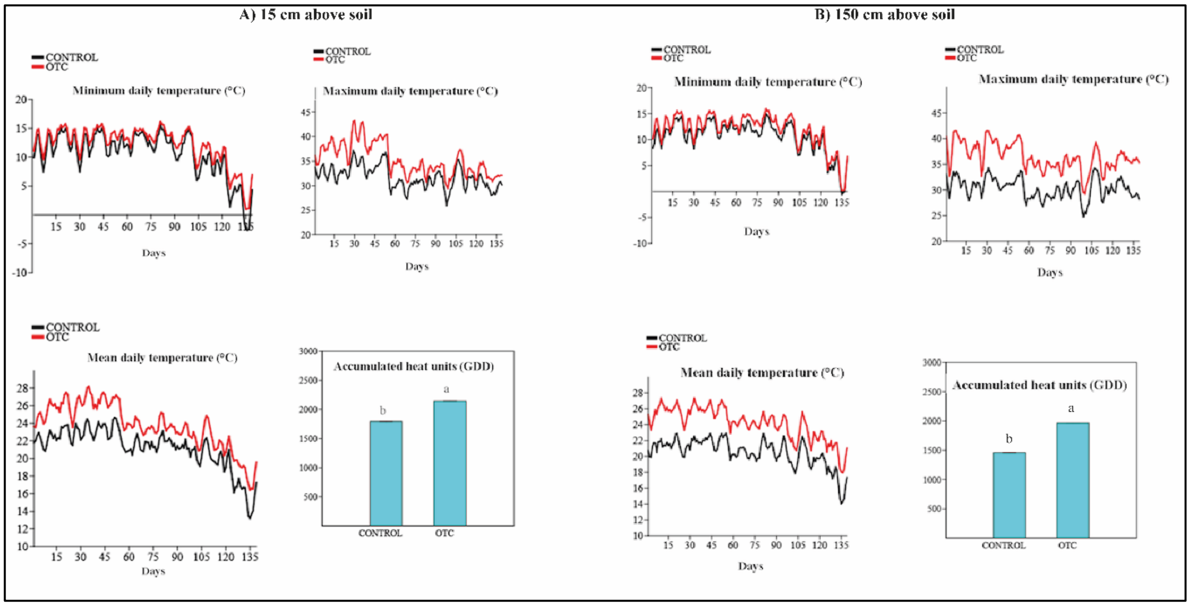

Fig 3. Average daily values of registered temperatures and accumulated heat units calculated in the Open Top Chamber (OTC) and in the control environments at A) 15 cm and B) 150 cm above the soil. Vertical bars indicate the standard error for the accumulated heat units during all the experiments (n = 2). Different letters represent significant difference among the means according to Tukey's test (*P* < 0.05).

Effect of the induced passive heat on maize + bean + squash growth and development

Significant effects of the genotypes and the environment on some of the physiological variables using analysis of variance were observed. The interactions Environment (E) x Genotypes (G) (E x G) were significant for plant height, width leaf and rate of growth for maize; number of leaves per plant and stem thickness for bean; and number of leaves per plant, stem thickness, plant height, and rate of growth were significant for squash (See supplementary data Table 1). When the interaction was not significant, the simple effect of the environmental and genotypic factors was considered.

In Figure 4, the mentioned interactions (E x G) respond to growth and development variables of each crop (maize+bean+squash) from each agro-ecological zone at each treatment.

The passive induced heat increased the plant height and rate of growth of the maize genotypes. The maize genotypes in the OTC plots reached a mean of 2.57±0.09 m for plant height while in the control plots it was 2.06±0.16 m; and 0.013±0.0008 m day^{-1} in OTC plots and 0.010±0.001 m day^{-1} in control plots. The genotypes from *Huasteca* (hot and humid climate) in the OTC and control plots showed the maximum plant height and rate of growth and were significantly superior to those from warm-dry (*Altiplano*) and template (*Media*) where the induced passive heat did not affect the plant height and rate of growth of the maize genotypes. The induced passive heat affected the width leaf of the maize where the genotypes grown in control plots showed a mean of 11.17±0.06 cm vs. 9.05±0.44 cm in OTC plots. However, the width of the leaf was statistically equal for the maize in control plots and superior to the ones reported in OTC for each genotype. Under control and OTC conditions, the E x G interaction for stem thickness reported no difference for the maize plants. That mean, the stem thickness reported under the two conditions were statistically equals for each genotype. However, more stem thickness was registered under control for genotypes from *Media* (template climate) and *Altiplano* (warm-dry climate), while for *Huasteca* (hot and humid climate), the maximum stem thickness was observed under OTC plots.

The number of leaves per plant decreased significantly under the OTC for the E x G of the squash plants, where in the control environment the mean was 60.5±1.42 vs. 35.38±4.5 under the OTC plots. That means the induced passive heat decreased by 41.52% the number of leaves per plant of the squash. The genotypes from the template climate (*Media*) were the most affected, with a significant difference under the induced passive heat. Under the E x G, the plant height and rate of growth were affected by the induced passive heat of the squash. The squash in control plots registered a plant height and rate of growth of 106.72±3.77 cm and 0.7±0.06 cm day^{-1} respectively against 97.92±0.56 cm and 0.6±0.00001 cm day^{-1} under OTC conditions. The genotypes from *Huasteca* (hot and humid climate) and *Altiplano* (warm-dry) reported significant differences for plant height and rate of growth, while the ones from *Media* (template climate) showed no difference. Also, for the stem thickness, only the genotypes from the hot and humid climate (*Huasteca*) registered significant differences under the effect of the passive heat, while for the template (*Media*) and warm-dry (*Altiplano*), no differences were observed.

For bean, the E x G revealed no differences. However, the bean from *Huasteca* (hot and humid climate) registered a significant difference of stem thickness in comparison to the ones from warm-dry and template climates (*Altiplano* and *Media*, respectively). A mean of 10.79±0.51 mm and 9.45±0.54 mm was observed for the bean from *Huasteca* grown under OTC and control environments, respectively. On the other hand, the means were 5.55±0.25mm (OTC) vs. 6.33±0.35mm (control) and 6.32±0.16mm (OTC) vs. 6.74±0.22 mm (control) for the beans from warm-dry (*Altiplano*) and template (*Media*) climates, respectively. Finally, the number of leaves per plant was affected by the induced passive heat. The E x G showed a significant difference for the beans from *Huasteca* (hot and humid climate) and *Altiplano* (warm-dry climate), where the number of leaves per plant for the bean grown under control was statistically superior to the ones under passive heat conditions, while no difference was observed between bean from *Media* (template climate). 34.04% more leaves were registered under control conditions for the beans from *Huasteca* (hot and humid climate) in comparison to OTC conditions, while for *Altiplano* (warm-dry climate), the effect of the passive heat decreased the number of leaves by 42.97%.

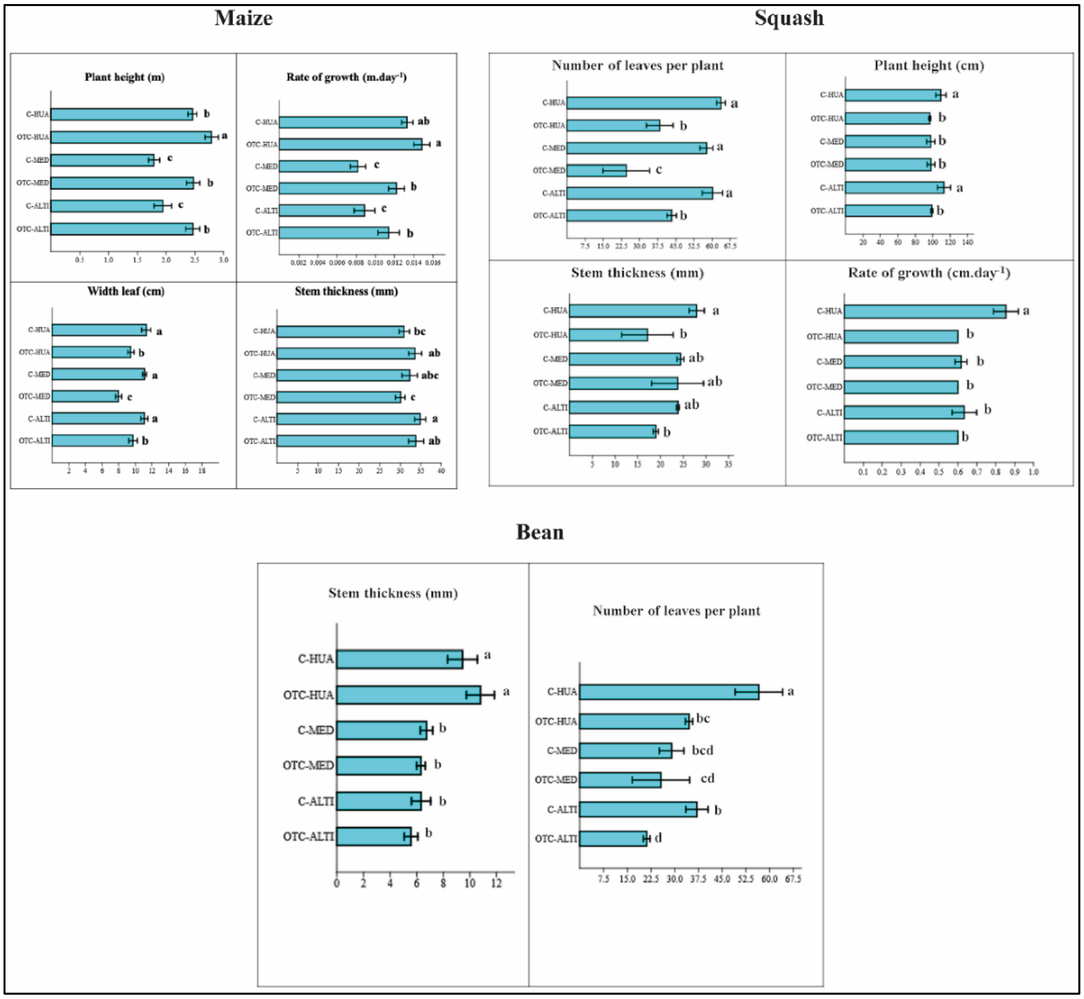

Fig 4. Effect of induced passive heating on plant height (m), rate of growth (m.day^{-1}), width leaf (cm) and stem thickness (mm) of maize; number of leaves per plant, plant height (cm), stem thickness (mm) and rate of growth (cm.day^{-1}) of squash and stem thickness (mm) and number of leaves per plant on bean from different climate of the state of San Luis Potosí (Mexico). OTC: Open top Chamber; C: Control; HUA: *Huasteca* (hot and humid climate); MED: *Media* (temperate climate); ALTI: *Altiplano* (warm-dry climate). The letters a, b, c, and d indicate significant differences according to the Tukey test ($P < 0.05$). Vertical bars indicate the standard error, (n= 20 for maize, n=10 for bean and n= 6 for squash).

Simple effects of the factors (Environment and Genotypes) were observed for leaf number per plant, leaf length, leaf area, days for female flowering per plot, days for male flowering per plot and height to ear insertion for maize; number of flowers per plant, plant height and rate of growth for bean and number of flowers per plant for squash (See supplementary data Table 1).

Table 3 shows the simple effect of passive heat and controlled environments over variables of growth and development for maize, bean, and squash plants. For the factor environment, the OTC decreased significantly the leaf number per plant, leaf area, days for male flowering per plot and height to ear insertion for maize plants, number of flowers per plant and rate of growth for beans and finally the number of flowers per plant for squash.

No differences were observed for the variables leaf length and days for female flowering per plot for maize and plant height for beans. The OTC decreased the leaf area of the maize up to 132.64 cm^2, but it significantly accelerated the days for male flowering per plot to 6.2 days and the height to ear insertion to a mean of 1.41±0.03 m vs. 0.98±0.03 m in the control conditions. For bean, the number of flowers per plant and rate of growth were affected by the passive heat and decreased by up to 7.3 and 0.05 cm day^{-1}, respectively. The squash was one of the crops most affected by the induced passive heat for the variables number of flowers per plant, where it decreased by up to 61.97% in comparison to control environments.

For the factor genotypes represented by the climate procedence of the crops, the genotypes from the hot and humid climate (*Huasteca*) registered a significant difference and were statistically superior to the ones from the warm-dry and template climates (*Altiplano* and *Media*, respectively) for the variables leaf number per plant, leaf length, leaf area, days for female flowering per plot, days for male flowering per plot, and height to ear insertion for maize plants. The genotypes from *Huasteca* (hot and humid climate) registered 103.9±1.35 cm of leaf length while the ones from *Altiplano* (warm-dry) and *Media* (template) were 93.0±0.3 and 90.4±0.2 cm, respectively. In addition, more leaf area was observed in the maize from *Huasteca* (hot and humid climate) with 810.29±20.9 cm^2 while for genotypes from *Altiplano* (warm-dry) it was 723.12±16.9 cm^2. The genotypes from *Media* (template) registered the least leaf area. On the other hand, the genotypes from *Huasteca* (hot and humid climate) took more time to reach the female and male flowering stages, with a mean of 67.2±1.51 days and 66.2±1.51 days, respectively, while the maize from *Altiplano* (warm-dry) and *Media* (template) took less time to reach their reproductive stage.

In addition, for the number of flowers per plant, the bean from the hot and humid and template climates (*Huasteca* and *Media*, respectively) registered the maximum flowers, while for the squash, no differences were observed between the three climates. For plant height, the bean from hot and humid and template climates (*Huasteca* and *Media*, respectively) showed the maximum values, while for rate of growth, it was the hot and humid and warm-dry climates (*Huasteca* and *Altiplano*, respectively) where the maximum values were registered with a mean of 0.16±0.01 and 0.13±0.01 cm day^{-1}, respectively.

Table 3. Effect of the induced passive heating on variables of growth and development for the *milpa* system (maize+bean+squash) from different climates [*Altiplano* (warm-dry), *Media* (template) and *Huasteca* (hot and humid climate)] of the state of San Luis Potosí (Mexico).

Maize				
Leaf number per plant				
Factor environment (N=60)		**Factor genotype (N=40)**		
OTC	Control	*Altiplano*	*Media*	*Huasteca*
12±0.25b	13±0.26a	12±0.3b	11±0.2b	14±0.2a
LSD =0.52		LSD =0.77		
Leaf length (cm)				
Factor environment (N=60)		**Factor genotype (N=40)**		
OTC	Control	*Altiplano*	*Media*	*Huasteca*
96.7±1.37a	95.1±1.26a	93±1.22b	90.4±1.42b	103.9±1.35a
LSD =3.1		LSD =4.5		
Leaf area (cm^2)				
Factor environment (N=60)		**Factor genotype (N=40)**		
OTC	Control	*Altiplano*	*Media*	*Huasteca*
664.3±14.62b	796.97±14.12a	723.12±16.9b	658.54±15.6c	810.29±20.9a
LSD =33.5		LSD =49.3		
Days for female flowering per plot				
Factor environment (N=60)		**Factor genotype (N=40)**		
OTC	Control	*Altiplano*	*Media*	*Huasteca*
61.7±2.93a	57.2±2.27a	55.7±2.01b	55.2±2.8b	67.2±1.51a
LSD =6.2		LSD =9.6		
Days for male flowering per plot				
Factor environment (N=60)		**Factor genotype (N=40)**		
OTC	Control	*Altiplano*	*Media*	*Huasteca*
57.5±2.67b	63.7±1.3a	56.5±2.01b	59±2.81b	66.2±1.51a
LSD =4.4		LSD =6.7		
Height to ear insertion (m)				
Factor environment (N=60)		**Factor genotype (N=40)**		
OTC	Control	*Altiplano*	*Media*	*Huasteca*
1.41±0.03a	0.98±0.03b	1.23±0.05ab	1.11±0.05b	1.25±0.04a
LSD =0.03		LSD =0.05		
Bean				
Number of flowers per plant				
Factor environment (N=60)		**Factor genotype (N=40)**		
OTC	Control	*Altiplano*	*Media*	*Huasteca*
12.9±0.76b	20.2±0.43a	14±1.49b	19.6±0.66a	18.08±0.72ab

LSD =1.67		LSD =2.46		
Plant height (cm)				
Factor environment (N=60)		**Factor genotype (N=40)**		
OTC	Control	*Altiplano*	*Media*	*Huasteca*
37.96±0.8a	36.68±0.71a	35.35±1.05b	37.32±0.71ab	39.28±0.77a
LSD =2.42		LSD =3.56		
Rate of growth (cm day^{-1})				
Factor environment (N=60)		**Factor genotype (N=40)**		
OTC	Control	*Altiplano*	*Media*	*Huasteca*
0.11±0.007b	0.16±0.007a	0.13±0.01ab	0.12±0.01b	0.16±0.01a
LSD =0.02		LSD =0.03		
Squash				
Number of flowers per plant				
Factor environment (N=60)		**Factor genotype (N=40)**		
OTC	Control	*Altiplano*	*Media*	*Huasteca*
5.11±0.75b	13.44±1.15a	12.58±1.94a	8.08±1.3a	7.17±1.32a
LSD =4.3		LSD =6.35		

OTC: Open top chamber; LSD: Least Significant Difference; The letters a, b, c, and d indicate significant differences according to the Tukey test ($P < 0.05$).

Effect of the induced passive heat on the yield and its component variables on *milpa* system (maize+bean+squash)

Significant effects of the genotypes and the environment over some of the yield and its component variables using analysis of variance were observed. The interactions Environment (E) x Genotypes (G) (E x G) were significant for cob diameter, cob weight and number of rows per cob for maize; yield for squash and bean (See supplementary data Table 2). When the interaction was not significant, the simple effect of the environmental and genotype factors was considered.

Figure 5 depicts the yield and its component variables' responses to the *milpa* system (maize+bean+squash) as a result of the combined effect of the factors environment and genotype.

The yield components of the maize showed different responses to the combination of different environment and genotypes for the cob diameter, the cobs from the template climate (*Media*) registered the maximum values and were statistically superior to the ones from warm-dry and hot and humid climates (*Altiplano* and *Huasteca*, respectively). That means, the passive induced heat beneficed the cob diameter of the maize from the template climate (*Media*), while for the two last ones, there were no differences of cob diameters between OTC and control treatments. The maximum values of cob weight were registered in the interaction control environment and the maize genotypes. Under this interaction, the cob weight were 297.32±19.87 g, 241.74±9.01 g and 183.67±6.65 g for *Altiplano* (warm-dry), *Media* (template), and *Huasteca* (hot and humid), respectively. That means the induced passive decreased the cob weight and the minimum values were recorded for genotypes from hot and humid and warm-dry climates (*Huasteca* and *Altiplano*, respectively).

The maximum number of rows per cob was recorded under the interaction OTC in cobs from warm-dry climate (*Altiplano*) with 11.75±0.31 and 11.1±0.27 under control conditions, and there was no statistical difference between them. Also, no statistical differences were observed for the number of rows per cob of the genotypes from *Huasteca* and *Media*. That means the induced passive heat did not affect their number of rows per cob of the maize.

The squash yield was one of the most affected by the induced passive heat (See supplementary data Photo 1). A significant difference was recorded in the E x G where, under OTC plots, the yield decreased in comparison to control plot values. The maximum yield was registered under control plots from *Altiplano* (warm-dry) and *Media* (template). The induced passive heat decreased the yield of the squash by up to 87.02% and 90.92% in the warm-dry (*Altiplano*) and template climates (*Media*), respectively (See supplementary data Photo 1). Also, for the squash from *Huasteca* (hot and humid), a loss of the yield was observed, with a value of 91.94% in comparison to control plots.

For bean, the yield was affected significantly and decreased under the effects of the passive heat for the genotypes from the hot and humid climate (*Huasteca*) with 1.12±0.03 t ha^{-1} in control plots vs. 0.77±0.04 t ha^{-1} in OTC conditions. On the other hand, no statistical differences were recorded for the genotypes from *Media* and *Altiplano* (template and warm-dry climates, respectively) under the OTC and control environments. However, the bean from *Altiplano* registered the lowest yield under OTC and control environments.

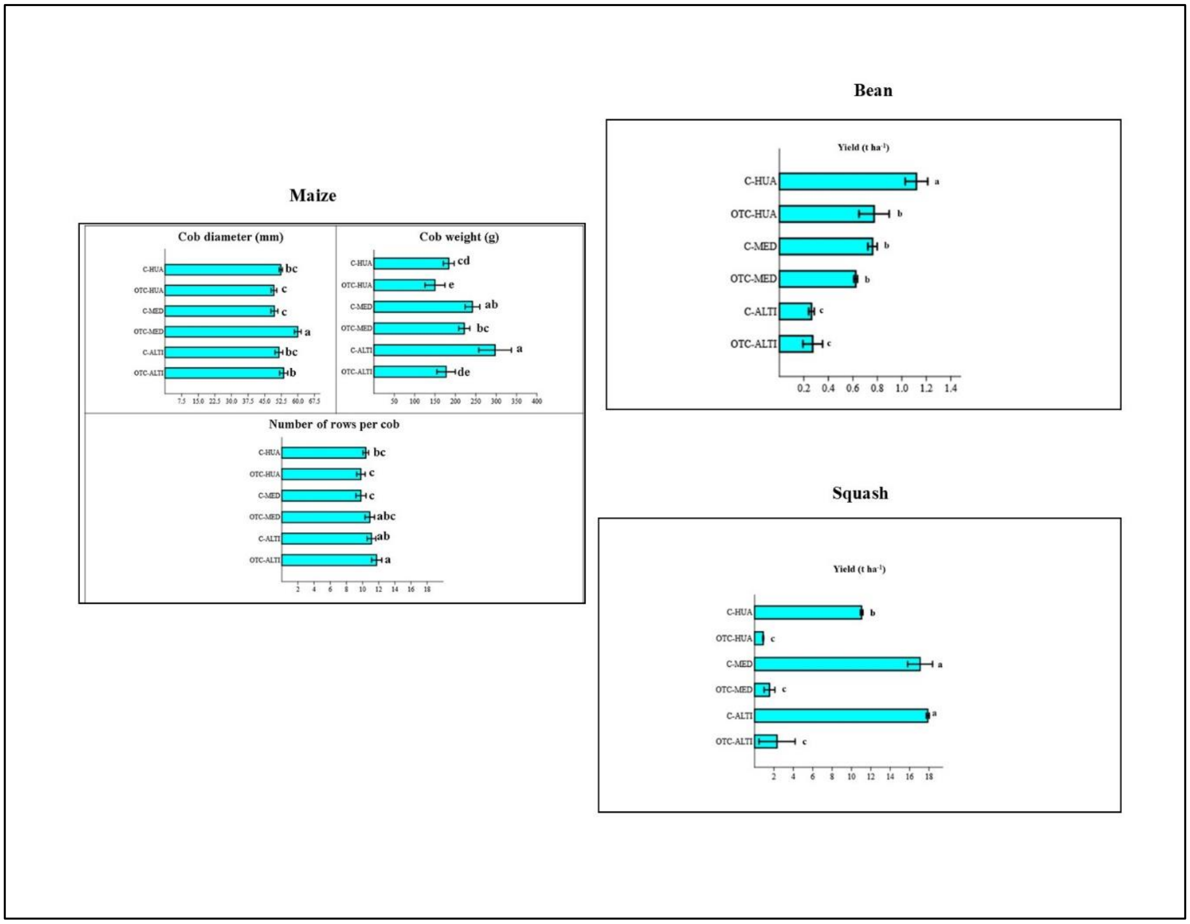

Fig 5. Effect of induced passive heating on cob diameter (mm), cob weight (g), number of rows per cob for maize plants; yield (t ha^{-1}) for squash and bean from different climate of the state of San Luis Potosí (Mexico). OTC: Open top Chamber; C: Control; HUA: *Huasteca* (hot and humid climate); MED: *Media* (temperate climate); ALTI: *Altiplano* (warm-dry climate). The letters a, b, c, and d indicate significant differences according to the Tukey test ($P < 0.05$). Vertical bars indicate the standard error.

Simple effects of the factors (Environment and Genotypes) were observed for number of cob per plant (NCP), cob length (CL), number of grains per row (NGR), 100 grains weight per plot (100GW), and yield (Y) for maize (See supplementary data Table 2).

Table 4 shows the simple effect of maize yield and its component variables under the effect of passive heat and control environments. Under the environmental factor, induced passive heat significantly reduced all yield and its component variables for maize.

The number of cob per plant, cob length, number of grains per row, 100 grains weight per plot, and yield decreased by up to 0.94, 3.95 cm, 6.95, 6.77 g, and 2.33 t ha^{-1} respectively, in comparison to control conditions.

Under the factor genotypes represented by the climate procedence of the maize, the genotypes from the hot and humid climate (*Huasteca*) showed significant differences for the number of cob per plant and number of grains per row and were statistically superior to those registered from *Altiplano* and *Media* (warm-dry and template climates, respectively), while for cob length no differences were registered for the factor genotype of the crops. In addition, the genotypes from *Altiplano* and *Media* (warm-dry and template climates, respectively) registered the maximum values of 100 grains weight per plot and yield, with means of 48.39±2.14 g and 49.55±0.43 g and 5.08±0.73 t ha^{-1} and 4.62±0.48 t ha^{-1} yield for *Altiplano* and *Media* (warm-dry and template climates, respectively) while from *Huasteca* (hot and humid); the values were 38.84±2.7 g (for 100 grains weight per) and 2.93±0.61 t ha^{-1} (for yield), being the one with the least yield and 100 grains weight per plot for maize genotypes (Table 4).

Table 4. Effect of the induced passive heating on yield and its component variables of the maize from different climates [*Altiplano* (warm-dry), *Media* (template) and *Huasteca* (hot and humid climate)] of the state of San Luis Potosí (Mexico).

Maize				
Number of cob per plant				
Factor environment (N=60)		**Factor genotype (N=40)**		
OTC	Control	*Altiplano*	*Media*	*Huasteca*
1.26±0.06b	2.2±0.08a	1.55±0.1b	1.75±0.1ab	1.9±0.13a
LSD =0.07		LSD =0.1		
Cob length (cm)				
Factor environment (N=60)		**Factor genotype (N=40)**		
OTC	Control	*Altiplano*	*Media*	*Huasteca*
14.36±0.29b	18.31±0.14a	16.08±0.43a	16.49±0.38a	16.42±0.45a
LSD =0.65		LSD =0.95		
Number of grains per row				
Factor environment (N=60)		**Factor genotype (N=40)**		
OTC	Control	*Altiplano*	*Media*	*Huasteca*
30.65±1b	37.6±0.5a	32.22±0.75b	33.42±0.96b	36.72±1.46a
LSD =2.21		LSD =3.24		
100 grains weight per plot (g)				
Factor environment (N=6)		**Factor genotype (N=4)**		
OTC	Control	*Altiplano*	*Media*	*Huasteca*
42.21±2.76b	48.98±1.71a	48.39±2.14a	49.55±0.43a	38.84±2.71b
LSD =4.22		LSD =6.48		
Yield (t ha^{-1})				
Factor environment (N=6)		**Factor genotype (N=4)**		
OTC	Control	*Altiplano*	*Media*	*Huasteca*
3.05±0.42b	5.38±0.53a	5.08±0.73a	4.62±0.48ab	2.93±0.61b
LSD =4.22		LSD =1.95		

OTC: Open top chamber; LSD: Least Significant Difference; The letters a, b, c, and d indicate significant differences according to the Tukey test ($P < 0.05$).

Effect of induced passive heat on photosynthetic capacity of *milpa* system (maize+bean+squash)

Effect of induced passive heat on chlorophyll fluorescence parameters measured at 45 days after emergence of each crop of the *milpa* (maize+bean+squash)

Significant effects of the genotypes and the environment on some of the chlorophyll fluorescence parameters using analysis of variance were observed. For the interactions Environment (E) x Genotypes (G) (E x G), Electron Transport Rate (ETR), Alternative non-photochemical quenching (NPQ), Quantum yield of the Photosystem II (PhiPS2), Non-photochemical quenching (qN), and Photochemical quenching **(**qP) were significant for beans and squash (except NPQ), but none of the parameters were significant for the interaction E x G for maize (See supplementary data Table 3). When the interaction was not significant, the simple effect of the environmental and genotypic factors was considered.

Table 5 shows the chlorophyll fluorescence parameters measured in each crop (maize+bean+squash) at 45 days after emergence.

No differences were recorded for the effect of the induced passive heat on ETR with 58.2±3.9 µmol m^{-2} s^{-1} in OTC plots and 61.1±3.3 µmol m^{-2} s^{-1} in control plots for maize genotypes. However, under the genotype effect, the maize from *Huasteca* (hot and humid climate) showed the maximum ETR (71.7±5.2 µmol m^{-2} s^{-1}) and statistically superior to those from warm-dry (*Altiplano*) and template climates (*Media*) with 54.2±3.3 and 53.1±3.5 µmol m^{-2} s^{-1}, respectively.

ETR was found to be higher in OTC plots from hot and humid climate (*Huasteca*) with a mean of 51.4±0.5 µmol m^{-2} s^{-1} and 41.4±1.01 µmol m^{-2} s^{-1} in control plots, which were statistically superior to the values recorded in the E x G from *Altiplano* and *Media* (warm-dry and template climates, respectively), where the lowest values were recorded in bean from *Altiplano* with 15.2±1.7 µmol m^{-2} s^{-1} in OTC and 12.3±0.5 µmol m^{-2} s^{-1} in control plots. That means, the induced passive heat increased the ETR of the bean from hot and humid climate (*Huasteca*).

On the other side, the ETR of the squash (from *Media* and *Huasteca*) was significantly impacted by the produced passive heat with a significant difference. The higher values were reported under control plots from *Media* and *Huasteca* (template and hot and humid climates, respectively), with values of 81.03±1.29 and 62.13±1.14 µmol m^{-2} s^{-1}, respectively. The induced passive heat decreased by up to 38.36 and 41.74 µmol m^{-2} s^{-1} in comparison to control plots from *Media* (template) and *Huasteca* (hot and humid), respectively. The squash from *Altiplano*, on the other hand, benefited from the influence of the produced passive heat with and was significantly higher than the squash planted in control plots.

The most important quenching parameters in assessing plant performance under stress circumstances are Fv/Fm, PhiPS2, and qP (Gallé and Flexas, 2010). In this approach, the produced passive heat harmed the bean and squash crops, lowering their Fv/Fm, which indicates photosystem II's maximal photochemical efficiency and potential activity in plant leaves.

For bean and squash, the decreases were 0.07 and 0.05, respectively. However, for maize, the passive heat increased the Fv/Fm with significant differences, and the values were 0.75±0.008 in OTC and 0.72±0.005 in control plots. Also for PhiPS2, the maximum value was reported in OTC with 0.08±0.006 and 0.05±0.005 in control conditions for maize genotypes. That indicates the position of the leaves inside the plots can influence the chlorophyll fluorescence parameters. Under the genotype factor, the maize from hot and humid (*Huasteca*) reported a significant difference and the mean was 0.08±0.008 while for the others from *Altiplano* (warm-dry) and *Media* (template), the mean was 0.06±0.008 for each.

The E x G indicated that the maximum value of PhiPS2 in bean was recorded in control plots from *Altiplano* (warm-dry) and *Media* (template) with 0.26±0.01 vs. 0.15±0.01 in OTC and 0.07±0.001 in control vs. 0.05±0.001 in OTC, respectively. In addition, for the bean from *Huasteca* (hot and humid), no difference was reported between control and OTC. For squash, the maximum PhiPS2 was recorded in control plants from *Altiplano* (warm-dry), but the differences were not significant for each genotype in the two environments.

Non-photochemical quenching (qN) and alternative non-photochemical quenching (NPQ) were impacted for the effect of the induced passive heat where their values under control conditions were significantly higher than the reported in OTC for maize genotypes. qN and NPQ in control were 0.91±0.003 and 1.84±0.04 while in OTC were 0.84±0.01 and 1.55±0.06, respectively.

For bean, the E x G reported the maximum values of qN in control conditions from *Huasteca* (hot and humid) but the difference was not significant for the two conditions. On the other hand, the induced passive heat significantly affected the bean from *Altiplano* and *Media* (warm-dry and template climates, respectively); they decreased by up to 24.24% and 50%, respectively, the qN in comparison to the control conditions.

In comparison to control conditions, the induced passive heat impacted the squash from *Media* (template), where they lost up to 62.07% of the qN. However, the induced passive heat significantly increased the qN of the squash from *Altiplano* (warm-dry), where the mean was 0.33±0.07 in OTC and 0.16±0.04 in control, while no difference was reported for the squash from *Huasteca* (hot and humid). That means, the procedence of the plants may influence the qN parameters.

The qP reported no difference for the maize genotypes under the effect of the passive heat, while for the factor genotype, the maize from a hot and humid climate (*Huasteca*) showed the maximum values with 0.37±0.02 and statistically superior to the qP of the genotypes from *Altiplano* and *Media* (warm-dry and template climates, respectively).

For bean, the E x G reported a significant difference for the plants from *Media* (template) where the induced passive heat increased the qP of the bean with 0.55±0.01 vs. 0.31±0.06 in control environment. On the other hand, no statistic differences were recorded for the bean from *Altiplano* and *Huasteca* (warm-dry and hot and humid climates, respectively) under the effect of the passive heat, however the ones from *Huasteca* reported up to 0.23 qP in comparison to OTC conditions.

The qP of the squash increased significantly under OTC conditions for the plants from a hot and humid climate (*Huasteca*), where the qP increased by up to 57.14% in comparison to control conditions, while no differences were reported for the squash from *Altiplano* and *Media* (warm-dry and template climates, respectively) under the effect of the passive heat (Table 5).

Table 5. Chlorophyll fluorescence parameters measured in different system of *milpa* (maize+bean+squash) from different environment under induced passive heat and controlled ambient at 45 days after emergence of each crop.

		Electron Transport Rate (ETR) (μmol m^{-2} s^{-1})			
			Genotypes		
Crops	**Environment**	***Altiplano***	***Media***	***Huasteca***	**Significance**
Maize	OTC		58.2±3.9a		Environment x
	Control		61.1±3.3a		Genotypes(ns)
	LSD		0.06		N=12
		54.2±3.3b	53.1±3.5b	71.7±5.2a	Environment(ns)
	LSD		0.08		N=36
					Genotypes** N=24
Bean	OTC	15.2±1.7d	23.5±2.58c	51.4±0.5a	Environment x
	Control	12.3±0.5d	24.4±1.11c	41.4±1.01b	Genotypes** N=6
	LSD		0.24		Environment*
					N=18
					Genotypes***
					N=12
Squash	OTC	40.93±6.65b	42.67±10.39b	20.39±1.6c	Environment x
	Control	18.26±1.51c	81.03±1.29a	62.13±1.14ab	Genotypes*** N=6
	LSD		24.34		Environment**
					N=18
					Genotypes***
					N=12
		Maximum efficiency of the Photosystem II (Fv/Fm)			
Maize			**Genotypes**		
		Altiplano	***Media***	***Huasteca***	Environment x
	OTC		0.75±0.008a		Genotypes(ns)
	Control		0.72±0.005b		N=12
	DMS		0.02		Treatment** N=36
		0.75±0.01a	0.73±0.007a	0.73±0.006a	Genotypes(ns)
	LSD		0.03		N=24
Bean	OTC		0.59±0.01b		Environment x
	Control		0.66±0.02a		Genotypes(ns)
	LSD		0.04		N=6
		0.62±0.02a	0.63±0.01a	0.63±0.02a	Environment**
					N=18
					Genotypes(ns)
					N=12

	LSD		0.06		
Squash	OTC		0.51±0.01b		
	Control		0.56±0.02a		Environment x Genotypes(ns) N=6
	LSD		0.04		
		0.51±0.01a	0.55±0.02a	0.55±0.02a	
	LSD		0.06		Environment* N=18
					Genotypes(ns) N=12
			Quantum yield of the Photosystem II (PhiPS2)		
Maize			**Genotypes**		
		Altiplano	***Media***	***Huasteca***	Environment x Genotypes(ns) N=12
	OTC		0.08±0.006a		
	Control		0.05±0.005b		
	LSD		0.02		Environment*** N=36
		0.06±0.008b	0.06±0.005b	0.08±0.008a	
	LSD		0.03		Genotypes** N=24
Bean	OTC	0.15±0.01b	0.05±0.001d	0.11±0.001b	Environment x Genotypes** N=6
	Control	0.26±0.01a	0.07±0.001c	0.16±0.01b	
	LSD		0.04		Environment*** N=18
					Genotypes*** N=12
Squash	OTC	0.34±0.08ab	0.35±0.03ab	0.31±0.04ab	Environment x Genotypes* N=6
	Control	0.52±0.03a	0.3±0.04ab	0.27±0.01b	
	LSD		0.19		Environment(ns) N=18
					Genotypes(ns) N=12
			Non-photochemical quenching (qN)		
Maize			**Genotypes**		
		Altiplano	***Media***	***Huasteca***	Environment x Genotypes(ns) N=12
	OTC		0.84±0.01b		
	Control		0.91±0.003a		
	LSD		0.03		Environment*** N=36
		0.89±0.006a	0.89±0.01a	0.85±0.02a	
	LSD		0.04		Genotypes* N=24
Bean	OTC	0.25±0.005c	0.23±0.008c	0.45±0.002a	Environment x Genotypes*** N=6
	Control	0.33±0.009b	0.46±0.012a	0.49±0.009a	

	LSD		0.04		Environment*** N=18 Genotypes*** N=12
Squash	OTC	0.33±0.07bc	0.22±0.04cd	0.47±0.01ab	Environment x Genotypes*** N=6
	Control	0.16±0.04d	0.58±0.02a	0.57±0.02a	Environment(ns) N=18
	LSD		0.18		Genotypes*** N=12
		Photochemical quenching (qP)			
Maize			**Genotypes**		
		Altiplano	***Media***	***Huasteca***	
	OTC		0.32±0.02a		Environment x Genotypes(ns) N=12
	Control		0.33±0.01a		
	LSD		0.04		
		0.3±0.02b	0.3±0.01b	0.37±0.02a	Environment(ns) N=36
	LSD		0.05		Genotypes* N=24
Bean	OTC	0.42±0.07ab	0.55±0.01a	0.32±0.02ab	Environment x Genotypes** N=6
	Control	0.42±0.06ab	0.31±0.06b	0.54±0.01a	
	LSD		0.18		Environment(ns) N=18 Genotypes(ns) N=12
Squash	OTC	0.5±0.09ab	0.68±0.03a	0.56±0.03a	Environment x Genotypes** N=6
	Control	0.66±0.06a	0.42±0.1ab	0.24±0.01b	
	LSD		0.22		Environment* N=18 Genotypes* N=12
		Alternative non-photochemical quenching (NPQ)			
Maize			**Genotypes**		
		Altiplano	***Media***	***Huasteca***	Environment x Genotypes(ns) N=12
	OTC		1.55±0.06b		
	Control		1.84±0.04a		
	LSD		0.06		Environment*** N=36
		1.8±0.04a	1.76±0.05a	1.53±0.08b	
	LSD		0.08		Genotypes** N=24
Bean	OTC	0.51±0.02c	0.95±0.001b	1.36±0.01a	

	Control	1.03±0.001b	1.03±0.001b	0.89±0.07b	Environment x
	LSD		0.16		Genotypes***
					N=6
					Environment(ns)
					N=18
					Genotypes***
					N=12
Squash	OTC		0.73±0.11a		Environment x
	Control		0.89±0.1a		Genotypes(ns)
	LSD		0.16		N=6
		0.42±0.09b	0.89±0.12a	1.13±0.02a	Environment(ns)
	LSD		0.23		N=18
					Genotypes***
					N=12

OTC: Open top chamber; LSD: Least Significant Difference; ns: no significant; *t-test, $p < 0.05$;**t-test, $p < 0.01$, and ***t-test, $p < 0.001$; The letters a, b, c, and d indicate significant differences according to the Tukey test ($P < 0.05$).

Effect of induced passive heat on gas exchange parameters measured at 45 days after emergence of each crop of the *milpa* (maize+bean+squash)

Significant effects of the genotypes and the environment on the gas exchange parameters using analysis of variance were observed. For the interactions Environment (E) x Genotypes (G) (E x G), stomatal conductance (Cond), intrinsic water use efficiency (iWUE), photosynthetic rate (Photo) and transpiration rates (Trmmol) were significant for beans and squash (except iWUE and Photo), but none of the parameters were significant for maize (See supplementary data Table 4). When the interaction was not significant, the simple effect of the environmental and genotypic factors was considered.

Figure 6 shows the gas exchange parameters under the effect of the passive heat on the *milpa* system (maize+bean+squash) at 45 days after emergence from different climates. The passive heat affected significantly the CO_2 assimilation, also known as the photosynthetic rate (Photo) of the maize, with a decrease of 8.25 µmol CO_2 m^{-2} s^{-1}. For the factor genotype, the maize from a hot and humid climate (*Huasteca*) showed the maximum values of CO_2 assimilation with a mean of 39.15±2.61 µmol CO_2 m^{-2} s^{-1} and was statistically superior to the reported from *Altiplano* and *Media* (warm-dry and template climates, respectively).

On the other hand, the E x G revealed different responses for bean and squash. For the two crops, the induced passive heat increased the photosynthetic rate with maximum values of 52.2±1.18 and 63.89±1.56 µmol CO_2 m^{-2} s^{-1} for *Huasteca* (hot and humid climate) in OTC conditions for bean and squash, respectively. In addition, the induced passive heat significantly reduced the photosynthetic rate of the bean from template climate (*Media*) where the values in control plots (42.96±0.93 µmol CO_2 m^{-2} s^{-1}) were significantly superior to the mean in OTC conditions (29.9±3.89 µmol CO_2 m^{-2} s^{-1}) while no differences were recorded for the squash from warm-dry and template climates (*Altiplano* and *Media*, respectively) and for bean from warm-dry climate (*Altiplano*).

The induced passive heat increased the stomatal conductance (Cond) of the maize genotypes. A significant difference of up to 42.31% in the stomatal conductance in comparison to control conditions. Also, in the maize from hot and humid climate (*Huasteca*) reported the maximum value of stomatal conductance with 0.25±0.02 mmol H_2O m^{-2} s^{-1} which was statistically superior to the others maize.

The E x G revealed different responses of the bean, where maximum values were reported for the plants from *Huasteca* (hot and humid climate) with 0.62±0.03 mmol H_2O m^{-2} s^{-1} in OTC plots vs. 0.55±0.05 mmol H_2O m^{-2} s^{-1} in control conditions which were statistically equals. In addition, the bean from the warm-dry climate (*Altiplano*) significantly increased the stomatal conductance under the effect of passive heat with 0.4±0.03 mmol H_2O m^{-2} s^{-1} and 0.22±0.014 mmol H_2O m^{-2} s^{-1} in control conditions, while no difference was recorded for the bean from the template climate (*Media*).

The induced passive heat increased the transpiration rates (Trmmol) of the maize and reported a significant difference in comparison to control environments. The value was 4.11±0.44 mmol H_2O m^{-2} s^{-1} in OTC and 3.27±0.33 mmol H_2O m^{-2} s^{-1} in control environments. For the factor genotypes, again the maize from a hot and humid climate (*Huasteca*) registered the highest Trmmol which was statistically superior to the maize from *Altiplano* and *Media* (warm-dry and template climates, respectively), which reported 3.20±0.17 and 3.56±0.16 mmol H_2O m^{-2} s^{-1}, respectively.

The bean reported maximum values also for the plants from *Huasteca* (hot and humid climate), where the means were 10.30±0.37 mmol H_2O m^{-2} s^{-1} in control and 9.28±0.5 mmol H_2O m^{-2} s^{-1} in OTC but no statistical difference was recorded between them. For squash plants, no differences were recorded under the two factors (environment and genotypes). That means the induced passive heat did not affect them and either the genotypes.

The maize's intrinsic water use efficiency (iWUE) was dramatically reduced by the induced passive heat. In comparison to the control environment, an iWUE reduction of up to 54.42% was reported. On the other hand, no difference was recorded in the maize climate. They responded as equals, no matter the characteristics of their climates for the gas exchange parameter iWUE.

For the bean, different responses were reported where the induced passive heat decreased the iWUE of the bean from template and warm-dry climates (*Media* and *Altiplano*, respectively).

The first one registered the maximum value under control conditions and reduced up to 59.69 µmol CO_2 mol^{-1} H_2O in OTC, while the bean from *Altiplano* (warm-dry climate) reduced up to 77.33 µmol CO_2 mol^{-1} H_2O in comparison to control conditions. Also, no difference was recorded for the bean from the hot and humid climate (*Huasteca*). That means, they were not influenced by the induced passive heat.

The induced passive heat favoured the iWUE of the squash from a hot and humid climate (*Huasteca*), where a maximum value was reported in OTC conditions with 169.16±15.73 µmol CO_2 mol^{-1} H_2O, which was statistically superior to that reported in the control environment. Finally, no statistical differences were found in the E x G for squash from *Altiplano* and *Media* (warm-dry and template climates, respectively). However, the values reported in the control environment were higher than those registered in OTC conditions.

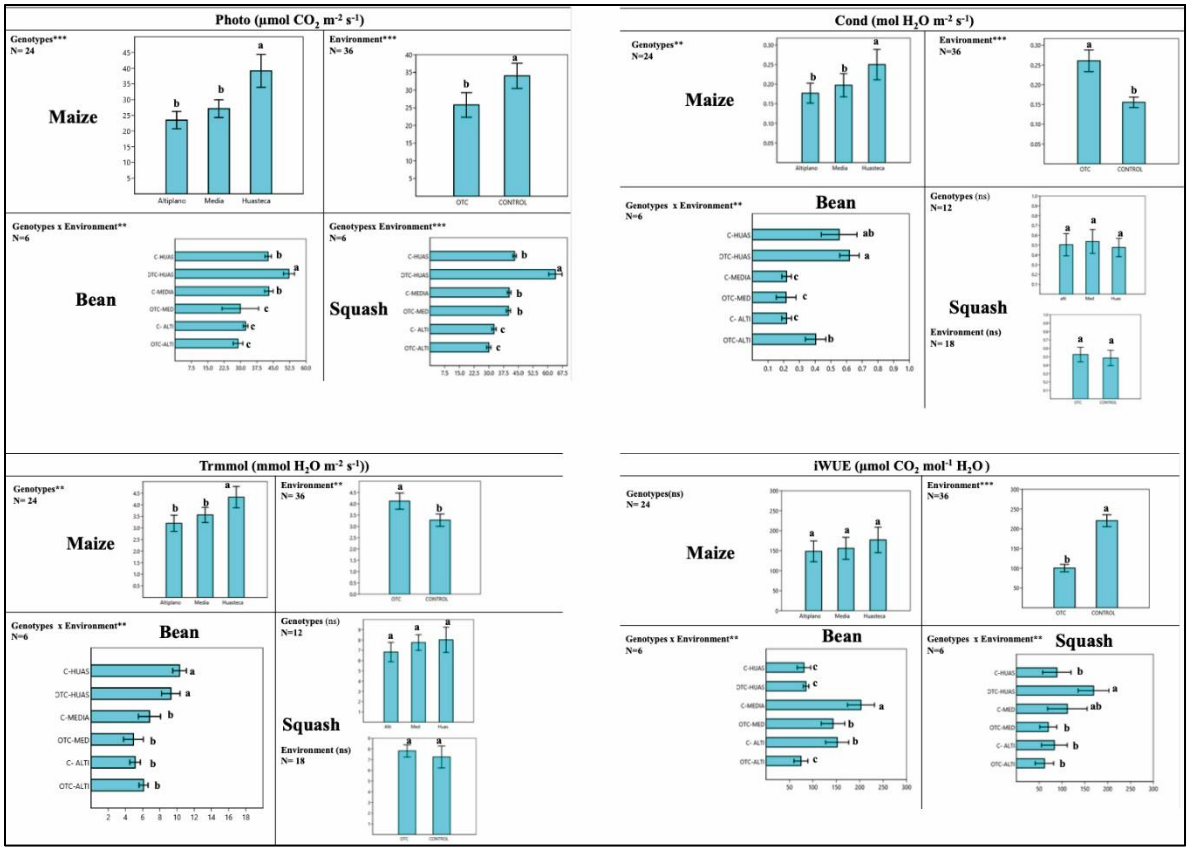

Fig 6. Effect of induced passive heating on gas exchange parameters of the *milpa* system (maize+bean+squash) at 45 days after emergence from different climate of the state of San Luis Potosí (Mexico). OTC: Open top Chamber; C: Control; HUAS: *Huasteca* (hot and humid climate); MED: *Media* (temperate climate); ALTI: *Altiplano* (warm-dry climate); Photo: photosynthetic rate; Cond: stomatal conductance; Trmmol: transpiration rates; iWUE: intrinsic water use efficiency; ns: no significant; *t-test, $p < 0.05$;t-test, $p < 0.01$, and ***t-test, $p < 0.001$. The letters a, b, c, and d indicate significant differences according to the Tukey test ($P < 0.05$). Vertical bars indicate the standard error.**

Effect of induced passive heat on chlorophyll fluorescence parameters measured at 75 days after emergence of each crop of the *milpa* (maize+bean+squash)

Significant effects of the genotypes and the environment on some of the chlorophyll fluorescence parameters at 75 days after emergence using analysis of variance were observed. For the E x G interactions, all of the evaluated parameters were significant for bean, but only the maximum efficiency of the Photosystem II (Fv/Fm), quantum yield of the Photosystem II (PhiPS2) and photochemical quenching (qP) were significant for squash. Finally, none of the parameters were significant for maize (See supplementary data Table 5). When the interaction was not significant, the simple effect of the environmental and genotypic factors was considered.

Table 6 shows the mentioned chlorophyll parameters for the *milpa* system (maize+bean+squash) at 75 days after emergence, which corresponds to the reproductive stage of the crops.

The induced passive heat decreased the electron transport rate (ETR), maximum efficiency of the Photosystem II (Fv/Fm), quantum yield of the Photosystem II (PhiPS2), non-photochemical quenching (qN) and alternative non-photochemical quenching (NPQ) of the maize. The results showed a significant difference of the ETR under OTC plots, with a mean of 47.8±0.06 µmol m^{-2} s^{-1} while in control conditions, the value was 61.42±0.04 µmol m^{-2} s^{-1}. The induced passive heat reduced the maize ETR by up to 22.17%. At the reproductive stage, the genotypes from *Altiplano* (warm-dry climate) recorded the maximum value of ETR with 61.6±2.87 µmol m^{-2} s^{-1} which was statistically higher than the reported for the maize from template and hot and humid climates (*Media* and *Huasteca*, respectively), where no differences were observed.

The induced passive heat greatly improved the ETR of the bean from a hot and humid region (*Huasteca*), with the greatest value reported in OTC environments at 61.69±0.45 µmol m^{-2} s^{-1}, which was statistically greater than the control. No differences were recorded for the bean from warm-dry and template climates (*Altiplano* and *Media*, respectively) in comparison to the two environments. However, the bean from the warm-dry climate (*Altiplano*) reported the lowest values of ETR in OTC. The bean responded differently in dependence on their climate.

The passive heat also reduced the ETR of the squash with a significant difference. A reduction of 38.76% of the squash ETR was reported by the effect of the heat conditions. For the factor genotypes, the squash from template (*Media*) reported the maximum mean with 94.6±10.29 µmol m^{-2} s^{-1} which was statistically superior to the results registered in *Huasteca* and *Altiplano*. The last one reported the lowest ETR with 34.76±6.24 µmol m^{-2} s^{-1}. That means the squash responded differently depending on the climate.

The maize reported the maximum mean of Fv/Fm under control conditions with 0.87±0.001 which was statistically higher than that reported in OTC. The climate features of the maize, on the other hand, showed no variations because they both responded equally well to the passive heat.

Different responses were reported in the E x G for the bean where the induced passive heat affected more the plants from the hot and humid climate (*Huasteca*). They decreased the Fv/Fm of the control environment (0.8±0.002) which is the maximum values in comparison to OTC. For the bean from *Altiplano* (warm-dry climate) and *Media* (template), no differences were recorded under the two conditions. However, higher values of Fv/Fm were reported under control conditions.

The squash plants showed different responses in the E x G where the induced passive heat increased the Fv/Fm at the reproductive stage for the plants from hot and humid climate (*Huasteca*). They significantly increased the Fv/Fm with a maximum of 0.75±0.005 in OTC vs. 0.66±0.02. The squash from *Huasteca* was the only one benefitted by the effect of the induced passive heat, while the others from *Altiplano* and *Media* (warm-dry and template climates, respectively) responded equally, with no differences in the two environments.

In compared to control environments, the maize lost up to 41.66% of its PhiPS2 when exposed to passive heat. The climate features of the maize for the variable PhiPS2, showed no variations because they both responded equally well to the passive heat.

The bean responded differently by the effect of the induced passive heat for PhiPS2. The bean from *Media* (template) beneficed up to 78.94% of PhiPS2 in OTC in comparison to control environments. They were statistically higher than those reported in the control environment. Bean from *Altiplano* and *Huasteca* (warm-dry and hot and humid climates, respectively) showed no differences in PhiPS2. However, maximum values were reported in control environments.

Also, the squash from the template and hot and humid climates (*Media* and *Huasteca*, respectively) significantly increased its PhiPS2. They reported 0.49±0.05 in OTC vs. 0.26±0.04 in control (*Media*) and 0.37±0.02 in OTC vs. 0.16±0.008 in control (*Huasteca*). In addition, no difference was recorded for the squash from warm-dry climate (*Altiplano*). The non-photochemical quenching (qN) and alternative non-photochemical quenching (NPQ) of the maize were reduced by up to 7.86% and 15.53% respectively, by the induced passive heat. However no differences were recorded for the factor genotypes of the maize for the two non-photochemical parameters.

At the reproductive stage, the induced passive heat increased the qN of the bean from the hot and humid climate (*Huasteca*). They registered the maximum in OTC conditions with 0.86±0.006 which was statistically higher than the reported in control with 0.63±0.04. On the other hand, no differences were recorded for bean from *Altiplano* and *Media* (warm-dry and template climates, respectively), but the values reported in control were higher than those recorded in OTC plots. In addition, for the alternative non-photochemical quenching (NPQ), the bean responded differently and were affected by the induced passive heat. The bean from the template climate (*Media*) significantly reduced their NPQ to 0.264 in comparison to control environments. No differences were reported for the bean from *Altiplano* and *Huasteca* (warm-dry and hot and humid climates, respectively).

The squash's qN dropped with passive heat, with a difference of 0.16 compared to control, whereas there were no variations between the two conditions for NPQ. For the factor genotypes, the squash from *Media* (template) and *Huasteca* (hot and humid) recorded the maximum values of qN and NPQ with 0.62±0.06 and 0.77±0.02 respectively, 1.09±0.13 and 1.53±0.11 respectively. The lowest values were reported for squash from *Altiplano* (warm-dry) for the two non-photochemical parameters.

At 75 days after emergence, the photochemical quenching (qP) parameter was the only one where the E x G was significant for maize. In this approach, the induced passive heat significantly decreased the qP of the maize. The maximum means were reported under control environment for the three genotypes with 0.44±0.008; 0.44±0.008 and 0.45±0.008 for *Altiplano* (warm-dry), *Media* (template) and *Huasteca* (hot and humid), respectively while in OTC; they were 0.32±0.002, 0.25±0.008 and 0.34±0.001. That means the induced passive heat affected the qP parameters and the maize responded differently to the characteristics of their climates (Table 6).

Table 6. Chlorophyll fluorescence parameters measured in different system of *milpa* (maize+bean+squash) from different environment under induced passive heat and controlled ambient at 75 days after emergence of each crop.

		Electron transport rate (ETR) (μmol m^{-2} s^{-1})			
		Genotypes			
Crops	**Environment**	***Altiplano***	***Media***	***Huasteca***	**Significance**
Maize	OTC	47.8±0.06b			Environment x Genotypes(ns) N=12 Environment*** N=36 Genotypes*** N=24
	CONTROL	61.42±0.04a			
	LSD	4.65			
		61.6±2.87a	49.05±2.22b	53.19±1.99b	
	LSD	6.84			
Bean	OTC	21.32±2.52d	36.87±2.76c	61.69±0.45s	Environment x Genotypes* N=6 Environment* N=18 Genotypes*** N=12
	CONTROL	18.25±1.51d	37.78±1.58c	51.43±0.89b	
	LSD	8.54			
Squash	OTC	50.33±6.39b	50.33±6.39b	50.33±6.39b	Environment x Genotypes (ns) N=6 Environment** N=18 Genotypes*** N=12
	CONTROL	82.19±9.02a	82.19±9.02a	82.19±9.02a	
	LSD	13.5			
		Maximum efficiency of the Photosystem II (Fv/Fm)			
Maize		**Genotypes**			
		Altiplano	***Media***	***Huasteca***	Environment x Genotypes (ns) Environment*** N=36 Genotypes (ns) N=24
	OTC	0.75±0.007b			
	CONTROL	0.87±0.001a			
	LSD	0.014			
		0.81±0.01a	0.81±0.01a	0.81±0.01a	
	LSD	0.02			
Bean	OTC	0.76±0.003bc	0.77±0.004abc	0.74±0.002c	Environment x Genotypes* N=6 Environment** N=18 Genotypes(ns) N=12
	CONTROL	0.77±0.016abc	0.78±0.003ab	0.8±0.002a	
	LSD		0.03		
Squash	OTC	0.76±0.006a	0.75±0.001a	0.75±0.005a	Environment x Genotypes** N=6 Environment** N=18 Genotypes** N=12
	CONTROL	0.76±0.007a	0.74±0.002a	0.66±0.02b	
	LSD	0.05			
Maize		**Quantum yield of the photosystem II (PhiPS2)**			
		Genotypes			
		Altiplano	***Media***	***Huasteca***	Environment x Genotypes (ns) N=12 Environment* N=36 Genotypes (ns) N=24
	OTC	0.75±0.007b			
	CONTROL	0.87±0.01a			
	LSD	0.014			
		0.81±0.01a	0.81±0.01a	0.82±0.02a	
	LSD	0.03			
Bean	OTC	0.41±0.09ab	0.38±0.05ab	0.19±0.009bc	Environment x Genotypes*** N=6 Environment* N=18 Genotypes** N=12
	CONTROL	0.5±0.051a	0.08±0.007c	0.35±0.07ab	
	LSD	0.21			
Squash	OTC	0.58±0.07ab	0.49±0.05ab	0.37±0.02bc	Environment x Genotypes** N=6 Environment** N=18 Genotypes*** N=12
	CONTROL	0.63±0.02a	0.26±0.04cd	0.16±0.008d	
	LSD	0.15			
		Non-photochemical quenching (qN)			
Maize		**Genotypes**			
		Altiplano	***Media***	***Huasteca***	Environment x Genotypes(ns) N=12 Environment*** N=36 Genotypes(ns) N=24
	OTC	0.82±0.01b			
	CONTROL	0.89±0.007a			
	LSD	0.03			
		0.83±0.01a	0.87±0.008a	0.86±0.02a	

	LSD	0.04			
Bean	OTC	0.52±0.08c	0.61±0.07bc	0.86±0.006a	Environment x Genotypes** N=6 Environment(ns) N=18 Genotypes(ns) N=12
	CONTROL	0.71±0.02abc	0.8±0.01ab	0.63±0.04bc	
	LSD	0.23			
Squash	OTC		0.49±0.06b		Environment x Genotypes(ns) N=6 Environment* N=18 Genotypes*** N=12
	CONTROL		0.65±0.05a		
	LSD	0.11			
		0.33±0.07b	0.62±0.06a	0.77±0.02a	
	LSD	0.16			
Maize		**Photochemical quenching (qP)**			
		Genotypes			
		Altiplano	***Media***	***Huasteca***	
	OTC	0.32±0.002b	0.25±0.008c	0.34±0.001b	Environment x Genotypes***N=12 Environment*** N=36 Genotypes*** N=24
	CONTROL	0.44±0.008a	0.44±0.008a	0.45±0.008a	
	LSD	0.04			
Bean	OTC	0.59±0.09b	0.69±0.05ab	0.53±0.01b	Environment x Genotypes*** N=6 Environment* N=18 Genotypes*** N=12
	CONTROL	0.71±0.04ab	0.17±0.007c	0.74±0.04a	
	LSD	0.14			
Squash	OTC	0.83±0.07ab	0.83±0.03ab	0.71±0.04bc	Environment x Genotypes** N=6 Environment** N=18 Genotypes*** N=12
	CONTROL	0.93±0.003a	0.58±0.06cd	0.4±0.03d	
	LSD	0.21			
Maize		**Alternative non-photochemical quenching (NPQ)**			
		Genotypes			
		Altiplano	***Media***	***Huasteca***	Environment x Genotypes (ns) N=12 Environment* N=36 Genotypes (ns) N=24
	OTC	1.36±0.05b			
	CONTROL	1.61±0.06a			
	LSD	0.07			
		1.37±0.007a	1.58±0.06a	1.51±0.08a	
	LSD	0.1			
Bean	OTC	0.89±0.1c	1.006±0.09c	1.44±0.009c	Environment x Genotypes*** N=6 Environment(ns) N=18 Genotypes(ns) N=12
	CONTROL	1.09±0.04abc	1.27±0.02ab	0.9±0.11c	
	LSD	0.36			

Squash	OTC	0.92±0.15a			Environment x Genotypes (ns) N=6 Environment(ns) N=18 Genotypes*** N=12
	CONTROL	1.16±0.13a			
	LSD	0.19			
		0.5±0.14b	1.09±0.13a	1.53±0.11a	
	LSD	0.26			

OTC: Open top chamber; LSD: Least Significant Difference; ns: no significant; *t-test, $p< 0.05$;**t-test, $p < 0.01$, and ***t-test, $p < 0.001$; The letters a, b, c, and d indicate significant differences according to the Tukey test ($P < 0.05$).

Effect of induced passive heat on gas exchange parameters measured at 75 days after emergence of each crop of the *milpa* (maize+bean+squash)

Significant effects of the genotypes and the environment on the gas exchange parameters at 75 days after the emergence of the crops using analysis of variance were observed. For maize, only the E x G of the transpiration rates (Trmmol) was significant (See supplementary data Table 6). When the interaction was not significant, the simple effect of the environmental and genotypic factors was considered.

Figure 7 shows the four gas exchange parameters used to evaluate the effect of the induced passive heat on the *milpa* system (maize+bean+squash) from different climates at 75 days after emergence. The passive induced heat did not affect the photosynthetic rate (photo) of the maize at the reproductive stage because no difference was recorded between the two environments. However, the maize from *Huasteca* (hot and humid) and *Media* (template) reported the maximum photosynthetic rate with 61.29±2.33 µmol CO_2 m^{-2} s^{-1} and 57.69±2.39 µmol CO_2 m^{-2} s^{-1} respectively, which was statistically different to the reported from *Altiplano* (warm-dry). The last ones registered the lowest photosynthetic rate with 40.44±3.23 µmol CO_2 m^{-2} s^{-1}.

The bean and squash were affected by the induced passive and significantly reduced their CO_2 assimilation rate. The genotypes responded differently under the effect of passive heat, where the squash and bean from hot and humid climate (*Huasteca*) reported the maximum values with 19.89±1.76 µmol CO_2 m^{-2} s^{-1} and 12.75±1.86 µmol CO_2 m^{-2} s^{-1} respectively, while those from *Altiplano* (warm-dry) recorded the lowest with 6.14±1.24 µmol CO_2 m^{-2} s^{-1} for squash and 4.58±0.56 for bean. That means the beans and squash from warm-dry climate were the most affected in the stage of reproduction for CO_2 assimilation.

For maize and bean, there was no variation in stomatal conductance (Cond) between genotypes and environments. That suggests the maize and bean reacted in the same way to the passive heat. In contrast, the squash benefited their stomatal conductance under the effect of the passive heat.

An increase of 0.21 mmol H_2O m^{-2} s^{-1} in OTC was recorded for the squash. The E x G was significant for transpiration rates (Trmmol) of the maize; however no differences statistics were observed. In addition, the maize from warm-dry climate (*Altiplano*) was the most affected and reported the lowest value in OTC with 3.11±0.69 mmol H_2O m^{-2} s^{-1} and 4.46±0.31 mmol H_2O m^{-2} s^{-1} in control conditions.

The bean from hot and humid climate (*Huasteca*) showed the minimum value of transpiration rates (Trmmol) with 3.68±0.28 mmol H_2O m^{-2} s^{-1} while those from template climate (*Media*) reported the highest values with 4.71±0.35 mmol H_2O m^{-2} s^{-1}.On the other side, the induced passive heat significantly impacted the Trmmol of the beans. A reduction of 1 mmol H_2O m^{-2} s^{-1} was reported comparing the two conditions. In contrast, the induced passive heat significantly increased the Trmmol of the squash. They reported an increase of 1.49 mmol H_2O m^{-2} s^{-1}.

In both environments, the maize intrinsic water use efficiency (iWUE) was affected by the induced passive heat with a significant difference. They decreased by up to 26.48% the iWUE in comparison to the control plots. Also, the crops bean and squash showed a reduction in their iWUE with significant differences. They reported a reduction of up to 43.56% and 57.43% for bean and squash, respectively. Furthermore, the genotypes of bean and squash were affected by the passive heat effect and behaved differently. The highest iWUE was reported for the squash from hot and humid climate (*Huasteca*) with 44.89±5.15 µmol CO_2 mol^{-1} H_2O which was statistically superior to those reported from *Media* and *Altiplano* (Template and warm-dry climates, respectively). The last reported the lowest iWUE with 11.52±2.34 µmol CO_2 mol^{-1} H_2O. Also, the beans from hot and humid climate (*Huasteca*) reported the maximum value of iWUE with 47.56±7.16 µmol CO_2 mol^{-1} H_2O while no differences were reported for those from template and warm-dry climates (*Media* and *Altiplano*, respectively).

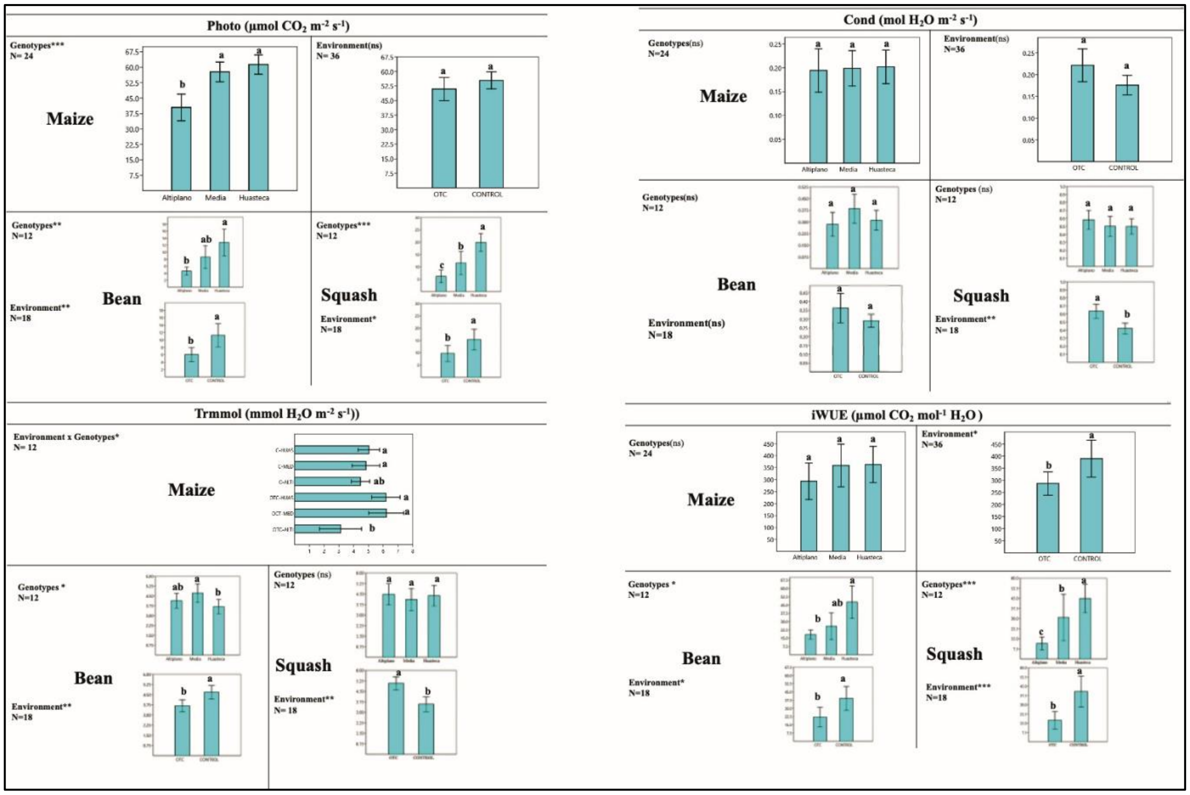

Fig 7. Effect of induced passive heating on gas exchange parameters of the milpa system (maize+bean+squash) at 75 days after emergence from different climate of the state of San Luis Potosí (Mexico). OTC: Open top Chamber; C: Control; HUAS: *Huasteca* (hot and humid climate); MED: *Media* (temperate climate); ALTI: *Altiplano* (warm-dry climate); Photo: photosynthetic rate; Cond: stomatal conductance; Trmmol: transpiration rates; iWUE: intrinsic water use efficiency; ns: no significant; *t-test, $p < 0.05$;t-test, $p < 0.01$, and ***t-test, $p < 0.001$. The letters a, b, c, and d indicate significant differences according to the Tukey test ($P < 0.05$). Vertical bars indicate the standard error.**

Correlation among abiotic variables and various growth, and development parameters of the *milpa* system (maize+bean+squash)

As physiological parameters are very interdependent for the *milpa* system, the correlations between them and the abiotic variables are necessary in determining the overall performance of the crops. An increase in temperature and accumulated heat units leads to an increased plant height of maize and bean plants but a decreased one on squash plants. Also, the increase in the abiotic variables leads to an increase in the rate of growth of maize but a decrease in this value for bean and squash. A significant but negative correlation was reported for the number of leaves of the squash, where the increase in the values of the abiotic variables considerably decreased the number of leaves (Figure 8A). In addition, an increase in temperature was negatively correlated with the yield of the *milpa* (maize+bean+squash). This negative correlation was significant for the squash, confirming that plants of this crop were the most affected by the induced passive heat (See supplementary data Photo 1) and mean that, the induced passive heat will decrease considerably the grain yield of the *milpa* system (maize+bean+squash) (Figure 8).

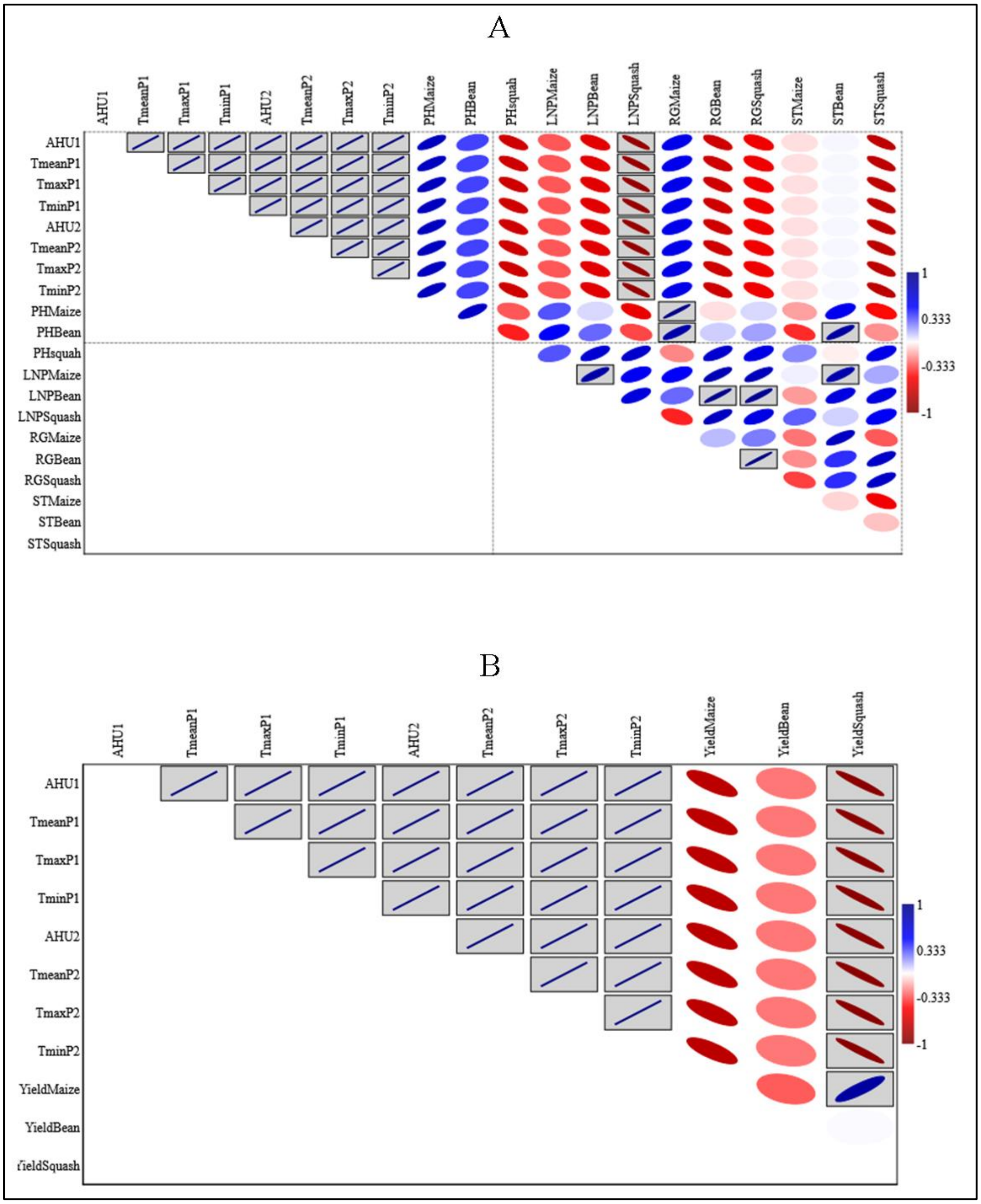

Fig 8. Plots of the statistic correlation of Pearson linear (r) among the abiotic variables and growth, and development parameters and yield of the *milpa* system (maize+bean+squash). AHU: accumulated heat units; Tmean: mean daily temperature; Tmax: Maximum daily temperature; Tmin: minimum daily temperature; P1: at 15 cm and P2: at 150 cm above the soil; PH: plant height; LNP: leaves number per plant; RG: rate of growth; ST: stem thickness. The boxed plots are significant at P< 0.05.

Correlation among abiotic variables and various photosynthetic parameters of the *milpa* system (maize+bean+squash)

Significant and negative correlations were reported for the maximum efficiency of the Photosystem II (Fv/Fm) for beans, intrinsic water use efficiency (iWUE) and non-photochemical quenching (qN) for maize, with the data of photosynthesis recorded 45 days after emergence in each crop, while a positive and significant correlation was only obtained for the stomatal conductance of the maize. The possible reason may be the increase in stomatal opening that is very directly associated with the photosynthetic rate. An increase of the abiotic variables, leads in a reduction of the photosynthetic capacity of the *milpa* system (maize+bean+squash) (Figure 9A).

At the reproductive stage of the crops, more chlorophyll fluorescence parameters had negative significant correlation with the abiotic variables and only for maize. Those parameters were efficiency of the photosystem II (Fv/Fm), photochemical quenching (qP) and non-photochemical quenching (qN). The possible reason may be related to the physiology of the maize, which is the one growing vertically and directly in contact with the light sun. In contrast, positive and significant correlations were showed in squash plants with some gas exchange parameters (stomatal conductance and transpiration rates). That means the increase in the abiotic variables promoted the gas exchange of the squash. The possible reason may also be related to the management of the system *milpa* where the maize plants protect the beans and squash plants against direct contact with the sun's light, because even though the correlations of the bean gas exchange parameters were not significant, they were positive (Figure 9B).

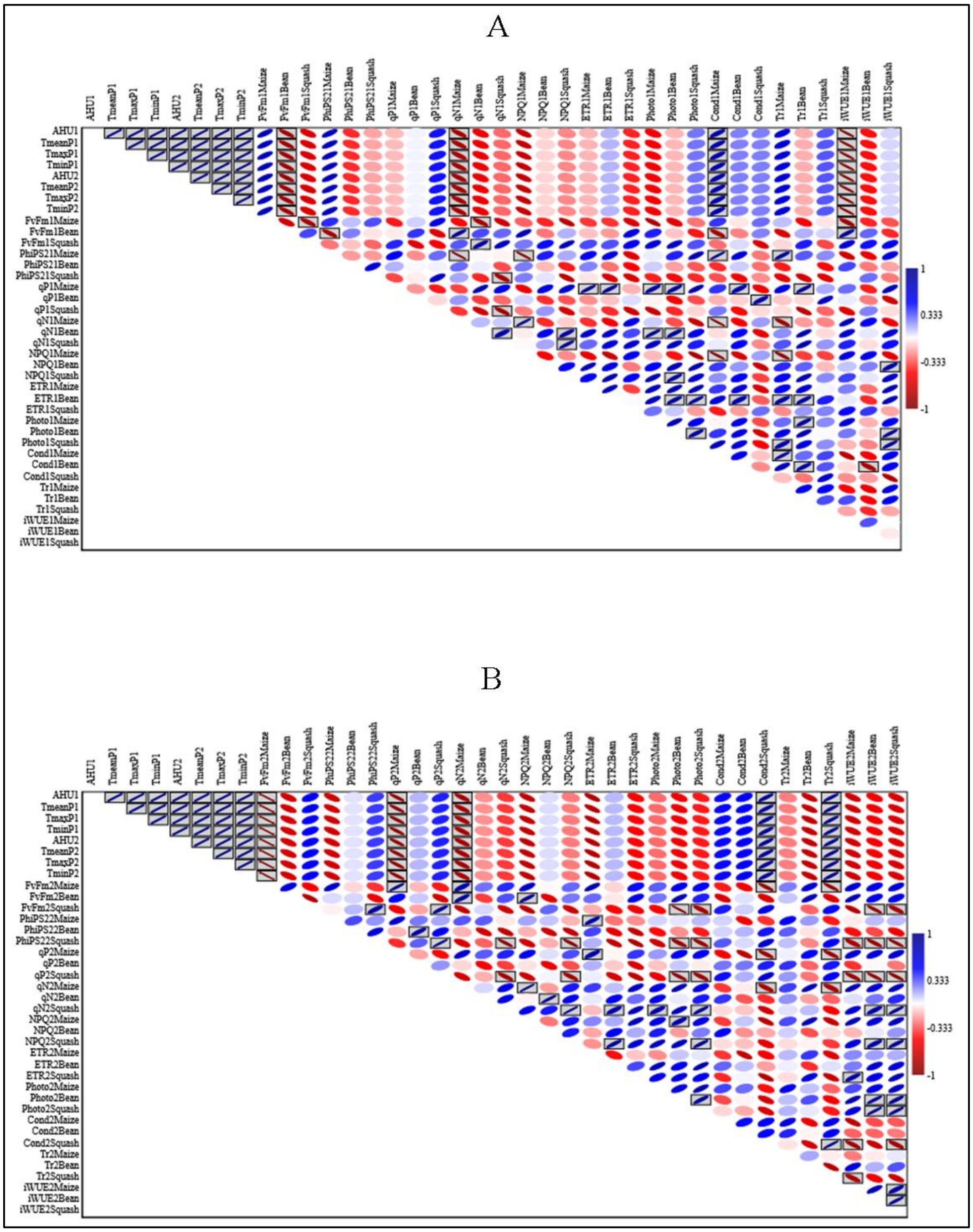

Fig 9. Plots of the statistic correlation of Pearson linear (r) among the abiotic variables and various photosynthetic parameters of the *milpa* system (maize+bean+squash). AHU: accumulated heat units; Tmean: mean daily temperature; Tmax: Maximum daily temperature; Tmin: minimum daily temperature; P1: at 15 cm and P2: at 150 cm

above the soil; ETR: Electron transport rate; Fv/Fm: Maximum PSII efficiency; PhiPS2: quantum yield of PSII; qN: Non-photochemical quenching; NPQ: Alternative non-photochemical quenching; qP: Photochemical quenching; Photo: photosynthetic rate; Cond: stomatal conductance; Trmmol: transpiration rates; iWUE: intrinsic water use efficiency; 1 and 2: measured at 45 and 75 days after emergence, respectively. The boxed plots are significant at P< 0.05.

Discussion

In this study we investigate the influence of increased air temperature (abiotic variable) under climate change scenarios on *milpa* systems (maize+bean+squash) from distinct climate (warm-dry, template and hot and humid) in the state of San Luis Potosí (Mexico). For the experiment, OTC was used to simulate the induced passive heat and allow evaluation of the *milpa* systems and their responses under a prognostic increase in temperature. In this approach, the employment of OTC appears to have resulted in accurate temperature projections (Cossani and Sadras, 2021). Our warming methods resulted in a maximum increase of 1.8°C in the mean daily air temperature for OTC at 15 cm above the soil while an increase of 3.65°C were reported at 150 cm above the soil. This was within the expected 1–3°C increase in global warming by the late twenty-first century (Chen, 2021; Kogo et al., 2021; Levine and Steele, 2021). Moreover, because there was more Growing Day Degrees found in OTC than in control (Figure 2A and B), most of the growth and development parameters were benefited for the crops of *milpa* system (Dan et al., 2020). In addition, the *milpa* system from a hot and humid climate (*Huasteca*) responded with more plant height, rate of growth, width leaf, height to ear insertion, number of leaves per plant, leaf area, leaf length and number of flowers per plant. The possible reason may be related to the adaptation characteristics of the genotypes to their climate, where more mean temperature and precipitation are reported (Figure 1). Then, this study therefore indicates that genotypes from different regions responded differently to the temperature effect (Diédhiou et al., 2021). In our case, the three different *milpa* systems responded differently to the effect of induced passive heat and increased most of the growth and development parameters of the crops that conformed to their *milpa* systems. Furthermore, the induced passive heat accelerated the time to flowering for the maize. It is important to remember that those variables were only measured for maize crops. Our results are consistent with those of Dong et al. (2021); Lizaso et al. (2018) and Wang et al. (2019), who stated that high temperatures can accelerate floret differentiation, reduce pollen shedding duration and delay silking.

The maize from a hot and humid climate (*Huasteca*) took more time to complete their reproductive stage. In this case, those from warm-dry (*Altiplano*) and template (*Media*) climates completed their reproductive stages faster than those from hot and humid climate. The results can be associated with the reason that the materials of dry and template (*Altiplano* and *Media*) environments with strong variation in the date of sowing have greater phenotypic plasticity than those of relatively more stable environments such as *Huasteca* (hot and humid).Furthermore, the current study clearly demonstrated that the induced passive heat during the intercropping *milpa* system resulted in yield loss. As a result, the squash was the most severely affected (see supplementary data Photo 1), with a loss of up to 91.94% of its yield recorded. The reason was that they used to abort under the OTC plots and that reduced their yield considerably. Most of the cucurbits are perishable and very sensitive to unpredictable climatic changes. An environmental stress like increasing (high) temperature is thought to be one of the major limiting factors in enhancing cucurbitaceous vegetables productivity (Kumar and Reddy, 2021). Additionally, the maize reported a reduction of up to 43.31% of the yield parameter. As mentioned in our OTC conditions, heat stress is a multifaceted challenge of strength (temperature degrees), duration, and rate of temperature augmentation and affected the *milpa* system. The reduction of the yield parameters is well correlated with the increase of the abiotic variables (Fig. 9B). Our results are in concordance with Murray-Tortarolo et al. (2018); Ureta et al. (2016); Ureta et al. (2012) Ureta et al. (2020) who stated that under climate change, temperature is expected to increase, and maize production could be heavily and negatively impacted by climate change (Liu et al., 2020b). The negative impact of the related effects of climate change on maize in Mexico has been largely studied (Aguirre-Liguori et al., 2019; Dendooven et al., 2012; Díaz-Álvarez et al., 2020; Diédhiou et al., 2021; Donatti et al., 2019; Eakin, 2000; Mercer et al., 2012; Ramirez-Cabral et al., 2017; Smale et al., 2001). Abiotic stresses have been also related to the effects of climate change in Mexico and will affect negatively maize germination (Castro-Nava et al., 2012; Reddy and Kakani, 2007), seedlings (Lizárraga-Paulín et al., 2011), growth and reproduction (Alam et al., 2017; Castro-Nava et al., 2012) and yield (Green et al., 2020; Ramirez-Cabral et al., 2017). The bean was the least affected crop by the induced passive heat because only those from hot and humid climate (*Huasteca*) reduced their yield. This result can be associated with the fact that the experiment was carried out in an area with a vapor pressure deficit greater than that which it normally faces in its region of origin. In the same way, for the ones from *Media* (template) and *Altiplano* (warm-dry), no differences were registered between control and OTC for the yield parameter.

With the objective of detecting how the yields of the three crops were affected by the induced passive heat, we made a correlation between the abiotic variables and the values of the obtained yields for each crop. We discovered that increasing values of the abiotic variables significantly reduced the squash, as well as the maize and bean yields. We found that the squash is the most affected by the warming effect (See supplementary Photo 1). During the experiment, the squash plants used to abort their flowers due to the consequences of the warming effect. That explains the loss of the yield for the squash plants and it is reported that high temperature is thought to be one of the major limiting factors in enhancing cucurbitaceous vegetables productivity (Kumar and Reddy, 2021).

Chlorophyll fluorescence analysis has become one of the most potent and extensively used tools in plant physiology research. The chlorophyll fluorescence parameters were represented by the measurement of the photosystem II, which is found in the thylakoid membranes and is intimately linked to instant plant damage caused by stress conditions (Maxwell and Johnson, 2000; Xu et al., 2020). In our study, the induced passive heat affected differently the chlorophyll fluorescence of the *milpa* system at the early and late stage of the crops. The induced passive heat increased the ETR, Fv/Fm and decreased the PhiPS2, qN, NPQ and qP of the maize plants. Furthermore, the response was different for bean and squash. The ETR increased by the effect of the induced passive heat in beans and squash, while Fv/Fm, PhiPS2 and qN reduced their values under the effect of the passive heat for the two crops. On the other hand, the qP was increased by the passive heat effect. Taking into account that under stress conditions Fv/Fm, PhiPS2, and qP are the most important parameters (Gallé and Flexas, 2010), our results are in accordance with that because the passive heat decreased those parameters for maize, bean, and squash (except qP). Our results agree with Xia et al. (2021) findings, that the qP of the two maize varieties decreased significantly under warming treatment. Schenone et al. (1994) indicated some differences in the measured of the physiological parameters of bean (*Phaseolus vulgaris* L.) due to the chambers effects which certainly caused by the physical structure of the OTC. In our investigation the photochemical quenching was affected by the passive induced heat. According to Silva et al. (2012a) OTC can reduce up to 25% the photosynthetically active radiation and increase the air temperature. These results are consistent with ours, as there was a reduction of photochemical quenching and an increase in air temperature with respect to the control environment. Yüzbaşıoğlu et al. (2017) reported similar results to ours for maize grown in high temperatures, keeping in mind that 20/25°C is close to our mean diurnal temperature during the experiment. Also, our results were similar to other researchers such as Li et al. (2020b) who found that an increase in temperature reduces photosynthesis in maize leaves. In the same way, Guidi et al. (2019) reported that photoinhibition occurs when light energy exceeds the amount of energy used for photosynthesis, characterized by a decline in the PhiPS2. In addition, Sales et al. (2013) and Trujillo et al. (2013) reported that the photosynthetic apparatus depends on the severity and duration of the stress.

In the current study, the gas exchange effect under passive heat stress has been reported to have different responses in the crops at 45 and 75 days after emergence. The photosynthetic rate, or CO_2 assimilation, and intrinsic water use efficiency were affected by the passive heat for all the crops in the system, while the stomatal conductance and transpiration rate were not affected at the early stage. Furthermore, the induced passive heat did not affect the maize photosynthetic rate at the reproductive stage; while the three other gas exchange parameters were affected. These results coincide with the analysis by Bradford et al. (2017) in which they conclude that increased temperature, while maintaining soil moisture, increases rainfed agriculture suitability in semiarid temperate regions (equivalent to *Altiplano* region). In our investigation, we show that a change in the development of photosynthesis apparatus exists in the milpa system for successful adaptation as measured by reduced CO_2 assimilation and higher water use efficiency appears to be involved in crop adaptation success (Ramazan et al., 2021). In addition, CO_2 exchange parameters act as chief indicators of plant growth due to their direct link to net productivity (Piao et al., 2008). The maize plants from a hot and humid climate (*Huasteca*) reported the highest values of the gas exchange parameters. That means they responded differently to the other genotypes. The genotypes from the warm-dry climate (*Altiplano*) were the most affected, even for the two other crops. Studies showed that early closure of stomata and decreasing transpiration were found to be thermal sensitive in maize plants grown at high temperatures (Correia et al., 2021; Yang et al., 2012), as we reported in our study. In various crop species, such as soybean, tobacco, and grape, global warming has been found to increase stomatal frequency while decreasing stomatal size, though no effect has been recorded in maize (Caine et al., 2019; Jumrani et al., 2017; Moore et al., 2021; Rodrigues et al., 2016; Zheng et al., 2013).

In our investigation, correlations were made between values of abiotic variables and photosynthetic variables at early and reproductive stages. Our results showed that the increase on the values of the abiotic variables leads to reduced specific variables such as Fv/Fm and qN for bean and maize at an early stage, while at the late stage, they were Fv/Fm, qP, and qN for maize. On the other hand, the increase on the values of the abiotic variables leads to improved stomatal conductance and transpiration rate of the squash (Figure 9 A and B). That means, in our case, the mentioned parameters were the most affected by the passive heat of the evaluated crops in our *milpa* system.

This study analyzed the effect of induced passive heat, which aims to simulate a scenario of global warming due to climate change, in *milpa* system from different climates of the state of San Luis Potosí (México). In the *milpa* system, maize is the most important crop and in Mexico, maize have an abundant genetic variability in all the country. In this approach, maize was originally categorized in different races and genotypes that have been related to particular environmental conditions (Wellhausen et al., 1952). Furthermore, Mexican maize was classified by Ruiz Corral et al. (2008) based on rainfall, photoperiod, and, most importantly, temperature of local adaptations or origins. These findings have crucial implications for thinking about the effects of climate change adaptation on maize in the country in general, and the state of San Luis Potosí in particular, because they highlight a way to contrast the negative effects of climate change while taking local conditions into account (Diédhiou et al., 2021). In our previous experiences (germination and emergence) (Diédhiou et al., 2021), the maize genotypes from hot and humid climates were the most affected. However, in the complete experience from emergence to yield, the maize from *Huasteca* (hot and humid climate) reported the highest values in growth and development parameters, photosynthetic and yield. The reason could be related to their origin environments' specific local adaptation. This is the first report to look into the effects of warming on the *milpa* system, taking into account the variability of the climates in San Luis

Potosí. Smallholders, in particular, are among those most affected by climate change. Our report is also a pioneer experiment in the state. From here, more investigation could be undertaken in each region using OTC as a model to simulate the increase in temperature. One of the limitations of the research was that the crops used by the *Media* are not the most representative climate of the region, whereas the most representative one is a semi-dry climate.

In conclusion, it was found that the use of the OTC structures increases the abiotic variables (minimum, maximum, mean daily temperature, and accumulated heat units). The growth and development parameters of the crops *milpa* system increased under the warming effect. Furthermore, the *milpa* from a hot and humid climate (*Huasteca*) was the least affected by the induced passive heat. In contrast, the warming considerably delayed the yield parameters of the crops. The squash was the most affected, while the bean most benefited from the yield parameters. The warming affected the chlorophyll and gas exchange differently for each crop. However, at an early stage (45 days after emergence), Fv/Fm and qN for beans and maize were reduced, while at the reproductive stage (75 days after emergence), they were Fv/Fm, qP, and qN for maize; stomatal conductance and transpiration rate of the squash were improved under the effect of warming.

Author contribution statement

HMRT project leader, obtained the financial resources for the study execution, supervised the research project. Coordinated the research work and revised/edited the manuscript. ID was mainly responsible for conducting literature review, research and wrote the first draft of the manuscript. JFM reviewed the manuscript and contributed to the final version of the manuscript. RFR reviewed the manuscript, revised and edited the final version of the manuscript. All authors read and approved the submitted version.

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Data availability

The datasets analyzed during the current study are available from the corresponding authors on reasonable request

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Supplementary data

Supplementary data Table 1. Results of the analysis of variance (ANOVA) of the physiological variables of the *milpa* system (maize+bean+squash)

Factor of variation for every crop	**PH**		**LNP**		**LL**		**WL**		**RG**		**LA**	
Maize	CM	Fvalue	CM	Fvalue	CM	Fvalue	CM	Fvalue	CM	Fvalue	CM	Fvalue
E	7.88	115.1***	27.07	12.8**	72.6	0.99ns	134.9	151.3***	0.005	47.7***	527764.5	61.31***
G	2.84	41.4***	108.16	51.3***	2046.5	27.8***	9.7	10.89***	0.005	42.4***	231974.9	26.95***
E x G	0.31	4.55**	5.5	2.6ns	44.9	0.61ns	8.28	9.29**	0.0005	4.55**	21520.4	2.5ns
CV(%)	11.3		11.9		8.9		9.34		9.8		12.7	
	DFF		**DMF**		**HEI**		**ST**					
	CM	Fvalue	CM	Fvalue	CM	Fvalue	CM	Fvalue				
E	60.7	3.1ns	114.08	11.9**	1.17	106.5***	1.19	0.1ns				
G	184.3	9.41**	102.6	10.7**	0.05	5.03**	104.07	8.45**				
E x G	4	0.2ns	28.08	2.93ns	0.02	1.67ns	64.87	5.27**				
CV(%)	7.4		5.1		9.7		10.75					
	NFP		**NLP**		**PH**		**RG**		**ST**			
Bean	CM	Fvalue	CM	Fvalue	CM	Fvalue	CM	Fvalue	CM	Fvalue		
E	1215	116.83***	2856.6	39.03***	24.77	1.13ns	0.04	11.54**	0.05	0.03ns		
G	38.06	3.66*	2027.92	27.71***	77.13	3.52*	0.01	3.89*	102.29	67.76***		
E x G	8.6	0.83ns	453.65	6.2**	1.23	0.06ns	0.0083	2.32ns	6.43	4.26**		
CV(%)	19		25.19		12.53		16.31		16.31			
	NFP		NLP		PH		RG		ST			

Squash	CM	Fvalue	CM	Fvalue	CM	Fvalue	CM	Fvalue	CM	Fvalue		
E	1.94	40.07***	5675.11	142.39***	696.96	19.97**	0.09	36.8***	266.88	14.81**		
G	0.16	3.25ns	425.36	10.67**	204.95	5.87**	0.05	20.94***	21.67	1.2ns		
E x G	0.03	0.67ns	200.19	5.02**	187.12	5.36**	0.05	20.94***	79.86	4.43*		
CV(%)	25.52		13.17		5.77		7.68		18.74			

PH: plant height; LNP: leaf number per plant; LL: leaf length; WL: width leaf; RG: rate of growth; LA: leaf area; DFF: days to female flowering; DMF: days to male flowering; HEI: height to ear insertion; ST: stem thickness; NFP: number of flowers per plant; NLP: number of leaves per plant; PH: plant height; NFP: number of flowers per plant; NLP: number of leaves per plant; CV: coefficient of variation; ns: no significant; *t-test, $p < 0.05$;**t-test, $p < 0.01$, and ***t-test, $p < 0.001$.

Supplementary data Table 2. Results of the analysis of variance (ANOVA) of the yield variables of the *milpa* system (maize+bean+squash)

	NCP		**CL**		**CD**		**CW**		**NRPC**		**NGPR**	
Maize	CM	Fvalue	CM	Fvalue	CM	Fvalue	CM	Fvalue	CM	Fvalue	CM	Fvalue
E	3.84	103.6***	468.07	145.17***	305.6	26.27***	0.47	35.72***	4.4	2.75ns	1442.13	38.64***
G	0.16	4.37**	1.98	0.62ns	156.3	13.44***	0.3	22.95***	19.82	12.38***	217.2	5.82**
E x G	0.07	2.02ns	3.43	1.07ns	477.5	41.05***	0.09	6.91**	7.75	4.84**	35.27	0.95ns
CV(%)	14.93		10.99		6.48		5		11.9			
	100GW		**YIELD**									
	CM	Fvalue	CM	Fvalue								
E	137.58	15.43**	0.2	30.05**								
G	138.21	15.5**	0.08	12.14**								
E x G	25.5	2.87ns	0.02	2.61ns								
CV(%)	6.5		14.19									
	YIELD											
Bean	CM	Fvalue										
E	0.07	26.73**										
G	0.47	168.37**										
E x G	0.03	11.43**										
CV(%)	8.33											
	YIELD											
Squash	CM	Fvalue										
E	1.93	114.89***										
G	0.2	11.95***										

E x G	0.03	2.37ns
CV(%)	8.16	

NCP: number of cob per plant; CL: cob length; cd: cob diameter; CW: cob weight; NRPC: number of rows per cob; NGPR: number of grains per row; 100GW: 100 grains weight for maize; CV: coefficient of variation; ns: no significant; *t-test, $p< 0.05$;**t-test, $p < 0.01$, and ***t-test, $p < 0.001$.

Supplementary data Table 3. Results of the analysis of variance (ANOVA) of the chlorophyll fluorescence parameters of the *milpa* system (maize+bean+squash) at 45 days after emergence.

	ETR		**Fv/Fm**		**NPQ**		**PhiPS2**		**qN**		**qP**	
Maize	CM	Fvalue	CM	Fvalue	CM	Fvalue	CM	Fvalue	CM	Fvalue	CM	Fvalue
Environment (E)	0.02	1.2ns	0.01	9.4**	0.23	15.63***	0.05	25.5***	0.09	29.9***	0.002	0.3ns
Genotypes(G)	0.11	6.97**	0.005	3.05ns	0.09	5.96**	0.01	5.63**	0.01	3.52*	0.02	4.41*
E x G	0.04	2.71ns	0.0002	0.13ns	0.03	2.01ns	0.004	2.07ns	0.008	2.9ns	0.001	0.29ns
CV	7.32		5.5		9.57		17.09		6.32		13.64	
Bean												
Environment (E)	142.02	9.6*	0.05	13.03**	0.01	1.86ns	0.04	110.05***	0.12	243.7***	0.0004	0.04ns
Genotypes(G)	3351.6	227.2***	0.0003	0.09ns	0.37	47.4***	0.13	303.4***	0.09	197.03***	0.0007	0.07ns
E x G	90.6	6.15**	0.007	2ns	0.72	91.6***	0.004	10.6**	0.03	63.8***	0.09	9.12**
CV	13.7		9.88		9.27		5.98		6.01		16.04	
Squash												
Environment (E)	0.26	13.7**	0.02	4.69*	0.12	2.17ns	0.007	0.62ns	0.03	3.11ns	0.11	7.22*
Genotypes(G)	0.3	15.9***	0.004	1.06ns	0.76	13.6***	0.02	2.42ns	0.18	17.2***	0.05	3.48*
E x G	0.57	30.5***	0.01	2.35ns	0.15	2.76ns	0.04	3.84*	0.17	16.1***	0.12	7.77**
CV	8.78		12.6		28.01		19.12		17.48		18.32	

ETR: Electron transport rate; Fv/Fm: Maximum PSII efficiency; PhiPS2: quantum yield of PSII; qN: non-photochemical quenching; NPQ: Alternative non-photochemical quenching; qP: Photochemical quenching; OTC: Open top chamber; LSD: Least Significant Difference; ns: no significant; *t-test, $p < 0.05$;**t-test, $p < 0.01$, and ***t-test, $p < 0.001$.

Supplementary data Table 4. Results of the Analysis of variance (ANOVA) of the gas exchange parameters of the *milpa* system (maize+bean+squash) at 45 days after emergence

	Cond		**iWUE**		**Photo**		**Trmmol**	
Maize	CM	Fvalue	CM	Fvalue	CM	Fvalue	CM	Fvalue
Environment (E)	0.22	58.42***	2.18	198.8***	0.32	19.8***	0.16	14.43**
Genotypes(G)	0.03	9.66**	0.03	2.99*	0.29	18.04***	0.1	9.1**
E x G	0.006	1.67ns	0.0007	0.07ns	0.01	0.61ns	0.005	0.46ns
CV	13.93		4.84		8.89		19.54	
Bean								
Environment (E)	0.04	9.6*	0.18	23.7***	0.02	4.2*	0.11	2.31ns
Genotypes(G)	0.28	66.7***	0.29	37.54***	0.11	23.09***	2.21	43***
E x G	0.02	5.53**	0.08	11.2**	0.05	11.03**	0.28	5.45**
CV	11.09		4.35		4.46		8.62	
Squash								
Environment (E)	0.008	0.49ns	0.00004	0ns	0.016	48.06***	0.13	1.39ns
Genotypes(G)	0.004	0.23ns	0.17	5.99**	0.15	439.54***	0.16	1.68ns
E x G	0.04	2.57ns	0.2	6.86**	0.03	107.67***	0.19	2.06ns
CV	19.07		8.95		1.15		11.43	

Photo: photosynthetic rate; Cond: stomatal conductance; Trmmol: transpiration rates; iWUE: intrinsic water use efficiency; ns: no significant; *t-test, $p < 0.05$;**t-test, $p < 0.01$, and ***t-test, $p < 0.001$.

Supplementary data Table 5. Results of the analysis of variance (ANOVA) of the chlorophyll fluorescence parameters of the *milpa* system (maize+bean+squash) at 75 days after emergence.

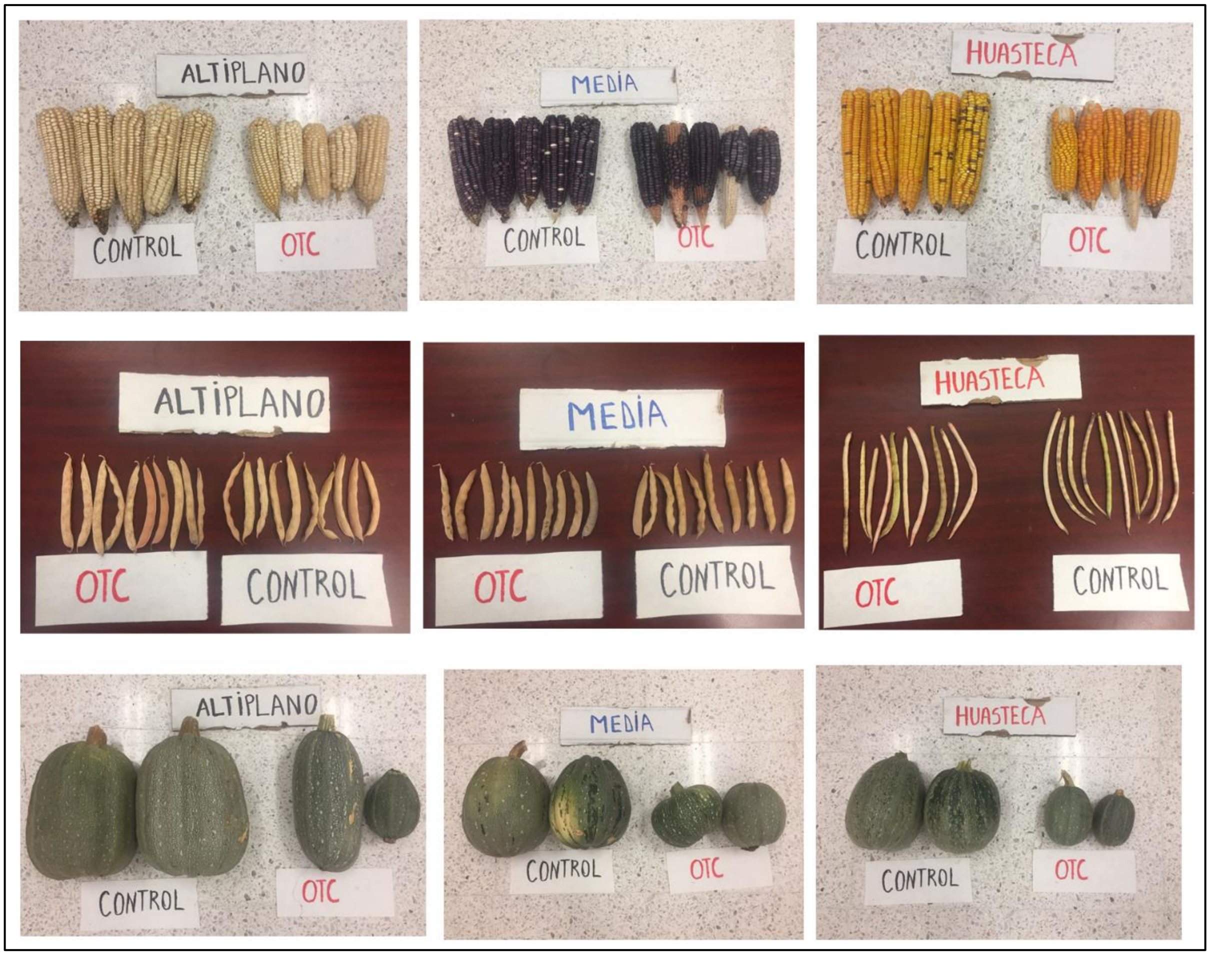
Maize	ETR		Fv/Fm		NPQ		PhiPS2		qN		qP	
	CM	Fvalue	CM	Fvalue	CM	Fvalue	CM	Fvalue	CM	Fvalue	CM	Fvalue
Environment (E)	0.19	42.3***	0.27	310.9***	0.19	9.16*	0.04	6.04*	0.07	21.4***	0.24	375.9***
Genotypes(G)	0.05	13.19***	0.0006	0.74ns	0.05	2.38ns	0.005	0.85ns	0.01	2.8ns	0.01	19.24***
E x G	0.0004	0.1ns	0.0003	0.4ns	0.03	1.74ns	0.007	1.1ns	0.005	1.52ns	0.008	13.15***
CV	3.9		3.67		12.13		27.8		7.01		4.24	
Bean												
Environment (E)	154.1	6.51*	0.0039	11.3**	0.006	0.15ns	0.009	0.66ns	0.02	1.34ns	0.03	4.74*
Genotypes(G)	4058.6	171.3***	0.0003	0.89ns	0.11	2.62ns	0.13	9.28**	0.04	3.01ns	0.13	20.55***
E x G	96.15	4.06*	0.002	6.34*	0.61	14.6***	0.19	13.05***	0.18	10.96**	0.26	40.4***
CV	12.8		2.41		18.58		22.8		18.68		10.96	
Squash												
Environment (E)	0.42	12.5**	0.01	15.47**	0.19	2.56ns	0.12	16.68**	0.11	4.29*	0.21	15.37**
Genotype(G)	0.67	19.67***	0.009	12.56**	1.16	15.39***	0.22	29.13***	0.39	14.85***	0.31	22.52***
G x E	0.06	1.86ns	0.006	8.78**	0.09	1.2ns	0.06	8.24**	0.02	0.83ns	0.14	10.2**
CV	10.6		3.64		29.02		14.09		22.45		16.5	

ETR: Electron transport rate; Fv/Fm: Maximum PSII efficiency; PhiPS2: quantum yield of PSII; qN: non-photochemical quenching; NPQ: Alternative non-photochemical quenching; qP: Photochemical quenching; OTC: Open top chamber; LSD: Least Significant Difference; ns: no significant; *t-test, $p< 0.05$;**t-test, $p < 0.01$, and ***t-test, $p < 0.001$.

Supplementary data Table 6. Results of the analysis of variance (ANOVA) of the gas exchange parameters of the *milpa* system (maize+bean+squash) at 75 days after emergence.

Maize	Cond		iWUE		Photo		Trmmol	
	CM	Fvalue	CM	Fvalue	CM	Fvalue	CM	Fvalue
Environment (E)	0.03	2.45ns	0.22	4.83*	0.07	3.65ns	0.008	0.04ns
Genotypes (G)	0.003	0.25ns	0.11	2.4ns	0.33	16.82***	1.74	9.64**
G x E	0.045	3.7ns	0.11	2.4ns	0.05	2.76ns	1.08	6*
CV	25.7		8.81		8.34		19.57	
Bean								
Environment (E)	0.02	1.36ns	0.82	8.99*	0.58	8.34**	0.1	9.8**
Genotypes (G)	0.02	1.64ns	0.41	4.57*	0.5	7.27**	0.03	3.1*
G x E	0.025	1.68ns	0.045	0.49ns	0.1	1.49ns	0.01	1.72ns
CV	21.89		22.38		32.25		17.3	
Squash								
Environment (E)	0.2	13.95**	1.58	22.01***	0.48	8.22*	0.24	14.69**
Genotypes (G)	0.01	0.86ns	1.2	16.69***	0.98	16.81***	0.005	0.33ns
G x E	0.01	0.82ns	0.02	0.3ns	0.036	0.63ns	0.01	0.69ns
CV	16.81		20.83		24.79		21.1	

Photo: photosynthetic rate; Cond: stomatal conductance; Trmmol: transpiration rates; iWUE: intrinsic water use efficiency; ns: no significant; *t-test, $p< 0.05$;**t-test, $p < 0.01$, and ***t-test, $p < 0.001$.



Supplementary data Photo 1. Effect of the induced passive heat on the harvested cobs (maize), pods (bean), and vegetables (squash) of the three *milpa* system.

Chapter VI: General Discussion and conclusions

Maize native genotypes: germination, emergence, initial growth and chlorophyll fluorescence under related effects of climate change

Maize is planted throughout Mexico, from very warm and humid climates at sea level to temperate and dry in the central plateau (equivalent to *Altiplano*). Distinct races and or genotypes of maize have been associated with particular environmental conditions since they were first classified (Wellhaussen et al., 1952). Corral et al. (2008) classified Mexican maize taking account rainfall, photoperiod and the most significantly temperature of their local adaptions or origins. These results have important implications for thinking about the effect of climate change adaptation of maize in the country because they indicated the way to take for contrasting the negative effects of climate change taking account the local conditions. Most notably, this is the first study to our knowledge to investigate effects of the increase of temperature and drought in creole genotypes during the germination and early growth stage of maize in San Luis Potosí taking account the three agroclimatic regions.

With the combination of the heat and water deficit stress, the results obtained were null or below 20% for percentage of germination. The mean germination time was delayed by the lower osmotic potential and the different temperature while for the growth variables most of them decreased under water stress conditions and depended to temperatures. However at high temperature and water stress (35°C/-0.5MPa), the results of the initial growth parameters decreased compared at 20, 25 and 30°C. In this work, some of the effects related to climate change (water deficit stress and high temperatures) drastically affected the germination and initial growth of creole genotypes of maize from the state of SLP under laboratory conditions. Then, it has documented how the increase of temperature and the decrease of precipitation will negatively affect the germination and initial growth of creole genotypes from different agroclimatic regions. Besides, the local particular conditions of each agroclimatic region have influenced the dynamic of germination and growth of the creole genotypes. Then, our results let select materials based on successful results from different environments, with different levels of water potential and thermal stress. Therefore, materials from less stressed areas (in this case *Huasteca*) will be less resilient to the related effect of climate change.

It is important to note that our experiment of germination and initial growth was conducted in laboratory conditions where the temperature and water deficit stress were controlled. In this sense, the limitations of our research are relative to the real conditions that the plants face in the field. The combinations of other factors, such as biotics, have not been taken into account.

Most importantly, this is the first study to investigate effects of the induced passive heating in young plants of maize (V9 and V12) emergence, initial growth and chlorophyll fluorescence of native genotypes of maize taking into account the three agro-ecological zones of the state of San Luis Potosí. Hernández et al. (2021) reported that a solid start to the plant cycle (initial stage) is critical for achieving a good end performance and a high grain yield. However, high seedling performance alone is insufficient to ensure a good grain production at the conclusion of the cycle. It is important to note that, in the *Huasteca* agro-ecological zone, the temperature oscillation in one day and in the year is much lower than in the *Altiplano* and *Media*. So the *Altiplano* and *Media* genotypes are adapted to tolerate extreme temperatures (which explains their best results) while the *Huasteca* genotypes are adapted to high temperatures, but with less variation and better climatic conditions for plant growth.

Maize metabolomic profiles under abiotic stress

Our research is a pioneer in determining the metabolic profile of native maize from different environments in the state of San Luis Potosí, Mexico. In the same way, the metabolomic profiles helped in classifying the native maize genotypes based on thermal variability. The combination of water deficit and heat stresses represents an excellent example of two different abiotic stress conditions that occur in the field simultaneously (Moffat, 2002). Sun et al. (2016) reported metabolomic profiles and metabolite levels in the leaves of three maize inbred lines grown in different temperatures [18/10°C (low temperature); 25/15°C (optimal temperature) and 35/25°C (high temperature)] conditions where our results were similar to those found by them because they mentioned a functional and metabolic plasticity may play different roles in maize plant adaptation to temperature variations. For example, tropical plants are damaged when exposed to temperatures below 10 ºC (chilling injury) and most species begin to have problems between 30 and 40°C. Small temperature increases (from 30 to 35ºC) can damage the reproductive organs of many crops, including wheat (*Triticum aestivum* (L). Thell), maize, rice (*Oryza sativa* L.), peanuts (*Arachis hypogaea* L.) and tomatoes (*Solanum lycopersicum* L.).

This study allowed to determine the metabolomic profiles of maize native genotypes seedlings from different environment of the state of SLP; and was able to identify differences related to the environment of origin (genetics) and the experimental conditions established in this work. Abiotic factors (increase in temperature and/or water stress combination) influenced both agronomic variables and molecular characteristics. To the best of our knowledge, this study is a first in determining the metabolomic profiles in the early growth of native maize seedlings in Mexico, despite the fact that 80 to 100% of the country smallholders "*campesinos*" use native seeds for maize production. However, even if it was possible to determine the metabolomic profile of the native maize genotypes from different climates and to evaluate the differences between them from the two factors such as water deficit stress, heat and their origin, we can say that our knowledge is limited. This is because this first research was conducted in laboratory conditions where the factors are controlled differently from what really happens in the field where the maize genotypes face during their emergence and growth.

Growth, development, photosynthetic capacity and grain yield and its component parameters of *milpa* (maize+bean+squash) under climate change

In this is study, we investigate the influence of increased air temperature (abiotic variable) under climate change scenarios on *milpa* systems (maize+bean+squash) from distinct climate in the state of San Luis Potosí, (México). In this present study, OTC was used to simulate the induced passive heat and allow evaluation of the *milpa* systems and their responses under a prognostic increase in temperature.

In the *milpa* system, maize is the most important crop and in Mexico, maize have an abundant genetic variability in all the country. In our previous experiences (germination and emergence), the maize genotypes from hot and humid climates were the most affected. However, in the complete experience from emergence to yield, the maize from *Huasteca* (hot and humid climate) reported the highest values in growth and development parameters, and photosynthetic.

Furthermore, the current study clearly demonstrated that the induced passive heat during the intercropping *milpa* system resulted in grain yield loss. As a result, the squash was the most severely affected (see supplementary data Photo 1), with a loss of up to 91.94% of its fruit yield recorded. The reason was that they aborted flowers under the OTC plots and that reduced their fruit yield. Most of the cucurbits are perishable and very sensitive to unpredictable climatic changes. An environmental stress like increasing (high) temperature is thought to be one of the major limiting factors in enhancing cucurbitaceous vegetables productivity (Kumar and Reddy, 2021). Additionally, the maize reported a reduction of up to 43.31% of the grain yield parameter. As mentioned in our OTC conditions, heat stress is a multifaceted challenge of strength (temperature degrees), duration, and rate of temperature augmentation and affected the *milpa* system. The reduction of the yield parameters is well correlated with the increase of the abiotic variables. Our results are in concordance with Murray-Tortarolo et al. (2018) and Ureta et al. (2020) who stated that under climate change, temperature is expected to increase, and maize production could be heavily and negatively impacted by climate change (Liu et al., 2020). The negative impact of the related effects of climate change on maize in Mexico has been largely studied. Abiotic stresses have been also related to the effects of climate change in Mexico and will affect negatively maize germination (Diédhiou et al., 2021), seedlings (Lizárraga-Paulín et al., 2011), growth and reproduction (Alam et al., 2017) and grain yield (Green et al., 2020). The bean was the least affected by the induced passive heat because only those from hot and humid climate (*Huasteca*) reduced their yield. The plants from *Altiplano* (warm-dry) provided a greater bean grain yield. Our results showed that warming favors pod parameters than ambient temperature. The reason could be related to their origin environments' specific local adaptation. This is the first report to look into the effects of warming on the *milpa* system, taking into account the variability of the climates in San Luis Potosí. Smallholders, in particular, are among those most affected by climate change. Our report is also a pioneer experiment in the state. From here, more investigation could be undertaken in each region using OTC as a model to simulate the increase in temperature.

The chlorophyll fluorescence parameters were represented by the measurement of the photosystem II fluorescence, which is found in the thylakoid membranes and is extremely linked to instant plant damage caused by stress conditions (Maxwell and Johnson, 2000; Xu et al., 2020). In our study, the induced passive heat affected differently the chlorophyll fluorescence of the *milpa* system at the early and late stage of the crops. The induced passive heat increased the ETR, Fv/Fm and decreased the PhiPS2, qN, NPQ and qP of the maize plants. Furthermore, the response was different for bean and squash. The ETR increased by the effect of the induced passive heat in beans and squash, while Fv/Fm, PhiPS2 and qN reduced their values under the effect of the passive heat for the two crops. On the other hand, the qP was increased by the passive heat effect. Taking into account that under stress conditions Fv/Fm, PhiPS2, and qP are the most important parameters, our results are in accordance with that because the passive heat decreased those parameters for maize, bean, and squash (except qP).

The gas exchange effect under passive heat stress has been reported to have different responses in the crops at 45 and 75 days after emergence. The photosynthetic rate, or CO_2 assimilation, and intrinsic water use efficiency were affected by the passive heat for all the crops in the system, while the stomatal conductance and transpiration rate were not affected at the early stage. Furthermore, the induced passive heat did not affect the maize at the reproductive stage; while the three other gas exchange parameters were affected. These results coincide with the analysis by Bradford et al. (2017) in which they conclude that increased temperature, while maintaining soil moisture, increases rainfed agriculture suitability in semiarid temperate regions (equivalent to *Altiplano* region) for beans specifically.

Research perspectives and constraints

This investigation evaluated maize genotypes from germination to grain yield. In addition, the intercropped crops bean and squash with maize were also evaluated under the warming effect. However, germination experiments were conducted in controlled conditions where others factors such as biotics were not taken into account. Also, the metabolomic profiles of maize seedlings grown under related conditions of climate change was determined. For that, shoots of the seedlings of 16 days after germination were used and were only determined using the GC/MS technique. Then, for future research, the use of more techniques such as nuclear magnetic resonance (NMR), Fourier transform-ion cyclotron resonance mass-spectrometry, capillary electrophoresis-mass spectrometry and pressurized liquid extraction, liquid chromatography tandem mass spectrometry (LC-MS/MS), high or ultrahigh performance liquid chromatography coupled to UV or fluorescent detection (HPLC/UPLC) and more aspects of the seedlings or plant parts (root, shoot, stem, leaf etc.), including the age of the crops, will be really interesting and bring more knowledge about maize native genotypes' metabolomics profiles grown under abiotic or/and biotic stresses and their combination. This kind of investigation has not been yet well studied in crops and specially in native genotypes of maize.

On the other hand, the use of the OTC to simulate the increase in the air temperature is a very good method in plants, but the small OTCs are limited for the maize crop because they can only be evaluated at an early stage of the maize. In the same way, OTC was created to evaluate the entire maize cycle. We were able to evaluate the maize's entire life cycle thanks to the OTC. Even so, the conditions they encountered, such as high relative humidity and the presence of more insects (data not evaluated), represented the constraints of the *milpa* experiments. In this research, in OTC experiments, only the temperature increase was evaluated. Future investigations can be conducted by combining the increase in temperature with the water deficit with the objective of simulating the real conditions that crops face in the fields. In addition, our field experiments with the OTC were conducted in the *Altiplano* region, which gave advantages for the crops from this region because they are already adapted to the conditions below, while the other two regions have been related to disadvantages. In the same way, future research must be conducted in conjunction with the construction of the OTC in each region of the state. Another constraint of this research is that the system *milpa* was evaluated for each crop and not as a system where there are relations between each element of the system. In this context, we also suggest evaluating the *milpa* as a system with the possible use of mathematical and statistical models.

In this research, only the negative effects of the related effects of climate change have been exposed. There have been no solutions proposed for farmers to mitigate the negative effects of climate change. For that, we propose using arbuscular mycorrhiza (AM) symbiosis, for example, under heat and/or water deficit stress. AM is known to be a nutrient-exchange symbiosis between plant roots and fungi of the phylum: the fungus receives organic carbon from its host and provides mineral nutrients, particularly phosphate, to the plant. The symbiosis has also been linked to increased plant resistance to abiotic stresses such as water deficit, salinity, and temperature extremes. Because of the benefits it provides for plant growth, the symbiosis is of great interest for use in sustainable agriculture.

In this context, several research questions and hypotheses to respond to for future investigations are:

Would there be differences between the metabolomic profiles of maize genotypes grown under climate change-related conditions with the use of different techniques (NMR, GC/MS, HPLC/UPLC, LC-MS/MS, etc.)? With the hypothesis that the use of different techniques will provide different metabolites, taking into account that each technique has disadvantages.

How would crops (maize+bean+squash) respond on physiology, growth and development, photosynthetic capacity, and yield (biomass, grains, and fruits etc.) to a combination of temperature increase and water deficit? This question can be answered with the use of the OTC to increase the air temperature and with the suspension of irrigation. In the same way, single-stress and multistress can be conducted in field conditions. In addition, we propose to conduct the experiments in each agroclimatic region of the state. The suggested hypothesis is that the combination of heat and water deficit stress and single-stress will affect the maize genotypes differently, and the genotypes with great responses can represent a key to counterattack the related negative effect of climate change in the state of SLP. The objective of the experiments must be to find the genotypes with more resistance to single and multistress in field conditions.

In the same way, after the determination of the genotypes more resistant to single and multistress, the metabolomic profiles of those genotypes can be determined and will provide more knowledge for the protection of the Mexican native maize. Therefore, the use of OTC can help to understand the crops' responses to future scenarios that are expected to happen in the future. In addition, to provide solutions for the smallholders "*campesinos*", the use of AM symbiosis under single and multistress experiments must be tested in field conditions.

Conclusions and final reports

The results of this thesis lead to the following conclusions:

1. The germination and initial growth of creole genotypes of maize coming from different agroclimatic regions were drastically affected by the increase of temperature and water stress. The creole genotypes from the region with more high mean annual temperature and precipitation (*Huasteca*) were the most affected and we consider this is associated to adaptations of the genetic material to the local environmental conditions with less stress in comparison to the materials from *Altiplano* and *Media*, that are adapted to regions of unfavorable conditions. Genotypes from the *Altiplano* and *Media* regions are associated not only with stress because of the combination of less precipitation and mean annual temperature but also with high temperature variations. The creole genotypes from *Altiplano* and *Media* can represent an important phylogenetic potential to counteract negative effects of the increase of temperature and water stress for being the less affected in laboratory conditions and coming from unfavorable conditions for the development of maize plants.
2. In the present, metabolomic profile in Mexican native maize have not yet well studied and most of the profile investigated was done on trans genetic, hybrid, wild ancestral maize. In addition, the response of maize to stress involves complex physiological and biochemical processes, and the molecular mechanism governing this response needs to be elucidated in depth via combinations of various analytical methods, such

as metabolomics, proteomics, genomics, transcriptomics, and bioinformatics. We conclude that the metabolomic profile of Mexican native maize have not been well studied and can be the key to understand how to face and how maize face the negative effect of climate change.

3. Untargeted metabolic profiling using gas chromatography/mass spectrometry in combination with multivariate data analysis provided molecular differentiation of the native genotypes of maize from warm-dry, temperate, and hot and humid environments. As a result, we now have a better understanding of the molecular diversity of these maize genotypes. Important metabolites in the different native maize genotypes were identified under heat, water stress and their combination and the origins of each genotype. The metabolite profiles, which show the relative content of the metabolites of the genotypes under related effects of climate change, will be useful baseline information for assessing the possible ways to counterattack abiotic stresses (water stress and heat) in native genotypes of maize.
4. Findings of the present study showed differential effects of warming on physiological attributes of native maize seedlings. The emergence of the seedlings and the photochemical quenching of the maize seedling genotypes were affected negatively by the increase in air temperature. The plant growth benefited from the increase in temperature, and it was accelerated. The genotypes from the *Huasteca* region (hot and humid climate), were the most affected. This is linked to the local conditions of adaptation of their genetic material, which is less stressed than the materials from the *Altiplano* (warm-dry climate) and the *Media* (temperate climate), which have unfavorable conditions and stressful environments for maize plant growth.
5. Finally, the growth and development parameters of the crops in the *milpa* system increased under the warming effect. Furthermore, the *milpa* from a hot and humid climate (*Huasteca*) was the least affected by the induced passive heat. In contrast, the warming considerably delayed the grain yield parameters of all the crops. The squash was the most affected crop, while the bean was the most benefited from the grain yield parameters. The warming affected the chlorophyll fluorescence of the PSII and gas exchange differently for each crop. However, at an early stage (45 days after emergence), Fv/Fm and qN for bean and maize were reduced, while at the reproductive stage (75 days after emergence), they were Fv/Fm, qP, and qN for maize; stomatal conductance and transpiration rate of the squash were improved under the effect of warming.

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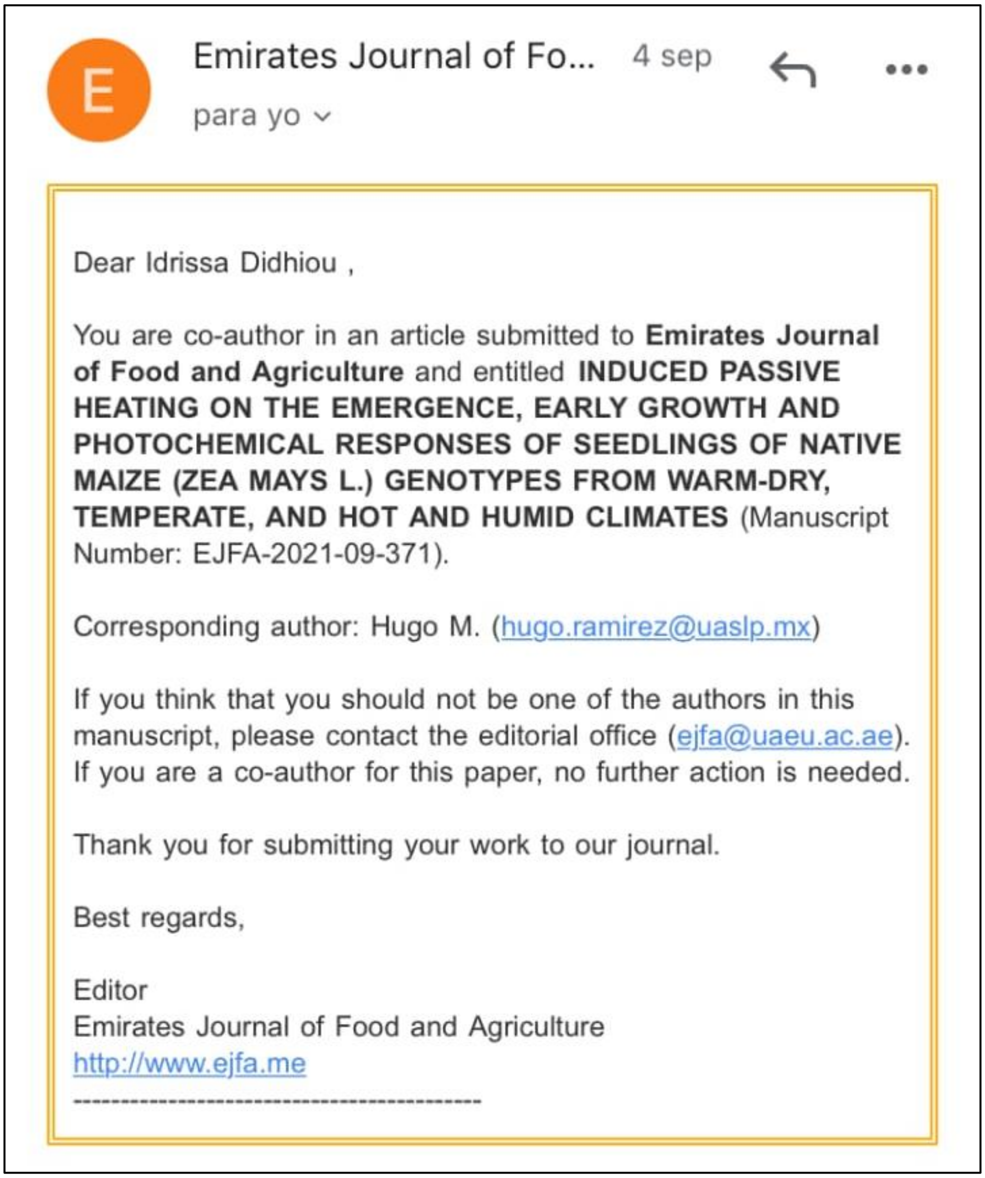
Annex

Original Article 3 send to Emirates Journal of Food and Agriculture (pISSN:2079-052X, eISSN: 2079-0538).



Dear Idrissa Didhiou ,

You are co-author in an article submitted to **Emirates Journal of Food and Agriculture** and entitled **INDUCED PASSIVE HEATING ON THE EMERGENCE, EARLY GROWTH AND PHOTOCHEMICAL RESPONSES OF SEEDLINGS OF NATIVE MAIZE (ZEA MAYS L.) GENOTYPES FROM WARM-DRY, TEMPERATE, AND HOT AND HUMID CLIMATES** (Manuscript Number: EJFA-2021-09-371).

Corresponding author: Hugo M. (hugo.ramirez@uaslp.mx)

If you think that you should not be one of the authors in this manuscript, please contact the editorial office (ejfa@uaeu.ac.ae). If you are a co-author for this paper, no further action is needed.

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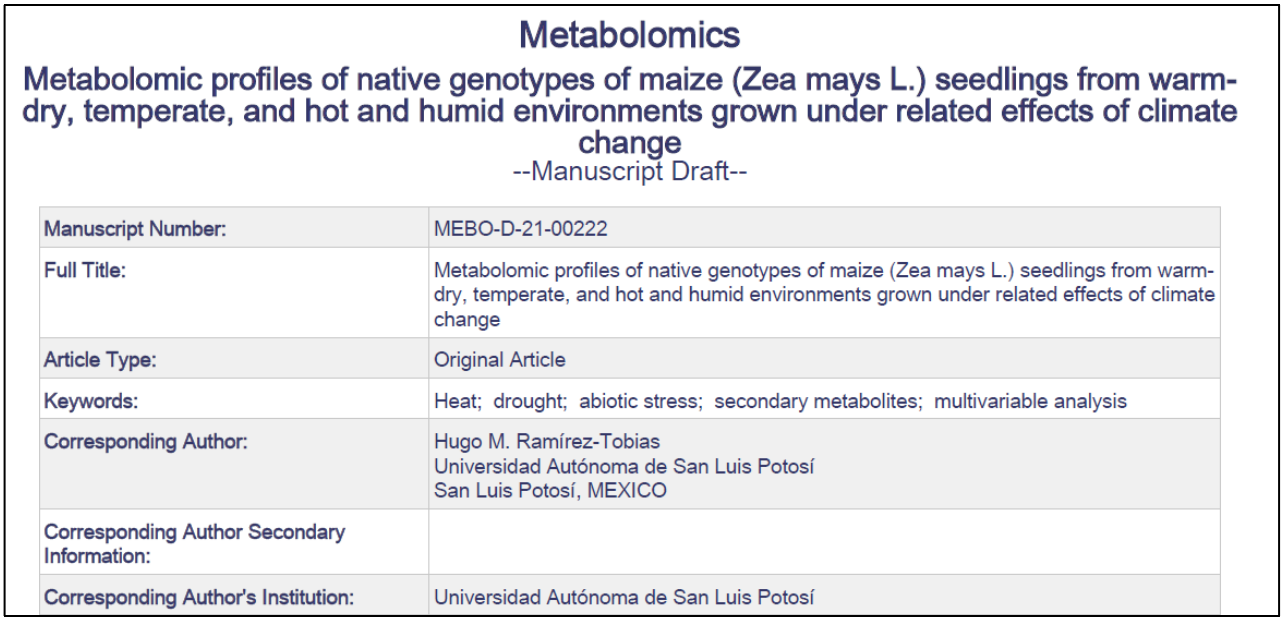


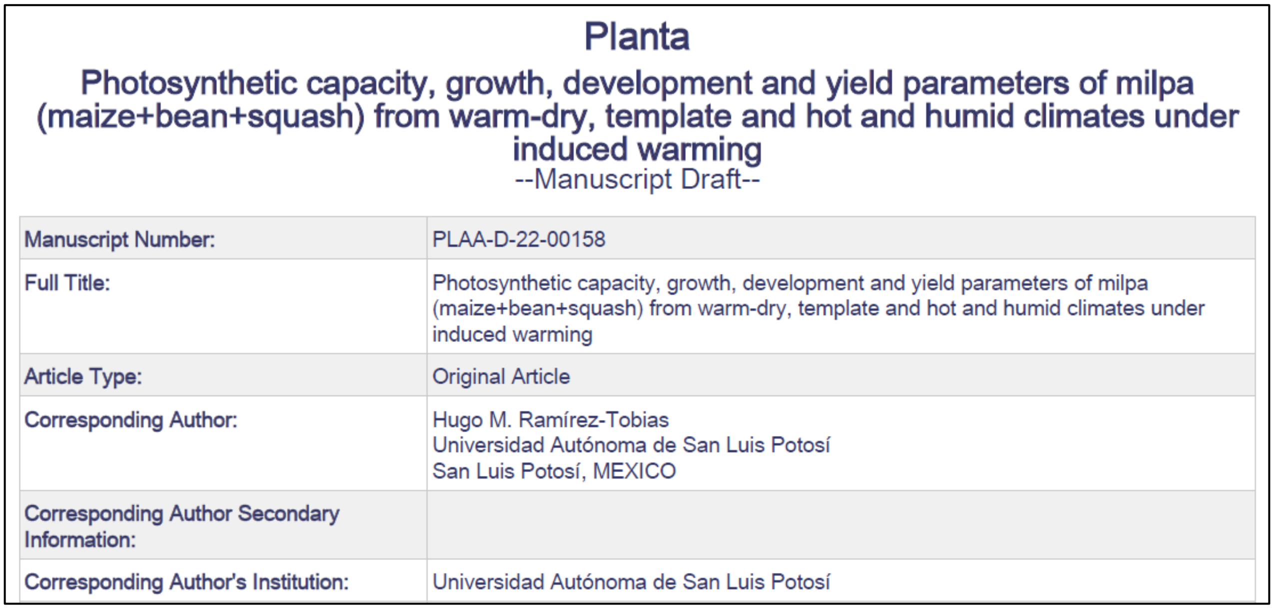
Metabolomics

Metabolomic profiles of native genotypes of maize (Zea mays L.) seedlings from warm-dry, temperate, and hot and humid environments grown under related effects of climate change

--Manuscript Draft--

Manuscript Number:	MEBO-D-21-00222
Full Title:	Metabolomic profiles of native genotypes of maize (Zea mays L.) seedlings from warm-dry, temperate, and hot and humid environments grown under related effects of climate change
Article Type:	Original Article
Keywords:	Heat; drought; abiotic stress; secondary metabolites; multivariable analysis
Corresponding Author:	Hugo M. Ramírez-Tobias Universidad Autónoma de San Luis Potosí San Luis Potosí, MEXICO
Corresponding Author Secondary Information:	
Corresponding Author's Institution:	Universidad Autónoma de San Luis Potosí

Original article 5 send to Planta (Journal Springer: electronic ISSN: 1432-2048, Print ISSN: 0032-0935) for the topical collection: Phenotyping photosynthetic capacity for crop improvement



Planta

Photosynthetic capacity, growth, development and yield parameters of milpa (maize+bean+squash) from warm-dry, template and hot and humid climates under induced warming

--Manuscript Draft--

Manuscript Number:	PLAA-D-22-00158
Full Title:	Photosynthetic capacity, growth, development and yield parameters of milpa (maize+bean+squash) from warm-dry, template and hot and humid climates under induced warming
Article Type:	Original Article
Corresponding Author:	Hugo M. Ramírez-Tobias Universidad Autónoma de San Luis Potosí San Luis Potosí, MEXICO
Corresponding Author Secondary Information:	
Corresponding Author's Institution:	Universidad Autónoma de San Luis Potosí

Photo 1: Experiments of germination, initial growth and metabolomic extraction

Photo 2: Experiment of maize seedlings in OTC

Photo 3: OTC constructions and *milpa* experiments