**Introduction**

Climate change is rapidly altering environmental conditions at the local level in particular, temperature and precipitation regimes and the severity of weather events. A major question for researchers throughout the world is how will plants cope with these rapid changes? Environmental conditions are even more impactful in plants than mobile organisms because of their sessile nature. Given the rapid change in local conditions, there are three ways plants can respond while avoiding extinction; quickly adapt, have the plasticity in phenotype that allows acclimation to the new conditions, or shift ranges.

The conditions across a species range are heterogeneous and likely have different selective pressures that act on the individuals of a population. This divergent selection can result in differing trait optima in two populations, which is known as local adaptation (Kawecki & Ebert, 2004). Temperature is a prominent variable that determines species distribution and varies greatly with geographic region in both severity and consistency. There have been many adaptations in different species to improve survival in extreme temperatures, but how do populations of the same species persist in different temperature regimes? To understand local adaptation to diverging temperature regimes, we must understand the biology of plants and ways in which they are vulnerable to extreme temperatures.

Intergenerational influences due to selection acting on both stages

Included adaptation during both stages

Cold and hot-thermotolerance

In this study, we compare temperature tolerance to extreme hot and cold conditions in plants from Minnesota and Texas. Since temperature tolerance selection can act on both the gametophytic and sporophytic stage, we incorporated variables from both stages. Sporophytic tolerance was measured using measurements on leaves including: net photosynthesis, chlorophyll fluorescence, and cell membrane stability. The gametophytic variables were pollen germination (viability) and pollen tube growth rate. The first objective was to 1) determine if local thermal conditions have selected for temperature tolerance traits fitting the conditions in the north and south. We hypothesized that if the temperature regimes in the north and south have resulted in divergent selection and local adaptation of temperature tolerance, then the plants in the north would be more tolerant of cold stress and plants from the south would be more tolerant of heat stress.

Is there variation in the traits

2) Inter-generational

The third objective was to 3) determine if there is a correlation between temperature tolerance in the gametophyte and sporophyte. If temperature stress is similar in both stages and gene expression patterns in the gametophytic and sporophytic life stages overlap, then there is a correlation between temperature tolerance in the gametophyte and sporophyte.

Temperature stress in plants largely occurs through oxidative stress via the production of reactive oxygen species (ROS) (Wahid, 2007; Wahid et al., 2007). Oxidative stress can hinder physiological mechanisms such as photosynthesis and metabolism, as well as the concentrations of primary and secondary metabolites. Primary metabolites are not only involved in physiological processes, but also in osmotic regulation and the integrity of cellular structures, including cell membranes (Gajanayake et al., 2011; Mishra et al., 2011; Valitova et al., 2019; Wahid, 2007; Zhu et al., 2018). While secondary metabolites in plants are often associated with defense and pollinator attraction, they are also central to photosynthesis. Pigments such as chlorophylls, carotenoids, and anthocyanins are secondary metabolites involved in absorbing light energy used for photosynthesis (Wahid, 2007). Some of these cellular processes are not unique to diploid cells of the plants (sporophyte), but also occur in the haploid cells such as pollen and ovules (gametophyte). Extreme temperatures can limit pollen production, tube growth rate, and viability (Gajanayake et al., 2011; Kakani et al., 2002; Singh et al., 2008). Although temperature stress can be damaging to these processes, there are adaptations that allow plants to withstand extreme temperatures such as the production of heat shock proteins (HSP).

Plants have life cycles that alternate between haploid and diploid stages (Bowman et al., 2016). The diploid stage, also referred to as the sporphyte, produces the genetically unique haploid gamete, also known as the gametophyte. For angiosperms, most of the plant’s life occurs in the sporophyte stage with a short period in the haploid stage during sexual reproduction. Many have found that natural selection can act both on the sporophyte and gametophyte stages and that the processes of selection are independent of one another (Beaudry et al., 2020; Walsh & Charlesworth, 1992).

In the sporophytic stage, selection can act through variation in the individual plant. Sporophytic traits include leaf morphology, biomass accumulation, plant size, competitiveness for resources, photosynthetic efficiency, water use efficiency, and other characteristics of the full plant. Many studies have compared temperature tolerance between cultivated varieties of crop or ornamental species, largely produced by selective breeding (Gajanayake et al., 2011; Poudyal et al., 2019). Poudyal et al. compared several cultivated varieties of hybridized lines and local accessions, some of which were selected and bred for high temperature tolerance. They found considerable differences between performance of certain genotypes over others after a high temperature treatment. The sporophytic traits with stark differences in performance between “temperature tolerant” accessions and “temperature sensitive” accessions were net photosynthesis, water use efficiency, and leaf cooling.

Gametophytic selection acts on the male gamete, pollen, and the female gamete, ovules. In the sexual reproduction of plants, pollen is produced in the anthers of a flower and is transferred via pollinators or wind to the stigma. The pollen grains then germinate by extending the cell in a tube-like projection, known as the pollen tube, through the style to the ovary, which encases a few to several ovules. The tubes fertilize the ovules by discharging sperm cells into the ovule (Bowman et al., 2016). In most cases, the number of pollen grains deposited on a stigma far outnumber the ovules, incurring competition between the male gametes to fertilize the ovules (Ottaviano et al., 1988; Ruane, 2009; Sarigorla et al., 1992). Traits in pollen that are linked to fitness are pollen production (number), pollen tube growth rate, pollen tube maximum length, and pollen viability.

Gametophytic selection is thought to contribute to the rate of evolution because the lack of dominance allows selection to directly act on single alleles (Beaudry et al., 2020). Selection at the gametophyte could then have pleiotropic effects that are adaptive or nonadaptive for the sporophyte. Since the gametophyte is exposed to environmental conditions, temperature could act as a selective pressure and contribute to how the sporophyte responds to thermal conditions. A few studies have found evidence of gametophytic selection for temperature tolerance. Paupiere et al. (2017) examined several cultivated tomatoes and wild accessions for temperature tolerance in the gametophyte. The cultivated tomatoes were either selectively breed for tolerance to high temperatures or overall hardiness. The wild accessions originated from low altitude populations in South America that grew in warm climates. There was considerable variation among the cultivated varieties and among the wild varieties for number of pollen grains per flower and pollen viability. The wild varieties had comparable values with cultivated varieties for both traits. These findings suggests that local adaptation through natural selection has led to populations with temperature tolerance to heat stress in pollen at these sites in South America. Similar results were found in other studies (Driedonks et al., 2018; Zamir et al., 1981). Zamir et al. (1981) compared cold and heat tolerance in pollen from a cultivated tomato variety and a wild, high altitude tomato species. They found that pollen from the high-altitude species, *Lycopersicon hirsutum*, was more successful in fertilization and had a higher germination percentage than the cultivated variety in cold conditions. The authors concluded that there had been local adaptation to cold in the gametophytic stage at the high-altitude locations. Several studies have found differences in temperature tolerance in pollen among cultivated varieties and genotypes for pollen tube growth rate, pollen germination, and fertilization success (Dominguez et al., 2005; Hedhly et al., 2005). These findings suggest that selection can occur at the gametophytic stage.

Though selection in the sporophyte and gametophyte are independent of one another, there is evidence of similarities between the two and the potential for selection to compound through the involvement of similar selective pressures at both stages (Beaudry et al., 2020; Evans et al., 1988). It has been shown that there is a substantial overlap in genes and gene expression between the sporophytic and gametophytic stages (Beaudry et al., 2020; Pedersen et al., 1987; Tanksley et al., 1981; Willing & Mascarenhas, 1984). However, not all studies have had the same results and Dominguez et al. (2005) found that temperature tolerance may not be as predictable as previously described. In a study on a cultivated tomato, they found that pollen selection for temperature tolerance to cold did not improve pollen viability and formation in cold conditions. The authors suggested that genes that mediate temperature tolerance may not be expressed in the gametophyte, but rather the sporophytic tissues surrounding the site of pollen formation.

Most research on the correlation of gametophytic and sporophytic temperature tolerance is in crop species, where artificial selection at the gametophytic stage would speed up the process of selective breeding (Dominguez et al., 2005; Dronavalli & Kang, 2019; Rani & Ravikumar, 2007). However, there are evolutionary implications for wild populations. If traits of temperature tolerance occur in the gametophyte and sporophyte, selective pressures could lead to the adaptation of traits that are more favorable in the local temperature regime for both life stages. Furthermore, if gene expression for these traits is similar in the two stages, selection on the gametophyte and sporophyte may increase rates of evolution for temperature tolerance, which is becoming increasingly important as the climate rapidly changes. To expand the inference space beyond crop species, we must incorporate wild species. Likewise, to fully understand how wild species will respond to climate change, we must understand all ways in which climate conditions could affect species local adaptation and persistence.

*Sporophytic Tolerance*

Photosynthetic rate is sensitive to temperature (Berry & Bjorkman, 1980), which becomes apparent through understanding the mechanisms involved in photosynthesis. Photosynthesis is the process by which plants convert light energy into chemical energy by fixing CO2 into carbohydrates. This process involves many enzymes, pigments, and proteins that are essential for absorbing and harvesting light energy. Photosynthesis begins with the light reaction in the thylakoid membrane of chloroplasts. Pigments, such as chlorophyll *a*, chlorophyll *b*, carotenoids, and anthocyanins, absorb light energy and transfer the energy to reaction centers, where the energy is used to excite electrons at both photosystems. The electrons are initially acquired through a water splitting reaction that takes place at photosystem II. The excited electrons move through an electron transport chain, in the process, creating a H+ gradient across the thylakoid membrane and converting NADP+ to NADPH. The membrane potential established by the H+ gradient is used by ATP synthase to produce ATP. The ATP and NADPH are then used for the light independent reaction, also known as the Calvin Cycle. The Calvin Cycle begins with an enzyme called rubisco which fixes CO2 to a ribulose sugar. The cycle continues and eventually produces fructose that is converted to glucose and is either used by the plant for energy or stored and used for growth.

Extreme temperatures can affect photosynthesis in multiple ways. High temperatures decrease the affinity of rubisco to CO2 and increase its affinity to O2 (Bauwe et al., 2010; Zhu et al., 2018). The fixation of O2 produces compounds that are needless and requires photorespiration to recycle components necessary for photosynthesis, in the process, reducing the efficiency of photosynthesis (Bauwe et al., 2010). In extreme temperatures, hot and cold, proteins and enzymes can be damaged or rendered inactive. This can have an immense effect on photosynthesis because the protein complexes in photosystem II and the electron transport chain can unfold (Zhu et al., 2018). The degradation of integral proteins and enzymes can also lead to the production of reactive oxygen species (ROS) through the excess absorption of light energy and prolonged excitation of chlorophyll molecules (Mishra et al., 2019). Reactive oxygen species damage membranes and other membrane proteins (Zhu et al., 2018).

In plants that are temperature tolerant, chlorophyll can adopt a transition state that reduces absorption and excitation of chlorophyll to reduce the production of ROS (Mishra et al., 2019). Chlorophyll transition can also reduce photosynthetic rate in stressful conditions. Many studies have found differences between genotypes in the maintenance of photosynthetic rates and recovery when exposed to extreme temperatures (Gurevitch, 1992; Mishra et al., 2019; Poudyal et al., 2019; Zhou et al., 2017). Though most studies have been preformed in sensitive and tolerant crop varieties, there is evidence of local adaptation in wild species of photosynthetic rates (Gurevitch, 1992) and responses in photosynthetic rate to temperature (Berry & Bjorkman, 1980; Zhu et al., 2018). Zhu et al. (2018) found that photosynthetic heat tolerance was generally higher in species adapted to hot environments in a study with 62 species from 5 distinct biomes in Australia. However, they also found that photosynthetic rate varied seasonally and that there was flexibility in this physiological trait.

*Gametophytic Tolerance*

Up until this point all processes that I have mentioned that are affected by temperature tolerance were in the sporophyte. However, the gametes of plants are also vulnerable to temperature and vary in temperature tolerance. Most studies on tolerance in the gametophyte focus on pollen, because of ease of study. Temperature can alter pollen production, pollen tube growth rate, and pollen viability (Hedhly et al., 2005). There have been multiple studies that have differentiated genotypes with more tolerant pollen grains from those that are more sensitive (Gajanayake et al., 2011; Hedhly et al., 2005; Paupiere et al., 2017; Poudyal et al., 2019; Singh et al., 2008; Zamir et al., 1982). Mechanisms of temperature tolerance in pollen have also been identified (Frank et al., 2009). Frank et al. (2009) used transcriptomics to determine ways the effects of heat stress are reduced in pollen grains. They found differential expression between heat sensitive and heat tolerant accessions of tomato in heat shock proteins, ROS scavengers, sugars, plant hormones, and regulatory genes. This suggests that even for the miniscule pollen grains there are complex mechanisms of temperature tolerance performed to survive and compete for fertilization. While understudied, there is also evidence of variation in temperature tolerance for the female gametophyte (Xu, Driedonks, et al., 2017; Xu, Wolters-Arts, et al., 2017). The female gametophyte is more difficult to study due to increased protection via the ovary and more conspicuous tolerance traits. Temperature can affect the female gametophyte through ovule formation, viability, and abortion rates.

*Mechanisms of tolerance: Cell membrane stability*

As mentioned previously, ROS affect the cell membrane integrity, but temperature stress itself can also affect the membrane fluidity (Zhu et al., 2018). High temperatures increase the fluidity of membranes and can result in leakage and disruption in the spatial organization of membrane proteins. Thylakoid membranes, the location of the light reaction in photosynthesis, are also composed of a phospholipid bilayer and is vulnerable to disruption (Berry & Bjorkman, 1980). Membrane stability is a trait that is variable among species and even individuals of the same species. The integrity of a cell membrane can be maintained by incorporating fatty acids with a higher degree of saturation. Zhu et al. (2018) found that 40% of the variation in heat tolerance threshold for plant species could be explained by fatty acid composition. They found evidence of local adaptation to temperature tolerance through differential production of saturated fatty acids among plant species resulting from the temperature range in which they reside. Most studies do not incorporate fatty acid composition, but rather use conductivity as a proxy for membrane disruption. Cytoplasm leakage, or electrolytic leakage as it is often referred to, has a higher concentration of solutes and therefore a higher conductivity. Less tolerant plants may have increased electrolytic leakage and a higher conductivity in the solution containing the plant material of interest. Multiple studies have used electrolytic leakage to determine the temperature tolerance of genotypes (Gajanayake et al., 2011; Xu et al., 2014; Zhao et al., 2005).

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