Interspecific Grafting of Tomato (*Solanum lycopersicum)* onto Wild Eggplant (*Solanum torvum)* for Increased Environmental Tolerances

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CHAPTER 1

INTRODUCTION AND OVERVIEW

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Vegetable Production in the US Virgin Islands

There is a rich culture and history of vegetables grown in the tropics, such as the US Virgin Islands (USVI) (Palada and Crossman, 1999). The USVI Agricultural Experiment Station states that the production and marketing of fruits and vegetables provides a primary or secondary source of income, and "many Virgin Islanders supplement their diets with fruits, vegetables and herbs grown in home gardens" (USVI Agricultural Experiment Station, 2000). These plants are rich sources of nutrients and, when exported to interested markets such as the continental US, can be a viable addition to domestic economies (Oomen and Grubben, 1978). Tropical leaf vegetables have unique adaptations that allow them to survive in tropical climates that have widely fluctuating amounts of rainfall throughout the year. According to Sands (1974), average monthly rainfall on the St. Croix Island of the USVI ranges from 4.26 to 6.08 inches August through November, and declines to a low of 1.71 inches in March and throughout most the summer. Tropical vegetables that can survive in these variable conditions include amaranth, eggplant (*Solanum melongena*), pak choi (*Brassica rapa*), malabar spinach (*Basella rubra*), sweet potato (*Ipomoea batatas*) and bush okra (*Abelmoschus esculentus*) (Palada and Crossman, 1999).

Staple vegetables of the continental United States, such as tomatoes (*Solanum lycopersicum)*, cabbage (*Brassica oleracea*), onions (*Allium cepa*) and peppers (*Piper nigrum*) are incredibly popular in the USVI as well, and several attempts at domestic production have been made (Pena and Hughes, 2007; Sands, 1974). Successful integration of these vegetables into tropical food production systems would have financial, cultural and nutritional benefits. The Asian Vegetable Research and Development Center (2006) states that, concerning tropical communities, "Vegetables are the best resource for overcoming micronutrient deficiencies and provide smallholder farmers with much higher income and more jobs per hectare than [native] crops". Sands (1974) points out that having a more diverse and fully developed agricultural system would complement the USVI's major industry –tourism- by offering visitors more fresh local products that wouldn't otherwise be available. He goes on to argue that from a cultural standpoint, expanded agriculture would preserve the natural environment of the USVI as well. Geographic potential of expanded agriculture exists- 14.7% of USVI land area exists as arable and permanent cropland, compared to an 11.3% world average (Earth Trends, 2003).

Expansion and diversification of USVI fruit and vegetable crops is limited and constrained, however, by a complex of biological, physical and socioeconomic factors. Crops must be able to handle a short period of extremely wet soils and harsh, rainy conditions followed by an extended dry season while the crops are maturing. Rainfall records at the Frederiksted USVI weather station show that less than once inch of rain fell in the months of February, March and May five times in a twelve year span from 1959-1972, and over six inches of rain averaged in October and November (Sands, 1974). Indeed, the problem still exists today, as the University of Virgin Islands Agricultural Experiment Station listed the short rainy season as the major limiting constraint of USVI agricultural production (2000), and Pena and Hughes (2007) state "environmental stress is the primary cause of crop losses worldwide, reducing average yields for most major crops by more than 50%". Most vegetable crops prefer cooler temperatures and constant moist soils (Ali, 2000), and the environmental extremes present in the USVI and other tropical areas pose a significant challenge. Vegetables, by definition, are succulent plants, and most are comprised of more than 90% water (AVRDC, 1990). Thus, water supply in the soil and the atmosphere has incredible influence on the size and quality of vegetables. The dry seasons common in the USVI climate lead to high rates of evapotranspiration and an increased solute concentration in the soils, causing an osmotic flow out of plant cells (Jipp et al., 1998). This lowers the water potential within the plant, and disrupts complex cell processes such as photosynthesis and respiration. Too much water in the rainy season poses yet another problem. Flooded soils inhibit oxygen processes in the root zone, and waterlogging is proven to produce endogenous ethylene that causes damage to tomatoes (Drew, 1979).

Temperature stress, in addition to water stress, reduces vegetable production, and climatologists believe that the combined environmental stress in the tropics will only get worse over time. Climate trend analysis in tomato growing regions by Bell et al. (2000) show that temperatures are going to rise, and the frequency and severity of above-optimal temperatures for vegetative growth are going to increase in the coming decades. This will prove to be detrimental to tomatoes specifically, as their growth and reproductive processes are strongly modified by increases in temperature alone, and also in conjunction with other changing environmental factors like water stress (Abdalla and Verderk, 1968). Maximum growth for most tomato plants occurs at day and night temperatures of 25 degrees Celsius (Max et al., 2009). The average temperature in the USVI however is 27 degrees Celsius, and average max temperatures often climb as high as 32 degrees Celsius (Brown and Lugo, 1990). Fundamental biochemical reactions are disrupted by high temperatures in most vegetable crops, such as a decrease in photosynthetic capabilities, reduced fruit set and pre-anthesis temperature stress leading to poorly developed flowers (Weis and Berry, 1988; Stevens and Rudich, 1978; Sato et al. 2002). In pepper, another solanaceous vegetable, high post-pollination temperatures inhibited fruit set, suggesting that fertilization is sensitive to high temperature stress (Erickson and Markhart, 2002). In summary, supra optimal temperatures in tomato crops induce fruit set failure by bud drop, abnormal flower development, poor pollen production, ovule abortion and poor viability, reduced carbohydrate availability, and reduced vegetative growth due to an inhibition of photosynthesis (Hazra et al. 2007).

Improving agricultural infrastructure would offset some of the environmental problems that face plant production in the USVI, but many are too expensive to be considered and government support for agricultural sectors has been declining for the past 50 years (McElroy et al., 1990; Sands, 1974). Due to financial constraints, the USVI has no wheeled or crawler tractors and zero percent irrigation (EarthTrends, 2000; Mwaijande et al., 2009). Greenhouses are used to change the microclimate around plants to create favorable growth conditions, but even if the USVI did improve its agricultural infrastructure with modern greenhouses, outside climatic pressures would still prove troublesome. Tropical greenhouses are often naturally ventilated to reduce energy costs (Max et al., 2009). This method of passive cooling relies on prevailing atmospheric conditions, especially wind, and ventilation openings need to have a large surface area in order to effectively cool the greenhouse (Kittas, 1996). According to Harmanto et al. (1996), ventilation openings in these types of greenhouses in lowland tropical areas also need to be covered with insect screens that decrease wind velocities and air exchange. This creates a less favorable microclimate within the greenhouse area, and would negatively affect plant growth (Harmanto et al., 1996). Thus, the expense of installing and maintaining greenhouses would not likely yield profitable results in the USVI.

Finally, cultural and economic shifts have reduced tax incentives and rural interest in USVI agriculture as well. Beginning in the postwar era, a decline in total farm acreage from 44,062 to 17,785 coincided with a 400% increase in tourism and 300% increase in hotels (McElroy and Tinsley, 1982). This increase is likely due to commercial tourism land being up to 1,000% more profitable per acre than land devoted to agriculture- tourism today accounts for more than 50% of the USVI GDP, up from 10% in 1960 (BEA, 2012; McElroy et al., 1990). Thus, agriculture has experienced a decline in favor from the native workforce, as available labor has fled from rural areas to work in the more lucrative tourism market.

These combined factors have all but destroyed large-scale vegetable production in the USVI. According to a 2003 report by EarthTrends, the USVI had no cereal or solanaceous crops in major commercial production, despite its geographic potential for expanded agriculture. The University of the Virgin Islands Agricultural Experiment (2000) Station found that the USVI only produces five percent of its total vegetable consumption. This has left the USVI with little to no food security. Multiple innovations in vegetable production that are simple, affordable and accessible will be needed if these obstacles are ever to be overcome in the USVI and tropical regions worldwide.

Vegetable Grafting

Improving environmental and climatic stress tolerance through grafting is an approach that has been in use in East Asia during the 20th century. In this context, grafting involves joining together two living plant parts- a rootstock and a scion- to produce a single, living plant. While grafting is an incredibly popular technique for increasing tomato and vegetable production in East Asia, it is almost nonexistent in the western hemisphere. According to a project report from Ohio State University (2006), “It is an accident of history that grafted vegetables dominate the high-tech hydroponic greenhouse industry and are very common in subsistence production in Asia, but are nearly absent from U.S. soil-based production systems”. The report goes on to speculate that conventional farmers in the U.S. would shy away from grafting as an alternative to traditional fumigation techniques, but since conventional farming is so limited in the USVI, it is unlikely that such a cultural anxiety would exist.

There are various techniques utilized to graft the scion onto the rootstock, and the proper selection of technique is dependent upon the size, growth stage and compatibility of the two plants in question.

Techniques

The three most common grafting techniques for tomato production are tube, cleft, and approach grafts (McAvoy, 2005; Toogood, 1999). In tube grafting, a 45-degree diagonal cut is made through the entire stem in both the rootstock and the scion. Ideally, both cuts are made below the cotyledon, as this reduces the chance of the rootstock suckering after the graft has healed (Bausher, 2011). The two pieces are joined together and the graft union is covered by either a grafting clip or plastic parafilm (Toogood, 1999). Newly grafted plants are immediately brought into a ‘healing chamber’- a low light environment with high relative humidity and a minimum of 18 degrees C at all times. After approximately seven days the plants can be removed from the chamber. Tube grafting is ideal for young plants with small stem diameters when only a single cut is manageable (McAvoy, 2005). Since the plants are smaller, tube grafting allows more plants to be put into the healing chamber at one time, but vascular contact in the graft union of tube grafts is minimal. Vascular regeneration reestablishes the continuity of water transport through the graft union, and a high level of vascular contact between the scion and rootstock expedites this process (Fernandez-Garcia, 2004). Since tube grafting has the least amount of vascular contact between the rootstock and scion among the three techniques, the risk of graft failure in the healing chamber is high.

Cleft grafting is most commonly used on solanaceous crops (Lee and Oda, 2003). Both the rootstock and scion are grown to larger minimum stem diameters than with tube grafting, when the plants are at about the 4-5 leaf stage (McAvoy, 2005). Similar to tube grafting, the rootstock is cut off below the cotyledon, but in cleft grafting a second, longitudinal cut is made 1.5 cm deep, about 75% the depth of the stem. The scion is pruned to 1-3 leaves, reducing transpiration in the healing chamber, and the lower stem is cut into a tapered wedge to place inside the depth cut of the rootstock (Lee and Oda, 2003). Since plants that are cleft grafted are larger and have more vascular contact at the graft union, success rates are higher than tube grafting. This success, however, comes at the expense of longer time needed to develop the plants before grafting, and the larger size of the plants, reducing the total number that can be grown in limited greenhouse space.

Approach grafting is a longer, two-step process that ensures the highest comparable survival rate, and is used often in both tomato and eggplant grafting systems (Yamakawa, 1982). In an approach graft, a 45-degree tongue is cut into the stem of both the scion and the rootstock without cutting off the entire plant. The two tongues are then fitted into each other and secured with a grafting clip or parafilm, and put into the healing chamber. While healing, the scion is still receiving water and nutrients from its own roots, and thus risk of graft failure is low (Oda, 2006). After 3 to 4 days in the healing chamber, the scion is completely removed from its roots. Approach grafting is slowly losing popularity among commercial growers because of the extra labor and time involved in cutting the rootstock twice, larger space demand compared to other methods, and a generally weaker graft union more prone to breaking or scion rooting after transplanting (Lee et al., 2010).

Disease Resistance

Grafting is an ideal technique for vegetable production because scions with desirable fruit-producing traits that are also susceptible to soil-borne disease or climatic pressures can be grafted onto rootstock that is more resistant to these pressures. The resulting union often results in a more productive plant (Cohen et al., 2002; Miller et al., 2005). This solution is preferable to breeding resistant varieties of desirable plants, which can be time consuming, expensive, technically demanding and sometimes controversial (Sleper et al, 1991). Grafting requires no herbicide or pesticide input, and thus would not affect the minimal agricultural infrastructure that exists in the USVI today (EarthTrends, 2003). Grafting has primarily been used to reduce the occurrence of soil-borne disease in non-native fruit vegetable plants, primarily tomato, pepper, eggplant and various *Cucurbitaceae* (Black et al., 2003; Palada and Wu, 2008; Rivard and Louws, 2008). In tomatoes specifically, grafting onto tolerant rootstock has been used to suppress verticillium dahlia infection since the 1960s (EarthTrends, 2003; Zhou et al., 2009). Rivard and Louws (2008) found that 'German Johnson' heirloom tomatoes had 0% fusarium wilt incidence in infested soils when grafted onto resistant CRA 66 or Hawaii 7996 tomato rootstock, compared to a 79% incidence on nongrafted controls. If an appropriate rootstock is used, grafting can also provide tolerance to soil related environmental stress such as drought, salinity and flooding- some of the primary environmental challenges posed by USVI agriculture. Romero et al. (1997) grafted melons onto a hybrid squash rootstock, and found that the grafted melons were more salt tolerant than non-grafted controls. Despite these advantages, vegetable grafting for disease resistance is still rare in the western hemisphere (Kubota et al., 2008), and no peer-reviewed research exploring the potential benefits vegetable grafting in the USVI could be found.

Environmental Tolerance

In addition to increased disease resistance, vegetable grafting has been found to reduce the detrimental effects of abiotic stresses as well, including sub-optimal temperature, moisture and salinity conditions (Schwarz et al., 2010). Temperature stresses, both too high and too low, have been shown to lead to inhibited plant growth and development, wilt, necrosis, and reduced overall yield of curcubit and solanaceous crops(Ahn, 1999). Sub-optimal temperatures have been shown to reduce root growth architecture, inhibit nutrient absorption, water absorption and translocation, disrupt sink/source relations and slow phytohormone transport (Ali et al., 1996; Bloom et al., 2004; Choi, 1995; Venema et al., 2008; Tachibana, 1982). Conversely, supra-optimal temperatures have observed deleterious effects on crops as well, including growth reduction, decrease in photosynthetic capacity accompanying increased respiration, osmotic damages and inhibited ion uptake/transport (Wang et al., 2003). Such conditions are of special concern to growers located in the lowland tropics such as the USVI (Palada and Wu, 2006).

One solution to these negative responses has been to alter the immediate growing environment of the crops by installing greenhouse systems utilizing active protection. These systems allow growers to bring temperatures back into their optimal threshold range for crops, but increasing energy costs has rendered this option inefficient and untenable in many areas of the world (Schwarz et al., 2010). Indeed, a statistical review by Winters and Martins (2004) states that territories with 'micro-economies', which includes the USVI and many other Caribbean countries, are at a 73.4% electricity cost disadvantage when compared to larger, more developed economies. The electricity rate for the USVI at the beginning of 2013 was 54.3 cents/KWh for commercial enterprises, compared to a US national average of 8.28 cents/KWh in 2011 (MCL, 2011; WAPA, 2013). Thus, it becomes apparent that lower-input solutions must be made in these areas.

One explored alternative is to breed cash crops with larger optimal temperature thresholds, instead of attempting to alter environmental temperature itself. This would allow plants to avoid detrimental physiological responses to normally suboptimal temperatures without active energy input. Though traditional breeding has increased production and made cash crop yields in greenhouses more efficient, little progress has been made on breeding plants with vastly expanded temperature tolerances (Van der Ploeg and Heuvelink, 2005). Temperature tolerance is developmentally regulated, growth stage specific, and involves many genes (Schwarz et al., 2010). Thus, the gene characterization of temperature tolerance is not well known, and efforts to successfully breed expanded temperature thresholds in plants, and tomatoes specifically, are limited (Foolad and Lin, 2001).

A method used to expedite the slow breeding process is to utilize vegetable grafting. High performance commercial scions can be grafted onto select rootstock with naturally wider optimal temperature thresholds. Multiple projects have demonstrated that tomato rootstock plants with high temperature tolerances have the ability to transfer tolerance to scions when appropriately grafted (Bloom et al., 2004; Venema et al., 2008; Zijlstra and Nijs, 1987). This resulted in a greater quantity of flowers, trusses and fruit production in grafted plants when compared to non-grafted controls at temperatures considered non-optimal for the scion. Venema et al. (2005) notes that for tomatoes, these naturally occurring wider temperature thresholds are much more common in wild species because of the reduced genetic diversity that is present in inbred, domesticated tomatoes.

Moisture stress is becoming an increasingly important issue in agriculture, especially in arid and semiarid regions of the world (Schwarz, 2010). In the USVI specifically, environmental flood and drought stresses are known to be two of the most limiting factors for vegetable production (UVI Ag. Experiment Station, 2000; Sands, 1974). Drought conditions lead to reduced metabolic activity and higher plant salinity, damaging plants and yields, while flood stresses lead to deoxygenation of soils, starving plants of the oxygen needed as a final electron acceptor in aerobic respiration. This slows photosynthetic rate, chlorophyll content and transpiration in the plant (Kato et al, 2001). Combined with a systemic lack of irrigation infrastructure, the USVI is left highly vulnerable to unfavorable moisture conditions (EarthTrends, 2000).

In grafted plants, the osmotic potential of dehydrated scions is determined by the drought tolerance of its rootstock (Sanders and Markhart, 1992). In kiwifruit, grapes and soybeans there are proven drought-tolerant rootstocks that are available and effective in commercial growing conditions, but little is known about the potential of grafted drought tolerance in fruit vegetables such as tomatoes (Clearwater et al., 1994; Schwarz et al, 2010; Serraj and Sinclair, 1996). Also, the depression in photosynthetic rate, stomatal conductance, transpiration and soluble proteins associated with flood stress has been lessened when crops are grafted onto flood-tolerant rootstock (Kato et al., 2001). Thus, improving water use efficiency in drought conditions and flood resistance of cash crops by grafting onto tolerant rootstocks is an appealing low-input option.

Recently, promising research has reported that grafting vegetables can alter their ability to filter uptake of potentially harmful organic pollutants. Otani and Seike (2007) found that when cucumber was grafted onto various *Cucurbita* spp. rootstock, certain combinations displayed a significant reduction in the uptake of aldrin, deildrin and endrin, highly toxic organic pollutants. As with temperature, drought and flood tolerances, the correct rootstock must be selected for optimal performance, as genetic diversity among rootstocks vary greatly.

Identification of Quantitative Trait Loci (QTLs) for Rootstock Resistance

Studies on the genetic basis for environmental tolerances in vegetables crops are sparse, but Venema et al. released a review of the genetics surrounding sub-optimal temperature tolerance in tomatoes in 2005. Through backcrossing, several genes and QTLs have been identified that control the plastochron index, shoot turgor pressure and root growth of tomatoes in suboptimal temperatures (Foolad and Lin, 2001; Goodstal et al., 2005; Truco et al., 2000; Vallejos and Tanksley, 1983). Further studies are needed to identify QTLs for environmental tolerances in tomatoes and other vegetable crops. Once accomplished, an efficient introgression of genes conferring specific environmental tolerances into rootstocks could be made, possibly via Marker Assisted Selection. Schwarz (2010) however points out that before such research can be done, we must first "…identify [the] physiological characteristics that reflect the complex underlying genetic make-up [of environmental tolerances]".

Yield Differences

The ultimate goal of any farmer is to adopt efficient cultural practices that maximize profit output with minimal resource input. Thus, grafted crops with enhanced environmental tolerances will only be utilized on a commercial scale if those tolerances lead to higher yields, and ultimately more profit. The following section explores the effect of vegetable grafting on increasing the yield of crops under disease, temperature and moisture pressures.

Grafting plants to the correct rootstock for resistance to microbial pathogens will result in higher total yields and increased profit for commercial farmers. An NCSU research project found that grafting with Maxifort tomato rootstock increased yield in high tunnels where disease pressure from Verticillium wilt was present (Groff, 2009). The grafted tomatoes allowed for an approximate 20 percent increase in yield, representing 9.4 more tons per acre. This increased yield translated into an additional gross income of $9,024 per high tunnel acre, or $1.88 per plant, more than offsetting the marginal added costs of growing grafted tomatoes opposed to control (Groff, 2009). Other diseases known to be suppressed by proper rootstock selection leading to higher yields are *Fusarium oxysporum* in cucurbit and tomato crops, verticillium wilt in eggplant, cucumber and watermelon, *Ralstonia solanacearum* bacterial wilt in tomato and *Phytophthora capsici* in cucumber (King et al., 2008).

Explorations of grafted plants growing in suboptimal temperature conditions on total yield have shown highly variable results. This affirms that one must select the correct rootstock from a diverse gene pool to target specific environmental stresses. Initial trials by Okimura et al. (1986) and Bulder et al. (1987) on *Cucurbitaceae* and *Solanaceae* showed that different scion-rootstock combinations don't respond with significantly different yields in suboptimal temperatures, but subsequent trials have identified rootstocks that lead to higher overall yields in tomato, cucumber and watermelon (Ahn et al., 1999; Davis et al., 2008; Tachibana, 1982; Ziljstra and Nijs, 1987). Not surprisingly, all grafted combinations that show suboptimal temperature tolerances are those with rootstocks with wide optimal temperature thresholds (Schwarz et al, 2010).

In supraoptimal temperature conditions, research has shown that grafting tomatoes onto heat-tolerant tomato rootstock increases vegetative growth, but with no significant difference in yield compared to non-grafted controls (Abdelmageed and Gruda, 2009). However, using eggplant rootstock may be more promising for supraoptimal temperature conditions, since eggplants are more adapted to live in hot, arid climates (Abdelmageed and Gruda, 2009; Schwarz et al., 2010). Indeed, Wang et al. (2007) observed yield increases of 10% on eggplant when grafted onto heat-tolerant eggplant rootstock. Chili pepper rootstock has been shown to be an effective option in supraoptimal temperature conditions as well (Palada and Wu, 2008).

Many tomato cultivars and lines are susceptible to supraoptimal temperatures that would be present in the USVI (Abdalla and Verderk, 1968). Most tomatoes grow under optimum day/night temperatures of 25 degrees Celsius (Max et al., 2009), however some tomato lines are tolerant well above that mark. Abdul-Baki (1991) found that several tomato lines genetically selected for heat tolerance produced a higher yield in high temperature conditions (38-40 degrees Celsius) than when they were grown in normal field conditions (26-28 degrees Celsius).

Even without the presence of temperature, moisture or pathogen stress it has been found that grafted tomatoes can still lead to increased yields compared to non-grafted controls, especially in older heirloom cultivars (Rivard and Louws, 2008). Thus, grafting tomatoes may be a financially viable cultural practice even in optimal production conditions. Possible explanations for vegetable yield increase in optimal conditions include increased water and macronutrient uptake by vigorous rootstock genotypes (Ruiz and Romero, 1999; Yetisir and Sari, 2003). Fernandez-Garcia et al. (2002) found that certain rootstocks can improve the stomatal conductance of tomato scions.

Interspecific Grafting

Interspecific grafting is a more recent development to help further the environmental tolerances of vegetable crops. While grafting vegetables onto tolerant rootstock of its own species has been proven to increase resistance to various environmental pressures such as flood, drought, cold, heat and pathogen stress (Bloom et al., 2004; Sanders and Markhart, 1992; Venema et al., 2008; Zijlstra and Nijs, 1987), in some cases the transferred tolerance is not strong enough, or a certain desired environmental tolerance does not yet exist within the rootstock germplasm of that species. Interspecific grafting can help to alleviate this problem. Vegetable species with certain environmental susceptibilities will sometimes have compatible relatives with a natural resistance to that stress. After grafting *Solanum melongena* L. eggplant scions onto a verticillium wilt resistant tomato rootstock *Lydl*, Liu and Zhou (2009) found a 0% incidence of the disease on grafted eggplant, compared to a 68.3% incidence on nongrafted controls. Allelopathic chemicals were also found in the tomato rootstock exudates, inhibiting spore germination and mycelium growth. Davis et al. (2008) states that watermelon grafted onto the rootstock of bottle gourd (*Lagenaria siceraria*) confer significant resistance to *Fusarium* spp. Interspecific grafting has been used successfully for many vegetables in the curcubit and solanaceous families (King et al., 2010).

Interspecific Grafting in Tomatoes and Potential for use in USVI

Tomatoes are one of the most lucrative cash crops worldwide, but they are especially sensitive to excessive flooding or drought, making them difficult to produce in tropical regions (EarthTrends, 2003; Max et al., 2009). Multiple accessions of tomato rootstock are in use commercially to confer temperature and salinity tolerances, but to date no tomato rootstock has significant resistance to flood conditions (Bhatt et al., 2002; Fernandez-Garcia et al., 2003; Schwarz et al., 2010). Thus, if a compatible rootstock of another species with drought tolerance could be found, it would help fill the gap of flood tolerance in tomato production. Eggplant (*Solanum melongena)* is a highly resilient and closely related solanaceous plant to tomato with many cultivars whose roots can survive for several days underwater.

There is a history of grafting tomato scions onto eggplant rootstock to mitigate unfavorable climatic conditions, and vice versa. Okimura et al. (1986) found that eggplants grafted onto *S. integrifolium x S. melongena* rootstocks grew better at lower temperatures (18oC to 21oC) than non-grafted plants, and Midmore et al. (1997) states "Tomato scions grafted onto eggplant rootstock grow well and produce acceptable yields during the rainy season." Black et al. (2003) recommends using eggplant rootstock for tomatoes when flooding or waterlogged soils are expected, and to select lines that are resistant to bacterial wilt and other soil borne diseases. The AVRDC has found that eggplant accessions EG195 and EG203 are compatible with most tomato scions and resistant to flooding, bacterial wilt, fusarium wilt and root-knot nematode, and Chetelat and Peterson (2003) have identified tomato accession 'Hawaii 7998' as broadly compatible with distantly related *solanaceous* crops, such as eggplant and pepper. Pena and Hughes also state "In addition to protection against flooding, some eggplant genotypes are drought tolerant and eggplant rootstocks can therefore provide protection against limited soil moisture stress." (2007). This is likely due to eggplant being more effective at water uptake than tomato root systems (Schwarz et al., 2010).

The identification of an ideal rootstock for interspecific grafting can be achieved by surveying available research, or by one's own experimental findings. When starting an initial search for interspecific rootstock, it may be wise to begin with plants native to the region where the crop will be cultivated. This way, the likelihood of compatible rootstock having appropriate environmental tolerances to be transferred to the non-native scion may be increased. If a compatible native rootstock also with a history of successful use can be found, then probability of success is even greater.

A USVI species of wild eggplant, *Solanum torvum*, may be an ideal rootstock candidate for tomatoXeggplant grafting in the USVI. As a native plant of St. Thomas and

St. Croix it already exhibits tolerance to the climatic pressures of tropical regions. There is also an established history of *S. torvum* for use as a rootstock in *S. melongena* cultivation for its resistance to a wide range of soil borne pathogens, including *Verticillium dahlia*, *Ralstonia solanacearum*, *Fusarium oxysporum* and *Meloidogyne* spp. root-knot nematodes (Bletsos et al., 2003; Gisbert et al., 2011; Singh and Gopalakrishnan, 1997). Uniform production of *S. torvum* rootstock seedlings can be challenging as a result of low germination rate leading to poor seedling emergence and slow early growth (Liu and Zhou, 2009). This potential hurdle can be overcome in the USVI, however, because of the vast wild population and cheap, easy access to seed year-round.

Using Experiential Education to Spread Farming Techniques

Global climate change has been predicted to negatively affect agricultural production worldwide, and it is likely that regions without developed agricultural infrastructure such as the USVI will be most damaged by these environmental changes (Bell et al., 2000). Thus, not only is there a need for research in low-input vegetable production techniques in environmental stress, but also an effective methodology for broadcasting this research to farmers. Utilizing progressive, experiential education may be effective in this case because the specific problem is narrow, specialized and location based. America's most respected educational scholars have argued for experiential education that places learners in a real-world context, engaging them in meaningful activities that focus on a specific interest (Dewey, 1916; Parr et al., 2007). Experiential education- the interaction of a learner with his/her environment- is thus intrinsically connected with the plant sciences, acquainting students with their natural environment. The use of experiential agroecology education has been suggested to efficiently spread the newest production techniques to the producers themselves; especially if the producers do not have direct access to published research (Francis et al., 2011).

Incorporating experiential education into an entire curriculum or even a single topic has been shown to increase learner retention and promote self-inquiry. Anderson and Piscitelli (2002) found that adding an informal learning environment to the formal teaching of a topic increased the quality and retention of overall curriculum objectives among students. Bauerle and Park (2012) showed that the addition of a place-based educational field trip increased the homework scores of students in a plant biology course at Cornell University compared to students who did not attend the trip. This increase was even more pronounced in students taking the class who were not majoring in plant sciences. Observed increases in retention and performance can likely be attributed to the theories of Lewin (1951), finding that learning is a continuous cycle when concrete experiences are involved, causing the learner to observe and reflect about the actual experience, rising to conceptual generalizations which can then be applied to future experiences.

Experiential techniques have already been used successfully in applied vegetable grafting education. Dissemination of grafting techniques to local farmers and gardeners increases grafting success rate and efficiency in the field (Heinrichs et al., 2008). The World Vegetable Center documents seminars given in India to provide training to staff and collaborating farmers on vegetable grafting technologies. In the same light, USVI grafting seminars would provide training to teachers at the University level and give direct, experiential learning to both commercial producers and interested backyard hobbyists. It is not unlikely that these experiential seminars would provide the same success and increase the likelihood of interspecific grafting being utilized in an area where it could be an effective production tool. Seminars would also be particularly important if using native eggplant rootstock (*S. torvum*) that is difficult to produce in greenhouse conditions.

CHAPTER 2

COMPATIBILITY OF *SOLANUM TORVUM* AS A ROOTSTOCK IN INTERSPECIFIC TOMATO GRAFTING

(for submission to *HortTechnology*)

Andrew Petran

Summary

Two tomato scions ('Celebrity' and 'CLN3212A') were grafted onto wild eggplant (*Solanum torvum*) rootstock to determine compatibility as a rootstock for interspecific grafting. *S. torvum* was compared against 'Maxifort', self grafted and non-grafted control rootstock in this experiment. Seed sown *S. torvum* rootstock was also compared against rooted vegetative cuttings of *S. torvum* to determine if there is a difference in compatibility based on method of rootstock propagation. Average days until graft fusion and survival rate was taken for each genotype. Vegetative *S. torvum* cuttings had the poorest grafting success rate as a rootstock (50% for both scions), while all other rootstock genotypes had statistically similar success rates. There was no significant difference in time to graft fusion among any grafted genotypes. High compatibility of seed sown *S. torvum* suggests it's potential use as an interspecific grafting rootstock with cultivated tomato.

Introduction

Plant grafting has been utilized in agriculture since the first millennium BCE (Mudge et al., 2009). The process involves joining together two parts (a rootstock and scion) from different plants to form a single, living plant. Over most of it's history, grafting was centered around woody perennials as a method to asexually propagate species that did not root well from vegetative cuttings, but starting in the 20th century grafting began to be used extensively on annual vegetable crops as well (AVRDC, 1990). Especially popular in East Asia, vegetable grafting allows a grower to combine a scion with desirable fruit producing traits with a rootstock that is resistant to a multitude of environmental pressures, such as climate and pathogen stress. The resulting union often results in higher yields (Cohen et al., 2002; Miller et al., 2005).

Grafting vegetable scions onto a rootstock of its own species is common because intraspecific compatibility is often very high (Black et al., 2003; Palada and Wu, 2008; Rivard and Louws, 2008). Intraspecific grafting has been shown to increase resistance to various environmental pressures such as flood, drought, cold, heat and pathogen stress, however in some cases the transferred tolerance is not strong enough, or a certain desired environmental tolerance does not yet exist within the rootstock germplasm of that species (Bloom et al., 2004; Sanders and Markhart, 1992; Venema et al., 2008; Zijlstra and Nijs, 1987). Intraspecific grafting would not be a viable cultural practice in these unique circumstances, but grafting is not always limited to intraspecific interactions. Vegetables with certain environmental susceptibilities will sometimes have graft-compatible relatives within the same genus that possess a natural resistance to that stress. Thus, interspecific grafting can be used to broaden rootstock diversity when environmental pressures surpass the advantages that can be provided by intraspecific grafting alone.

While not as common as intraspecific grafting, the successful use of interspecific grafting in vegetable production is well documented (King et al., 2010). After grafting *Solanum melongena* L. eggplant scions onto a verticillium wilt resistant tomato (*Solanum lycopersicum*) rootstock *Lydl*, Liu and Zhou (2009) found a 0% incidence of the disease on grafted eggplant, compared to a 68.3% incidence on nongrafted controls. Allelopathic chemicals were also found in the tomato rootstock exudates, inhibiting spore germination and mycelium growth. Davis et al. (2008) states that watermelon grafted onto the rootstock of bottle gourd (*Lagenaria siceraria*) confer significant resistance to *Fusarium* spp.

To identify a useful rootstock for interspecific grafting, first a relative with unique environmental resistances must be found, and then tested for rootstock compatibility.

Interspecific grafting compatibility is difficult to predict because the degree of taxonomic affinity necessary for compatibility varies widely across different taxa (Mudge et al., 2009). Four potential mechanisms of interspecific incompatibility are identified by Andrews and Marquez (1993): cellular recognition, wounding response, plant growth regulators, and incompatibility toxins. Since prediction is difficult, individual grafting trials must assess compatibility.

Tomatoes are lucrative cash crops with worldwide appeal, but they are sensitive to excessive flooding or drought, making them difficult to produce in tropical regions (EarthTrends, 2003; Max et al., 2009). Multiple accessions of tomato rootstock are in use commercially to confer temperature and salinity tolerances, but to date no tomato rootstock has significant resistance to flood conditions (Bhatt et al., 2002; Fernandez-Garcia et al., 2003; Schwarz et al., 2010). Thus, the identification of a flood tolerant rootsotck would help fill the gap of flood tolerance in tomato production. One potential candidate is eggplant (*Solanum melongena)*, a highly resilient and closely related solanaceous plant to tomato with many cultivars whose roots can survive for several days underwater (reference for this?).

Tomato/eggplant interspecific grafting has a history of successful use for conferring environmental tolerances to fruit producing scions. Okimura et al. (1986) found that eggplants grafted onto S. integrifolium x S. melongena rootstocks grew better at lower temperatures (18°C to 21°C) than non-grafted plants, and Midmore et al. (1997) observed tomato/eggplant interspecific grafts produce acceptable yields during the Taiwan rainy season. Black et al. (2003) recommends using eggplant rootstock for tomatoes when flooding or waterlogged soils are expected, and to select lines that are resistant to bacterial wilt and other soil borne diseases.

An especially promising eggplant rootstock for tomato interspecific grafting is *Solanum torvum*, or wild eggplant. *S. torvum* is native to the western tropics and India, and already exhibits tolerance to the climatic pressures of tropical regions (Gousset et al., 2005). This makes *S. torvum* an ideal candidate for tomato interspecific grafting in equatorial regions, where environmental conditions can make tomato production difficult (Max et al., 2009). There is also an established history of *S. torvum* for use as an intraspecific grafting rootstock in *S. melongena* cultivation for its resistance to a wide range of soil borne pathogens, including *Verticillium dahlia*, *Ralstonia solanacearum*, *Fusarium oxysporum* and *Meloidogyne* spp. root-knot nematodes (Bletsos et al., 2003; Gisbert et al., 2011; Singh and Gopalakrishnan, 1997). The compatibility of *S. torvum* as a tomato interspecific grafting rootstock, however, has yet to be quantified. If tomato/*S. torvum* compatibility were as high as commercially viable ISG rootstocks, it would allow farmers and researchers to explore the use of tomato/*S. torvum* interspecific grafting for production in areas with high risk of flood and drought stress. Thus, *S. torvum* was selected as the rootstock of interest in this compatibility study, and will be tested against other rootstocks of known high compatibility.

Uniform production of *S. torvum* rootstock seedlings can be challenging as a result of low germination rate leading to poor seedling emergence and slow early growth (Liu and Zhou, 2009). This potential hurdle may be overcome by rooting vegetative cuttings of uniform size for use as rootstock. If there is no difference between the compatibility of seed-sown *S. torvum* and vegetative propagated *S. torvum* in tomato interspecific grafting, then the difficulties of seed production can be eliminated by maintaining *S. torvum* stock plants for taking rootstock cuttings. Thus, the overall objectives of this study were to assess the compatibility of S. torvum as a rootstock for tomato interspecific grafting, and to determine any difference in graft compatibility based on method of rootstock propagation.

Materials and Methods

The experiment was conducted at the University of Minnesota in Saint Paul, MN, 44.94 N and 93.09 W. In early May of 2013, 48 seeds of *S.torvum* were planted into a plastic seed tray containing the soilless media ‘Sunshine Mix #8’ LC8’ (Sun Gro Horticulture). All seed were covered with coarse vermiculite, lightly watered and placed into a greenhouse. Greenhouse conditions were maintained at 21 C and 175 µmol PAR light from 0700 to 1800 hours. *S. torvum* seeds were acquired from the Virgin Islands Sustainable Farming Institute in St Croix, US Virgin Islands. Seeds were watered daily until time of grafting.

Seven days after planting *S. torvum* seeds, 10 cuttings were taken from a stock *S. torvum* plant and rooted in 4” tall pots containing the soilless media ‘Sunshine Mix #8’ LC8 (Sun Gro Horticulture). The bottom 6” of cuttings were dusted with Hormodin® 1 root inducing powder before placement into pots. Cuttings rooted in a mist house until grafting procedures began. All leaves except meristems were removed from cuttings.

Twenty days after the planting of *S. torvum* seeds, all remaining seeds for the experiment were planted using the methods stated above. This included 48 ‘Maxifort’ rootstock tomato seeds, 72 ‘CLN 3212A’ tomato seeds, and 72 ‘Celebrity’ tomato seeds. ‘Maxifort’ and ‘Celebrity’ seeds were acquired from Johnny’s Selected Seeds (955 Benton Avenue, Winslow, ME 04901), and ‘CLN3212A’ seeds were acquired from the Asian Vegetable Research and Development Center (Shanhua, Tainan 74199, Taiwan).

By late July 2013, all seeds had germinated and seedlings had grown to appropriate grafting size, the 4-5 true leaf stage (McAvoy, 2005). All *S. torvum* cuttings had rooted. Cleft grafting was used for all plants; the most commonly used method for solanaceous crops (Lee and Oda, 2003). With a razor blade, rootstocks were cut below the cotyledon and a longitudinal cut was made 1.5 cm deep, about 75% the depth of the stem. Scions were pruned to 1-3 leaves and the lower stem was cut into a tapered wedge to place inside the depth cut of the rootstock (Lee and Oda, 2003). After insertion, graft unions were wrapped with plastic parafilm to improve stability, reduce chance of infection and ensure vascular contact (Toogood, 1999). The scion and rootstock combinations that were joined to create the 10 different experimental genotypes are shown in Table 1. Newly grafted plants were immediately brought into a low light chamber with high relative humidity and a minimum of 18 degrees C at all times (Lee and Oda, 2003). The chamber was constructed by wrapping clear and black plastic around a PVC skeleton and placed into the greenhouse. Humidity was maintained by sub-irrigating grafted plants on .35" deep Sure To Grow® capillary mats, which were flushed to saturation with water every day (Gutierrez, 2008).

Each plant was evaluated daily to determine time until graft fusion and survival in the chamber. Due to inconsistent rooting, only 8 *S. torvum* cuttings were available for grafting. This resulted in "3212x*S.torvum* Veg" and "Celebrityx*S.torvum* Veg" having only 4 replications each. Evaluation involved observing changes in turgor pressure of each plant. When scion turgor pressure was restored in the chamber, the plant was moved outside the chamber. If the plant maintained turgor outside the chamber for 24 hours, graft fusion was considered completed.

Analysis of variance (ANOVA) was used to compare the differences in survival and days to fusion (DTF) between the 10 plants of Celebrity and 3212 genotypes. ANOVA has been used to compare differences in graft compatibility through DTF in perennial and annual crops (Estrada-Luna et al., 2002; Gisbert et al., 2011).

Results

A summary of average DTF and survival values for each scion genotype are shown in Tables 2 and 3. In all Celebrity scions, the *S. torvum* rootstock had the highest average DTF (12.3 days), but was not significantly higher than any other grafted genotype. All grafted genotypes had a significantly higher DTF than the non-grafted Celebrity control, which intrinsically had a DTF of 0 days. The Celebrity scion had the lowest survival percentage when grafted onto rooted vegetative *S. torvum* rootstock (0.5). This percentage was significantly lower than all other rootstock genotypes with the exception of the self-grafted Celebrity genotype.

In 3212 scions, there was also no significant difference in DTF between all grafted genotypes. The non-grafted 3212 control had a significantly shorter DTF (0 days) than all other rootstock genotypes. Though the 3212 scion also had the lowest survival percentage when grafted onto rooted vegetative cuttings of *S. torvum* (0.5), the difference was not enough to confer statistical significance from any other rootstock genotype.

Discussion

When comparing days to graft fusion among all rootstock genotypes, there is no significant difference in the amount of time it takes for any successfully grafted plant to form a healed graft union (Tables 2 and 3). *S. torvum* rootstock had the largest average days to fusion for both Celebrity and 3212 scions, but the difference from other rootstock genotypes was not significant . The largest average difference in days to fusion in all grafts was between 3212xMaxifort and 3212x*S.torvum* Veg (2.1 days), though again this was not statistically different from any other genotype comparison.

In both Celebrity and 3212 scions, vegetative *S. torvum* rootstock had a lower survival rate to seed sown *S. torvum* rootstock, Maxifort, self grafted and non-grafted rootstocks. The reason for vegetative *S. torvum* rootstock being less compatible than seed sown *S. torvum* rootstock in interspecific grafting may be twofold. Initial adventitious roots formed from cuttings are more adept at oxygen gas exchange and less adept at water uptake than primary root systems (Jackson, 1955). Thus it is possible that the scions grafted onto vegetative *S. torvum* lost turgor pressure and wilted because of this diminished hydraulic capability. Also, since rootstock derived from *S. torvum* cuttings would be older growth overall (with possible secondary growth), the formation of a vascular cambium in the vegetative rootstock may have inhibited proper graft fusion. More research is needed to determine the exact cause of reduced compatibility in vegetative *S. torvum* rootstock.

Because of the low survival percentage of vegetative *S. torvum* rootstock with both Celebrity and 3212 tomatoes, we do not recommended these combinations for commercial production. Seed sown *S. torvum* may still be a viable option for interspecific grafting based on the results in this experiment. If seed sown *S. torvum* is shown to be compatible to a wide variety of tomato scions and an effective means of providing strong environmental tolerances to the plant, it could be a valuable tool for growers worldwide. This would be especially true in regions with minimal agricultural infrastructure, such as tropical regions, where access to greenhouses and other environmentally controlled enclosures is declining or unavailable (Schwarz et al., 2010; McElroy et al., 1990; Sands, 1974).

Previous research documenting the effectiveness of seed sown *S. torvum* in intraspecific grafting is promising. *S. torvum* rootstock confers resistance to a wide array of environmental pressures (Bletsos et al., 2003; Gisbert et al., 2011; Singh and Gopalakrishnan, 1997). Because of the lack of environmental tolerances in tomato rootstock germplasm that *S. torvum* could provide, further exploration of *S. torvum* as a flood and drought resistant rootstock for tomato scions is merited. The highly variable germination rate of *S. torvum* seeds, however, would make production scheduling difficult (Liu and Zhou, 2009). This potential hurdle may be overcome by grafting within native distributions of *S. torvum* because of the vast wild population and cheap, easy access to seed year-round.

Seed-sown *S. torvum* is a compatible rootstock with the two tomato scion cultivars tested, Celebrity and CLN 3212A. Vegetative *S. torvum* rootstock showed moderate compatibility as an interspecific grafting rootstock, but had a significantly reduced grafting success rate when compared to seed sown *S. torvum*, Maxifort and self-grafted rootstocks. All successfully grafted plants had similar days until graft fusion. We recommend that the effectiveness of *S. torvum* rootstock in providing flood and drought tolerances to tomato scions be explored further.

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Table 1. Scion and rootstock combinations analyzed for grafting compatibility.			
Scion	Rootstock	Final 'Genotype'	Number of Plants
CLN 3212A	none (non-grafted)	3212	10
CLN 3212A	CLN 3212A	3212x3212	10
CLN 3212A	'Maxifort®'	3212xMaxifort	10
CLN 3212A	*Solanum torvum* seed	3212x*S.torvum*	10
CLN 3212A	*Solanum torvum* cutting	3212x*S.torvum* Veg	4
Celebrity	none (non-grafted)	Celebrity	10
Celebrity	'Celebrity'	CelebrityxCelebrity	10
Celebrity	'Maxifort®'	CelebrityxMaxifort	10
Celebrity	*Solanum torvum* seed	Celebrityx*S.torvum*	10
Celebrity	*Solanum torvum* cutting	Celebrityx*S.torvum* Veg	4

Table 2. Average days to fusion and survival (%) among all 'Celebrity' rootstock genotypes. Letters denote statistical differences (p<0.05) within rows.					
	Rootstock				
Celebrity Scion	Non-grafted	Celebrity	Maxifort	*S. torvum*	*S. torvum* Veg
(n)	10	10	10	10	4
Days to Fusion	0 a	12.14 b	10.5 b	12.3 b	12 b
Survival %	100 a	70 ab	100 a	100 a	50 b

Table 3. Average days to fusion and survival (%) among all 3212 rootstock genotypes. Letters denote statistical differences (p<0.05) within rows.					
	Rootstock				
3212 Scion	Non-grafted	3212	Maxifort	*S. torvum*	*S. torvum* Veg
(n)	10	10	10	10	4
Days to Fusion	0 a	11 b	9.9 b	11.2 b	12 b
Survival %	100	80	100	80	50

CHAPTER 3

UTILIZATION OF INTERSPECIFIC GRAFTING FOR INCREASED FLOOD AND DROUGHT RESISTANCE IN TOMATOES

(for submission to *HortTechnology*)

Andrew Petran

Summary

Two tomato scions ('Celebrity' and 'CLN3212A') were grafted onto eggplant rootstock to determine the effect of interspecific grafting on flood and drought tolerance of tomatoes. Wild eggplant *Solanum torvum* was selected as the interspecific rootstock of interest, and was compared against 'Maxifort', self-grafted and non-grafted control rootstock in flood stress, drought stress, and optimal soil moisture conditions. Plant height, internode length, and stomatal resistance of all scion/rootstock combinations in each environmental condition were measured for 25 days. No significant differences in plant height, internode length and stomatal resistance among related scion genotypes occured in optimal conditions. In flood conditions, Celebrityx*S.torvum* had significantly shorter height and internode length, and reduced visible symptoms of deoxygenation stress. Drought conditions revealed that plants grafted on all rootstock genotypes except *S. torvum* had permanently wilted by day 22, while no plants grafted onto *S. torvum* wilted for the duration of the experiment. Further research is needed to determine if the observed resistance to flood and drought conditions conferred by *S. torvum* would also effect flower bud initiation, fruit set and yield.

Introduction

Improving the environmental and climatic stress tolerance of vegetable crops through grafting is a novel approach that has been used extensively in East Asia during the 20th century (AVRDC, 1990). In this context, grafting involves joining together two living plant parts- a rootstock and a scion- to produce a single, living plant. Grafting is an ideal technique for vegetable production because scions with desirable fruit-producing traits that are also susceptible to soil-borne disease or climatic pressures can be grafted onto rootstock that is more resistant to these pressures. The resulting union often results in a more productive plant (Cohen et al., 2002; Miller et al., 2005). This solution can be preferable to breeding resistant varieties of desirable plants because it is far less time consuming, expensive, and technically demanding (Sleper et al, 1991). Since grafting enhances environmental tolerances without altering the environment itself, it would intrinsically reduce the input requirement of pesticides for optimal production. Thus, this technique would not tax the minimal agricultural infrastructure that exists in many tropical regions today (EarthTrends, 2003).

Grafting vegetables onto tolerant rootstock of its own species is the most common grafting technique since intraspecific compatibility is high (Black et al., 2003; Palada and Wu, 2008; Rivard and Louws, 2008). While intraspecific grafting has been proven to increase resistance to various environmental pressures such as flood, drought, cold, heat and pathogen stress, in some cases the transferred tolerance is not strong enough, or a certain desired environmental tolerance does not yet exist within the rootstock germplasm of that species (Bloom et al., 2004; Sanders and Markhart, 1992; Venema et al., 2008; Zijlstra and Nijs, 1987). However, vegetable species with certain environmental susceptibilities will sometimes have grafting-compatible relatives within the same family that possess a natural resistance to that stress. Thus, interspecific grafting can be used to broaden rootstock diversity when environmental pressures surpass the advantages that can be provided by intraspecific grafting alone.

The utilization of interspecific grafting as an alternative, low-input means of vegetable production in regions with high environmental pressures is promising, and merits further exploration. Interspecific grafting has been used successfully for many vegetables in the curcubit and solanaceous families (King et al., 2010). After grafting *Solanum melongena* L. eggplant scions onto a verticillium wilt resistant tomato rootstock *Lydl*, Liu and Zhou (2009) found a 0% incidence of the disease on grafted eggplant, compared to a 68.3% incidence on non-grafted controls. Allelopathic chemicals were also found in the tomato rootstock exudates, inhibiting spore germination and mycelium growth. Davis et al. (2008) states that watermelon grafted onto the rootstock of bottle gourd (*Lagenaria siceraria*) confer significant resistance to *Fusarium* spp.

The identification of an ideal rootstock for interspecific grafting compatibility trials can be achieved by surveying available research for a history of compatibility, and giving preference to plants native to the region the grafted crop will be cultivated. This way, the likelihood of compatible rootstock having appropriate environmental tolerances to be transferred to the non-native scion may be increased. If a compatible native rootstock also with a history of successful use can be found, then probability of successful trials grows even more.

Tomatoes are one of the most lucrative cash crops worldwide, but they are especially sensitive to excessive flooding or drought, making them difficult to produce in tropical regions (EarthTrends, 2003; Max et al., 2009). Multiple accessions of tomato rootstock are in use commercially to confer temperature and salinity tolerances, but to date no tomato rootstock has significant resistance to flood conditions (Bhatt et al., 2002; Fernandez-Garcia et al., 2003; Schwarz et al., 2010). Thus, the identification of a flood tolerant interspecific graft would help fill the gap of flood tolerance in tomato production. One potential candidate is eggplant (*Solanum melongena)*, a highly resilient and closely related solanaceous plant to tomato with many cultivars whose roots can survive for several days underwater.

There is a history of tomato/eggplant interspecific grafting to mitigate unfavorable climatic conditions, and vice versa. Okimura et al. (1986) found that eggplants grafted onto S. integrifolium x S. melongena rootstocks grew better at lower temperatures (18°C to 21°C) than non-grafted plants. Midmore et al. (1997) observed tomato/eggplant Interspecific grafting produces acceptable yields during the rainy season. Black et al. (2003) recommends using eggplant rootstock for tomatoes when flooding or waterlogged soils are expected, and to select lines that are resistant to bacterial wilt and other soil borne diseases. The AVRDC has found that eggplant accessions EG195 and EG203 are compatible with most tomato scions and resistant to flooding, bacterial wilt, fusarium wilt and root-knot nematode, and Chetelat and Peterson (2003) have identified tomato accession 'Hawaii 7998' as broadly compatible with distantly related *solanaceous* crops, such as eggplant and pepper. No tomato/eggplant interspecific grafting trials have been performed analyzing for drought tolerance, but Pena and Hughes state that some eggplant genotypes are drought tolerant and eggplant rootstocks may therefore provide protection against soil moisture stress (2007). This is likely due to eggplant being more effective at water uptake than tomato root systems (Schwarz et al., 2010).

A variety of wild eggplant, *Solanum torvum*, has been selected as a rootstock candidate for tomato/eggplant interspecific grafting in this experiment. *Solanum* torvum is native to the western tropics and India, and already exhibits tolerance to the climatic pressures of tropical regions (Gousset et al., 2005). There is also an established history of *S. torvum* for use as a rootstock in *S. melongena* cultivation for its resistance to a wide range of soil borne pathogens, including *Verticillium dahlia*, *Ralstonia solanacearum*, *Fusarium oxysporum* and *Meloidogyne* spp. root-knot nematodes (Bletsos et al., 2003; Gisbert et al., 2011; Singh and Gopalakrishnan, 1997). Uniform production of *S. torvum* rootstock seedlings can be challenging as a result of low germination rate leading to poor seedling emergence and slow early growth (Liu and Zhou, 2009). This potential hurdle may be overcome by rooting vegetative cuttings of stock plants for use as rootstock, or by grafting within native distributions of *S. torvum*, such as the U.S. Virgin Islands, because of the vast wild population and cheap, easy access to seed year-round.

If tomato crops grafted onto *S. torvum* produces a plant able to withstand flood and drought, then it could be utilized as a low-input tool to optimize production in tropical regions such as the U.S. Virgin Islands. Possible advantages of growing rootstocks in these areas include diversifying local cultivar availability and low-input season extension. Extending the season for local produce allows for off-season price premiums, sometimes as high as 50% (Jett, 2006; Rowley, 2010; Rowley et al., 2010).

Stomatal conductance and resistance is the quantitative measurement of plant gas exchange on the leaf. Because water leaves the stomata during this gas exchange, stomatal conductance and resistance has also been used to measure flood tolerance, drought tolerance and overall water use efficiency in plants (Kato et al., 2001; Sivritepe et al., 2005). A porometer measuring stomatal resistance can be used to determine the physiologic response of each genotype under controlled moisture conditions. Porometer readings are taken on newly unfurled leaves at the same time of day, as changes in age of the leaf and time of day can alter the consistency of resistance readings and confound statistical analysis (Ferreira and Katerji, 1992).

The tomato rootstock ‘Maxifort’ is a commercial standard for grafting tomato (Rivard and Louws, 2008), and was utilized as a control rootstock. Non-grafted Celebrity and 3212 were also used as a control. Two tomato scions, ‘Celebrity’ and ‘CLN 3212A’ (3212) were chosen for this project. Celebrity was chosen because of its wide use, and 3212 was chosen because the Asian Vegetable Research and Development Center’s classification as a heat tolerant cultivar. If interspecific grafting onto *S. torvum* rootstock would confer moisture tolerance to either cultivar, this technique could be used to increase the adaptation of this vegetable crop. The objective of this research was to determine whether *S. torvum* as an interspecific rootstock can impart flood and drought tolerance of tomato scions.

Materials and Methods

The experiment was conducted at the University of Minnesota in Saint Paul, MN, 44.94 N and 93.09 W. In June of 2012, 48 seeds of *S.torvum* were planted into a 48-count plastic seed tray containing the soilless media 'Sunshine Mix #8' LC8' (Sun Gro Horticulture). All seed were covered with coarse vermiculite, lightly watered and placed into a greenhouse maintained at 21°C and 175 μmol PAR light from 0700 to 1800 hours. *S. torvum* seeds were acquired from the Virgin Islands Sustainable Farming Institute in St Croix, US Virgin Islands. Seeds were watered daily until time of grafting.

Twenty days after the planting of *S. torvum*, all remaining seeds for the experiment were planted using the methods stated above. This included 48 'Maxifort' rootstock tomato seeds, 72 'CLN 3212A' tomato seeds, and 72 'Celebrity' tomato seeds. 'Maxifort' and 'Celebrity' seeds were acquired from Johnny's Selected Seeds (955 Benton Avenue, Winslow, ME 04901), and 'CLN3212A' seeds were acquired from the Asian Vegetable Research and Development Center (Shanhua, Tainan 74199, Taiwan).

In early July 2012, all seeds had germinated and seedlings had grown to appropriate grafting size, the 4-5 true leaf stage (McAvoy, 2005). Plants were grafted using the cleft grafting technique, which is most commonly used on solanaceous crops (Lee and Oda, 2003). With a razor blade, rootstocks were cut below the cotyledon and a longitudinal cut was made 1.5 cm deep, about 75% the depth of the stem. Scions were pruned to have 1-3 leaves and the lower stems were cut into a tapered wedge to place inside the depth cut of the rootstock (Lee and Oda, 2003). After insertion, graft unions were wrapped with plastic parafilm to improve stability, reduce chance of infection and ensure vascular contact (Toogood, 1999). The scion and rootstock combinations that were joined to create the 8 different experimental genotypes are shown in Table 1. Newly grafted plants were immediately brought into a low light environment with high relative humidity and a minimum of 18 degrees C at all times (Lee and Oda, 2003). This chamber was constructed by wrapping clear and black plastic around a PVC skeleton and placed into the greenhouse. Humidity was maintained by sub-irrigating grafted plants on .35" deep Sure To Grow® capillary mats, which were flushed to saturation with water every day (Gutierrez, 2008). After approximately seven days the plants were removed from the chamber to be grown on in experimental conditions.

After graft unions had healed, plants were taken out of the healing chamber and potted into 6" pots filled with LC8 media (Sun Gro Horticulture). Plants were divided into 3 different moisture treatments (Drought Stress, Flood Stress and Optimal Conditions), each treatment having 3 replications of the 8 different combinations (3212, 3212x3212, 3212x*S.torvum*, 3212xMaxifort, Celebrity, CelebrityxCelebrity, Celebrityx*S.torvum*, CelebrityxMaxifort). Plants were arranged in a randomized complete block design, with each block representing a different moisture treatment.

Optimal soil moisture conditions were maintained by calculating how many mL of water were needed to increase soil moisture in the pot by 1%. This was done by, first, measuring the mL of water lost from a 6" pot with LC8 soilless media 24 hours after saturation, and dividing it by the percentage of soil moisture lost over the same time period. With this figure, each plant could be measured for soil moisture every day and be given the exact amount of water needed to bring the soil moisture content back to the optimal level (known as container capacity) observed 24 hours after saturation (White and Mastalerz, 1966). It was calculated that container capacity for the media in 6" pots was 34% soil moisture. Soil moisture was read daily with an SM100 Soil Moisture Sensor plugged into a Watchdog 1000 Series Micro Station.

Drought stress conditions were maintained by using the same daily watering technique used for optimal conditions, except water was given to maintain soil moisture in between 1% and 2%, unlike the optimal soil moisture treatment, which in this experiment was soil moisture of 34%.

Flooded conditions were created by placing the plants directly into plastic basins half the height of the pots, and filling the basins with water every day. This ensured that the soil moisture levels were at saturation for the duration of the experiment.

Immediately after potting and establishment of each environmental condition, plants were measured for morphological and physiological changes over a 25-day period. Plant height (cm), number of nodes, internode length and stomatal resistance (mmol/m2/s) readings were taken on day 1, 5, 10, 15, 20, and 25, along with plant survival. Stomatal resistance was measured with a Delta T® AP4 porometer. Resistance readings were taken on the terminal leaflet of the youngest fully-unfurled branch each measurement day at 1 pm.

On the final day, fresh weight, dry weight and leaf area (cm2) measurements were taken. Leaf area was measured using a Li-Cor LI-3100 area meter prior to placing plants in a Hot Pack® drying oven at 170 degrees F for 48 hours. Dry weight was taken after XXX days.

Data was subjected to multiple methods of statistical analysis. Analysis of variance (ANOVA) was used to compare the differences in stomatal resistance between the four Celebrity and 3212 genotypes in each environmental condition (flood, drought, optimal) on each measurement day. ANOVA has been used to compare differences in stomatal conductance in tomatoes exposed to different categorical treatments (Sivritepe et al., 2005). ANOVA was also used to compare the differences in final plant height and internode lengths (day 25) between the four Celebrity and 3212 genotypes in each environmental condition. Linear regression analysis was used to determine the significance of correlation between dry weight and leaf area in each environmental condition, and also to determine the significance of a stomatal resistance regression of the four Celebrity and 3212 genotypes in each environmental condition (flood, drought, optimal) over time. Rootstock genotype may have an effect on the resistance of the scion in stressed conditions (Borel et al., 2001). Statistical significance for ANOVA and regression was calculated at the $p < 0.05$ level. All analyses were carried out using the statistical program R.

Results

ANOVA- Plant Height and Internode Length

Under optimal conditions, the final plant height of 3212x*S.torvum* was significantly different ($p < 0.05$) than 3212x3212, and Celebrityx*S.torvum* was not significantly different than any other Celebrity genotype (Figure 1). There was no significant difference in internode length among any genotypes in optimal conditions (Figure 2). In flood stress conditions, final plant height of 3212x*S.torvum* was not significantly different than any other 3212 genotypes, and Celebrityx*S.torvum* was significantly different than all other Celebrity genotypes (Figure 1). Final internode length of Celebrityx*S.torvum* was significantly different than Celebrity and CelebrityxCelebrity

(Figure 2). In drought stress conditions, no genotype had a significantly different plant height or internode length than any other genotype within its group (Figures 1 and 2).

When analyzing stomatal resistance, data taken from day 20 was used as all plants in the drought treatment were dead by day 25. In optimal conditions, *3212xS.*torvum was significantly different than 3212xMaxifort (Figure 3). In both flood and drought stress conditions there was no significant difference between any related genotypes (Figure 3).

Linear Regression Analysis

A highly significant correlation between dry weight and leaf area among all 3 treatments was determined with regression analysis. Correlation in optimal conditions had a p-value of 0.047, compared to a correlation in drought conditions of p=0.046 and flooded conditions of p=0.087. When all treatments were combined, correlation between dry weight and leaf area had an R-squared value of .71 with a p-value of 2.2e-16 (Figure 4). No significant differences among the average stomatal resistance of any related genotypes over time occurred, but certain observable trends could be seen. In optimal conditions there was general inconsistency regarding which genotypes had the highest and lowest graft combinations as time progressed, but in flooded conditions 3212x*S.torvum* consistently had the highest stomatal resistance and in drought stress Celebrityx*S.torvum* consistently had the lowest stomatal resistance.

Discussion

Optimal Conditions

Under optimal conditions both final plant height and internode length of 3212 and Celebrity genotypes are reduced when grafted onto *S.torvum* rootstock, though the only statistically significant difference was between 3212x*S.torvum* and 3212x3212. This observable reduction in height may be due to the grafting procedure itself. Time from sowing to transplant of grafted tomatoes is 30 to 33 days, while non-grafted tomatoes take less time, 14 to 21 days (Black et al., 2003; McAvoy and Giacomelli, 1985). In the procedure of this experiment, scions and non-grafted controls were sown on the same day so non-grafted plants would have a height advantage over grafted transplants. Intraspecific grafted plants were able to make up for this deficit by day 25, but 3212x*S. torvum* and Celebrityx*S. torvum* still had the lowest mean plant height and internode length, most likely due to the increased time it takes for graft unions to fuse in *S. torvum* interspecific grafting (Masayuki et al., 2005). In the future, if scion sowing for *S. torvum* interspecific grafting is started before other genotypes, it would likely offset this initial height difference. Also, since internode length of all related scion genotypes were so similar, it is unlikely that this reduction in height was due to environmental stress (Figure 2).

No Celebrity genotype had a significantly different stomatal resistance than other Celebrity genotypes over the course of the experiment, but in day 20 3212x*S. torvum* had a significantly higher resistance than 3212xMaxifort. This may have led to 3212xMaxifort having a higher median plant height than 3212x*S. torvum* by the end of the experiment (Figure 1), but by day 25 there was no difference in stomatal resistances.

The overall lack of significant differences imply that in optimal moisture conditions, grafting onto *S. torvum* or Maxifort rootstock does not confer a distinct morphological or physiological growth advantage or disadvantage compared to each other or to an non1grafted control. These results differ from those found by Fernandez-Garcia et al. (2002) that grafted tomatoes experience superior stomatal conductance compared to non-grafted controls of the same cultivar, even in optimal conditions. Since this project did not quantify flowering, total or marketable yield, we cannot determine whether this insignificant difference in growth also results in yield differences among genotypes. A second trial of this experiment, conducted in February 2013, yielded the same optimal condition results among genotypes as the initial 2012 trial.

Photograph 1 shows the observable differences within each genotype. Previous research has found that even without the presence of temperature, moisture or pathogen stress grafted tomatoes can still lead to increased yields compared to non-grafted controls, especially in older heirloom cultivars (Rivard and Louws, 2008). Thus, grafting tomatoes may be a financially viable cultural practice even in optimal production conditions. Possible explanations for vegetable yield increase in optimal conditions include increased water and macronutrient uptake by vigorous rootstock genotypes (Ruiz and Romero, 1999; Yetisir and Sari, 2003). Fernandez-Garcia et al. (2002) found that certain rootstocks can improve the stomatal conductance of tomato scions. Fernandez-Garcia et al. (2002) found that certain rootstocks can improve the stomatal conductance of tomato scions and Leonardi and Giuffrida (2006) observed increased phosphorus and calcium uptake with particular rootstock genotypes as well.

Flood Conditions

Flood stress causes various physiological and morphological responses in tomatoes. Waterlogged soils inhibit oxygen and nutrient uptake, which causes leaf chlorosis and necrosis, starting in mature leaves and slowly making it's way up the plant (Ezin et al., 2010). Waterlogged soils sometimes cause the underside of tomato leaves to turn purple as a result of phosphorus deficiency (Dumas, 1989). Flood stressed tomatoes also temporarily close their stomata, until the formation of adventitious roots as a mechanism to alleviate the stress (Aloni and Rosenshtein, 1982; Kozlowski, 1984).

The formation of adventitious roots increase oxygen uptake, and stomatal conductance levels return to near normal. In this project, adventitious roots were observed in all genotypes, along the soil line and in some cases on the scion at the point of graft union. ANOVA testing revealed that although grafting didn't appear to have an effect on 3212 genotypes in flooded conditions, grafting Celebrity onto *S. torvum* had a profound effect when soils were waterlogged. CelebrityX *S. torvum* had a significantly shorter plant height and internode length than all other Celebrity genotypes (Figures 1 and 2). Also, when comparing treatment differences of specific genotypes, almost all genotypes experience increased or similar plant heights and internode lengths when flood stress is applied compared to optimal conditions, while CelebrityX*S. torvum* decreases in these categories. Thus, flood stress resulted in taller or leggier plants in most tomato genotypes, but result in a shorter, more compact plant when grafted onto *S. torvum*.

Visible differences in leaf color can be observed as well (Photograph 2). As mentioned before, flood stress symptoms in tomatoes include chlorosis and necrosis of mature leaves along with purple undersides of leaves and veins (Ezin et al., 2010). All these symptoms were seen to a high degree in every genotype with the exception of Celebrityx*S. torvum*, where mature leaves were still green and had limited purpling of veins. Visual differences show that while waterlogged soils lead Celebrityx*S. torvum* to be shorter and more compact, fewer visual symptoms were noted when compared to all other genotypes. Further exploration should include a leaf tissue analysis of all genotypes, so more precise reasons for visual differences can be quantified. A second trial of this experiment, conducted in February 2013, yielded the same flood tolerance results as the initial 2012 trial.

Drought Conditions

There was no statistical difference among related scion genotypes in any of the measurements taken in drought conditions. As in other treatments, Celebrity*xS. torvum* had the lowest median plant height and internode length, but unlike in optimal or flooded conditions 3212x*S. torvum* had the highest median plant height and internode length under drought stress (Figures 1 and 2). This trend difference may be attributed to 3212 being known as a heat tolerant tomato variety by its distributer, the Asian Vegetable Research and Development Center. It has been shown before that increasing heat tolerance in tomato can result in an increase in water use efficiency (Lukic et al., 2012).

Stomatal resistance of all genotypes in drought stress is high when compared to optimal and flooded conditions, although there is no significant difference among related genotypes within the drought treatment (Figure 3). These results are consistent with the literature, that stomatal resistance is known to increase when tomatoes are exposed to drought stress conditions to conserve water (Camejo et al., 2005; Sobeih et al., 2004).

Photograph 3 shows the differences among scions grafted onto *S. torvum* and other rootstocks in drought stress. 3212 scions grafted onto *S torvum* have noticeably more turgor pressure than 3212, Maxifort and non-grafted rootstock. In Celebrity, all rootstock except *S. torvum* reached permanent wilting point by day 22. Celebrity scions reaching permanent wilting before 3212 may be attributed to the increased heat tolerance in 3212 raising water use efficiency as well (Lukic et al., 2012). A second trial of this experiment, conducted in February 2013, yielded the same drought tolerance results as the initial 2012 trial.

A thorough review of the literature yielded no available research exploring rootstock induced drought tolerance in tomatoes, so the exact mechanism leading to the tolerance observed in this experiment is not yet known. In apples, dwarfing and semidwarfing rootstock use less water due to higher leaf-specific, soil-stem hydraulic resistance (Cohen and Naor, 2002). Since *S. torvum* appears to have a dwarfing effect on both Celebrity and 3212, it is possible the same phenomenon may be occurring here.

In this experiment, we found that *S. torvum* rootstock does not effect plant height, internode length or stomatal resistance of tomato scions Celebrity and CLN 3212A in optimal moisture conditions. In flood conditions, Celebrityx*S.torvum* had significantly shorter height and internode length, and reduced visible symptoms of deoxygenation stress. Drought conditions revealed that plants grafted on all rootstock genotypes except *S. torvum* had permanently wilted by day 22, while no plants grafted onto *S. torvum* wilted for the entirety of the experiment. Based on these findings, we recommend using *S. torvum* as a rootstock for interspecific tomato grafting to increase drought tolerance. This practice would be particularly useful for producers located in regions of considerable drought stress.

Future research could investigate root architecture of *S. torvum* rootstock against rootstocks not shown to be drought tolerant, plant nutrient differences among genotypes via plant tissue analysis, and chemical root-to-shoot signaling that controls water use efficiency in *S. torvum* versus other rootstock.

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Table 1. 8 different scion and rootstock combinations were analyzed for morphological and physiological responses to different environmental pressures.

Scion	Rootstock	Final 'Genotype'	# Replications per Environmental Treatment
CLN 3212A	none (non-grafted)	"3212"	3
CLN 3212A	CLN 3212A	"3212x3212"	3
CLN 3212A	Maxifort®	"3212xMaxifort"	3
CLN 3212A	*Solanum torvum*	"3212x*S.torvum*"	3
Celebrity	none (non-grafted)	"Celebrity"	3
Celebrity	Celebrity	"CelebrityxCelebrity"	3
Celebrity	Maxifort®	"CelebrityxMaxifort"	3
Celebrity	*Solanum torvum*	"Celebrityx*S.torvum*"	3

Figure 1. Boxplot of plant height (cm) of all genotypes in each treatment, day 25. Star indicates a significant difference (p<0.05) from all related scion genotypes in that condition.

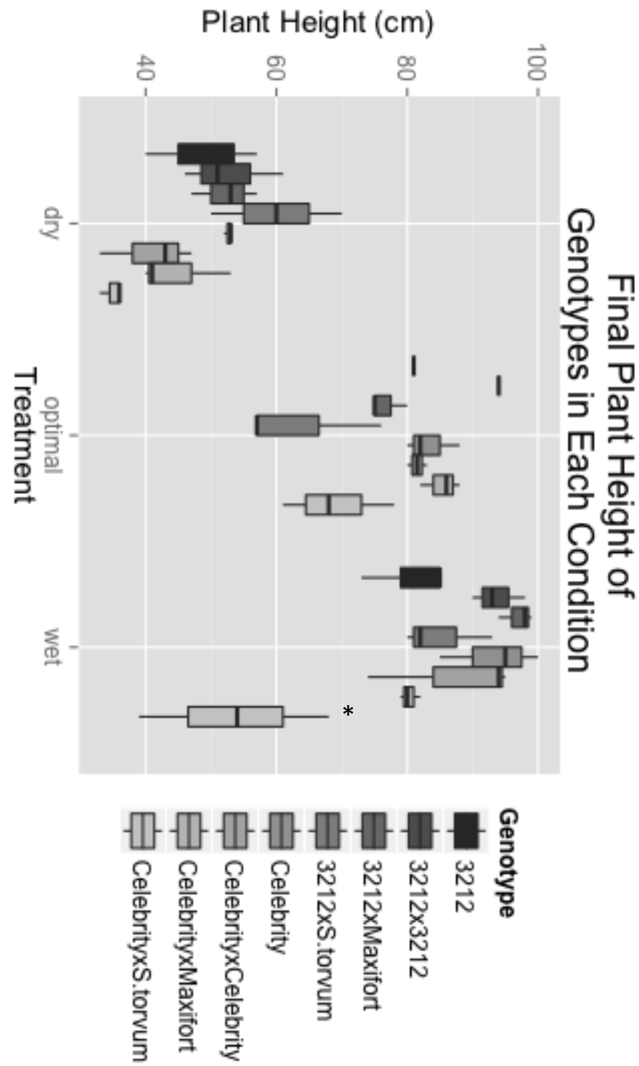


Figure 2. Boxplot of internode length (cm) of all genotypes in each treatment, day 25. Star indicates a significant difference (p<0.05) from all related scion genotypes in that condition.

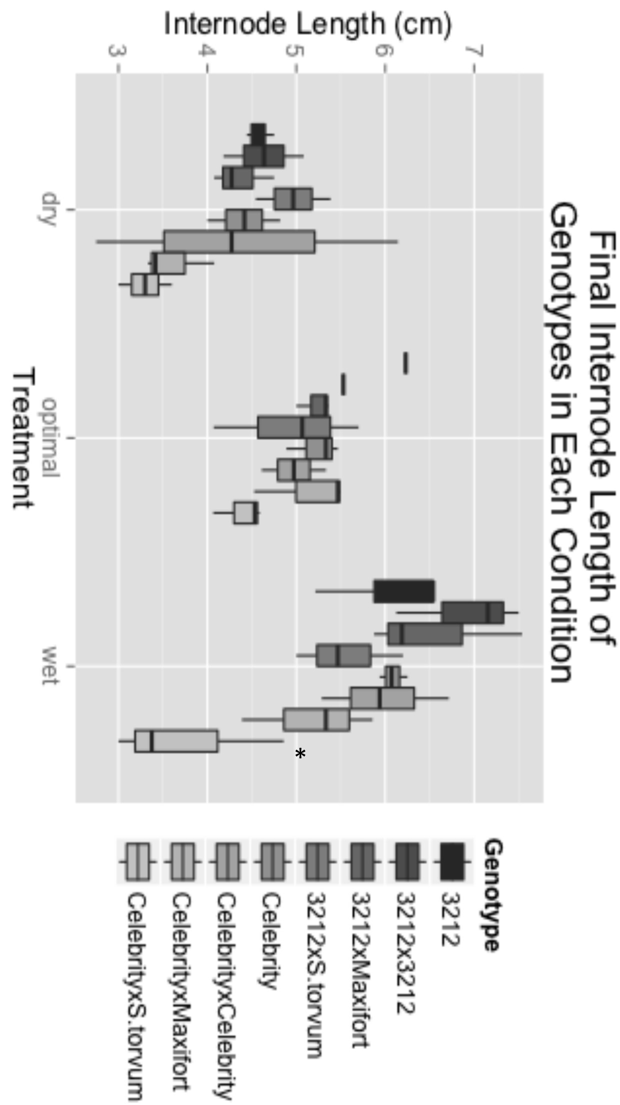


Figure 3. Boxplot of stomatal resistance (mmol/m2/s) of all genotypes in each condition, day 25.

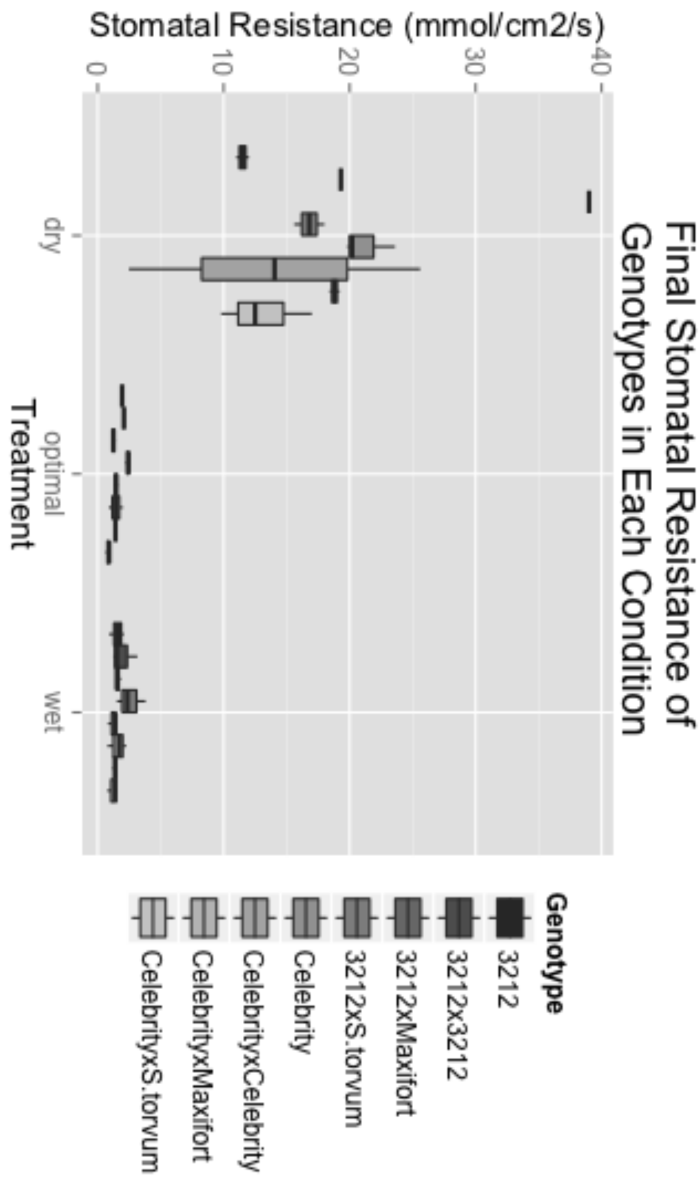
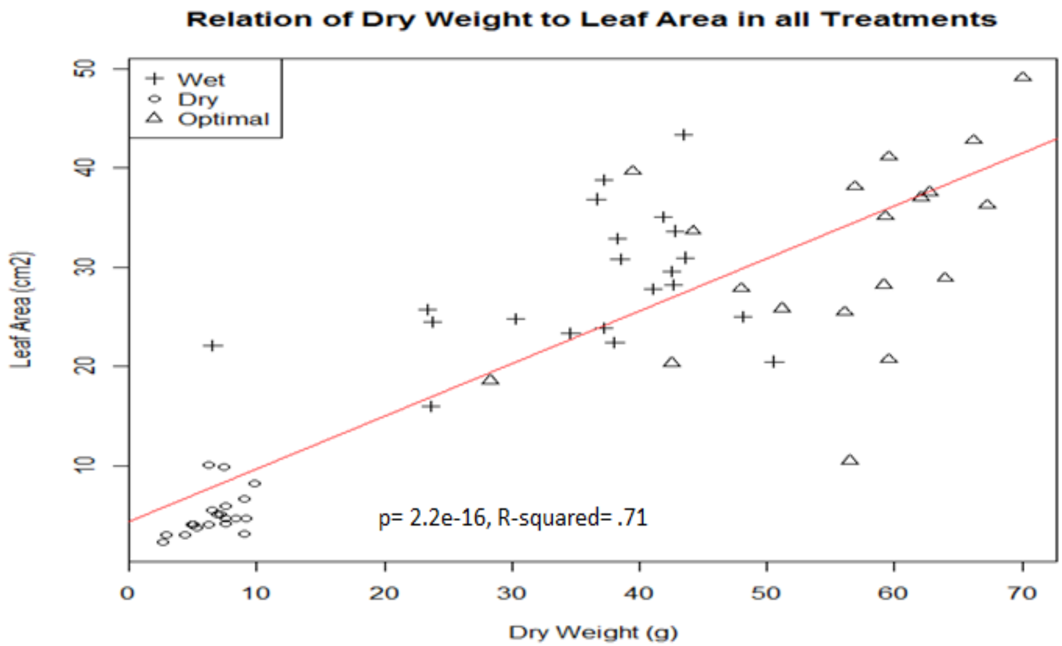
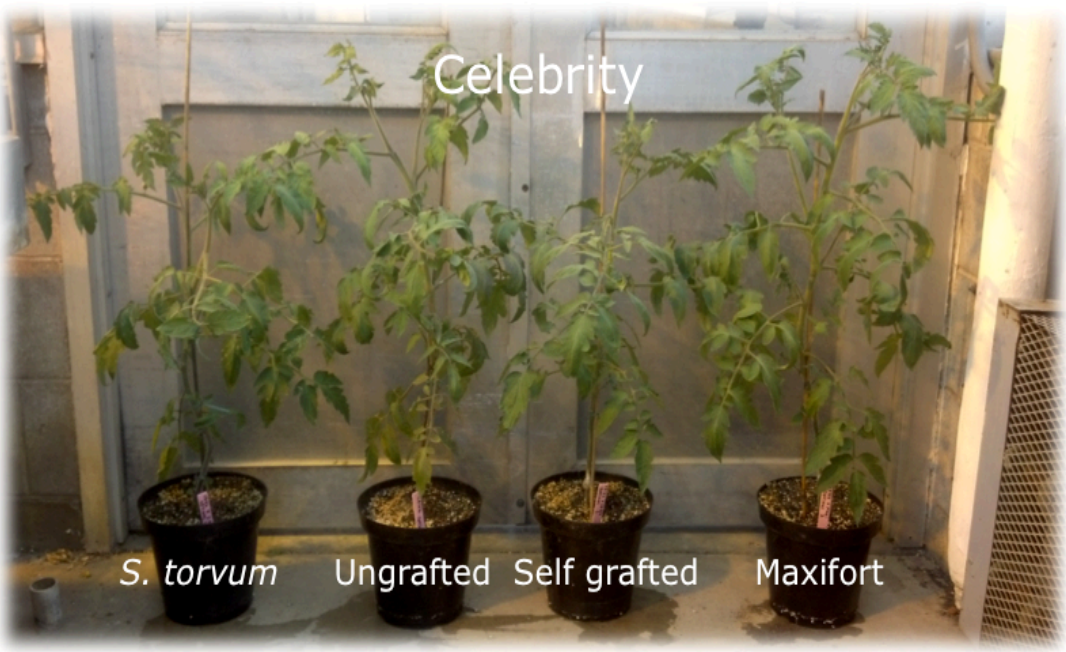
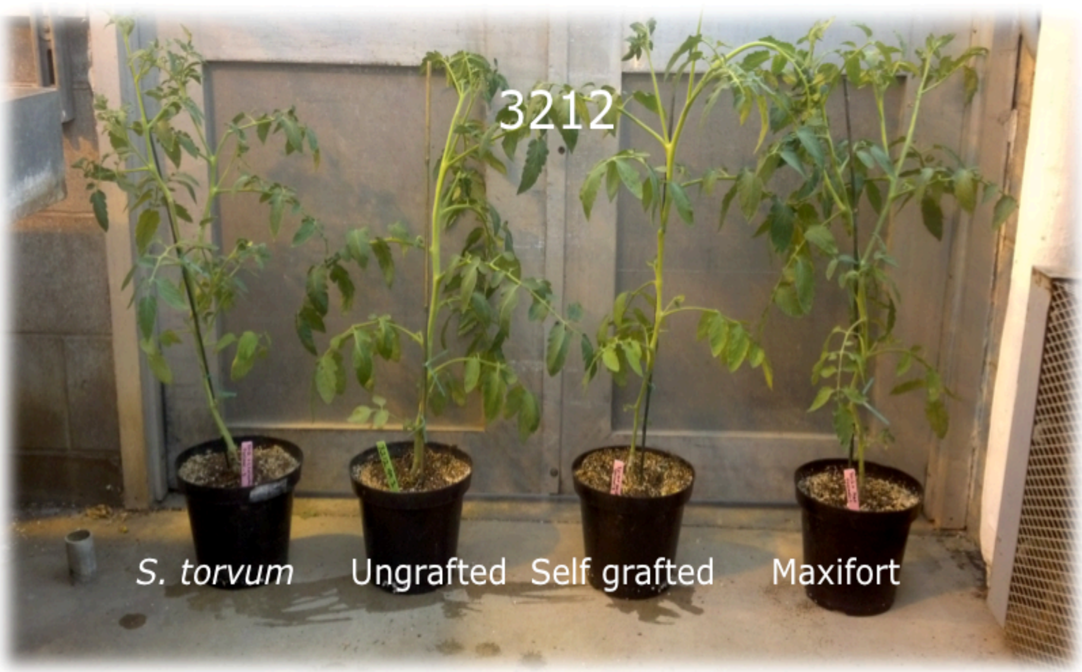


Figure 4. Scatter plot showing the correlation of dry weight (g) to leaf area (cm2) of all treatments.



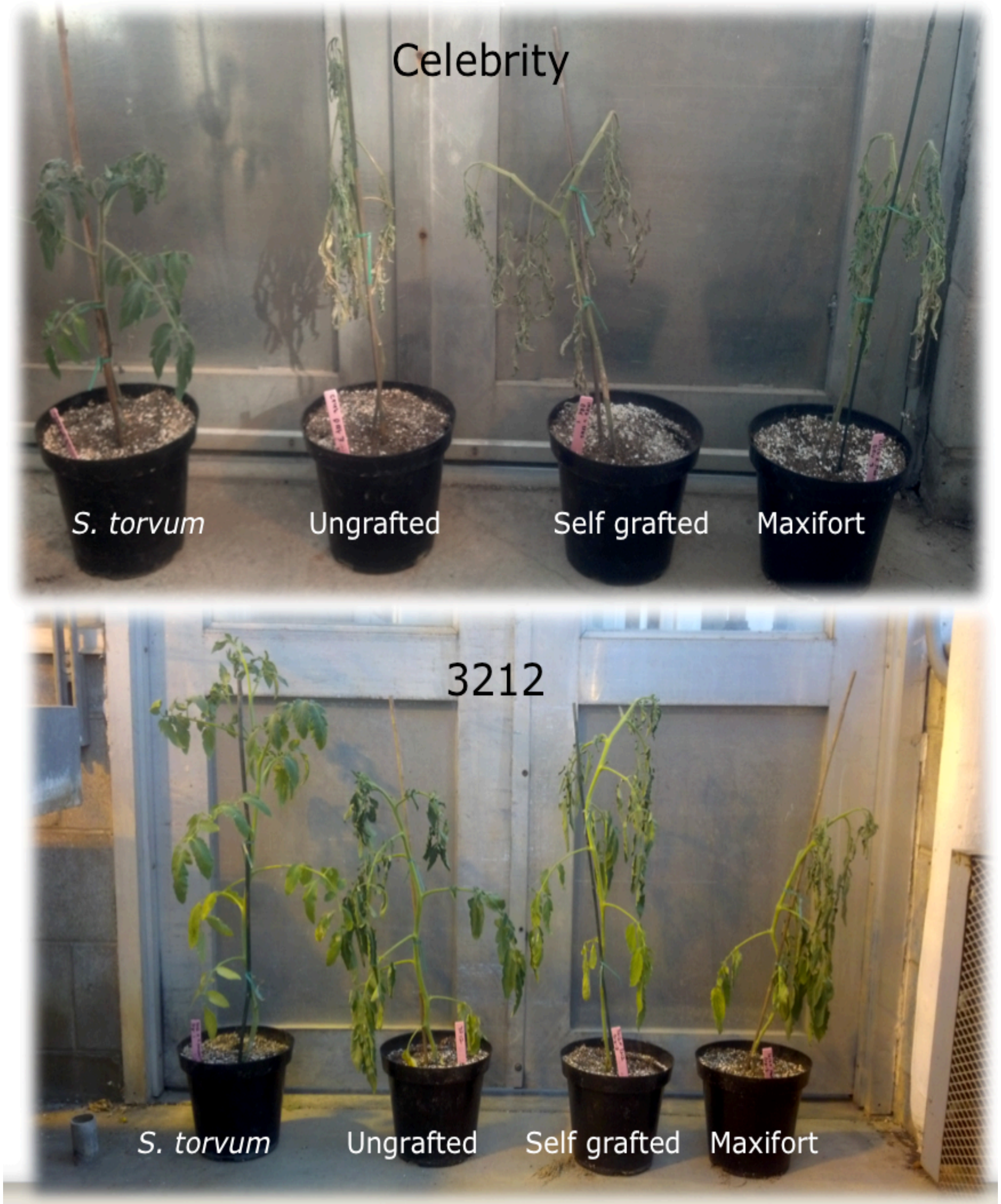
Photograph 1. Randomized selection of each genotype in optimal conditions, Trial 1, Day 22.





Photograph 2. Randomized selection of each genotype in flooded conditions, Trial 1, Day 22. Star placed above Celebrityx*S. torvum* to indicate significant difference in plant height and internode length.

Photograph 3. Randomized selection of each genotype in drought conditions, Trial 1, Day 22.



CHAPTER 4

UTILIZATION OF INTERSPECIFIC GRAFTING FOR INCREASED HEAT TOLERANCE IN TOMATOES

(for submission to *HortTechnology*)

Andrew Petran

Summary

Two tomato scions (‘CLN 3205A’ and ‘CLN3212A’) were grafted onto eggplant rootstock to determine the effect of interspecific grafting on heat tolerance of tomatoes. Wild eggplant *Solanum torvum* was selected as the interspecific rootstock of interest, and was compared against an non-grafted control rootstock in plant growth chambers set at optimal (26 C day, 20 C night) and supraoptimal temperatures (37 C day, 28 C night) for tomato vegetative growth. Plant height, internode length, and stomatal resistance of all genotypes in each environmental condition were measured for 35 days. Changes in plant height and internode length of tomatoes placed in supraoptimal temperatures was similar for both *S. torvum* and non-grafted rootstock, but non-grafted tomatoes experienced a significant decrease in stomatal resistance when placed in supraoptimal temperatures, while tomatoes grafted onto *S. torvum* did not. Further research is needed to determine if the observed stomatal stability in supraoptimal temperature conditions of grafted plants could lead to an increase in yield through flower initiation and fruit set.

Introduction

Temperature stresses, both too high and too low, have been shown to lead to inhibited plant growth and development, wilt, necrosis, and reduced overall yield of curcubit and solanaceous crops, including tomato (Ahn, 1999). Specifically, supra-optimal temperatures have observed deleterious effects on crops as well, including growth reduction, decrease in photosynthetic capacity accompanying increased respiration, osmotic damages and inhibited ion uptake/transport (Wang et al., 2003). Such conditions are applicable in many areas of the world, but of special concern to growers located in the lowland tropics (Palada and Wu, 2006).

Improving the environmental and climatic stress tolerance of vegetable crops through grafting is a novel approach that has been in used extensively in East Asia during the 20th century (AVRDC, 1990). In this context, grafting involves joining together two living plant parts- a rootstock and a scion- to produce a single, living plant. Grafting is an ideal technique for vegetable production because scions with desirable fruit-producing traits that are also susceptible to soil-borne disease or climatic pressures can be grafted onto rootstock that is more resistant to these pressures. The resulting union often results in a more productive plant (Cohen et al., 2002; Miller et al., 2005). Grafting, thus, this technique would not tax the minimal agricultural infrastructure that exists in many tropical regions today (EarthTrends, 2003).

Tomatoes are one of the most lucrative cash crops worldwide, but many cultivars and genotypes are affected when exposed to supraoptimal temperatures similar to conditions in the USVI (Abdalla and Verderk, 1968; EarthTrends, 2003). Most tomatoes grow under optimum day/night temperatures of 25 degrees Celsius (Max et al., 2009), however some tomato genotypes are tolerant at higher temperatures. Abdul-Baki (1991) found that several tomato lines genetically selected for heat tolerance produced a higher yield in high temperature conditions (38-40° Celsius) than when they were grown in normal field conditions (26-28° Celsius). These selected genotypes would likely produce well under high heat stress, but if a producer wanted to confer heat tolerance to other, exotic heirloom varieties, interspecific grafting may be a viable option.

Explorations of grafted plants growing in expanded temperature conditions on total yield have shown highly variable results. Initial trials by Okimura et al. (1986) and Bulder et al. (1987) on *Cucurbitaceae* and *Solanaceae* showed that different scion-rootstock combinations don't respond with significantly different yields in suboptimal temperatures, but subsequent trials have identified rootstocks that lead to higher overall yields in tomato, cucumber and watermelon (Ahn et al., 1999; Davis et al., 2008; Tachibana, 1982; Ziljstra and Nijs, 1987). Not surprisingly, all grafted combinations that show sub and supra-optimal temperature tolerances are those with rootstocks with wide optimal temperature thresholds (Schwarz et al, 2010).

In supraoptimal temperature conditions, research has shown that grafting tomatoes onto heat-tolerant tomato rootstock increases vegetative growth, but with no significant difference in yield compared to non-grafted controls (Abdelmageed and Gruda, 2009). However, using eggplant as an interspecific grafting rootstock may be a more promising candidate for supraoptimal temperature conditions, since eggplants are more adapted to live in hot, arid climates (Abdelmageed and Gruda, 2009; Schwarz et al., 2010). Indeed, Wang et al. (2006) observed yield increases of 10% on eggplant when grafted onto heat-tolerant eggplant rootstock. If similar results could be observed for tomato-eggplant interspecific grafting, it could increase local tomato production, cultivar availability, and growing season in areas of supraoptimal temperature for tomato.

A species of wild eggplant, *Solanum torvum*, has been selected as a rootstock candidate for tomato/eggplant interspecific grafting in this experiment. *Solanum* torvum is native to the western tropics and India, and exhibits tolerance to the climatic pressures of tropical regions (Gousset et al., 2005). There is also an established history of *S. torvum* for use as a rootstock in *S. melongena* cultivation for its resistance to a wide range of soil borne pathogens, including *Verticillium dahlia*, *Ralstonia solanacearum*, *Fusarium oxysporum* and *Meloidogyne* spp. root-knot nematodes (Bletsos et al., 2003; Gisbert et al., 2011; Singh and Gopalakrishnan, 1997). If evidence of increased temperature tolerance could be confirmed as well, it would make *S.* torvum an even more appealing candidate for commercial interspecific grafting production in the tropics. Uniform production of *S. torvum* rootstock seedlings can be challenging due to low germination rate leading to poor seedling emergence and slow early growth (Liu and Zhou, 2009).

Stomatal conductance and resistance is the quantitative measurement of plant gas exchange of the leaf. Because water leaves the stomata during this gas exchange, stomatal conductance and resistance has also been used to measure flood tolerance, drought tolerance and overall water use efficiency in plants (Kato et al., 2001; Sivritepe et al., 2005). A porometer was used in this project to measure stomatal resistance of each genotype under controlled temperature conditions. Porometer readings are taken on newly unfurled leaves at the same time of day since changes in leaf age and time of day can alter the consistency of resistance readings and confound statistical analysis (Ferreira and Katerji, 1992).

Two tomato scions, 'CLN 3205A' (3205) and 'CLN 3212A' (3212) were chosen for this project. These cultivars were chosen because of their classification as heat tolerant cultivars by the Asian Vegetable Research and Development Center. If interspecific grafting onto *S. torvum* rootstock would confer moisture tolerance to either cultivar, this technique could be used to increase the adaptation of this vegetable crop. Non-grafted Celebrity and 3212 will also be tested to serve as an unaltered, general control for statistical comparison.

If tomato crops grafted onto *S. torvum* are able to confer supraoptimal temperature tolerances that are greater than other available rootstock and non-grafted tomatoes, then it could possibly be utilized as a low-input tool to optimize production in regions of high temperature stress. The objective of this study, thus, was to determine the effect of *S. torvum* as an interspecific grafting rootstock for improving the heat tolerance of tomatoes.

Materials and Methods

The experiment was conducted at the University of Minnesota in Saint Paul, MN, 44.94 N and 93.09 W. In December of 2012, 24 seeds of *S.torvum* were planted into a 48-count seed tray containing the soilless media 'Sunshine Mix #8' LC8' (Sun Gro Horticulture). All seed were covered with coarse vermiculite, lightly watered and placed into a greenhouse. Greenhouse conditions were maintained at 21° C and 175 µmol PAR light from 0700 to 1800 hours. *S. torvum* seeds were acquired from the Virgin Islands Sustainable Farming Institute in St Croix, US Virgin Islands. Seeds were watered daily until time of grafting.

Twenty days after the planting of *S. torvum*, all remaining seeds for the experiment were planted using the methods stated above. This included 24 'CLN 3205' tomato seeds and 24 'CLN 3212A' tomato seeds. Scion tomato seeds were acquired from the Asian Vegetable Research and Development Center.

In early January 2013, all seeds had germinated and seedlings had grown to appropriate grafting size, the 4-5 true leaf stage (McAvoy, 2005). Plants were grafted using the cleft grafting technique, which is most commonly used on solanaceous crops (Lee and Oda, 2003). With a razor blade, rootstocks were cut below the cotyledon and a longitudinal cut was made 1.5 cm deep, about 75% the depth of the stem. Scions were pruned to 1-3 leaves, and the lower stem was cut into a tapered wedge to place inside the depth cut of the rootstock (Lee and Oda, 2003). After insertion, graft unions were wrapped with plastic parafilm to improve stability, reduce chance of infection and ensure vascular contact (Toogood, 1999). The scion and rootstock combinations that were used in experiment are explained in Table 1. Newly grafted plants were immediately brought into a low light environment with high relative humidity and a minimum of 18° C at all times (Lee and Oda, 2003). This chamber was constructed by wrapping clear and black plastic around a PVC skeleton and placed into the greenhouse. Humidity was maintained by sub-irrigating grafted plants on 0.35” deep Sure To Grow® capillary mats, which were flushed to saturation with water every day (Gutierrez, 2008). After approximately seven days the plants were removed from the chamber to be grown on in experimental conditions, described below.

Plants were placed in plant growth chambers and measured for morphological and physiological changes over a 35-day period. All environmental conditions in both growth chambers were the same, with the exception of temperature. One growth chamber was set at 26° C day, 20° C night (designated ‘control’) and the second chamber was set at 37° C day, 28° C night (designated ‘hot’). Plant height (cm), number of nodes, internode length and stomatal resistance (mmol/m2/s) readings were taken on day 1, 5, 15, 25, and 35, along with plant survival. Stomatal resistance was measured with a Delta T® AP4 porometer. Resistance readings were taken on the terminal leaflet of the youngest fully unfurled branch each measurement day at 1 pm, as changes in age of the leaf and time of day can alter the consistency of resistance readings and confound statistical analysis (Ferreira and Katerji, 1992).

On the final day, fresh weight, dry weight and leaf area (cm2) readings were taken as well. Dry weight was taken after plants had been placed in a Hot Pack® drying oven at 170 degrees F for 48 hours, and leaf area was measured using a Li-Cor LI-3100 area meter. All measurements for this set of replications were finished by February 2013.

Data was subjected to multiple methods of statistical analysis. Analysis of variance (ANOVA) was used to compare the differences in stomatal resistance between all replications of the two 3205 and 3212 genotypes in each environmental condition (control, hot) on each measurement day. ANOVA has been used to compare differences in stomatal conductance in tomatoes exposed to different categorical treatments (Sivritepe et al., 2005). ANOVA was also used to compare the differences in final plant height and internode lengths (day 35) between the two 3205 and 3212 genotypes in each environmental condition. Linear regression analysis was used to determine the significance of correlation between dry weight and leaf area in each environmental condition, and also to determine the significance of a stomatal resistance regression of the two 3205 and 3212 genotypes in each environmental condition over time. Rootstock genotype may have an effect on the resistance of the scion in stressed conditions (Borel et al., 2001). Statistical significance for ANOVA and regression was calculated at the $p < 0.05$ level. All analyses were carried out using the statistical program R.

Results

Control conditions with 3205 was the tallest plant on average (72 cm), and was significantly taller than both 3212 and 3212x*S.torvum*, but not significantly taller than 3205x*S.torvum* (Table 2). There were no significant differences in average plant height among any of the genotypes in hot conditions. 3205 and 3205x*S.torvum* were significantly shorter in hot conditions than in control conditions (Table 3). There were also no significant differences in internode length among any genotypes within each environmental condition, but when comparing the same genotype in different conditions, both 3205 and 3205x*S.torvum* had longer average internode lengths in control conditions than in hot conditions (Table 4).

Analyzing stomatal resistance revealed that all average resistances of genotypes were higher in control conditions than in hot conditions, but those differences were only significant for non-grafted 3205 and 3212 genotypes (Table 3). There was no statistical difference among scion genotypes in the same environmental condition.

Discussion

Regardless of temperature conditions, grafting a genotype onto *S. torvum* rootstock usually reduced average plant height compared to the non-grafted control, with the exception of the 3212 scion in control conditions. This observable yet insignificant reduction in height may be due to the grafting procedure itself. Time from sowing to transplant of grafted tomatoes is 30 to 33 days, while non-grafted tomatoes take less time, 14 to 21 days (Black et al., 2003; McAvoy and Giacomelli, 1985). In the procedure of this experiment, plants destined to be grafted as well as non-grafted control seeds were sown on the same day, so it is understandable that non-grafted plants would have a height advantage at the time of grafted transplant. The reason for 3212x*S.torvum* having a significantly higher average plant height than 3212 in control conditions cannot be confirmed, but it is possible that 3212 is a more compatible scion for *S. torvum* interspecific grafting than 3205.

Interspecific graft compatibility is highly variable among genotypes and difficult to predict; the degree of taxonomic affinity necessary for compatibility varies widely across different taxa (Mudge et al., 2009). Four potential mechanisms of interspecific incompatibility are identified by Andrews and Marquez (1993): cellular recognition, wounding response, plant growth regulators, and incompatibility toxins. If the 3205 scion experienced a degree of incompatibility through any of these mechanisms that the 3212 scion did not, it may have resulted in the comparatively stunted plant growth observed in this experiment.

Average internode length was greater for every genotype in control conditions compared to hot conditions, and for 3205 and 3205x*S.torvum* the difference was significant (Table 3). Internode length of tomatoes decreases in heat stress (Wahid et al., 2007), but since both scion genotypes experienced the same internode length reduction as their non-grafted controls, we can not determine whether grafting onto *S. torvum* has any effect on tomato internode length when grown under heat stress conditions.

The analysis of stomatal resistances among genotypes demonstrates increased heat tolerance when *S. torvum* is utilized as a rootstock. For both cultivars, average stomatal resistance was significantly reduced in hot conditions for the non-grafted controls while there was an insignificant reduction when grafted onto *S. torvum* rootstock (Table 4). Stomatal resistance is known to increase when tomatoes are exposed to drought stress conditions in order to conserve water, but will decrease as temperatures rise, as the plant intakes more carbon dioxide to accommodate increased respiration (Camejo et al., 2005; Sobeih et al., 2004). Diligent irrigation ensured there was no drought stress in this experiment. Thus, since the drop in stomatal resistance was significantly more in the non-grafted controls than the grafted genotypes, we concluded the grafted genotypes were not reacting to the same extent as the heat stress treatments. The lower resistances of the non-grafted plants in heat stress may also have contributed to the observed height increase when compared to grafted plants in hot conditions (Table 2). As mentioned before, the lower resistances likely accommodated higher respiration rates, which could have led to a faster rate of growth.

Increasing temperatures worldwide make the development of heat-tolerant plants and cultural practices a pressing need. The insignificant drop in stomatal resistance of both tomato scions tested, CLN 3205A and CLN 3212A, when grafted onto *S. torvum* imply that they do not react as strongly to heat stress compared to non-grafted controls of the same genotype. Further research needs to be conducted to determine if this observed stomatal stability would result in increased flower bud initiation, fruit set, and ultimately higher yields.

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Table 1. Scion and rootstock combinations were analyzed for morphological and physiological responses to different environmental pressures.			
Scion	Rootstock	Final 'Genotype'	# Replications per Environmental Treatment
CLN 3205A	none (non-grafted)	"3205"	3
CLN 3205A	*Solanum torvum*	"3205x*S. torvum*"	3
CLN 3212A	none (non-grafted)	"3212"	3
CLN 3212A	*Solanum torvum*	"3212x*S. torvum*"	3

Table 2. Average final plant height of all genotypes in each environmental condition. Letters denote statistical differences (p<0.05) within rows. Stars denote statistical differences (p<0.05) within columns.

Plant Height (cm)	Genotype			
	3205	3205x*S.torvum*	3212	3212x*S.torvum*
(n)	3	3	3	3
Control	72 a	64 ac	46 b	58 c
	*	*		
Hot	60	52.33	57	52.67

Table 3. Average final internode length of all genotypes in each environmental condition. Stars denote statistical significance (p<0.05) within columns.

Internode Length (cm)	Genotype			
	3205	3205x*S.torvum*	3212	3212x*S.torvum*
(n)	3	3	3	3
Control	5.7	6.22	4.83	4.73
	*	*		
Hot	4.39	4.5	4	4.66

Table 4. Average final stomatal resistance of all genotypes in each environmental condition. Letters denote statistical differences ($p<0.05$) within rows. Stars denote statistical significance ($p<0.05$) within columns.

Stomatal Resistance (mmol/m2/s)	Genotype			
	3205	3205x*S.torvum*	3212	3212x*S.torvum*
(n)	3	3	3	3
Control	2.26 *	1.09	1.42 *	1.08
Hot	0.24	0.32	0.38	0.52

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APPENDIX

Data Tables for ANOVA and Regression Analysis

Table A1: Rootstock Compatibility Trials

Scion	Rootstock	Replication	Days to Fusion	Survival
3212	non-grafted	1	0	1
3212	non-grafted	2	0	1
3212	non-grafted	3	0	1
3212	non-grafted	4	0	1
3212	non-grafted	5	0	1
3212	non-grafted	6	0	1
3212	non-grafted	7	0	1
3212	non-grafted	8	0	1
3212	non-grafted	9	0	1
3212	non-grafted	10	0	1
3212	3212	1		0
3212	3212	2	11	1
3212	3212	3	11	1
3212	3212	4	11	1
3212	3212	5	11	1
3212	3212	6	11	1
3212	3212	7		0
3212	3212	8	11	1
3212	3212	9	11	1
3212	3212	10	11	1
3212	Maxifort	1	8	1
3212	Maxifort	2	8	1
3212	Maxifort	3	8	1
3212	Maxifort	4	8	1
3212	Maxifort	5	8	1
3212	Maxifort	6	10	1
3212	Maxifort	7	10	1
3212	Maxifort	8	13	1
3212	Maxifort	9	13	1
3212	Maxifort	10	13	1
3212	S. torvum	1	10	1
3212	S. torvum	2	10	1
3212	S. torvum	3	10	1
3212	S. torvum	4	10	1
3212	S. torvum	5	10	1
3212	S. torvum	6	14	1
3212	S. torvum	7	13	1
3212	S. torvum	8		0
3212	S. torvum	9	13	1
3212	S. torvum	10	11	0

Celebrity	non-grafted	1	0	1
Celebrity	non-grafted	2	0	1
Celebrity	non-grafted	3	0	1
Celebrity	non-grafted	4	0	1
Celebrity	non-grafted	5	0	1
Celebrity	non-grafted	6	0	1
Celebrity	non-grafted	7	0	1
Celebrity	non-grafted	8	0	1
Celebrity	non-grafted	9	0	1
Celebrity	non-grafted	10	0	1
Celebrity	Celebrity	1	11	1
Celebrity	Celebrity	2	11	1
Celebrity	Celebrity	3	11	1
Celebrity	Celebrity	4	19	1
Celebrity	Celebrity	5		0
Celebrity	Celebrity	6	11	1
Celebrity	Celebrity	7		0
Celebrity	Celebrity	8	11	1
Celebrity	Celebrity	9	11	1
Celebrity	Celebrity	10		0
Celebrity	Maxifort	1	8	1
Celebrity	Maxifort	2	8	1
Celebrity	Maxifort	3	8	1
Celebrity	Maxifort	4	8	1
Celebrity	Maxifort	5	8	1
Celebrity	Maxifort	6	13	1
Celebrity	Maxifort	7	13	1
Celebrity	Maxifort	8	13	1
Celebrity	Maxifort	9	13	1
Celebrity	Maxifort	10	13	1
Celebrity	S. torvum	1	10	1
Celebrity	S. torvum	2	14	1
Celebrity	S. torvum	3	10	1
Celebrity	S. torvum	4	10	1
Celebrity	S. torvum	5	10	1
Celebrity	S. torvum	6	14	1
Celebrity	S. torvum	7	10	1
Celebrity	S. torvum	8	15	1
Celebrity	S. torvum	9	15	1
Celebrity	S. torvum	10	15	1
3212	S. torvum Veg	1		0
3212	S. torvum Veg	2	12	1
3212	S. torvum Veg	3		0

3212	S. torvum Veg	4	12	1
Celebrity	S. torvum Veg	1		0
Celebrity	S. torvum Veg	2		0
Celebrity	S. torvum Veg	3	12	1
Celebrity	S. torvum Veg	4	12	1

Table A2: Moisture Condition Trials

Genotype	Day	Replication	Treatment	Resistance	Height	Nodes
3212	1	1	wet	0.95	30	7
3212	1	2	wet	0.98	43	10
3212	1	3	wet	0.46	52	9
3212x3212	1	1	wet	1.81	61	9
3212x3212	1	2	wet	1.3	34	8
3212x3212	1	3	wet	1.73	50	9
3212xS.torvum	1	1	wet	1.33	50	10
3212xS.torvum	1	2	wet	2.66	51	11
3212xS.torvum	1	3	wet	1.24	49	11
3212xMaxifort	1	1	wet	0.66	56	10
3212xMaxifort	1	2	wet	0.94	57	10
3212xMaxifort	1	3	wet	0.42	65	9
Celebrity	1	1	wet	0.92	50	10
Celebrity	1	2	wet	0.66	44	10
Celebrity	1	3	wet	1.86	54	10
CelebrityxCelebrity	1	1	wet	1.11	40	7
CelebrityxCelebrity	1	2	wet	1.34	42	8
CelebrityxCelebrity	1	3	wet	0.93	49	10
CelebrityxS.torvum	1	1	wet	11.8	18	4
CelebrityxS.torvum	1	2	wet	1.04	33	7
CelebrityxS.torvum	1	3	wet	1.01	26	7
CelebrityxMaxifort	1	1	wet	1.36	51	11
CelebrityxMaxifort	1	2	wet	1.22	49	11
CelebrityxMaxifort	1	3	wet	1.3	45	10
3212	1	1	dry	1.27	39	10
3212	1	2	dry	1.2	57	10
3212	1	3	dry	1.07	26	7
3212x3212	1	1	dry	0.74	31	7
3212x3212	1	2	dry	0.47	58	11
3212x3212	1	3	dry	1.05	36	8
3212xS.torvum	1	1	dry	0.62	51	10
3212xS.torvum	1	2	dry	0.83	42	8
3212xMaxifort	1	1	dry	0.98	46	9
3212xMaxifort	1	2	dry	0.93	52	9
3212xMaxifort	1	3	dry	0.9	46	10
Celebrity	1	1	dry	0.68	47	9
Celebrity	1	2	dry	1.65	43	9
Celebrity	1	3	dry	1.14	47	11
CelebrityxCelebrity	1	1	dry	1.53	47	10
CelebrityxCelebrity	1	2	dry	6.2	25	4
CelebrityxCelebrity	1	3	dry	2.18	43	8
CelebrityxS.torvum	1	1	dry	1.14	22	6
CelebrityxS.torvum	1	2	dry	3.75	24	6

CelebrityxS.torvum	1	3	dry	3.15	25	6
CelebrityxMaxifort	1	1	dry	2	37	10
CelebrityxMaxifort	1	2	dry	2.66	49	12
CelebrityxMaxifort	1	3	dry	1.82	38	9
3212	1	1	optimal	2.64	31	7
3212x3212	1	1	optimal	2.22	46	9
3212xS.torvum	1	1	optimal	4.9	41	11
3212xS.torvum	1	2	optimal	1.5	32	6
3212xS.torvum	1	3	optimal	1.4	48	10
3212xMaxifort	1	1	optimal	1.67	52	9
3212xMaxifort	1	2	optimal	1.18	43	9
3212xMaxifort	1	3	optimal	1.61	32	8
Celebrity	1	1	optimal	0.77	46	12
Celebrity	1	2	optimal	1.57	45	11
Celebrity	1	3	optimal	1.52	41	12
CelebrityxCelebrity	1	1	optimal	2.04	33	8
CelebrityxCelebrity	1	2	optimal	1.68	40	9
CelebrityxS.torvum	1	1	optimal	1.37	38	7
CelebrityxS.torvum	1	2	optimal	2.2	38	9
CelebrityxS.torvum	1	3	optimal	1.36	25	8
CelebrityxMaxifort	1	1	optimal	1.5	44	10
CelebrityxMaxifort	1	2	optimal	1.22	46	10
CelebrityxMaxifort	1	3	optimal	0.8	44	12
3212	5	1	wet	0.68	40	8
3212	5	2	wet	0.83	49	10
3212	5	3	wet	1.25	59	11
3212x3212	5	1	wet	1.77	72	8
3212x3212	5	2	wet	1.65	43	9
3212x3212	5	3	wet	0.91	58	9
3212xS.torvum	5	1	wet	1.16	57	11
3212xS.torvum	5	2	wet	5	58	12
3212xS.torvum	5	3	wet	0.82	59	13
3212xMaxifort	5	1	wet	0.65	68	12
3212xMaxifort	5	2	wet	1.55	72	12
3212xMaxifort	5	3	wet	0.96	72	9
Celebrity	5	1	wet	0.92	58	11
Celebrity	5	2	wet	0.5	52	12
Celebrity	5	3	wet	1.21	57	13
CelebrityxCelebrity	5	1	wet	1.21	50	9
CelebrityxCelebrity	5	2	wet	0.7	54	11
CelebrityxCelebrity	5	3	wet	0.7	61	12
CelebrityxS.torvum	5	1	wet	5.4	17	5
CelebrityxS.torvum	5	2	wet	1.28	41	11
CelebrityxS.torvum	5	3	wet	1.92	31	9
CelebrityxMaxifort	5	1	wet	1.24	59	10
CelebrityxMaxifort	5	2	wet	1.09	55	13

CelebrityxMaxifort	5	3	wet	1.36	53	12
3212	5	1	dry	10.2	50	9
3212	5	2	dry	1.61	62	11
3212	5	3	dry	8.1	37	8
3212x3212	5	1	dry	2.36	40	9
3212x3212	5	2	dry	2.78	65	11
3212x3212	5	3	dry	0.85	45	10
3212xS.torvum	5	1	dry	7.9	61	11
3212xS.torvum	5	2	dry	6.3	48	9
3212xMaxifort	5	1	dry	16.3	52	11
3212xMaxifort	5	2	dry	1.25	56	11
3212xMaxifort	5	3	dry	6.3	50	9
Celebrity	5	1	dry	6.9	56	11
Celebrity	5	2	dry	4.85	50	13
Celebrity	5	3	dry	5.8	56	13
CelebrityxCelebrity	5	1	dry	13.8	51	11
CelebrityxCelebrity	5	2	dry	5.7	25	5
CelebrityxCelebrity	5	3	dry	12.9	48	9
CelebrityxS.torvum	5	1	dry	1.49	24	8
CelebrityxS.torvum	5	2	dry	1.34	28	8
CelebrityxS.torvum	5	3	dry	1.97	30	8
CelebrityxMaxifort	5	1	dry	1.63	47	9
CelebrityxMaxifort	5	2	dry	7.7	56	13
CelebrityxMaxifort	5	3	dry	2.42	45	10
3212	5	1	optimal	1.81	46	10
3212x3212	5	1	optimal	1.1	57	12
3212xS.torvum	5	1	optimal	2.7	48	10
3212xS.torvum	5	2	optimal	4.35	44	9
3212xS.torvum	5	3	optimal	7.3	55	11
3212xMaxifort	5	1	optimal	1.88	55	11
3212xMaxifort	5	2	optimal	1.32	55	11
3212xMaxifort	5	3	optimal	1.89	42	11
Celebrity	5	1	optimal	0.35	47	13
Celebrity	5	2	optimal	1.45	53	10
Celebrity	5	3	optimal	1.51	51	11
CelebrityxCelebrity	5	1	optimal	1.71	43	12
CelebrityxCelebrity	5	2	optimal	1.57	49	10
CelebrityxS.torvum	5	1	optimal	0.69	43	11
CelebrityxS.torvum	5	2	optimal	0.4	44	10
CelebrityxS.torvum	5	3	optimal	0.64	28	9
CelebrityxMaxifort	5	1	optimal	0.68	48	11
CelebrityxMaxifort	5	2	optimal	0.44	55	10
CelebrityxMaxifort	5	3	optimal	1.33	55	14
3212	10	1	wet	1.08	56	13
3212	10	2	wet	0.46	59	13
3212	10	3	wet	0.61	71	12

3212x3212	10	1	wet	0.82	68	12
3212x3212	10	2	wet	0.91	55	11
3212x3212	10	3	wet	0.75	68	13
3212xS.torvum	10	1	wet	1.4	66	12
3212xS.torvum	10	2	wet	1.87	68	15
3212xS.torvum	10	3	wet	0.85	75	15
3212xMaxifort	10	1	wet	1.08	75	15
3212xMaxifort	10	2	wet	1.34	82	14
3212xMaxifort	10	3	wet	1.05	77	12
Celebrity	10	1	wet	0.68	70	12
Celebrity	10	2	wet	0.74	66	13
Celebrity	10	3	wet	0.95	67	15
CelebrityxCelebrity	10	1	wet	0.57	62	12
CelebrityxCelebrity	10	2	wet	1.07	70	13
CelebrityxCelebrity	10	3	wet	0.76	70	12
CelebrityxS.torvum	10	1	wet	1.22	20	7
CelebrityxS.torvum	10	2	wet	0.48	46	11
CelebrityxS.torvum	10	3	wet	1.54	36	10
CelebrityxMaxifort	10	1	wet	1.14	69	15
CelebrityxMaxifort	10	2	wet	1.17	63	15
CelebrityxMaxifort	10	3	wet	1.08	65	14
3212	10	1	dry	8.2	53	11
3212	10	2	dry	6.7	63	11
3212	10	3	dry	10.4	40	9
3212x3212	10	1	dry	3.65	52	10
3212x3212	10	2	dry	9.6	59	14
3212x3212	10	3	dry	4.75	53	12
3212xS.torvum	10	1	dry	4.25	63	11
3212xS.torvum	10	2	dry	1.55	59	10
3212xMaxifort	10	1	dry	2.62	52	11
3212xMaxifort	10	2	dry	6.1	55	11
3212xMaxifort	10	3	dry	9	56	12
Celebrity	10	1	dry	6.2	57	13
Celebrity	10	2	dry	3.8	54	15
Celebrity	10	3	dry	7.6	57	15
CelebrityxCelebrity	10	1	dry	7.9	53	14
CelebrityxCelebrity	10	2	dry	1.83	26	5
CelebrityxCelebrity	10	3	dry	6.3	57	10
CelebrityxS.torvum	10	1	dry	1.38	30	10
CelebrityxS.torvum	10	2	dry	1.47	32	9
CelebrityxS.torvum	10	3	dry	1.16	32	10
CelebrityxMaxifort	10	1	dry	4.5	49	12
CelebrityxMaxifort	10	2	dry	6.8	57	12
CelebrityxMaxifort	10	3	dry	6.4	49	11
3212	10	1	optimal	0.69	55	12
3212x3212	10	1	optimal	0.8	70	14

3212xS.torvum	10	1	optimal	1.15	50	10
3212xS.torvum	10	2	optimal	0.77	59	10
3212xS.torvum	10	3	optimal	1.43	64	11
3212xMaxifort	10	1	optimal	0.97	64	12
3212xMaxifort	10	2	optimal	0.76	65	14
3212xMaxifort	10	3	optimal	0.88	57	13
Celebrity	10	1	optimal	0.73	67	17
Celebrity	10	2	optimal	0.63	63	14
Celebrity	10	3	optimal	0.33	59	12
CelebrityxCelebrity	10	1	optimal	0.46	54	12
CelebrityxCelebrity	10	2	optimal	0.67	61	12
CelebrityxS.torvum	10	1	optimal	0.73	55	12
CelebrityxS.torvum	10	2	optimal	0.58	53	12
CelebrityxS.torvum	10	3	optimal	0.62	34	10
CelebrityxMaxifort	10	1	optimal	0.45	60	12
CelebrityxMaxifort	10	2	optimal	0.49	64	13
CelebrityxMaxifort	10	3	optimal	0.68	64	13
3212	15	1	wet	0.72	79	15
3212	15	2	wet	0.46	72	14
3212	15	3	wet	1.39	67	13
3212x3212	15	1	wet	1.07	82	12
3212x3212	15	2	wet	1.06	70	12
3212x3212	15	3	wet	0.58	77	14
3212xS.torvum	15	1	wet	1.33	75	13
3212xS.torvum	15	2	wet	0.94	75	14
3212xS.torvum	15	3	wet	0.92	84	15
3212xMaxifort	15	1	wet	0.44	89	12
3212xMaxifort	15	2	wet	0.46	86	13
3212xMaxifort	15	3	wet	0.53	70	11
Celebrity	15	1	wet	0.39	80	12
Celebrity	15	2	wet	0.28	75	13
Celebrity	15	3	wet	0.62	79	14
CelebrityxCelebrity	15	1	wet	0.25	67	13
CelebrityxCelebrity	15	2	wet	0.37	75	13
CelebrityxCelebrity	15	3	wet	0.28	78	11
CelebrityxS.torvum	15	1	wet	0.17	25	8
CelebrityxS.torvum	15	2	wet	0.44	61	12
CelebrityxS.torvum	15	3	wet	0.72	40	10
CelebrityxMaxifort	15	1	wet	0.73	80	15
CelebrityxMaxifort	15	2	wet	0.7	70	14
CelebrityxMaxifort	15	3	wet	0.39	77	15
3212	15	1	dry	3.85	52	10
3212	15	2	dry	3.4	65	11
3212	15	3	dry	10.1	41	9
3212x3212	15	1	dry	18.7	58	10
3212x3212	15	2	dry	4.5	66	9

3212x3212	15	3	dry	8	55	10
3212xS.torvum	15	1	dry	5.1	73	10
3212xS.torvum	15	2	dry	2.62	50	12
3212xMaxifort	15	1	dry	6.2	56	12
3212xMaxifort	15	2	dry	15.9	59	11
3212xMaxifort	15	3	dry	25.6	49	12
Celebrity	15	1	dry	12	55	13
Celebrity	15	2	dry	15.3	51	13
Celebrity	15	3	dry	14.2	53	13
CelebrityxCelebrity	15	1	dry	14.5	48	12
CelebrityxCelebrity	15	2	dry	0.73	27	6
CelebrityxCelebrity	15	3	dry	3.65	47	11
CelebrityxS.torvum	15	1	dry	6.9	35	10
CelebrityxS.torvum	15	2	dry	4.8	38	11
CelebrityxS.torvum	15	3	dry	4.15	36	11
CelebrityxMaxifort	15	1	dry	11	42	11
CelebrityxMaxifort	15	2	dry	5.1	53	12
CelebrityxMaxifort	15	3	dry	13.1	50	13
3212	15	1	optimal	1.24	68	12
3212x3212	15	1	optimal	1.14	84	14
3212xS.torvum	15	1	optimal	1.07	61	12
3212xS.torvum	15	2	optimal	0.86	62	14
3212xS.torvum	15	3	optimal	0.77	71	13
3212xMaxifort	15	1	optimal	1.17	75	12
3212xMaxifort	15	2	optimal	1.03	76	13
3212xMaxifort	15	3	optimal	1.26	69	12
Celebrity	15	1	optimal	0.65	79	15
Celebrity	15	2	optimal	0.58	70	12
Celebrity	15	3	optimal	0.44	69	13
CelebrityxCelebrity	15	1	optimal	0.3	68	13
CelebrityxCelebrity	15	2	optimal	0.85	68	14
CelebrityxS.torvum	15	1	optimal	0.38	61	12
CelebrityxS.torvum	15	2	optimal	0.49	64	14
CelebrityxS.torvum	15	3	optimal	0.43	48	10
CelebrityxMaxifort	15	1	optimal	0.6	71	13
CelebrityxMaxifort	15	2	optimal	0.7	78	16
CelebrityxMaxifort	15	3	optimal	0.47	70	13
3212	20	1	wet	1.67	73	12
3212	20	2	wet	0.91	81	12
3212	20	3	wet	2.08	83	14
3212x3212	20	1	wet	3.15	81	12
3212x3212	20	2	wet	1.52	82	12
3212x3212	20	3	wet	1.23	79	13
3212xS.torvum	20	1	wet	1.52	80	15
3212xS.torvum	20	2	wet	3.8	80	15
3212xS.torvum	20	3	wet	2.36	92	16

3212xMaxifort	20	1	wet	1.85	83	15
3212xMaxifort	20	2	wet	1.52	94	16
3212xMaxifort	20	3	wet	1.5	94	13
Celebrity	20	1	wet	1.39	94	16
Celebrity	20	2	wet	0.82	85	13
Celebrity	20	3	wet	1.5	86	14
CelebrityxCelebrity	20	1	wet	0.78	78	13
CelebrityxCelebrity	20	2	wet	2.26	86	16
CelebrityxCelebrity	20	3	wet	1.7	89	14
CelebrityxS.torvum	20	1	wet	1.36	32	10
CelebrityxS.torvum	20	2	wet	1.59	68	11
CelebrityxS.torvum	20	3	wet	0.77	45	11
CelebrityxMaxifort	20	1	wet	1.52	83	13
CelebrityxMaxifort	20	2	wet	1.17	73	14
CelebrityxMaxifort	20	3	wet	1.4	75	17
3212	20	1	dry	12	50	11
3212	20	2	dry	0	57	12
3212	20	3	dry	11	40	9
3212x3212	20	1	dry	19.3	51	11
3212x3212	20	2	dry	0	61	12
3212x3212	20	3	dry	0	46	11
3212xS.torvum	20	1	dry	15.6	70	13
3212xS.torvum	20	2	dry	18	50	11
3212xMaxifort	20	1	dry	39	53	13
3212xMaxifort	20	2	dry	0	57	12
3212xMaxifort	20	3	dry	0	47	11
Celebrity	20	1	dry	20.2	53	11
Celebrity	20	2	dry	19.8	53	12
Celebrity	20	3	dry	23.6	52	13
CelebrityxCelebrity	20	1	dry	0	43	7
CelebrityxCelebrity	20	2	dry	2.48	33	12
CelebrityxCelebrity	20	3	dry	25.6	47	11
CelebrityxS.torvum	20	1	dry	12.5	33	10
CelebrityxS.torvum	20	2	dry	9.8	36	10
CelebrityxS.torvum	20	3	dry	17	36	12
CelebrityxMaxifort	20	1	dry	18.4	40	12
CelebrityxMaxifort	20	2	dry	0	53	13
CelebrityxMaxifort	20	3	dry	19.2	41	12
3212	20	1	optimal	1.94	77	13
3212x3212	20	1	optimal	2.08	90	16
3212xS.torvum	20	1	optimal	2.44	66	12
3212xS.torvum	20	2	optimal	2.5	62	12
3212xS.torvum	20	3	optimal	2.22	77	14
3212xMaxifort	20	1	optimal	1.24	79	14
3212xMaxifort	20	2	optimal	1.43	81	14
3212xMaxifort	20	3	optimal	1.12	77	14

Celebrity	20	1	optimal	1.45	83	14
Celebrity	20	2	optimal	1.3	75	14
Celebrity	20	3	optimal	1.62	76	13
CelebrityxCelebrity	20	1	optimal	0.88	70	14
CelebrityxCelebrity	20	2	optimal	2	63	14
CelebrityxS.torvum	20	1	optimal	0.92	70	13
CelebrityxS.torvum	20	2	optimal	0.91	63	13
CelebrityxS.torvum	20	3	optimal	0.63	55	13
CelebrityxMaxifort	20	1	optimal	1.31	77	13
CelebrityxMaxifort	20	2	optimal	1.56	82	13
CelebrityxMaxifort	20	3	optimal	1.41	77	15
3212	25	1	wet	1.38	85	13
3212	25	2	wet	1.03	85	13
3212	25	3	wet	1.25	73	14
3212x3212	25	1	wet	1.21	98	16
3212x3212	25	2	wet	1.04	90	12
3212x3212	25	3	wet	1.56	93	13
3212xS.torvum	25	1	wet	1.11	93	15
3212xS.torvum	25	2	wet	1.42	82	15
3212xS.torvum	25	3	wet	1.22	80	16
3212xMaxifort	25	1	wet	1.32	99	16
3212xMaxifort	25	2	wet	1.1	94	16
3212xMaxifort	25	3	wet	1.72	98	13
Celebrity	25	1	wet	1.36	100	16
Celebrity	25	2	wet	0.97	95	16
Celebrity	25	3	wet	1.2	85	14
CelebrityxCelebrity	25	1	wet	0.79	74	14
CelebrityxCelebrity	25	2	wet	0.81	94	14
CelebrityxCelebrity	25	3	wet	0.75	95	16
CelebrityxS.torvum	25	1	wet	0.59	39	13
CelebrityxS.torvum	25	2	wet	1.67	68	14
CelebrityxS.torvum	25	3	wet	0.53	54	16
CelebrityxMaxifort	25	1	wet	1.05	82	14
CelebrityxMaxifort	25	2	wet	0.68	79	18
CelebrityxMaxifort	25	3	wet	0.78	80	15
3212	25	1	dry	0	50	11
3212	25	2	dry	0	57	12
3212	25	3	dry	0	40	9
3212x3212	25	1	dry	0	51	11
3212x3212	25	2	dry	0	61	12
3212x3212	25	3	dry	0	46	11
3212xS.torvum	25	1	dry	0	70	13
3212xS.torvum	25	2	dry	0	50	11
3212xMaxifort	25	1	dry	0	53	13
3212xMaxifort	25	2	dry	0	57	12
3212xMaxifort	25	3	dry	0	47	11

Celebrity	25	1	dry	0	53	11
Celebrity	25	2	dry	0	53	12
Celebrity	25	3	dry	0	52	13
CelebrityxCelebrity	25	1	dry	0	43	7
CelebrityxCelebrity	25	2	dry	0	33	12
CelebrityxCelebrity	25	3	dry	0	47	11
CelebrityxS.torvum	25	1	dry	0	33	10
CelebrityxS.torvum	25	2	dry	0	36	10
CelebrityxS.torvum	25	3	dry	0	36	12
CelebrityxMaxifort	25	1	dry	0	40	12
CelebrityxMaxifort	25	2	dry	0	53	13
CelebrityxMaxifort	25	3	dry	0	41	12
3212	25	1	optimal	0.76	81	13
3212x3212	25	1	optimal	0.77	94	17
3212xS.torvum	25	1	optimal	1.79	57	14
3212xS.torvum	25	2	optimal	1.09	57	10
3212xS.torvum	25	3	optimal	1.4	76	15
3212xMaxifort	25	1	optimal	1.25	75	14
3212xMaxifort	25	2	optimal	1.16	75	15
3212xMaxifort	25	3	optimal	0.86	80	15
Celebrity	25	1	optimal	1.31	88	18
Celebrity	25	2	optimal	0.64	80	15
Celebrity	25	3	optimal	0.85	82	15
CelebrityxCelebrity	25	1	optimal	0.81	80	15
CelebrityxCelebrity	25	2	optimal	0.89	83	18
CelebrityxS.torvum	25	1	optimal	0.59	78	17
CelebrityxS.torvum	25	2	optimal	0.84	68	15
CelebrityxS.torvum	25	3	optimal	0.36	61	15
CelebrityxMaxifort	25	1	optimal	1.22	82	15
CelebrityxMaxifort	25	2	optimal	1.07	88	16
CelebrityxMaxifort	25	3	optimal	0.7	86	19

Table A3: Moisture Trial Final Day Calculations

Genotype	Replication	Treatment	Fresh Weight	Dry Weight	Leaf Area
3212	1	wet	198.71	38.47	30.78
3212	2	wet	202.37	42.8	33.62
3212	3	wet	102.42	23.59	15.96
3212x3212	1	wet	192.3	37.2	23.87
3212x3212	2	wet	199.4	30.24	24.75
3212x3212	3	wet	201.52	38.06	22.42
3212xS.torvum	1	wet	172.8	41.02	27.75
3212xS.torvum	2	wet	188.7	34.6	23.31
3212xS.torvum	3	wet	214.36	43.58	30.93
3212xMaxifort	1	wet	238.98	42.6	28.16
3212xMaxifort	2	wet	238.2	48.05	24.99
3212xMaxifort	3	wet	211.75	36.6	36.84
Celebrity	1	wet	190.01	43.4	43.36
Celebrity	2	wet	177.36	38.31	32.85
Celebrity	3	wet	192.63	43.85	
CelebrityxCelebrity	1	wet	217.91	37.77	
CelebrityxCelebrity	2	wet	175.06	37.22	38.74
CelebrityxCelebrity	3	wet	186.86	41.8	34.99
CelebrityxS.torvum	1	wet	79.87	6.54	22.09
CelebrityxS.torvum	2	wet	115.85	23.78	24.49
CelebrityxS.torvum	3	wet	152.3	23.35	25.69
CelebrityxMaxifort	1	wet	240.6	45.95	
CelebrityxMaxifort	2	wet	244.73	50.55	20.46
CelebrityxMaxifort	3	wet	201.72	42.57	29.56
3212	1	dry	9.88	8.98	6.67
3212	2	dry	10.57	9.16	4.63
3212	3	dry	7.41	6.93	5.08
3212x3212	1	dry	6.68	6.19	10.06
3212x3212	2	dry	9.02	8.31	4.62
3212x3212	3	dry	6.55		4.02
3212xS.torvum	1	dry	11.12	9.81	8.15
3212xS.torvum	2	dry	7.48	6.25	4.09
3212xMaxifort	1	dry	5.7	4.95	4.02
3212xMaxifort	2	dry	7.59	6.42	5.51
3212xMaxifort	3	dry	8.34		5.7
Celebrity	1	dry	8.28	7.4	9.89
Celebrity	2	dry	8.08	7.48	4.7
Celebrity	3	dry	8.37	7.54	4.12
CelebrityxCelebrity	1	dry	10.45	8.98	3.13
CelebrityxCelebrity	2	dry	2.95	2.69	2.23
CelebrityxCelebrity	3	dry	7.74	7.21	5.04
CelebrityxS.torvum	1	dry	3.48	2.9	3
CelebrityxS.torvum	2	dry	4.51	4.29	3.05

CelebrityxS.torvum	3	dry	5.41	5.01	4.02
CelebrityxMaxifort	1	dry	7.13		4.86
CelebrityxMaxifort	2	dry	7.93	7.5	5.94
CelebrityxMaxifort	3	dry	5.63	5.25	3.75
3212	1	optimal	202.05	28.31	18.57
3212x3212	1	optimal	238.48	44.19	33.65
3212xS.torvum	1	optimal	236.55	39.44	39.62
3212xS.torvum	2	optimal	286.53	42.55	20.32
3212xS.torvum	3	optimal	292.78	47.94	27.84
3212xMaxifort	1	optimal	245.55	51.12	25.82
3212xMaxifort	2	optimal	279.9	59.14	28.21
3212xMaxifort	3	optimal	288.43	56.85	38.11
Celebrity	1	optimal	304.11	63.98	28.86
Celebrity	2	optimal	276.15	62.1	37
Celebrity	3	optimal	230.32	56.51	10.47
CelebrityxCelebrity	1	optimal	304.94	59.52	20.7
CelebrityxCelebrity	2	optimal	276.12	59.3	35.08
CelebrityxS.torvum	1	optimal	570	67.23	36.21
CelebrityxS.torvum	2	optimal	450	56.07	25.44
CelebrityxS.torvum	3	optimal	522	62.75	37.51
CelebrityxMaxifort	1	optimal	484	70.03	49.09
CelebrityxMaxifort	2	optimal	487	66.21	42.73
CelebrityxMaxifort	3	optimal	467	59.5	41.11

Table A4: Heat Condition Trials

Genotype	Day	Replication	Treatment	Resistance	Height	Nodes
3205	1	1	control	3.1	19	4
3205	1	2	control	3.55	18	5
3205	1	3	control	3.35	22	5
3205	1	4	hot	5.7	23	5
3205	1	5	hot	11.3	25	8
3205	1	6	hot	3.65	22	6
3212	1	1	control	1.82	15	5
3212	1	2	control	1.33	18	5
3212	1	3	control	1.53	17	5
3212	1	4	hot	2.04	17	6
3212	1	5	hot	1.2	16	5
3212	1	6	hot	1.27	14	5
3205xS.torvum	1	1	control	4.7	21	5
3205xS.torvum	1	2	control	1.68	21	5
3205xS.torvum	1	3	control	1.85	17	5
3205xS.torvum	1	4	hot	3.95	22	4
3205xS.torvum	1	5	hot	1.57	22	5
3205xS.torvum	1	6	hot	1.8	25	7
3212xS.torvum	1	1	control	1.78	20	5
3212xS.torvum	1	2	control	2.02	26	8
3212xS.torvum	1	3	control	2.8	19	5
3212xS.torvum	1	4	hot	1.27	20	6
3212xS.torvum	1	5	hot	1.88	18	5
3212xS.torvum	1	6	hot	2.02	18	5
3205	5	1	control	0.68	26	8
3205	5	2	control	0.67	23	8
3205	5	3	control	0.46	29	8
3205	5	4	hot	0.83	30	9
3205	5	5	hot	0.76	32	10
3205	5	6	hot	1	30	9
3212	5	1	control	0.6	21	7
3212	5	2	control	0.64	23	7
3212	5	3	control	0.5	23	7
3212	5	4	hot	0.65	26	9
3212	5	5	hot	0.48	25	7
3212	5	6	hot	0.75	21	7
3205xS.torvum	5	1	control	0.66	21	6
3205xS.torvum	5	2	control	0.63	20	6
3205xS.torvum	5	3	control	0.63	21	8
3205xS.torvum	5	4	hot	1	26	7
3205xS.torvum	5	5	hot	1	28	8
3205xS.torvum	5	6	hot	1	25	8
3212xS.torvum	5	1	control	0.86	22	6

3212xS.torvum	5	2	control	0.87	28	7
3212xS.torvum	5	3	control	0.81	23	6
3212xS.torvum	5	4	hot	0.71	26	9
3212xS.torvum	5	5	hot	0.8	26	7
3212xS.torvum	5	6	hot	0.92	21	7
3205	15	1	control	0.53	49	11
3205	15	2	control	0.49	43.5	11
3205	15	3	control	0.35	51	10
3205	15	4	hot	0.37	41	12
3205	15	5	hot	1.1	44	13
3205	15	6	hot	0.35	42	11
3212	15	1	control	0.15	39	11
3212	15	2	control	0.14	45	8
3212	15	3	control	0.24	39	8
3212	15	4	hot	0.035	45	12
3212	15	5	hot	0.28	34	9
3212	15	6	hot	0.25	35	9
3205xS.torvum	15	1	control	0.17	33	10
3205xS.torvum	15	2	control	0.19	28	10
3205xS.torvum	15	3	control	0.09	30	10
3205xS.torvum	15	4	hot	0.095	32	10
3205xS.torvum	15	5	hot	0.18	35	13
3205xS.torvum	15	6	hot	0.13	35	11
3212xS.torvum	15	1	control	0.064	35	10
3212xS.torvum	15	2	control	0.49	43	11
3212xS.torvum	15	3	control	0.065	34	10
3212xS.torvum	15	4	hot	0.1	39	12
3212xS.torvum	15	5	hot	0.17	35	9
3212xS.torvum	15	6	hot	0.18	32	10
3205	25	1	control	0.66	68	13
3205	25	2	control	0.67	64	12
3205	25	3	control	0.78	61	12
3205	25	4	hot	0.24	53	15
3205	25	5	hot	0.25	47	14
3205	25	6	hot	0.62	54	15
3212	25	1	control	0.49	60	13
3212	25	2	control	2.04	59	11
3212	25	3	control	2.52	57	12
3212	25	4	hot	0.36	54	13
3212	25	5	hot	0.33	47	12
3212	25	6	hot	0.35	48	11
3205xS.torvum	25	1	control	0.81	45	11
3205xS.torvum	25	2	control	0.37	35	10
3205xS.torvum	25	3	control	0.78	42	10
3205xS.torvum	25	4	hot	0.45	45	12
3205xS.torvum	25	5	hot	1.19	59	15

3205xS.torvum	25	6	hot	0.61	51	13
3212xS.torvum	25	1	control	0.69	50	11
3212xS.torvum	25	2	control	0.97	55	12
3212xS.torvum	25	3	control	1.24	50	12
3212xS.torvum	25	4	hot	1.14	55	13
3212xS.torvum	25	5	hot	0.34	50	12
3212xS.torvum	25	6	hot	1.25	44	10
3205	35	1	control	1.7	75	14
3205	35	2	control	2.32	71	12
3205	35	3	control	2.78	70	12
3205	35	4	hot	0.31	59	13
3205	35	5	hot	0.21	55	14
3205	35	6	hot	0.2	66	14
3212	35	1	control	1.42	52	9
3212	35	2	control	1.39	42	11
3212	35	3	control	1.45	44	9
3212	35	4	hot	0.38	50	12
3212	35	5	hot	0.46	60	16
3212	35	6	hot	0.29	61	15
3205xS.torvum	35	1	control	0.75	61	11
3205xS.torvum	35	2	control	0.72	68	10
3205xS.torvum	35	3	control	1.8	63	10
3205xS.torvum	35	4	hot	0.51	56	13
3205xS.torvum	35	5	hot	0.3	50	11
3205xS.torvum	35	6	hot	0.15	51	11
3212xS.torvum	35	1	control	0.66	58	11
3212xS.torvum	35	2	control	1.57	62	14
3212xS.torvum	35	3	control	1.02	54	12
3212xS.torvum	35	4	hot	0.39	57	13
3212xS.torvum	35	5	hot	1.01	54	11
3212xS.torvum	35	6	hot	0.15	47	10