INTRASPECIFIC VARIATION OF ABOVEGROUND WOODY BIOMASS INCREMENT IN HYBRID POPLAR AT HIGH TEMPERATURE

by

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ABSTRACT

In the continental United States, mean surface air temperature is expected to increase by up to 5 ºC within 100 years. With hotter temperatures, leaf budbreak is expected to occur earlier in forests, and leaf area is expected to increase in locations where temperature is limiting. The response of plant photosynthesis to hotter temperatures is less certain; plant productivity could increase or decrease. Past studies have found intraspecific variation in the responses of forest tree productivity, phenology, canopy leaf area, and leaf isoprene emission to warming, which all influence carbon uptake and yield for agricultural tree species; it is therefore important to understand not only how hot climates affect carbon uptake and biomass production between different tree species, but also in different genotypes of the same species. We conducted a common garden study at the Biosphere 2 research center near Oracle, AZ, USA. We created a hybrid poplar plantation of 168 trees, which were planted as cuttings in January 2013. The trees used in this study are comprised of 5 distinct genotypes of *Populus deltoides* × *trichocarpa* from a range of average annual air temperatures. We measured photosynthetic capacity, leaf phenological timing, canopy leaf area and aboveground woody biomass in 2014 growing season, and leaf isoprene emission in the 2015 growing season. We observed a strong effect of genotype on aboveground woody biomass increment, implying strong local adaptation to the home range and limited phenotypic plasticity in terms of physiological and biometric responses to high temperature environments. Our study suggests that genotypes from hotter home ranges are able to maintain photosynthetic capacity and canopy leaf area late into the growing season, despite high temperatures, and thus produce more aboveground woody biomass. This study may have implications for agricultural management—as temperatures warm where managers currently grow hybrid poplar for agricultural or other purposes, the genotypes from those home ranges

would likely have reduced yield; managers could investigate the use of genotypes from home ranges with higher average temperatures to replace the vulnerable local varieties.

CHAPTER 1: INTRODUCTION

In the continental United States, mean surface air temperature could increase by between 0.5 and 5 ºC within 100 years (IPCC, 2013); this change is likely to impact tree productivity (Lu *et al.*, 2013). This would have implications for the carbon cycle, as carbon uptake is generally related positively to forest tree productivity, and increased productivity could serve as a negative feedback to climate change due to increased carbon uptake (Rustad *et al.*, 2001; Melillo *et al.*, 2002; Luo *et al.*, 2009). However, the opposite would be true if productivity were reduced, for instance due to extreme heat stress (Cox *et al.*, 2000; Luo, 2007). Productivity in forests is responsible for more than 50% of net terrestrial vegetative carbon uptake (Geider *et al.*, 2001) and more than 75% of carbon storage on agricultural land (Zomer *et al.*, 2016). Agriculture already claims nearly half of the world's potentially-vegetated land surface (Foley *et al.*, 2005; Johnson, *et al.*, 2014) and this is expected to increase in the future (FAO, 2015). Trees grown agriculturally—whether for biofuel production, paper production, environmental remediation, or other uses—are bred for maximum yield, which is often measured by the amount of aboveground woody biomass that can be produced per hectare of land in one year (Lombard *et al.*, 2005; O'Neill *et al.*, 2006; O'Neill *et al.*, 2013; O'Neill *et al.*, 2014). In general, aboveground woody biomass increases as an effect of hotter temperatures (Rustad *et al.*, 2001; Melillo *et al.*, 2002; Luo *et al.*, 2009). Past studies have found differences in productivity and biomass not only between tree species, but also within populations of the same species (Alberto *et al.*, 2013), including when trees are subjected to warmer temperatures (Lombard *et al.*, 2005; O'Neill *et al.*, 2006; O'Neill *et al.*, 2013; O'Neill *et al.*, 2014); it is thus important to understand how hot climates affect tree productivity and aboveground woody biomass within species that are used for agricultural production.

Differences in aboveground woody biomass within species may be due to respective differences in phenology, photosynthetic productivity, or canopy leaf area, which are all sensitive to changes in temperature. Phenology, which refers to the timing of lifecycle events, regulates carbon uptake in forest trees—phenological events are triggered by environmental cues, and thus are sensitive to climate change (Walther *et al.*, 2002). Changes in phenology can have implications for the ability for plants—and ecosystems as a whole—to mitigate the effects of rising anthropogenic CO_2 concentrations in the atmosphere. An increase in the length of the leaf production period due to an earlier start to spring would likely be accompanied by increased CO_2 uptake (Churkina *et al.*, 2005), which would contribute to increased aboveground woody biomass production. With hotter temperatures, leaf budbreak is expected to occur earlier in forests (Kramer *et al.*, 2000), and leaf area is expected to increase if cold temperatures limit leaf area (Morison and Lawlor, 1999); both of these increases would likely cause increases in aboveground woody biomass. The responses of plant photosynthesis to changing temperatures are also sensitive to changes in temperature, and this response varies between individuals of a species (Kirschbaum, 2014), as it is likely locally adapted (Berry & Björkman, 1980). Under hotter temperatures, plant productivity could increase (Shaver *et al.*, 1998; Rustad *et al.*, 2001; Wan *et al.*, 2005; Sullivan *et al.*, 2008) or decrease (Klein *et al.*, 2007; Saxe *et al.*, 2001) potentially due to heat stress. The effects across species ranges of changing plant productivity, phenology, and canopy leaf area under hot conditions on carbon uptake and aboveground woody biomass production are influenced by intraspecific variation; in order to anticipate the impacts of future high temperatures, it is not sufficient to understand only differences between species, but also within species.

Intraspecific differences can be caused by phenotypic plasticity—individuals display different phenotypes depending on environmental conditions (Nicotra *et al.*, 2010)—or local adaptation—individuals from a given area perform better there than individuals from other areas due to differences in genotype (Kawecki & Ebert, 2004). Local adaptation to temperature and insolation (Albert *et al.*, 2010) has been observed in many tree species (Alberto *et al.*, 2013), and results in different genotypes, each specifically adapted to the local climate.

The poplar species *Populus deltoides* is ideal for studying intraspecific variation, as it is broadly distributed across a temperature gradient in North America—its genotypes occur across a range of climates, from the hotter southern latitudes (i.e. Texas) to the cooler northern latitudes (i.e. Minnesota). The broad distribution of this species, combined with its rapid growth, allows us to determine whether variability of productivity and carbon uptake between genotypes is due to local adaptation or phenotypic plasticity.

To characterize the intraspecific variability between genotypes, they can be exposed simultaneously to the same conditions, such as in a common garden experiment (de Villemereuil *et al.*, 2016). Common garden experiments have been used to disentangle the effects of environmental influences and genetics on plant productivity (Kawecki & Ebert, 2004; Alberto *et al.*, 2013; Rehfeldt *et al.*, 2002) and phenological variation (Brachi *et al.*, 2013; Vander Mijnsbrugge *et al.*, 2016; Elferjani *et al.*, 2016). Common gardens can also be used to explore intraspecific differences along home range temperature gradients, either due to latitudinal (Toräng *et al.*, 2015; Elferjani *et al.*, 2016) or altitudinal gradients (Alberto *et al.*, 2011). When used in a hot climate, a common garden offers a method to explore the differences in terms of productivity and carbon uptake between genotypes from different home ranges under high temperatures.

The hot climate of southern Arizona offers an opportunity to determine how high temperature might affect aboveground woody biomass production in different hybrid poplar genotypes which currently grow successfully in cooler climates (Lombard *et al.*, 2005; O'Neill *et al.*, 2006; O'Neill *et al.*, 2013; O'Neill *et al.*, 2014). The purpose of this work is to determine whether local adaptation constrains the range of physiological and biometric responses to high temperature environments. To test this, we brought 5 genotypes of *Populus deltoides* (hybridized with *P. tremuloides*), which were bred for biomass production across a range of temperatures, to a common garden at the Biosphere 2 research center in southern Arizona. If tree response to rising temperature is plastic, the genotypes will likely respond similarly to a hot climate, but genetic adaptation may be a critical factor in their response. If plant productivity is strongly controlled by genotypic adaptation to the home range, then genotypes from hotter origins will produce the most aboveground woody biomass, because the extreme heat stress of southern Arizona will prevent high photosynthetic capacity and large canopy leaf area in the genotypes that are adapted to colder annual average temperatures. We expect that the pattern in aboveground woody biomass production will follow the average annual average temperature gradient of the home ranges of the chosen hybrid poplar genotypes. However, earlier onset of spring in southern Arizona relative to the average seasonal air temperature that the genotypes are adapted to may cause earlier budbreak, particularly in the genotypes that are adapted to colder annual average temperatures. Additionally, hybrid poplar trees are among the tree species that release the volatile organic compound isoprene, which is thought to help trees regulate extreme leaf temperature stress (Sharkey *et al.*, 2008). If photosynthetic capacity, canopy leaf area, and isoprene emission are phenotypically plastic, then hot- and cold-adapted genotypes will produce the same amount of aboveground woody biomass, because trees break bud earlier—and thus

have longer leaf production periods—when grown in locations with earlier spring than their home ranges.

CHAPTER 2: PRESENT STUDY

Appendix A details the background, methods, results, and conclusions of this study, and is formatted for submission to *Environmental and Experimental Botany*. This section outlines the major findings of this study.

We conducted our study at the Biosphere 2 research center near Oracle, AZ, USA. We created a hybrid poplar plantation of 168 trees, which were planted as cuttings. The trees used in this study are comprised of 5 distinct genotypes, each originating in a different region of the United States. We planted the trees in January 2013. We measured photosynthetic capacity, leaf phenological timing, canopy leaf area and aboveground woody biomass in 2014 growing season, and leaf isoprene emission in the 2015 growing season.

To measure photosynthetic capacity, we used an infrared gas analysis system (LI-6400; LI-COR, Inc., Lincoln, NE, USA). We measured the youngest fully expanded leaf on five trees of each of the five genotypes over the course of the 2014 growing season. To quantify the leaf production period, we made phenological observations of each study tree to determine the approximate date of budbreak and the cessation of new leaf production. To estimate leaf area, we photographed the leaves of a subset of branches and used a software program (ImageJ; U. S. National Institutes of Health, Bethesda, MD, USA) to convert the images to area estimates. To quantify aboveground woody biomass, we destructively harvested the trees at the end of the growing season and weighed the dried stems. To estimate leaf-level isoprene emission rates, we used a portable gas-exchange system (LI-6400) attached to a chemiluminescence continuous isoprene detector (Fast Isoprene Sensor; Hills Scientific, Boulder, CO, USA). We measured the youngest fully expanded leaf on five trees of each of the five genotypes.

We observed a strong effect of genotype on aboveground woody biomass increment, implying strong local adaptation to the home range and limited phenotypic plasticity in terms of physiological and biometric responses to high temperature environments. In general, genotypes from hotter home ranges produced more aboveground woody biomass, had larger canopy leaf area, and had higher late-season photosynthetic capacity. Our results indicate that differences in aboveground woody biomass increment between genotypes are related more closely to canopy leaf area and late-season photosynthetic capacity than leaf phenology or mid-season photosynthetic capacity. The results of our study indicate that local adaptation to different climates will affect the way that species respond to climate change. Our study suggests that genotypes from hotter home ranges are able to maintain photosynthetic capacity and canopy leaf area late into the growing season, despite high temperatures, and thus produce more aboveground woody biomass. This implies a carbon cycle feedback as well, as trees that are more productive also take up more CO_2, thus potentially reducing further climate change (Rustad *et al.*, 2001; Melillo *et al.*, 2002; Luo *et al.*, 2009). This study may have implications for agricultural management—as temperatures warm where managers currently grow hybrid poplar for agricultural or other purposes, the genotypes from those home ranges would likely have reduced yield; managers could investigate the use of genotypes from home ranges with higher average temperatures to replace the vulnerable local varieties.

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APPENDIX A: Intraspecific variation of aboveground woody biomass increment in hybrid poplar at high temperature

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Abstract

In the continental United States, mean surface air temperature is expected to increase by up to 5 ºC within 100 years. This temperature increase is likely to impact tree productivity and thus the carbon cycle, as well as yield in tree species used for agriculture. Past studies have found intraspecific variation in the response of forest tree productivity to warming; it is therefore important to understand not only how hot climates affect tree productivity and biomass production in different tree species, but also in different genotypes of the same species. We conducted a common garden study at the Biosphere 2 research center near Oracle, AZ, USA. We created a hybrid poplar plantation of 168 trees, which were planted as cuttings in January 2013. The trees used in this study are comprised of 5 distinct genotypes of *Populus deltoides* × *trichocarpa* from a range of average annual air temperatures. We measured photosynthetic capacity, leaf phenological timing, canopy leaf area and aboveground woody biomass in 2014 growing season, and leaf isoprene emission in the 2015 growing season. We observed a strong effect of genotype on aboveground woody biomass increment, implying strong local adaptation

to the home range and limited phenotypic plasticity in terms of physiological and biometric responses to high temperature environments. Our study suggests that genotypes from hotter home ranges are able to maintain photosynthetic capacity and canopy leaf area late into the growing season, despite high temperatures, and thus produce more aboveground woody biomass. This study may have implications for agricultural management—as temperatures warm where managers currently grow hybrid poplar for agricultural or other purposes, the genotypes from those home ranges would likely have reduced yield; managers could investigate the use of genotypes from home ranges with higher average temperatures to replace the vulnerable local varieties.

Introduction

In the continental United States, mean surface air temperature is expected to increase by between 0.5 and 5 ºC within 100 years (IPCC, 2013); this change is likely to impact tree productivity (Lu *et al.*, 2013). The effects of hot temperatures on tree productivity are variable; in general, productivity could increase (Shaver *et al.*, 1998; Rustad *et al.*, 2001; Wan *et al.*, 2005; Sullivan *et al.*, 2008) or decrease (Klein *et al.*, 2007). This would have implications for the carbon cycle, as carbon uptake is generally related positively to forest tree productivity, and increased productivity could serve as a negative feedback to climate change due to increased carbon uptake (Rustad *et al.*, 2001; Melillo *et al.*, 2002; Luo *et al.*, 2009). However, the opposite would be true if productivity were reduced, for example due to extreme heat stress (Cox *et al.*, 2000; Luo, 2007). Productivity in forests is responsible for more than 50% of net terrestrial vegetative carbon uptake (Geider *et al.*, 2001) and more than 75% of carbon storage on agricultural land (Zomer *et al.*, 2016). Agriculture already claims nearly half of the world's

potentially-vegetated land surface (Foley *et al.*, 2005; Johnson, *et al.*, 2014) and this is expected to increase in the future (FAO, 2015). Trees grown agriculturally are bred for maximum yield, which is often measured by the amount of aboveground woody biomass that can be produced per hectare of land in one year (Lombard *et al.*, 2005; O'Neill *et al.*, 2006; O'Neill *et al.*, 2013; O'Neill *et al.*, 2014). In general, aboveground woody biomass increases as an effect of hotter temperatures (Rustad *et al.*, 2001; Melillo *et al.*, 2002; Luo *et al.*, 2009). Past studies have found differences in productivity and biomass not only between tree species, but also within populations of the same species (Alberto *et al.*, 2013), including when trees are subjected to warmer temperatures (Lombard *et al.*, 2005; O'Neill *et al.*, 2006; O'Neill *et al.*, 2013; O'Neill *et al.*, 2014). This intraspecific variation could cause varying responses in populations of the same species under hotter conditions; it is thus important to understand how hot climates affect tree productivity and carbon uptake in different genotypes of the same species used for agricultural production.

The poplar species *Populus deltoides* is broadly distributed across a temperature gradient in North America—its genotypes are adapted to a range of climates (Sixto *et al.*, 2011), from the hotter southern latitudes (i.e. Texas) to the cooler northern latitudes (i.e. Minnesota). This allows for the characterization of the intraspecific variability of productivity and carbon uptake between genotypes. Intraspecific differences can be caused by phenotypic plasticity—individuals display different phenotypes depending on environmental conditions (West-Eberhard, 2003; Nicotra *et al.*, 2010)—or local adaptation—individuals from a given area perform better there than individuals from other areas (Kawecki & Ebert, 2004). Local adaptation to temperature and insolation (Albert *et al.*, 2010) has been observed in many tree species (Alberto *et al.*, 2013), and results in different genotypes, each specifically adapted to the local climate. To characterize the

intraspecific variability between genotypes, they can be exposed simultaneously to the same conditions, such as in a common garden experiment. Common garden experiments have been used to disentangle the effects of environmental influences and genetics on plant productivity (Kawecki & Ebert, 2004; Alberto *et al.*, 2013; Rehfeldt *et al.*, 2002) and phenological variation (Brachi *et al.*, 2013; Vander Mijnsbrugge *et al.*, 2016; Elferjani *et al.*, 2016). Common gardens can also be used to explore intraspecific differences along home range temperature gradients, either due to latitudinal (Toräng *et al.*, 2015; Elferjani *et al.*, 2016) or altitudinal gradients (Alberto *et al.*, 2011). When used in a hot climate, a common garden offers a method to explore the performance (in terms of productivity and carbon uptake) of genotypes from a range of temperatures under high temperatures.

Aboveground woody biomass increment—which is controlled by temperature-sensitive factors including leaf phenology, photosynthesis, and canopy leaf area—is measure of yield for agricultural tree species. With hotter temperatures, leaf budbreak is expected to occur earlier in forests (Kramer *et al.*, 2000), and leaf area is expected to increase in locations where temperature is limiting (Morison and Lawlor, 1999); both of these increases would likely cause increases in aboveground woody biomass. However, predictions for photosynthesis with hotter temperatures are less clear: photosynthesis would likely increase at first along with increasing temperature, but would later decline at very high temperatures (Kirschbaum, 2014). When combined, the impacts of all of these responses on aboveground woody biomass can be complex, as phenology, photosynthesis, and leaf area all influence aboveground woody biomass production. However, past studies have indicated that aboveground biomass generally increases with warming (Rustad *et al.*, 2001; Melillo *et al.*, 2002; Luo *et al.*, 2009).

Hybrid poplar trees are among the tree species that release the volatile organic compound isoprene, which is thought to help the tree regulate extreme leaf temperature stress (Sharkey *et al.*, 2008). Isoprene emission increases with high temperatures (Tingey *et al.*, 1979). Thus, hybrid poplar trees grown at high temperature that have high leaf isoprene emission rates may also have high photosynthesis rates and high aboveground woody biomass production. Past study has shown that higher photosynthesis is generally correlated positively with higher isoprene (Eller *et al.*, 2012). In this study, we expect the genotypes with the highest leaf isoprene emission rates to have the highest photosynthetic capacity and the highest seasonal aboveground woody biomass production.

The hot climate of southern Arizona offers an opportunity to determine how high temperature might affect aboveground woody biomass production in different hybrid poplar genotypes which currently grow successfully in a range of climates (Lombard *et al.*, 2005; O'Neill *et al.*, 2006; O'Neill *et al.*, 2013; O'Neill *et al.*, 2014) that may experience hotter temperatures in the future. The purpose of this work is to determine whether phenotypic plasticity or local adaptation predicts physiological and biometric performance in high temperature environments. To test this, we brought 5 genotypes of *Populus deltoides* (hybridized with *P. tremuloides*), which were bred for biomass production across a range of temperatures (Table 1), to a common garden at the Biosphere 2 research center in southern Arizona. If plant productivity is strongly controlled by genotypic adaptation to the home range, then genotypes from hotter origins will produce the most aboveground woody biomass, because the extreme high air temperatures of southern Arizona will prevent high photosynthetic capacity and large canopy leaf area in the genotypes that are adapted to colder average annual temperatures. We expect that the pattern in aboveground woody biomass production will follow the average annual

average temperature gradient of the home ranges of the chosen hybrid poplar genotypes (Table 1). However, earlier onset of spring in southern Arizona relative to the average seasonal air temperature that the genotypes are adapted to may cause earlier budbreak, particularly in the genotypes that are adapted to colder annual average temperatures. If high temperatures do not prevent high photosynthetic capacity and canopy leaf area in cold-adapted genotypes due to phenotypic plasticity, then cold-adapted genotypes will produce at least the same amount of aboveground woody biomass as hot-adapted genotypes, because earlier budbreak is associated with increased carbon uptake.

Materials and Methods

Study Site

We established a common garden experiment outdoors at the Biosphere 2 Research Center near Oracle, AZ, USA (32 34 51 N 110 50 57 W; 1189 m). To prepare the site, which was previously a landscaped dirt parking lot, we removed 8 ornamental trees and excavated the soil to a depth of 1 m. We mixed topsoil with the existing soil. The common garden consisted of 168 trees from 14 genotypes of hybrid poplar crosses, including 5 genotypes of the hybrid *Populus deltoides* × *trichocarpa* (D × T). We obtained ~20–30 cm bare stem cuttings (Segal Ranch Hybrid Poplar growers, Grandview, WA, USA), and planted ~12 trees of each genotype in a random arrangement with 1 × 1 m spacing during January, 2013. The D × T genotypes we studied consisted of a *P. trichocarpa* female parent from Washington state, and a *P. deltoides* male parent from one of several states. To create a latitude, temperature, and USDA planting zone gradient, we chose the specific genotypes 50-194 from Illinois (IL), 57-276 from Missouri (MO), 180-372 from Minnesota (MN), 49-177 from Texas (TX), and 199-586 from Oklahoma

(OK) (Table 1). For clarity, we use the state abbreviation of the male *P. deltoides* parent to refer to each genotype. We studied five individuals from each genotype, which were randomly selected before the start of the 2014 growing season. The trees were exposed to ambient climatic conditions, including full sun, temperature, and precipitation. Between April and mid-June, we supplied an additional 20 liters of water per tree each morning predawn via a drip irrigation system which was fed from an on-site well with a reverse osmosis system. From mid-June onwards we supplied 40 liters of water per tree per day. We provided fertilization with 3 liters of Hoagland's solution, a mixture of micro and macronutrients, approximately once per month. To determine the average climatological conditions during the study period, we used a meteorological station with sensors to measure air temperature (Rotronic HygroClip2 Temperature/RH Probe HC2S3-L6; Rotronic Instrument Corp., Hauppauge, NY, USA) and precipitation (Texas Electronics Rain Gage TE525WS-L30; Texas Electronics, Inc., Dallas, TX, USA). The study site is located in a region characterized by a hot desert climate, and mean precipitation was 634 mm, with the majority falling during the summer monsoon in July and August. The mean annual high temperature is 23.4 ºC, and the mean annual low temperature is 9.9 ºC.

Aboveground Woody Biomass

To estimate total aboveground woody biomass production by each tree during the 2014 growing season, we destructively harvested each study tree, then removed and discarded the leaves. We stored the stems at room temperature until they were dry, then weighed them.

Phenology

To estimate the start of the leaf production period, we recorded manual measurements of the protocol outlined by the US National Phenology Network (www.usanpn.org; Tucson, AZ, USA) for the budbreak leaf phenophase. Briefly, on each measurement day, we recorded whether or not breaking buds were present on each study tree. To estimate the end of the leaf production period, we recorded the date that each tree ceased to produce new leaves. On each measurement day, we recorded whether or not there were new leaves present on each tree. We observed each study tree twice per week at the beginning and end of the 2014 leaf production period.

Photosynthetic Capacity

To quantify photosynthetic capacity, we used an open gas exchange system with a 6 cm^2 leaf cuvette (LI-6400; LI-COR, Inc., Lincoln, NE, USA) to measure leaf gas exchange *in situ* at the common garden. We measured the youngest fully expanded leaf of each study tree during the 2014 growing season. To determine the optimal photosynthetic photon flux density (PPFD) level for photosynthesis measurements, we produced light curves at a constant CO_2 level (400 μmol mol^{-1}) and varied the PPFD level from 0 to 2800 mmol m^{-2} s^{-1} with stepwise increases between values. We estimated a saturating PPFD of 2000 mmol m^{-2} s^{-1}, so we used this value for all future photosynthetic capacity measurements. The LI-6400 uses a built-in red–blue led light source to control PPFD, which it calibrates against an internal photodiode (LI-6400–03; LI-COR, Inc.). To determine the optimal time of day for photosynthesis measurements, we produced a diurnal pattern of instantaneous photosynthesis at a constant CO_2 level (400 μmol mol^{-1}) but with ambient PPFD levels, which changed throughout the day. We measured photosynthesis with the LI-6400 set to a leaf temperature of 25 ºC, and we used the built-in chromel–constanten

thermocouple to measure the leaf temperatures the machine was actually able to achieve. To measure the maximum rate of carboxylation (Vc_{max}) and electron transport (J_{max}), we produced *A* vs C_i curves with CO_2 values ranging from 50 to 2000 μmol mol^{-1}, with stepwise increases between each value. We measured photosynthetic capacity three times during the 2014 growing season: during June, before cessation of leaf production; during July, soon after cessation of leaf production began; and during September, after the majority of the study trees had ceased leaf production. During each measurement campaign, we measured five trees of each of the five genotypes. To estimate Vc_{max} and J_{max} from *A* vs C_i curves we used the plantecophys (plantecophys R package, Duursma) and PEcAn (PEcAn.photosynthesis R package, Dietze *et al.*) packages in the R programming language (R Software Environment, R Foundation for Statistical Computing).

Canopy Leaf Area

To characterize average canopy leaf area during the 2014 growing season, we photographed the flattened leaves of two mature branches of two randomly selected study trees within each genotype against a reference scale, which was in this case a gridded background. We then calculated leaf area from the 2-dimensional image (ImageJ; U. S. National Institutes of Health, Bethesda, MD, USA) to generate a leaf area estimate in m^2. To obtain an estimate of the total canopy leaf area of each tree, we multiplied the estimated average leaf area per branch by the number of branches on each tree. While this method introduced uncertainty into the measurement, it allowed for an estimate of leaf area with minimal destructive sampling and avoided some of the drawbacks to other methodologies which were designed for larger, more developed tree canopies (Bréda, 2003).

Isoprene

To measure leaf isoprene emission rates, we used a portable gas-exchange system (LI-6400) which we attached to a chemiluminescence continuous isoprene detector (Fast Isoprene Sensor; Hills Scientific, Boulder, CO, USA) (Monson *et al.*, 2016). We measured the youngest fully expanded leaf on each study tree during the 2015 growing season.

Statistics

To determine whether or not there were statistical differences between genotypes in terms of aboveground woody biomass, phenology, photosynthetic capacity, canopy leaf area, and leaf isoprene emission rates, we used one-way ANOVAs (R v. 3.2.2; R Foundation for Statistical Computing, Vienna, Austria). Briefly, one-way ANOVAs indicate significant differences between means. We report degrees of freedom as the subscripts to the *F*-statistic. If we found significant differences ($p < 0.05$) between genotypes, we used Tukey post-hoc tests (R v. 3.2.2) to determine which particular genotypes were statistically different from one another ($p < 0.05$). Briefly, Tukey post-hoc tests identify significant differences between means within a sample. Unless otherwise noted, the sample size is $n = 5$ trees per genotype. To determine how well phenology, photosynthetic capacity, and canopy leaf area correlated with aboveground woody biomass, we calculated Pearson product-moment correlation coefficients (R v. 3.2.2). Briefly, the Pearson product-moment correlation function indicates the direction and strength of linear relationships between variables. We report correlation strength on a scale from very weakly correlated ($0.00 < r < 0.19$) to very strongly correlated ($0.80 < r < 1.0$; Evans, 1996).

Results

Aboveground Woody Biomass

The production of aboveground woody biomass varied between genotypes during the 2014 growing season ($F_{4,20} = 10.98$, $p < 0.05$; Fig. 1). The TX genotype produced the most biomass, followed by MO; the TX genotype produced significantly more biomass than the IL, MN, and OK genotypes ($p < 0.05$) and the MO genotype produced significantly more biomass than the MN genotype ($p < 0.05$).

Phenology

Budbreak varied between genotypes in 2014 ($F_{4,20} = 8.35$, $p < 0.05$), but neither the end of the leaf production period ($F_{4,20} = 0.64$, $p > 0.05$) nor did the total length of the leaf production period ($F_{4,20} = 0.36$, $p > 0.05$) varied significantly. Budbreak occurred earliest in 2014 for the trees of the MN genotype and latest for IL (Fig. 2). However, the only significant differences in budbreak were between the MN genotype and IL ($p < 0.05$), and MN and MO ($p < 0.05$). Budbreak was only weakly positively correlated with aboveground woody biomass ($r = 0.22$, $r^2 = 0.05$, $n = 25$, $p > 0.05$), but the end of the leaf production period ($r = 0.6$, $r^2 = 0.36$, $n = 25$, $p < 0.05$) and the length of the leaf production period ($r = 0.57$, $r^2 = 0.32$, $n = 25$, $p < 0.05$) were strongly and moderately positively correlated, respectively (Fig. 3).

Photosynthetic Capacity

In 2014, we found that neither Vc_{max} nor J_{max} varied between genotypes before ($F_{4,17} = 0.9$, $p > 0.05$; $F_{4,17} = 1.41$, $p > 0.05$ respectively) nor during ($F_{4,19} = 1.32$, $p > 0.05$; $F_{4,19} = 1.05$, $p > 0.05$ respectively) the end of the leaf production period. However, both Vc_{max} and J_{max} varied between genotypes in September, after the end of the leaf production period for most trees ($F_{4,20}$

= 8.99, $p < 0.05$; $F_{4,20} = 5.97$, $p < 0.05$ respectively). During September 2014, the TX genotype had higher Vc_{max} and J_{max} than MN and OK ($p < 0.05$), and MO had higher Vc_{max} than MN and OK ($p < 0.05$). Vc_{max} and J_{max} were both lower in September than in June or July for OK and TX (Fig. 4). We found a weak positive correlation between Vc_{max} and biomass in both June ($r = 0.3$, $r^2 = 0.09$, $n = 25$, $p > 0.05$) and July ($r = 0.24$, $r^2 = 0.06$, $n = 25$, $p > 0.05$). We found a weak negative correlation between J_{max} and biomass in June ($r = -0.26$, $r^2 = 0.07$, $n = 25$, $p > 0.05$), but a weak positive correlation in July ($r = 0.27$, $r^2 = 0.07$, $n = 25$, $p > 0.05$). We found moderate, positive, and significant correlations between both September Vc_{max} and aboveground woody biomass ($r = 0.52$, $r^2 = 0.27$, $n = 25$, $p < 0.05$; Fig. 5a), and between September J_{max} and aboveground woody biomass ($r = 0.46$, $r^2 = 0.21$, $n = 25$, $p < 0.05$; Fig. 5b).

Canopy Leaf Area

Canopy leaf area varied between genotypes ($F_{4,20} = 28.66$, $p < 0.05$). The TX genotype had the largest canopy leaf area, followed by MO. The leaf area of TX was significantly larger than each of the other genotypes ($p < 0.05$). MO was significantly higher than OK and MN ($p < 0.05$), but not IL. IL had significantly higher leaf area than only MN ($p < 0.05$). We found a very strong positive correlation between canopy leaf area and aboveground woody biomass ($r = 0.85$, $r^2 = 0.72$, $n = 25$, $p < 0.05$; Fig. 6).

Isoprene

Leaf isoprene emission rates varied between genotypes ($F_{4,20} = 13.86$, $p < 0.05$). Leaf isoprene emission rates were highest in the MO genotype, followed by the TX genotype. The only genotype with significant differences from the others was OK, which had lower isoprene

emission than each of the other four (IL, MN, MO, and TX; $p < 0.05$). We found weak positive and not significant correlations between leaf isoprene emission and Vc_{max} in September 2014 ($r = 0.35$, $r^2 = 0.12$, $n = 25$, $p > 0.05$), and between leaf isoprene emission and aboveground woody biomass ($r = 0.28$, $r^2 = 0.08$, $n = 25$, $p > 0.05$; Fig. 7).

Discussion

We found that aboveground woody biomass production under high temperatures was strongly affected by genotype—aboveground woody biomass increment generally increased with increasing home range temperature. Genotypes from cooler home ranges did break bud earlier, but had lower aboveground woody biomass production than genotypes from warmer home ranges. Our results indicate that differences in aboveground woody biomass increment between genotypes are related more closely to canopy leaf area and late-season photosynthetic capacity than phenology, mid-season photosynthetic capacity, or leaf isoprene emission rates. The hybrid poplar genotypes that produced the most aboveground woody biomass had larger leaf areas and were able to maintain higher photosynthetic capacity late into the season—even after leaf production ceased—than the other genotypes. This implies that for the genotypes adapted to colder home ranges, phenotypic plasticity in photosynthetic capacity, canopy leaf area, or isoprene emission was not a sufficient response to the high temperatures in southern Arizona, nor did earlier budbreak compensate for reduced canopy leaf area or late-season photosynthetic capacity.

Annual aboveground woody biomass values were consistent with previous studies from other climates (Laureysens *et al.*, 2004; Pellis *et al.*, 2004; Zabek and Prescott, 2006). We found that aboveground woody biomass production generally reflected the expected pattern of increasing aboveground woody biomass with increasing average annual air temperature of the

home range (Fig. 1), although OK was expected to produce more than MO. Neither phenology nor mid-season photosynthetic appeared to contribute significantly to differences in aboveground woody biomass increment between genotypes. The genotypes with the highest aboveground woody biomass production, TX and MO, had large leaf canopies and maintained their high photosynthetic capacities after cessation of leaf production than the other genotypes (Fig. 4). Past study has found similar patterns in productivity; TX was the most productive, followed by IL, MO, and genotypes from Oklahoma (184-411 and 195-529) when grown in New Mexico (O'Neill *et al.*, 2006; Lombard *et al.*, 2005); in a follow-up study, which used TX, IL, and the other genotypes from Oklahoma, only TX and one of the Oklahoma genotypes survived the experiment (O'Neill *et al.*, 2013; O'Neill *et al.*, 2014). In the follow-up experiment, aboveground woody biomass differed between TX and 195-529 by only 3.42 Mg ha^{-1} yr^{-1} (O'Neill *et al.*, 2013), while in our study, TX produced 40.05 Mg ha^{-1} yr^{-1} more biomass than OK. Average air temperatures in the New Mexico study area are much cooler (10 – 12 °C) than temperatures in our study area (20 – 22 °C; PRISM Climate Group, 2015). This indicates that the cold-adapted genotypes do not always produce less biomass than the others, and that the differences we observed between genotypes are influenced by the high temperatures of the study site in southern Arizona.

Budbreak occurred earlier than in the poplar specimens used in other studies (Thitithanakul *et al.*, 2012; Luo and Polle, 2009), likely because the requirements for budbreak, including daylength and temperature accumulation (Rohde *et al.*, 2011), are met earlier in southern Arizona than in the locations of the other studies. Ecosystem carbon uptake may increase with earlier onset of spring (Churkina *et al.*, 2005), but this may not be true for all genotypes of locally adapted tree species. Previous common garden experiments have shown that

different species show different patterns in intraspecific variation in budbreak; trees from colder home ranges were found to break bud earlier in some species and later in others (Vitasse *et al.*, 2009). However, warming has often been observed to cause earlier leaf flushing (Ahas *et al.*, 2002; Chmielewski and Rotzer, 2002; Menzel *et al.*, 2006; Delbart *et al.*, 2008; Linderholm, 2006). We expected the genotypes from cooler climates to break bud earlier and have the longest leaf production periods, because we expect the hot climate of southern Arizona to effectively be a proxy for earlier spring—heat accumulation thresholds for the start of budbreak will likely be reached earlier in southern Arizona because the winters are shorter and milder than in the cooler home ranges. We found that the earliest genotype to break bud, MN, was from the coolest climate, but contrary to our expectations, it also had the lowest aboveground woody biomass production (Fig. 1), implying a reduced tolerance to the high temperature conditions in southern Arizona. There were no significant differences between genotypes in terms of the length of the leaf production period nor the end of the leaf production period, which may indicate that the observed differences in aboveground woody biomass increment were due to differences in photosynthetic capacity or canopy leaf area.

There is generally a link between higher temperatures and higher photosynthetic productivity, although extremely hot temperatures can cause photosynthesis to decrease (Saxe *et al.*, 2001; Berry & Björkman, 1980). We expected that photosynthetic capacity would be lower in genotypes from cooler climates throughout the growing season. We did not find any significant differences between genotypes in mid-season photosynthetic capacity, but photosynthetic capacity did vary between genotypes late in the season (Fig. 4), and the variability matched the differences we found in biomass (Fig. 1)—the genotypes from cooler climates generally had lower photosynthetic capacity after cessation of leaf production. In

general, both Vc_{max} (Fig. 5a) and J_{max} (Fig. 5b) were positively correlated with aboveground woody biomass, but this relationship was only significant in Vc_{max} and J_{max} from September 2014.

Canopy leaf area has been observed to increase with warming temperatures (Morison and Lawlor, 1999; Gunn & Farrar, 1999; Marshall *et al.*, 1992), but can be reduced under extreme high temperature (Shah & Paulsen, 2003). Due to the higher average temperature in southern Arizona than in their home ranges, we expected that canopy leaf area would be lower in the cold-adapted genotypes, and we did observe this pattern. We found significant differences between genotypes in leaf area, and this variability was strongly positively correlated with aboveground woody biomass (Fig. 6).

Isoprene emission rates were similar to previous studies on mature poplar leaves (Eller *et al.*, 2012; Centritto *et al.*, 2004). Isoprene emission has been observed to increase under hotter temperatures (Tingey *et al.*, 1979), and is thought to confer thermotolerance to leaves (Sharkey *et al.*, 2008). We expected to find higher leaf isoprene emission in the genotypes from hotter home ranges, and also in the genotypes with the greatest aboveground woody biomass increment. We did find significant differences between genotypes in leaf isoprene emission rates, but no significant correlations with either photosynthetic capacity or aboveground woody biomass production (Fig. 7).

Conclusion

We observed a strong effect of genotype on aboveground woody biomass increment, implying local adaptation to the home range and limited phenotypic plasticity in terms of physiological and biometric responses to high temperature environments. In general, genotypes

from hotter home ranges produced more aboveground woody biomass, had larger canopy leaf area, and had higher late-season photosynthetic capacity. Genotypes from cooler home ranges generally broke bud earlier, but did not have longer leaf production periods, had smaller leaf canopies, and were unable to maintain photosynthetic capacity after cessation of leaf production. The results of our study indicate that local adaptation to different climates will affect the way that species respond to climate change, as plasticity in phenological responses to early springtime temperatures cannot compensate for differences between genotypes in tolerance to high temperatures. Our study suggests that genotypes from hotter home ranges are able to maintain photosynthetic capacity and canopy leaf area late into the growing season, despite high temperatures, and thus produce more aboveground woody biomass. This may imply a carbon cycle feedback; if these patterns held true for all trees, we might expect a negative feedback to climate change in genotypes from hotter home ranges—as trees that are more productive over the entire growing season also uptake more CO_2—but a positive feedback for genotypes from cooler home ranges. This study may have implications for agricultural management—as temperatures warm where managers currently grow hybrid poplar for paper or biofuel production, or for other purposes such as carbon sequestration, the genotypes from those home ranges would likely have reduced yield. Managers could investigate the use of genotypes from home ranges with higher average temperatures to replace the vulnerable local varieties.

Tables and Figures

Table 1. Parentage of five hybrid poplar clones, planted in 2013 and irrigated with a drip system.

Clone	Female Parent	Source	Male Parent	Source	USDA Plant Hardiness Zone*	30-yr Normal Mean Annual Temperature (°C)†
180-372	*P. trichocarpa*	Washington	*P. deltoides*	Minnesota	4b	6-8
50-194	*P. trichocarpa*	Washington	*P. deltoides*	Illinois	6a	12-14
57-276	*P. trichocarpa*	Washington	*P. deltoides*	Missouri	6b	14-16
199-586	*P. trichocarpa*	Washington	*P. deltoides*	Oklahoma	7b	16-18
49-177	*P. trichocarpa*	Washington	*P. deltoides*	Texas	8b	18-20

* (Daly *et al.*, 2010)

† (PRISM Climate Group, 2015)

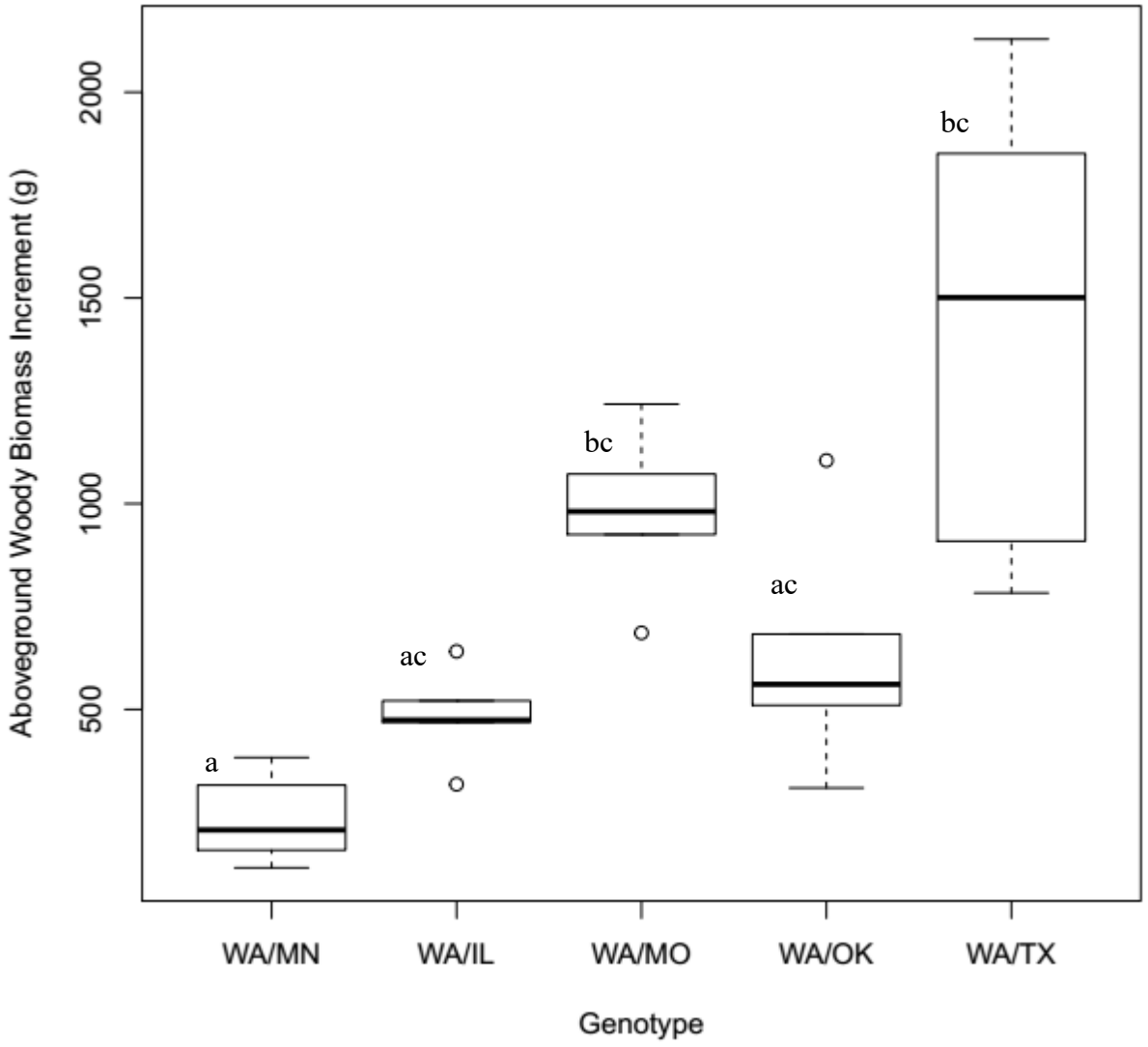


Figure 1. Aboveground woody biomass increment in five hybrid poplar clones grown in southern Arizona during the 2014 growing season. Genotypes are ordered from coolest average air temperature (left) to warmest (right). Different letters indicate statistically significant differences between genotypes (Tukey post-hoc tests, $p < 0.05$).

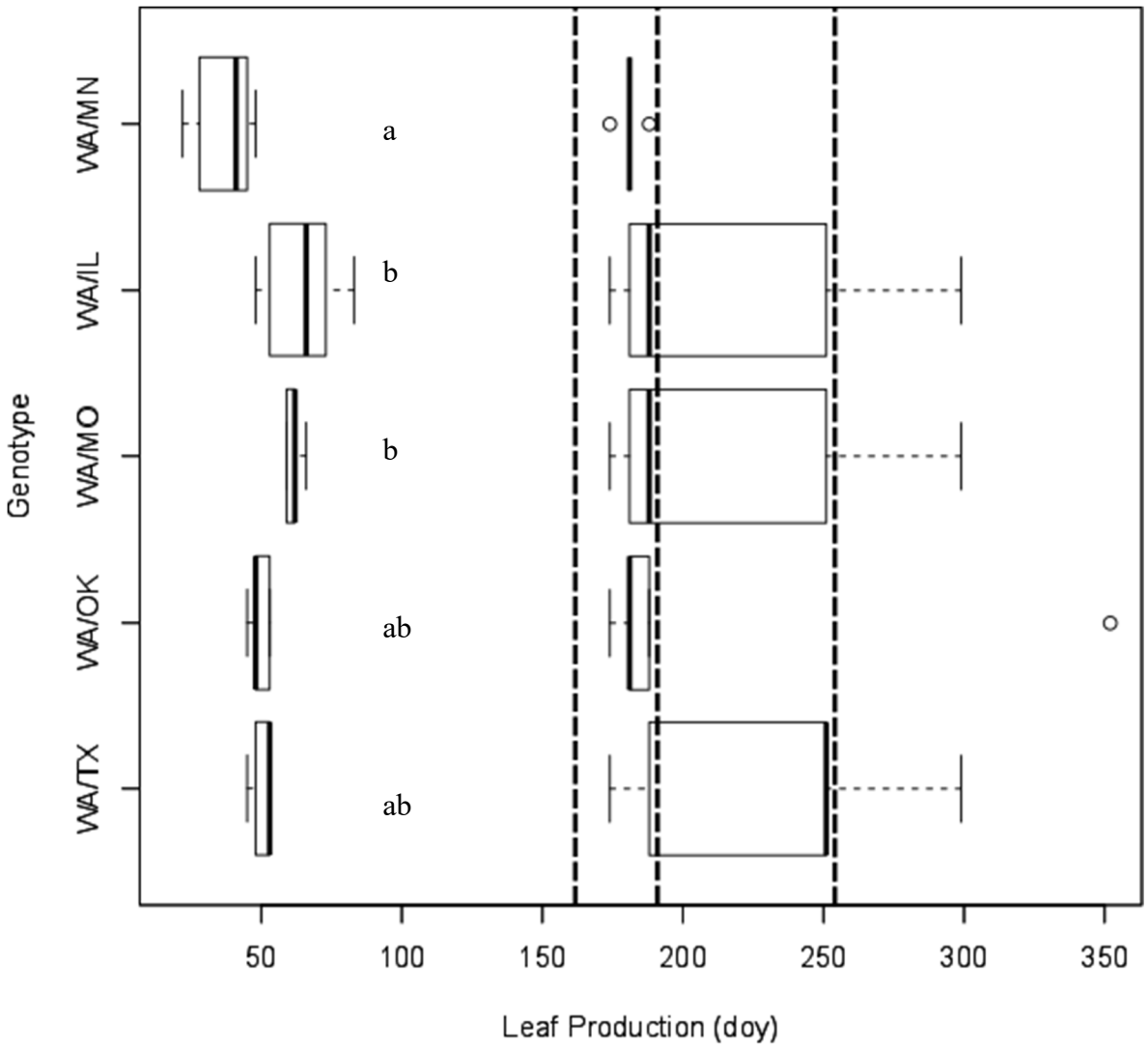


Figure 2. Budbreak (left) and cessation of leaf production (right) in five hybrid poplar clones grown in southern Arizona during the 2014 growing season. Vertical dashed lines indicate the timing of photosynthetic capacity measurements (see Fig. 3). The distance between the budbreak and cessation of leaf production boxplots constitutes the leaf production period for each genotype. Different letters indicate statistically significant differences between genotypes in budbreak (Tukey post-hoc tests, $p < 0.05$); there were no significant differences between genotypes in cessation of leaf production.

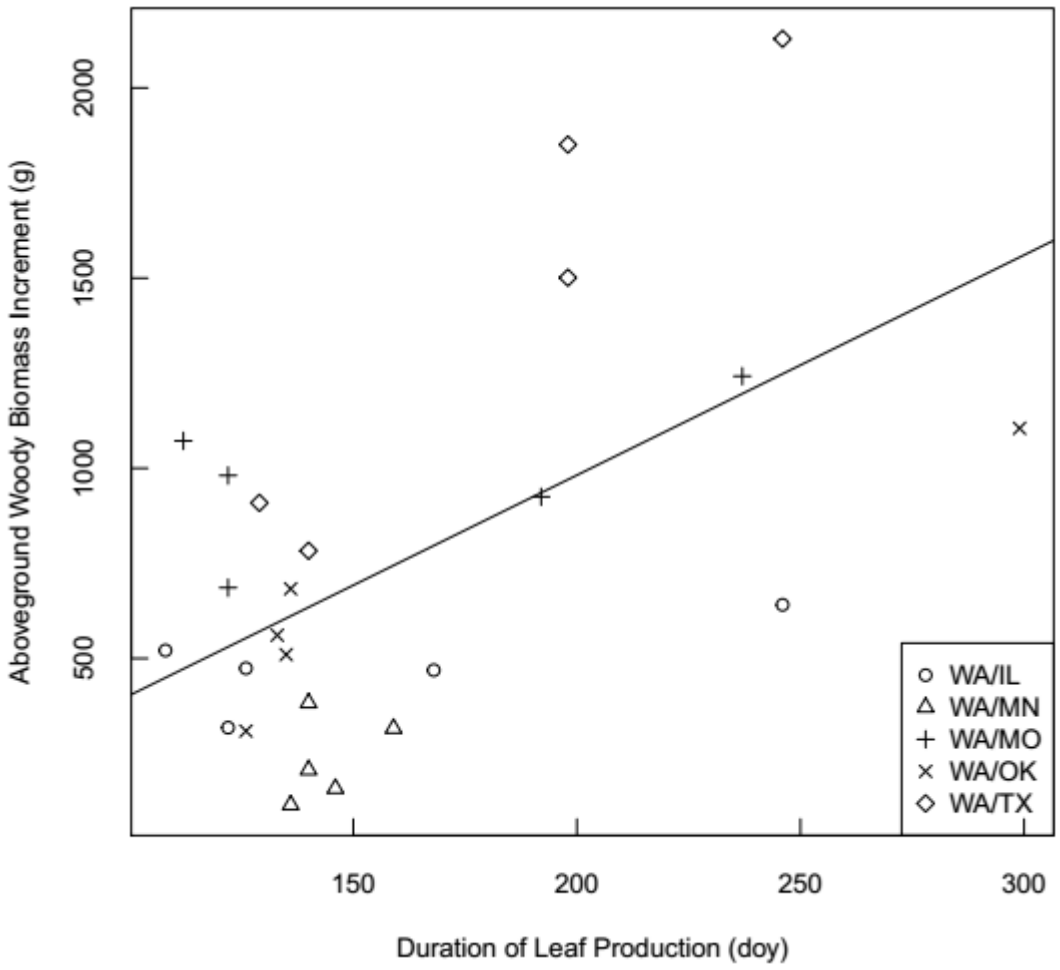
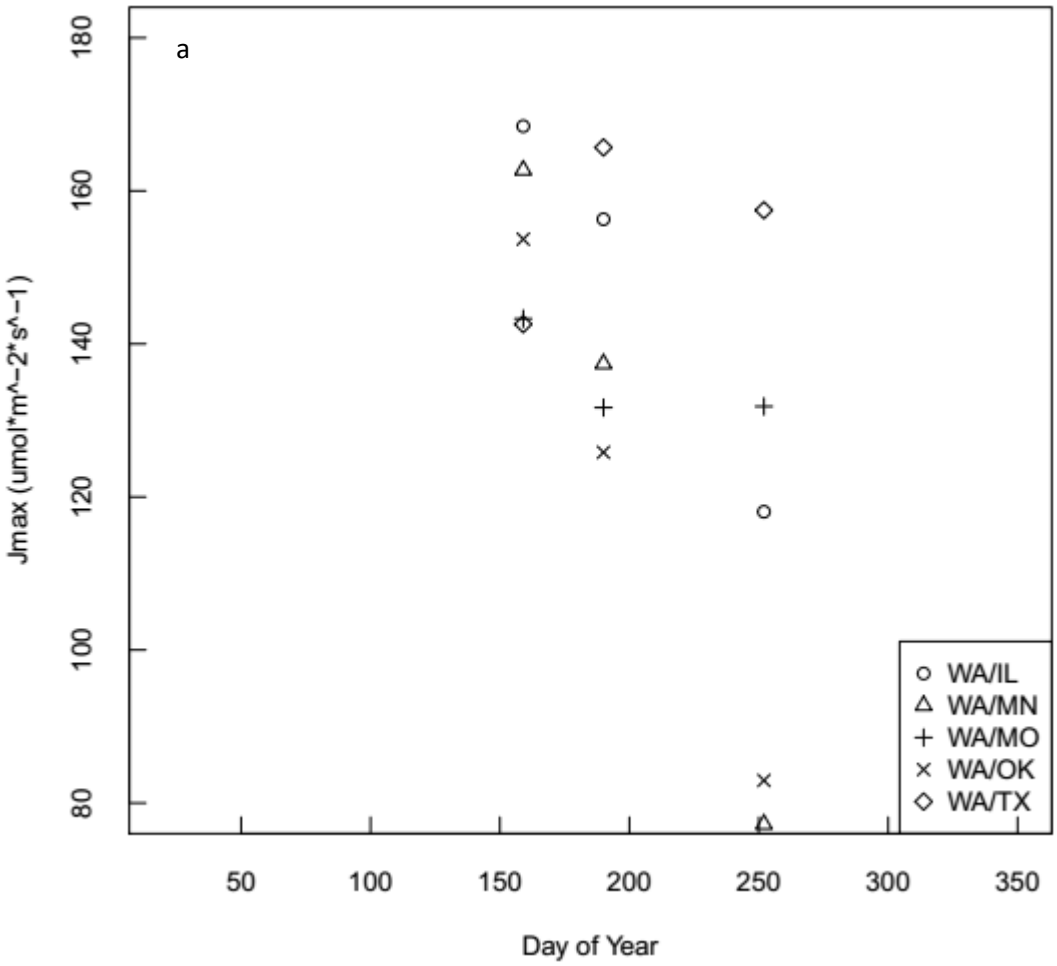


Figure 3. Aboveground woody biomass increment versus leaf production period in five hybrid poplar clones grown in southern Arizona during the 2014 growing season.


a
Jmax (umol*m^−2*s^−1)
80
100
120
140
160
180
50
100
150
200
250
300
350
Day of Year
WA/IL
WA/MN
WA/MO
WA/OK
WA/TX

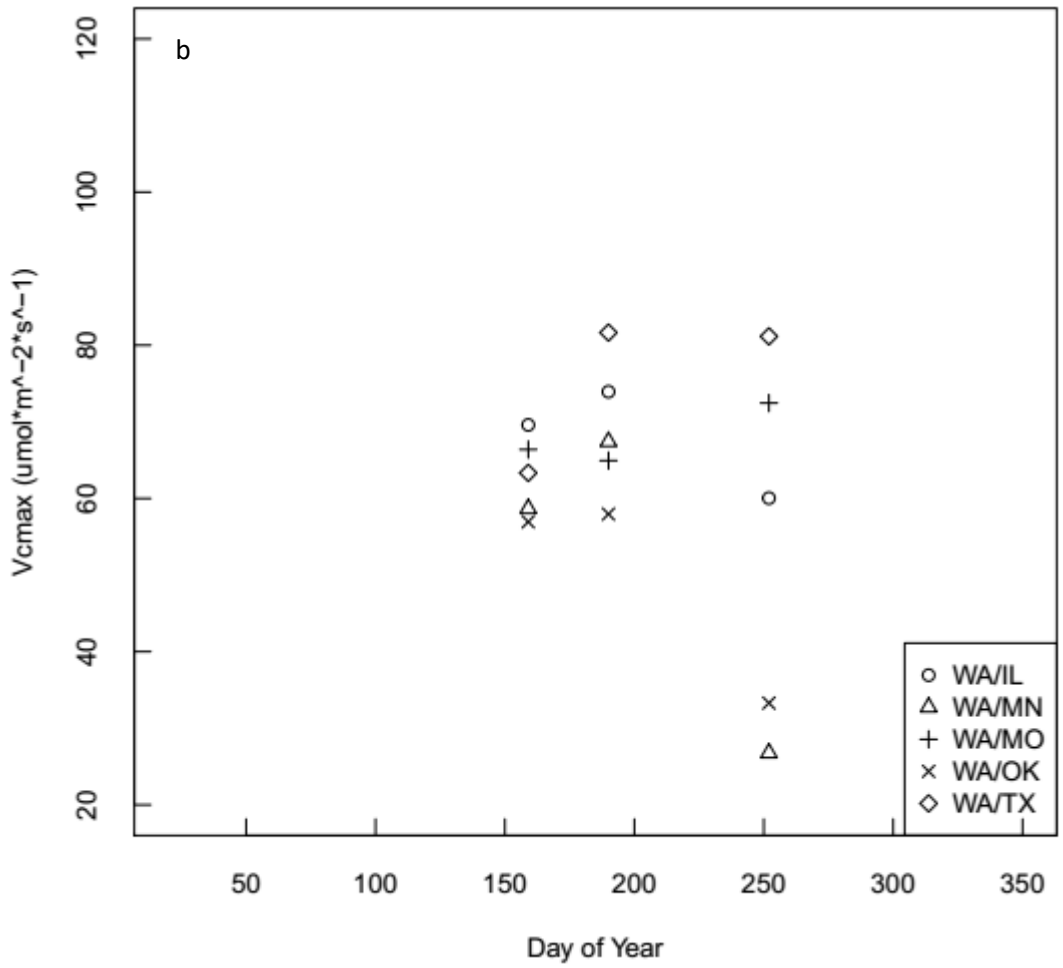
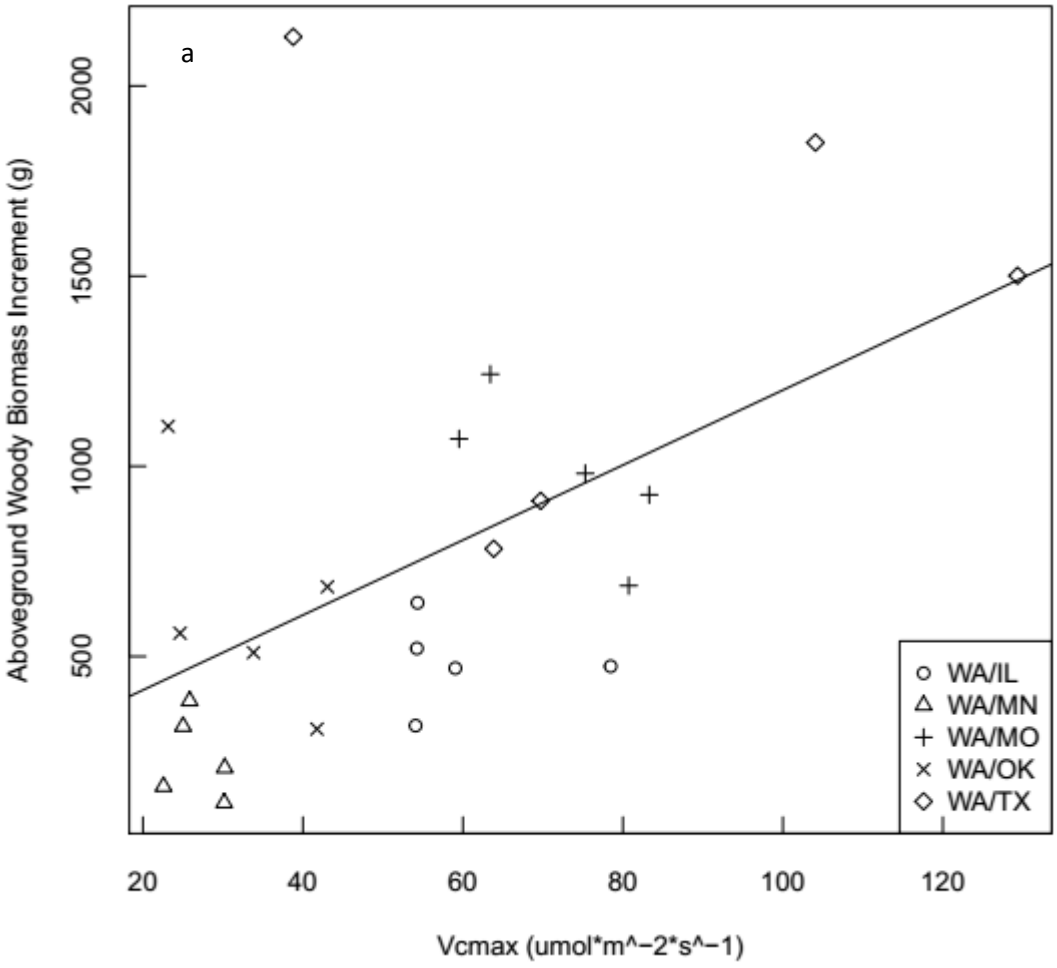


Figure 4. Photosynthetic capacity in five hybrid poplar clones grown in southern Arizona during the 2014 growing season. (a) Maximum rate of electron transport (J_{max}); (b) maximum rate of carboxylation (Vc_{max}).


a
Aboveground Woody Biomass Increment (g)
500
1000
1500
2000
20
40
60
80
100
120
Vcmax (umol*m^−2*s^−1)
WA/IL
WA/MN
WA/MO
WA/OK
WA/TX

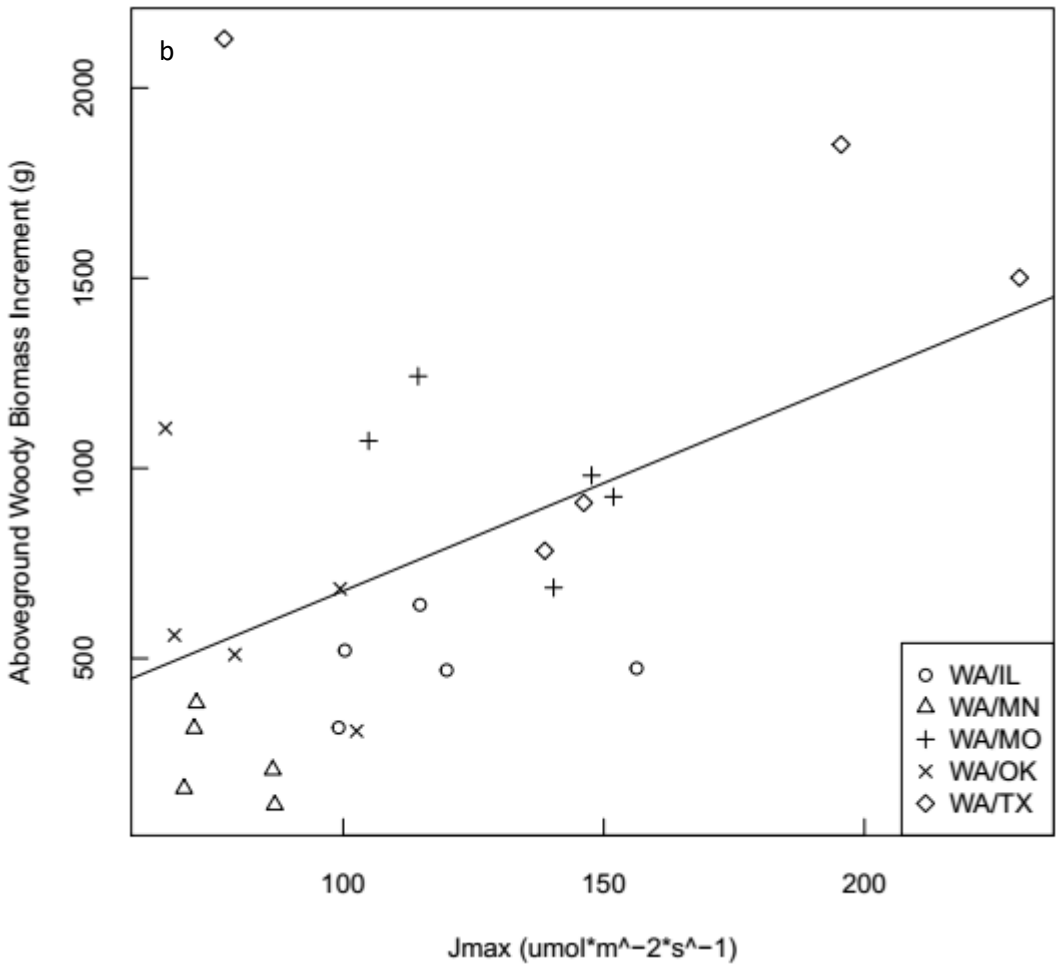


Figure 5. Aboveground woody biomass increment versus photosynthetic capacity in five hybrid poplar clones grown in southern Arizona during the 2014 growing season. (a) Maximum rate of carboxylation (Vc_{max}); (b) maximum rate of electron transport (J_{max}).

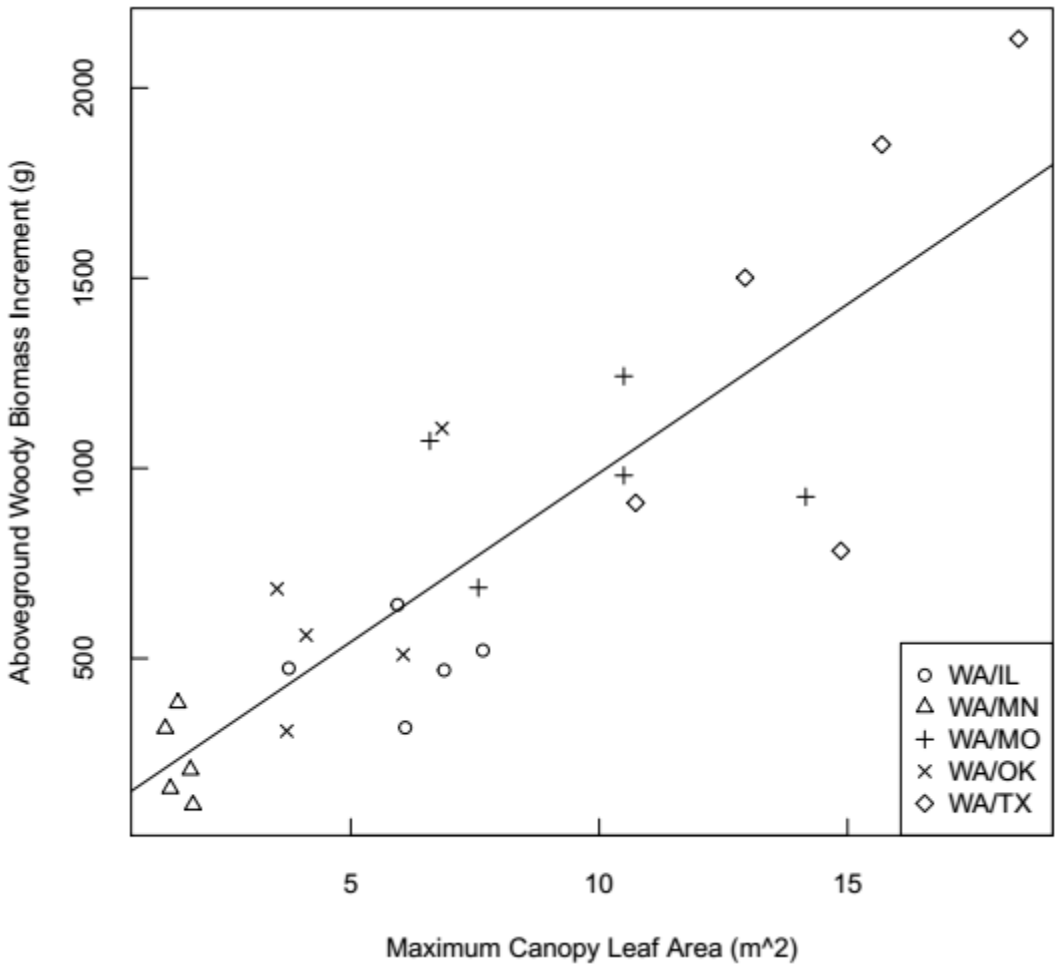


Figure 6. Aboveground woody biomass increment versus canopy leaf area in five hybrid poplar clones grown in southern Arizona during the 2014 growing season.

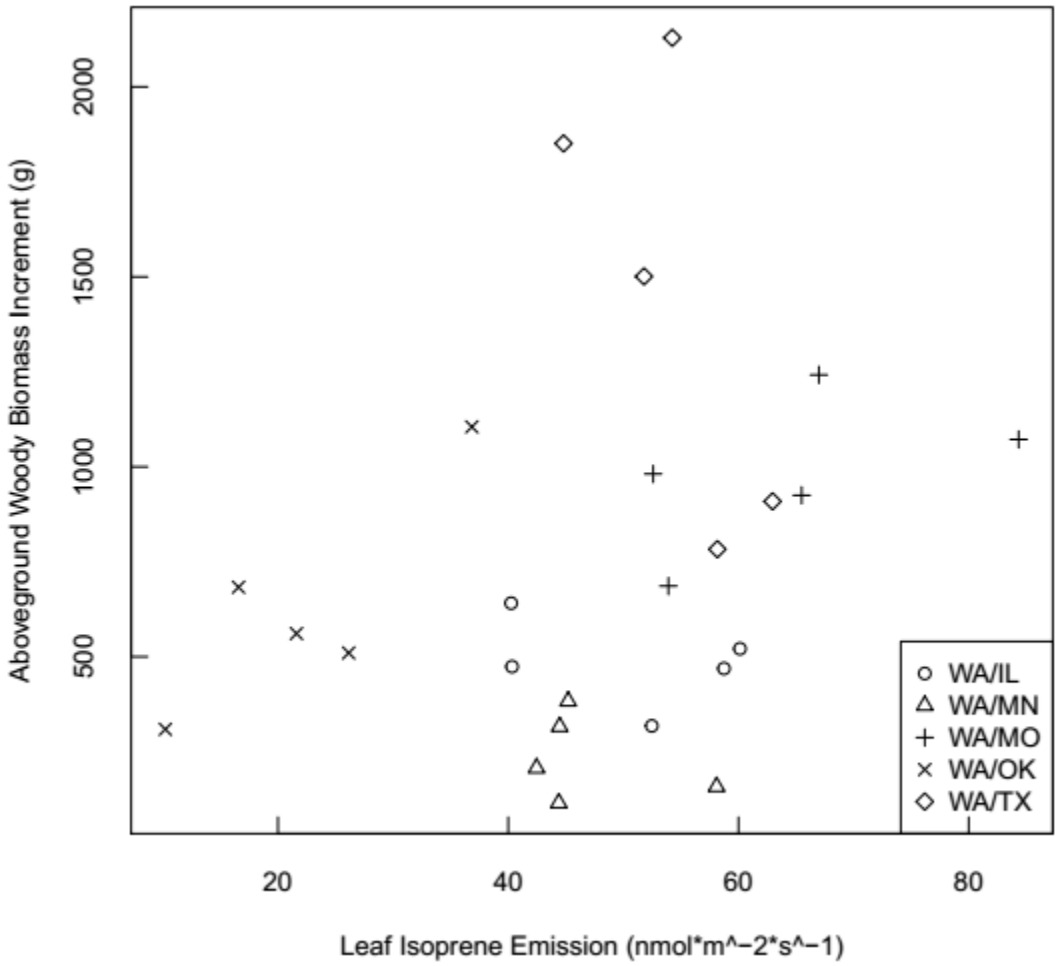


Figure 7. Aboveground woody biomass increment versus leaf isoprene emission in five hybrid poplar clones grown in southern Arizona during the 2014 growing season.

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