POPULATION-LEVEL VARIATION OF *FRAXINUS AMERICANA* L. IS INFLUENCED BY CLIMATE DIFFERENCES ACROSS THE NATIVE RANGE

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Abstract.—This paper reviews population variation in *Fraxinus americana* (white ash) to determine whether intraspecific variation in various physiological traits affects growth and survival in *F. americana* and to correlate any intraspecific variation in *F. americana* with temperature or precipitation differences throughout the species range. Beginning in the 1980s, results from common garden studies indicated that differences in growth and survival in *F. americana* are the result of ecotypic variation in the species. Recently, further insights into the mechanisms controlling these ecotypic differences in growth were made in a common garden at the edge of the species range. This project in northeastern Kansas found significant differences in morphology, phenology, and stomatal regulation among 44 *F. americana* populations. Even after 30 years of growth in the common garden, these population differences were well-correlated with climatic differences (temperature and precipitation) at the location of population origin. Temperature requirements for leaf emergence of *F. americana* populations in the common garden were positively correlated with the latitude of population origin. Differences in water use efficiency among other *F. americana* populations were observed and may be caused by morphological traits, such as variation in leaf mass per area and foliar nitrogen concentration. Thus, the original observations of differences in growth among *F. americana* ecotypes are likely caused by adaptive differentiation among populations.

INTRODUCTION

Interest in the ecology of *Fraxinus* (ash) species has increased due to the recent discovery of an exotic insect pest, the emerald ash borer (*Agrilus planiplennis*), in North America. The wood-boring beetle has caused the death of millions of ash trees (MacFarlane and Meyer 2005) and has seriously threatened the survival of native North American *Fraxinus* species. When tools to conserve and manage ash species are being developed, it is important to consider how ecologically important traits vary among natural populations. High levels of intraspecific variation in morphology, physiology, growth, and phenology are commonly observed in tree species with large ranges that cover different climatic, edaphic, and biotic regions (Donselman and Flint 1982, Geber and Dawson 1993, Abrams 1994, Aspelmeier and Leushner 2004).

Tree physiology often changes along climatic gradients and may be driven by adaptation to temperature differences and/or differences in water availability throughout the species range. In the case of the temperate deciduous tree *F. americana* L. (white ash), the natural species range includes the eastern half of the United States and extends into parts of southern Canada (Fig. 1). Even without accounting for the devastation caused by *A. planiplennis*, models predicting future suitable habitat for the species indicate that its range will decrease in the future as a result of a northward shift in optimum growing conditions (Prasad et al. 2007). An understanding of the natural variation in traits that affect growth, susceptibility to *A. planiplennis*, and survival of *Fraxinus* species is necessary for directing management strategies and conservation efforts.

Figure 1.—Natural range of F. americana in North America (shaded region, USDA Forest Service, www.na.fs.fed.us). Sources (● and o) of the 44 *F. americana* populations grown in the common garden (*) at Nelson Environmental Study Area in northeastern Kansas are also indicated. Ten populations originating from along an east-west precipitation gradient are identified by open circles. From Marchin et al. 2008.

F. americana is a ring-porous angiosperm native to the temperate deciduous forests of the eastern United States. This hardwood is an early successional species that is often one of the first trees to colonize abandoned fields and thus is important for forest regeneration across its range (Schlesinger 1990). The wood of *F. americana* is valued for its strength and is used for furniture and baseball bats (Nesom 2000).

Prior to this century, not much was known about the extent of intraspecific variation in the physiology and growth of *F. americana*. Recent work in a *F. americana* common garden in northeastern Kansas, however, revealed intraspecific variation for several important ecological traits (Marchin 2006, Marchin et al. 2008). Located in a marginal habitat at the western edge of the species range where the required degree of adaptation may exceed the limits of phenotypic plasticity in some genotypes, this study site likely allowed a full expression of range-wide genetic variation in response to abiotic stresses (Paschke et al. 2003, Stanton et al. 2000).

The main focus of this review is to (1) determine whether there are differences in morphology, phenology, gas exchange, and stomatal regulation among *F. americana* populations, (2) determine whether intraspecific variation in these traits affects growth and survival in the species, and (3) correlate intraspecific variation in *F. americana* with a corresponding climate variable to define the causal mechanism driving genetic divergence in the species.

METHODS: THE COMMON GARDEN APPROACH

For many years, it has been known that *F. americana* is genetically variable throughout its range, partly owing to the presence of polyploidy (Wright 1944). These differences in ploidy level vary across the species range, with diploids (46 chromosomes) occurring throughout the species range. Tetraploids (92 chromosomes), however, are restricted to regions south of latitude 35°N, and hexaploids (138 chromosomes) are found between latitudes 35° and 40°N (Black and Beckmann 1983, Schlesinger 1990). Triploid and pentaploid embryos have also been observed, although the prevalence of these individuals in natural populations is unknown (Black and Beckmann 1983).

To better understand how this genetic variation affected growth and to identify the best seed sources for various geographical locations, the U.S. Forest Service, North Central Forest Experiment Station initiated a range-wide provenance test of *F. americana* in 1976 (Clausen 1980, Clausen et al. 1981). Open-pollinated seeds were collected from native parent trees at 59 locations throughout the species' range and planted in a nursery in Illinois. It was observed that under the common environment of the nursery, tetraploids grew taller than other ploidy levels (Clausen et al. 1981). These 1-year-old seedlings were later transplanted to 22 plantations throughout the eastern United States and Canada.

This review primarily focuses on one of the *F. americana* common gardens, located in Kansas at the western edge of the species range (University of Kansas, Nelson Environmental Study Area, 39.0°N, 95.2°W, 299 m asl). At this common garden site, mean annual precipitation is 879 mm, with large interannual variation (± 200 mm SD). Mean annual temperature is 11.9°C, and mean temperature during the growing season (April–September) is 20.4°C (see Jefferson County, Table 1).

Table 1.—Climatic data from the common garden (located in Jefferson County, KS and the locations represented in the common garden. From Marchin et al. (2008 Populations in the latitudinal gradient are indicated by a single cross (†); populations in the east-west precipitation gradient are indicated by a double cross (‡).

Location	Latitude (°N)	Longitude (°W)	Elevation (m)	Annual Precipitation (mm)	Annual Temperature (°C)	Growing Season VPD (kPa)
Jefferson, KS	39.0	95.0	299	879	11.9	0.633
Ontonagon, MI †	46.6	89.5	408	820	4.3	0.400
Forest, WI (2) † †	45.7	89.0	511	777	5.6	0.428
Presque Isle, MI	45.3	83.6	198	749	6.1	0.509
Penobscot, ME (2)	44.8	69.0	85	1083	6.2	0.519
Benzie, MI	44.7	86.0	236	793	6.4	0.530
Onondaga, NY	42.7	76.1	381	940	8.3	0.579
Washtenaw, MI (2)	42.2	83.7	259	799	9.0	0.637
Wayne, OH ‡	40.7	82.0	265	969	9.7	0.592
Otoe, NE ‡	40.6	95.7	259	765	10.8	0.639
Adams, IL ‡	39.8	90.7	213	943	10.9	0.633
Preble, OH ‡	39.6	84.7	305	1035	11.7	0.699
Tucker, WV ‡	39.1	79.5	762	1261	9.3	0.463
Effingham, IL † ‡	39.1	88.4	183	1025	11.9	0.631
Effingham, IL † ‡	39.0	88.4	177	1025	11.9	0.631
Randolph, WV ‡	38.9	79.7	975	1261	9.3	0.463
Jackson, IN ‡	38.9	86.0	191	1142	12.3	0.670
Jackson, IL (2) ‡	37.7	89.4	158	1097	13.3	0.760
Gallatin, IL †	37.6	88.3	152	1125	13.3	0.680
Muhlenberg, KY	37.3	87.2	128	1220	13.9	0.547
Hopkins, KY (2)	37.3	87.6	139	1220	13.9	0.547
Overton, TN (3)	36.5	85.4	357	1408	13.6	0.627
Marion, AR (2)	36.4	92.8	274	1155	14.5	0.672
Boone, AR	36.4	93.0	274	1164	14.2	0.652
Bledsoe, TN (2)	35.5	85.2	396	1408	13.6	0.680
McMinn, TN	35.3	84.5	251	1263	13.9	0.690
Franklin, TN (2)	35.2	85.9	357	1408	13.6	0.680
Pickens, SC	35.0	83.0	229	1295	15.6	0.779
Union, GA	34.8	83.9	914	1378	15.3	0.738
Oktibbeha, MS (3) † † †	33.4	88.8	116	1383	17.2	0.639
East Baton Rouge, LA (2)	31.5	91.0	9	1559	19.3	0.686
George, MS †	30.8	88.8	76	1602	19.4	0.732

Trees in the common garden were 30 years old at the time of the study. The common garden is set up in a block design, with each of the 44 populations (Fig. 1) represented by 25 trees (5 blocks with 5 replicate trees from each population). In 2004, 40 of the 44 populations were still represented by at least 10 individuals, although one population (East Baton Rouge, LA) had no surviving trees in the common garden.

To determine possible mechanisms driving genetic variation in *F. americana*, two subsets of populations were selected *a priori*. One subset of 10 populations formed a north-south latitudinal gradient that ranged from 30.8° to 46.6°N and originated within a narrow longitudinal range (approximately 89°W). Similarly, the second subset of 10 populations formed an east–west precipitation gradient ranging from 79.5° to 95.7°W and originating within a narrow latitudinal range (approximately 39°N). These subsets of populations can indicate the climatic control over known trait variation by maximizing differences caused by one climate parameter (e.g., precipitation) and minimizing differences caused by other factors (e.g., temperature, photoperiod). All physiological measurements were performed on three to five individuals per population, and when possible, all measured trees were located in one block to minimize microsite differences among trees.

RESULTS

Population-level Responses in Growth and Survival

After only 3 years of seedling growth in the originally established 22 *F. americana* common gardens, height varied significantly among populations and plantations, revealing a strong genotype × environment interaction (Clausen 1980). The patterns of variation in height indicated the presence of northern and southern

ecotypes divided at approximately 39°N (Roberds et al. 1990). Populations of the southern ecotype had greater growth than the northern ecotype throughout most of the *F. americana* range, excluding the extreme northern latitudes (Clausen et al. 1981, Roberds et al. 1990). Therefore, foresters recommended collecting seed up to 300 km south of a *F. americana* plantation location.

As the *F. americana* trees aged, the height differences among populations became more accentuated at most plantation sites. The mean percentage of total variation attributed to provenance, taken across 10 common gardens, increased from 28.6 percent at age 3 to 38.5 percent at age 13 (Clausen 1984, Rink and Kung 1991). In contrast, the mean variance component attributed to populations-within-provenances decreased from 11.9 percent at age 3 to 7.5 percent at age 13 in the same study sites (Clausen 1984, Rink and Kung 1991), indicating that mean between-provenance variation is more than three times greater than within-provenance variation. Interestingly, the common garden in Kansas was an exception to this trend. Here, the between-provenance variance component for height of 13-year-old trees was 10 percent, while the within-provenance variance component was 31 percent (Rink and Kung 1991.

In the central zone between the northern and southern ecotype, at approximately 39°N, growth and survival are highest among populations that originated from locations closest to the common garden (Schuler 1994, Marchin et al. 2008). This result was confirmed by two common gardens located at opposite edges of the species range. At the common garden in north-central West Virginia, Schuler (1994) examined trees 15 years after establishment and found height and survival were highest in populations originating from the immediate vicinity of the common garden. Among 30-year-old trees in the Kansas common garden, similar results were found: Stem circumference and survival were highest in populations originating closest to the common garden (Fig. 2) (Marchin et al. 2008). In both studies, survival and growth in the common garden were lower in provenances originating either to the north or south of the common garden (Fig. 2).

Taken together, these studies indicate that adaptive differentiation has occurred in *F. americana* in response to range-wide climatic variation. Evidence suggests that the genetically controlled differences in growth and survival among *F. americana* populations are related to differences in temperature and/or precipitation patterns throughout the species' range. There are high degrees of variation in climatic variables throughout the *F. americana* range (Table 1), with mean annual temperature ranging from 4.3 to 19.4 °C and mean annual precipitation ranging from 749 to 1602 mm.

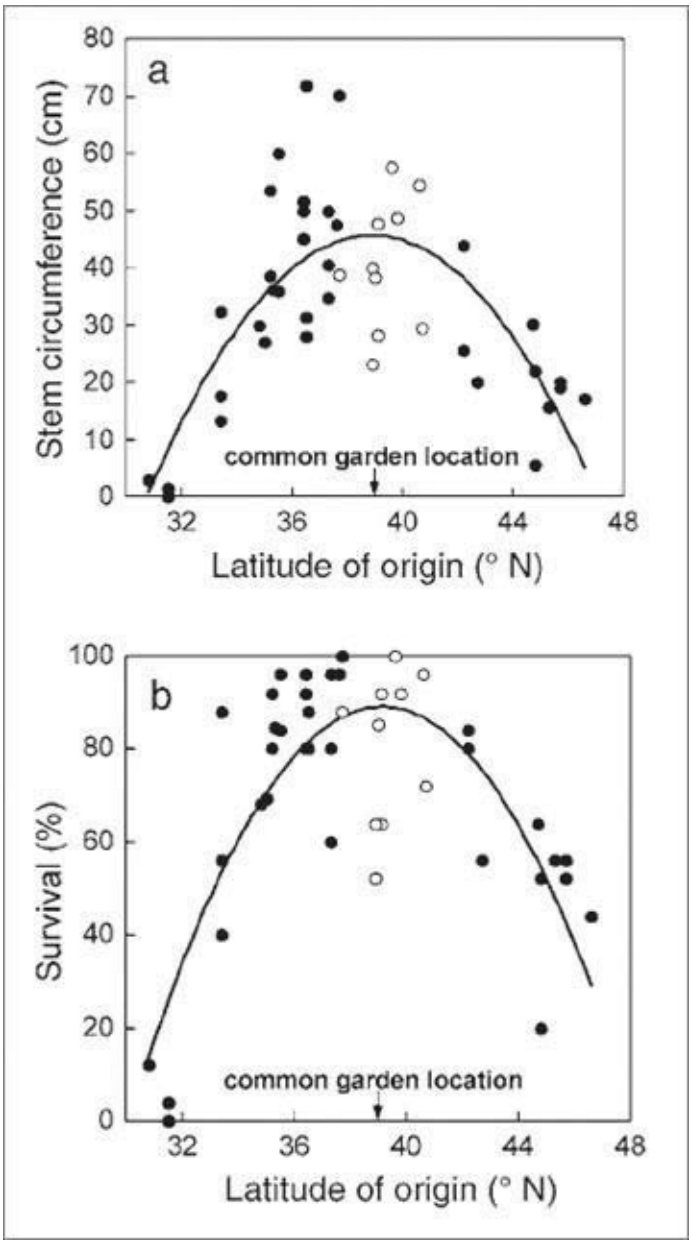

Figure 2.—(a) Stem circumference (n = 1-25) and (b) survival (n = 25) regressed against latitude of origin for 44 *Fraxinus americana* populations grown in a common garden located in Jefferson County, KS. Populations representing an east-west precipitation gradient along latitude 39ºN are identified by open symbols. From Marchin et al. 2008.

Temperature-influenced Intraspecific Variation

As indicated by the differences in survival among ecotypes of *F. americana*, there is variation in cold tolerance among *F. americana* populations. Alexander et al. (1984) found that stem tissue of the northernmost populations had lower killing temperatures (–42.6 °C, –41.4 °C) than did the southernmost populations (–33.7 °C, –30.8 °C) in two different years. This result suggests that southern tree populations require lower temperatures or more time to reach maximum potential cold hardening than do northern tree populations. Additionally, it has been shown that southern populations have lower temperature requirements for bud break in the spring in Kansas (Marchin 2006), indicating that these populations may be more susceptible to damaging late-spring frosts. The lower growth and survival of southern *F. americana* populations in the Kansas common garden is likely at least partially controlled by temperature-related traits.

Because killing temperatures of northern *F. americana* populations are low (Alexander et al. 1984), the mechanism controlling differential growth and survival among northern populations is likely different from that of southern populations. The lower stem circumference of northern populations may still be controlled by temperature-related traits, however, because there are phenological differences among populations. The range for mean date of leaf emergence among populations in the Kansas common garden was 26 days, which is comparable to reported time intervals for other deciduous temperate tree species (Scotti-Saintagne et al. 2004, Borchert et al. 2005). A significant linear relationship was found between temperature sum for spring leaf emergence and latitude of origination among *F. americana* populations, where northern populations had higher temperature requirements for bud break than southern populations (Marchin 2006). In forest ecosystems, early greening of canopies is critical for net ecosystem primary production. A difference of a few days in canopy development accounted for more than 20 percent of the interannual change in net photosynthetic production in a northeastern North American forest (Myneni et al. 1997).

Another possible cause of the differential growth and survival observed among *F. americana* populations is differences in photosynthetic capacity or rates of light-saturated photosynthesis (A_{sat}). Leaf gas exchange parameters, such as net photosynthesis (A) and stomatal conductance (g_s), have been found to vary significantly among populations of the closely related species *F. pennsylvanica* (green ash; Abrams et al. 1990). This variation among genotypes in A_{sat} is maintained by simultaneous changes in biochemical and stomatal characteristics during photosynthesis (Geber and Dawson 1997).

Because the amount and intensity of solar radiation in different habitats is a source of population variation in A_{sat} (Fitter and Hay 2002), it is possible that *F. americana* populations along a north-south latitudinal gradient would have differences in A_{sat}. One study comparing 10 *F. americana* populations that originated along such a latitudinal gradient found no significant variation in A_{sat} or g_s (p=0.35, p=0.25, respectively) among *F. americana* populations (Table 2; Marchin 2006). The sample size analyzed in this study was low (n=3-5 individuals), however, and perhaps better sampling would reveal significant differences among populations. Indeed, there does appear to be a trend between mean A_{sat} and latitude, where northern *F. americana* populations have the lowest mean A_{sat} (Table 2). Populations with lower inherent rates of photosynthesis would also have lower potential growth rates (Larcher 2003).

Precipitation-influenced Intraspecific Variation

Changes in water availability across a species range have been found to drive intraspecific differences in drought tolerance in a number of tree species (Schmidtling and Froelich 1993, Roupsard et al. 1998, Adams and Kolb 2004). Water is one of the most important resources for tree growth; up to 90 percent of the variation in the annual width of tree rings can be explained by variations in rainfall (Kozlowski et al. 1991). It is not surprising then to observe population variation in *F. americana* that is related to precipitation differences across the species' range.

Table 2.—Leaf gas exchange (n = 3-5) in *Fraxinus americana* populations originating from locations along a latitudinal gradient and grown in a common garden in Jefferson County, KS

Location	Latitude	A_{sat} (± SD)	g_s (± SD)	Slope of A_{sat}-N Relationship
Ontonagon, MI	46.6	7.94 ± 4.26	0.127 ± 0.136	9.6
Forest, WI	45.7	6.46 ± 1.67	0.062 ± 0.018	2.6
Forest, WI	45.7	8.20 ± 2.09	0.080 ± 0.027	-4.6
Effingham, IL	39.1	9.35 ± 3.30	0.111 ± 0.078	12.5
Effingham, IL	39.0	9.98 ± 2.11	0.118 ± 0.037	3.1
Gallatin, IL	37.6	11. 27 ± 2.68	0.150 ± 0.076	3.2
Oktibbeha, MS	33.4	11. 25 ± 1.83	0.159 ± 0.068	1.3
Oktibbeha, MS	33.4	9.18 ± 3.71	0.118 ± 0.082	-2.7
Oktibbeha, MS	33.4	10.04 ± 2.52	0.104 ± 0.033	2.3
George, MS	30.8	9.85 ± 4.26	0.164 ± 0.101	10.2

Genetic differentiation for water-related traits in *F. americana* can be analyzed in a common garden by choosing a subset of populations where precipitation is known to differ among the locations of origin, but temperature variation is minimized. In the east–west precipitation gradient analyzed here, mean annual precipitation at the source of these populations ranges from 765 mm year^{-1} in the west (Otoe, NE) to 1261 mm year^{-1} in the east (Tucker, WV; Table 1). Among these 10 populations, survival in the common garden was only about 50 percent for the easternmost population (Randolph, WV) but rose to 96 percent for the westernmost population, which originated closest to the common garden (Otoe, NE; Fig. 2). Similarly, stem circumference in the easternmost populations (Tucker, WV; Randolph, WV; Wayne, OH) was only about half that in the westernmost populations (Otoe, NE; Adams, IL).

The stable carbon isotope ratio of leaves (foliar $\delta^{13}C$) provides a time-integrated measure of the ratio of leaf inter-cellular CO_2 concentration to atmospheric CO_2 concentration (c_i/c_a). The c_i/c_a ratio depends on stomatal conductance and photosynthetic demand for CO_2 and thus indicates water-use efficiency (Farquhar et al. 1989, Ehleringer 1991). In the Kansas common garden, foliar $\delta^{13}C$ values were significantly negatively correlated with annual precipitation at the location of origin (Fig. 3; Marchin et al. 2008). Eastern populations from wetter regions exhibited lower $\delta^{13}C$ values and were therefore less conservative in their water use when compared with western populations that originated from drier climates. A more conservative strategy for water use may have contributed to higher survival, particularly when considering that the common garden experienced periods of extreme drought in the past 30 years.

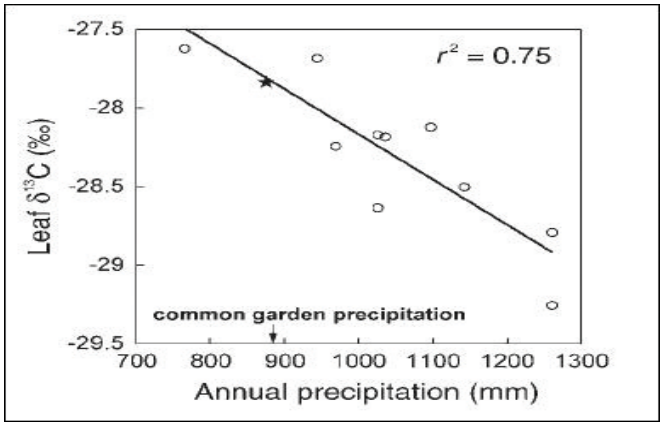

Figure 3.—Foliar carbon isotope ratios of *Fraxinus americana* populations (n = 3-6) from an east-west precipitation gradient when grown in a common garden. The population originating from Jefferson County, KS, near the common garden is indicated by the filled star. (Marchin et al. 2008)

The responses of these *F. americana* populations suggest wide-range adaption of *F. americana* to the local moisture regime. Differentiation in leaf mass per area (LMA) and foliar nitrogen (N) concentration (on an area basis, N_a) was also evident among *F. americana* populations from across the east–west precipitation gradient (Marchin et al. 2008). Increases in LMA and N_a indicate increases in the quantity of photosynthetic apparatus per unit leaf area (Fitter and Hay 2002) and, thus, increases in water-use efficiency (Li et al. 2000, 2004). The superior growth and survival of provenances originating from the western edge of the species range where the climate is driest is thus likely attributable, at least in part, to their high LMA and N_a.

CONCLUSIONS

Genetically based differences in morphology, phenology, and stomatal regulation among populations of *F. americana* are correlated with temperature and/or precipitation differences at the site of population origin. The physiological responses of *F. americana* trees, which are still apparent after 30 years in a different climate, affect the ability of individual populations to grow and survive in novel climates. Populations with the highest growth and survival at the edge of the species range originated from climates of similar annual temperature and precipitation to that of a Kansas common garden. A thorough understanding of population variation can be used to determine the potential for adaptive evolution in *F. americana*, as well as the genotypes that may be most successful in a given region under predicted future climatic and biotic conditions.

The spread of *A. planipennis* to new sites has seriously threatened the continued existence of *Fraxinus* species in North America. The current situation for *Fraxinus* has been compared to the past devastation of *Castanea dentata* (American chestnut) trees by the fungal chestnut blight. Knowledge of the physiological variation among populations can direct seed-collection efforts aimed at conserving diversity in *F. americana*. While we face a difficult challenge in preserving *Fraxinus* species in North American temperate forests, the cultural and ecological importance of these species provides a strong incentive for solving the problem.

LITERATURE CITED

Abrams, M.D.; Kubiske, M.E.; Steiner, K.C. 1990. **Drought adaptations and responses in 5 genotypes of *Fraxinus pennsylvanica* Marsh - Photosynthesis, water relations, and leaf morphology**. Tree Physiology. 6: 305-315.

Abrams, M.D. 1994. **Genotypic and phenotypic variation as stress adaptations in temperate tree species - a review of several case-studies**. Tree Physiology. 14: 833-842.

Adams, H.D.; Kolb, T.E. 2004. **Drought responses of conifers in ecotone forests of northern Arizona: tree ring growth and leaf sigma C-13.** Oecologia. 140: 217-225.

Alexander, N.L.; Flint, H.L.; Hammer, P.A. 1984. **Variation in cold-hardiness of *Fraxinus americana* stem tissue according to geographic origin.** Ecology. 65: 1087-1092.

Aspelmeier, S.; Leuschner, C. 2004. **Genotypic variation in drought response of silver birch (*Betula pendula*): leaf water status and carbon gain**. Tree Physiology. 24: 517-528.

Black, C.L.; Beckmann, R.L. 1983. **The variability of nuclear DNA and its implications for polyploidy in white ash (*Fraxinus americana* L, Oleaceae).** American Journal of Botany. 70: 1420-1423.

Borchert, R.; Robertson, K.; Schwartz, M.D.; Williams-Linera, G. 2005. **Phenology of temperate trees in tropical climates.** International Journal of Biometeorology. 50: 57-65.

Clausen, K.E. 1980. **Survival and early growth of diploid white ash planted in the central hardwood region**. In: Garrett, H; Cox, G., eds. Proceedings, Third Central Hardwood Forest Conference, Columbia, MO: 374-383.

Clausen, K.E. 1984. **Nonlinear regressions and contour plots: Techniques for selection and transfer of white ash provenances**. Forest Science. 30: 441-453.

Clausen, K.E.; Kung, F.H.; Bey, C.F.; Daniels, R.A. 1981. **Variation in white ash.** Silvae Genetica. 30: 93-97.

Donselman, H.M.; Flint, H.L. 1982. **Genecology of eastern redbud (*Cercis canadensis*)**. Ecology. 63: 962-971.

Ehleringer, J.R. 1991. **$^{13}C/^{12}C$ fractionation and its utility in terrestrial plant studies.** In: Coleman, D.; Fry, P., eds. **Carbon isotope techniques**. New York, NY: Chapman and Hall: 187-200.

Farquhar, G.D.; Ehleringer,J.R.; Hubick, K.T. 1989. **Carbon isotope discrimination and photosynthesis.** Annual Review of Plant Physiology and Plant Molecular Biology. 40: 503-537.

Fitter, A.; Hay, R. 2002. **Environmental physiology of plants**. San Diego, CA: Academic Press.

Geber, M.A.; Dawson, T.E. 1993. **Evolutionary responses of plants to global change.** In Kareiva, P.; Kindolver, J.; Huey, R., eds. **Biotic interactions and global change.** Sunderland, MA**:** Sinauer Associates, Inc.: 179-197.

Geber, M.A.; Dawson, T.E. 1997. **Genetic variation in stomatal and biochemical limitations to photosynthesis in the annual plant, *Polygonum arenastrum*.** Oecologia. 109: 535-546.

Kozlowski, T.T.; Pallardy, S.G. 1997. **Physiology of woody plants.** 2nd ed. San Diego, CA. Academic Press.

Larcher, W. 2003. **Physiological plant ecology.** 4th ed. Berlin, Germany: Springer. 540 p.

Li, C.Y.; Berninger, F.; Koskela, J.; Sonninen, E. 2000. **Drought responses of *Eucalyptus microtheca* provenances depend on seasonality of rainfall in their place of origin.** Australian Journal of Plant Physiology. 27: 231-238.

Li, C.Y.; Liu, S.R.; Berninger, F. 2004. ***Picea* seedlings show apparent acclimation to drought with increasing altitude in the eastern Himalaya.** Trees-Structure and Function. 18: 277-283.

MacFarlane, D.W.; Meyer, S.P. 2005. **Characteristics and distribution of potential ash tree hosts for emerald ash borer.** Forest Ecology and Management. 213: 15-24.

Marchin, R. 2006. **Population variation in *Fraxinus americana* L. (white ash) in a common garden at the edge of the species range.** Lawrence, KS: University of Kansas. M.A. Thesis.

Marchin, R.M.; Sage, E.L.; Ward, J.K. 2008. **Population-level variation of *Fraxinus americana* (white ash) is influenced by precipitation differences across the native range.** Tree Physiology. 28: 151-159.

Myneni, R.B.; Keeling, C.D.; Tucker, C.J.; Asrar, G.; Nemani, R.R. 1997. **Increased plant growth in the northern high latitudes from 1981 to 1991.** Nature. 386: 698-702.

Nesom, G. 2000. **White ash: *Fraxinus americana* L.** In: Plants Database. Washington, DC: U.S. Department of Agriculture, Natural Resources Conservation Service.

Paschke, M.; Bernasconi, G.; Schmid, B. 2003. **Population size and identity influence the reaction norm of the rare, endemic plant *Cochlearia bavarica* across a gradient of environmental stress.** Evolution. 57: 496-508.

Prasad, A.; Iverson, L.; Matthews, S.; Peters, M. 2009. **A climate change atlas for 134 forest tree species of the eastern United States** [Database]. http://www.nrs.fs.fed.us/atlas/tree.

Rink, G.; Kung, F.H.1991. **Height and diameter variation in twelve white ash provenance/progeny tests in eastern United States.** In: McCormick, L; Gottschalk, K., eds. Proceedings, 8th Central Hardwood Forest Conference. Gen. Tech. Rep. NE 148. Radnor, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station: 179-187.

Roberds, J.H.; Hyun, J.O.; Namkoong, G.; Rink, G. 1990. **Height response functions for white ash provenances grown at different latitudes.** Silvae Genetica. 39: 121-129.

Roupsard, O.; Joly, H.I.; Dreyer, E. 1998. **Variability of initial growth, water-use efficiency and carbon isotope discrimination in seedlings of *Faidherbia albida* (Del.) A. Chev., a multipurpose tree of semi-arid Africa. Provenance and drought effects.** Annales Des Sciences Forestieres. 55: 329-348.

Schlesinger, R.C. 1990. ***Fraxinus americana* L. White Ash.** In: Burns, R.M.; Honkala, B.H., tech. coords. **Silvics of North America. Vol. 2, Hardwoods.** Agric. Handbk. 654. Washington, DC: U.S.Department of Agriculture: 333-338.

Schmidtling, R.C.; Froelich, R.C. 1993. **Thirty-seven year performance of loblolly pine seed sources in eastern Maryland.** Forest Science. 39: 706-721.

Schuler, T.M. 1994. **Survival and growth of white ash families and provenances 15 years after establishment in West Virginia.** Res. Pap. NE-684. Radnor, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 7 p.

Scotti-Saintagne, C.; Bodenes, C.; Barreneche, T.; Bertocchi,E.; Plomion, C.; Kremer, A. 2004. **Detection of quantitative trait loci controlling bud burst and height growth in *Quercus robur* L.** Theoretical and Applied Genetics. 109: 1648-1659.

Stanton, M.L.; Roy, B.A.; Thiede, D.A. 2000. **Evolution in stressful environments. I. Phenotypic variability, phenotypic selection, and response to selection in five distinct environmental stresses.** Evolution. 54: 93-111.

Wright, J. 1944. **Genotypic variation in white ash.** Journal of Forestry. 42: 489-495.