



Growth and Physiology Vary Little Among North American, an Asian, and a North American x Asian Hybrid Ash in a Common Garden in Ohio, U.S.A.

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Abstract. The emerald ash borer (EAB) (*Agrilus planipennis* Fairmaire) invasion of North America has increased interest in ash (*Fraxinus*, Oleaceae) phylogeny, ecology, and physiology. In a common garden in central Ohio, we compared the performance of three North American ash cultivars that are highly susceptible to EAB (*F. pennsylvanica* ‘Patmore,’ *F. americana* ‘Autumn Purple,’ and *F. nigra* ‘Fall Gold’), one North American species that is less susceptible to EAB (*F. quadrangulata*), and two taxa that are resistant to EAB (*F. mandshurica* and *F. mandshurica* × *F. nigra* ‘Northern Treasure’). During the 2015 growing season, we measured diameter growth, foliar N concentration, specific leaf area, and on four dates (two with adequate and two with low precipitation) we measured CO₂ assimilation rate (A), stomatal conductance (g_s), intercellular CO₂ concentration (C_i), photosynthetic nitrogen use efficiency (PNUE), variable fluorescence (Fv'/Fm': efficiency of energy harvested by open photosystem II reaction centers), and the fraction of photons absorbed by photosystem II that were used for photosynthesis (φPSII). *F. pennsylvanica* grew fastest and on most sampling dates was superior in physiological performance (A, g_s, and φPSII). Generally, however, there was little interspecific variation in growth and physiology among the different ash taxa tested, as all performed well. This suggests that the EAB-resistant *F. mandshurica* and *F. mandshurica* × *F. nigra* hybrid, as well as the moderately resistant blue ash, are as physiologically well-suited to growing conditions in the Midwestern United States as green and white ash cultivars that had been widely planted prior to the EAB invasion.

Keywords. Emerald Ash Borer; North American x Asian Ash Hybrid; Plant Performance; Tree Ecophysiology.

Ash (*Fraxinus*, Oleaceae) is one of the most widely distributed tree genera in North America, with white (*F. americana*), green (*F. pennsylvanica*), black (*F. nigra*), and blue ash (*F. quadrangulata*) being the most common species in eastern North American forests (MacFarlane and Meyer 2005). Furthermore, prior to the emerald ash borer (EAB) (*Agrilus planipennis* Fairmaire, Coleoptera: Buprestidae) invasion, green and white ash cultivars were broadly planted in North American urban forests because of their wide environmental tolerance (Raupp et al. 2006; Aiello 2012). EAB, a wood-boring beetle native to eastern Asia, was discovered killing ash trees in Michigan, U.S.A. and Ontario, Canada in 2002 (Cappaert et al. 2005). EAB has spread rapidly in North America (Herms and McCullough 2014) where it is causing mortality of healthy as well as stressed trees (Cappaert et al.

2005; Klooster et al. 2014). All North American ash species that EAB has encountered thus far are susceptible to the beetle to varying degrees (Villari et al. 2016).

There is a clear need to determine whether ash species and cultivars that are resistant to EAB are also physiologically suited to growing conditions where susceptible species and cultivars grew or were planted. In its native range, EAB is a secondary pest of its coevolved hosts, preferentially colonizing stressed trees (Wei et al. 2007). Manchurian ash (*F. mandshurica*), which is a primary host in Asia, has been shown to be highly resistant to EAB in common garden studies (Rebek et al. 2008; Herms 2015; Tanis and McCullough 2015), as has the hybrid ‘Northern Treasure’ (Herms 2015), which is a Manchurian ash × black ash (*F. nigra*) cross (Davidson 1999). Breeding

programs aimed at producing EAB-resistant cultivars will be essential to preserve ash trees in North America. These programs have focused on Asian species as a source of resistant germplasm to hybridize and back cross with North American species (Koch et al. 2012). The degree to which Asian ash species and North American x Asian hybrids are physiologically suited to growing conditions in North America relative to common North American ash species has not been empirically tested.

Manchurian ash grows in open woodlands and valleys and is considered an adaptable and stress-tolerant species that is widespread in northeastern China, Japan, Korea, and eastern Russia (Aiello 2012). Green ash is the most widely-distributed ash species in North America; it is fast-growing and capable of surviving under a wide range of moisture conditions, although it is generally considered a wetland and riparian species (MacFarlane and Meyer 2005). White ash is a common component in many forest types; it occupies bottomlands, open up-slope woodlands, and mixed hardwood forests (MacFarlane and Meyer 2005). White ash grows well in rich, well-drained, moist soils (Woodcock et al. 1993; MacFarlane and Meyer 2005). Black ash is a hydric species found in swamps and along streams that tolerates flooding, poorly drained areas, and grows well in shallow, organic peat, fine sands, and loam soils (Wright and Rauscher 1990; Iverson et al. 2016). Blue ash is tolerant of high soil pH and drought and generally grows in upland forests on calcareous soils, but is also found in moist and riparian forests (Braun 1961). Blue ash appears to be more resistant to EAB than other North American ash species, as it has experienced lower mortality in forest stands (Tanis and McCullough 2012) and common garden studies (Herms 2015; Tanis and McCullough 2015).

Comparisons of physiological traits among ash species and cultivars resistant and susceptible to EAB will inform planting decisions in urban forests. Hence, our objective was to characterize the physiological performance of North American ash cultivars highly susceptible to EAB including 'Autumn Purple' white ash, 'Patmore' green ash, and 'Fall Gold' black ash, with the more resistant blue ash, Manchurian ash, and Manchurian x black ash hybrid 'Northern Treasure' in a common garden plantation in northeast Ohio, U.S.A. White and green ash are both native to northeast Ohio and grow in the forest immediately adjacent to

the common garden. White and green ash served as reference species to compare physiological performance of the other ash species sampled. Over the growing season under differing precipitation levels, we measured growth and key leaf physiological traits, including leaf nitrogen (N) and specific leaf area (Reich et al. 1998), net photosynthetic rate and stomatal conductance (Lambers et al. 1998; Larcher 2003), photosynthetic nitrogen use efficiency (PNUE) (Poorter and De Jong 1999), and chlorophyll fluorescence as an indicator of the efficiency of photosynthesis (Krause and Weis 1991; Mohammed et al. 1995; Sanchez and Quiles 2006).

MATERIALS AND METHODS

Study Site

In 2015, we measured growth and physiological traits of six ash taxa growing in a common garden in northeast Ohio located at the Ohio Agricultural Research and Development Center campus in Wooster (UTM Zone 17T; 422253 E, 4514605 N). These included the North American blue ash (seedling origin), white ash (*F. americana* 'Autumn Purple'), green ash (*F. pennsylvanica* 'Patmore'), black ash (*F. nigra* 'Fall Gold'), the Asian species Manchurian ash (seedling origin), and the Manchurian x black ash hybrid 'Northern Treasure' (Table 1). The garden was established in 2011 on a field previously planted to forage crops. Ash saplings were planted in a randomized complete block design. We sampled eight replicates of each taxa for a total of 48 trees in the study (Table 1). EAB was present in the common garden at low levels, as indicated by captures of beetles in intercept traps, but none of the trees we sampled exhibited signs or symptoms of infestation (crown dieback, cracked bark, visible larval galleries, or adult emergence holes).

Growth and Physiology Measurements

To quantify growth during the 2015 growing season, we measured stem diameter at breast height (dbh at 1.4 m [4.5 feet] from the ground) before and then again after the 2015 growing season. In July of 2015, we collected 10 to 12 leaflets from sun-exposed leaves on each of the 48 ash trees and stored them in a cooler during collection and transport to the laboratory, where we measured area (LA, cm²) of individual leaves with a leaf area meter (LI-3100, LI-COR®, Lincoln, Nebraska). We then dried the leaves at 70°C

Table 1. Ash (*Fraxinus*) species, cultivar, and diameter at breast height (dbh \pm standard error) of trees at the start of the 2015 growing season in Wooster, Ohio, U.S.A.

Ash species	Cultivar	Sample size Mean	dbh (cm)
Green, <i>F. pennsylvanica</i>	Patmore	8	3.91 \pm 0.71
White, <i>F. americana</i>	Autumn Purple	8	1.38 \pm 0.07
Black, <i>F. nigra</i>	Fall Gold	8	4.02 \pm 0.31
Blue, <i>F. quadrangulata</i>	seedling origin	8	1.98 \pm 0.16
Manchurian \times black, <i>F. mandshurica</i> \times <i>F. nigra</i>	Northern Treasure	8	1.56 \pm 0.16
Manchurian, <i>F. mandshurica</i>	seedling origin	8	1.90 \pm 0.10

(158°F) for seventy two hours, recorded dry mass (g) with a semi-micro analytical balance (Mettler Toledo AT 261, Artisan Scientific Corp., Champaign, Illinois), ground them with a Wiley mill to pass 40-mesh, and stored them in airtight containers until analysis by the Service Testing and Research (STAR) Laboratory at the Ohio State University for N concentration. We calculated specific leaf area (SLA) as LA/dry mass (cm²/g), and foliar nitrogen on a dry mass (mg/g) and leaf area (mg/cm²) basis.

We measured leaf gas exchange traits from one leaf on each of the 48 trees on four dates (Figure 1)

between 10 am and 12 pm, including net CO₂ assimilation rate (A, $\mu\text{mol mol}^{-2} \text{s}^{-1}$), stomatal conductance (g_s, $\text{mmol m}^{-2} \text{s}^{-1}$), intercellular CO₂ concentration (C_i, $\mu\text{mol CO}_2/\text{mol air}$), variable fluorescence (Fv'/Fm', efficiency of energy harvested by open photosystem II reaction centers), and the fraction of photons absorbed by photosystem II that are used for photosynthesis (φPSII). Measurements were made on an east-facing, fully expanded terminal leaflet with a portable photosynthesis system (LI-6400, LI-COR®, Lincoln, Nebraska). On each of the four sampling dates, photosynthetic nitrogen use efficiency (PNUE) was calculated as A/N per unit LA ($\mu\text{mol mol}^{-2} \text{s}^{-1}$).

Temperature and precipitation were recorded throughout the growing season by a weather station located immediately adjacent to the common garden. Weather data were recorded by the National Oceanic and Atmospheric Administration (NOAA) and made available to the public (www.ncdc.gov).

Data Analyses

We conducted all data analyses in R, version 3.1.1 (R development Core Team 2015). For all linear or generalized linear models (package = stats), appropriate error distributions were chosen based on the shape of the frequency distribution of the response variable.

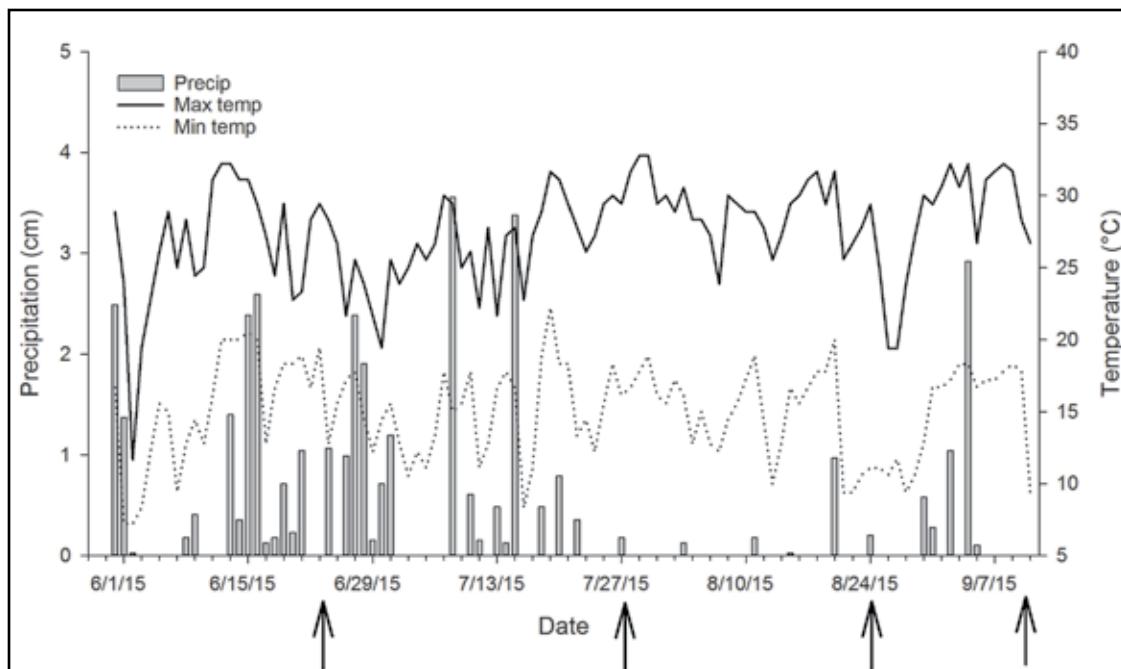


Figure 1. Precipitation (gray bars) and minimum (dotted line) and maximum (solid line) temperatures during the 2015 growing season in Wooster, Ohio. Arrows indicate dates on which gas exchange physiological measurements of ash trees were taken.

Not all ash taxa were present in all blocks of the common garden, so we could not use block as a factor in analyses. To examine whether differences in diameter growth with initial diameter (in 2014) as a covariate (normal distribution), SLA (normal distribution), and N per unit LA (gamma distribution) existed among taxa, we used Tukey's HSD (package = multcomp) to separate means. We used Pearson's pairwise

correlations to explore relationships between measures of growth and physiology on each sampling date and for each ash taxa. We used a repeated measures two-way ANOVA (normal distribution, package = nlme) followed by contrasts of interest to test for the effects of taxa and date and their interaction on A, g_s , PNUE, and ϕ_{PSII} . For all tests of significance, $\alpha = 0.05$.

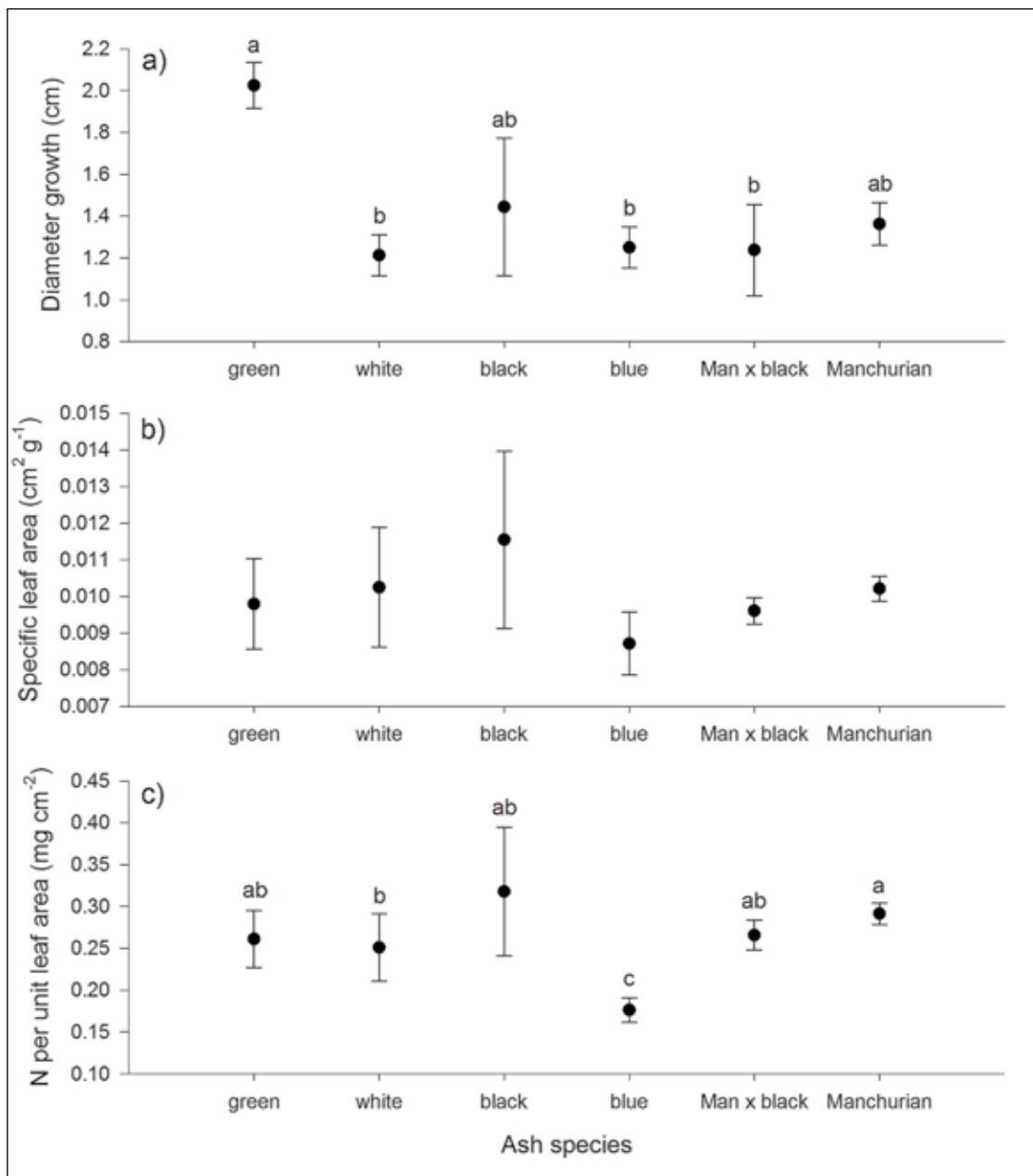


Figure 2. (a) Diameter (at breast height), (b) Specific leaf area (SLA), and (c) N per unit leaf area (LA) by ash taxa. Dots represent means of eight trees (seven for Man x black), and error bars are one standard error from the mean. Different letters indicate significant differences according to Tukey's HSD. Man x black = Manchurian x black ash.

RESULTS

Total annual precipitation (rainfall) in 2015 was 93 cm (36.5 inches). Mean minimum temperature was 4°C (39°F) and mean maximum temperature was 17°C (62.5°F). The 1981 to 2010 climate means were similar: total precipitation (rainfall) = 102 cm (40 inches), mean minimum temperature = 4°C (39°F), and mean maximum temperature = 16°C (60.5°F). Precipitation was adequate for the first two sampling dates and low for the final two sampling dates (Figure 1).

In 2015, there were significant differences in diameter growth among some ash taxa ($F = 2.83$; $df = 5.41$; $P = 0.030$). Diameter growth was greater for green ash than for blue, white, or Manchurian × black ash (Figure 2a). Diameter of trees prior to the start of the 2015 growing season did not vary significantly by taxon ($F = 0.07$; $df = 1.41$; $P = 0.790$). There were no differences in SLA among ash taxa (Figure 2b; $\chi^2 = 0.34$; $df = 5.41$; $P = 0.764$). Nitrogen per unit LA was lower in blue ash than in the other taxa and lower in white ash than in Manchurian ash (Figure 2c; $\chi^2 = 0.56$; $df = 5.41$; $P < 0.001$).

SLA was highly positively correlated with leaf N on a leaf area basis ($r \geq 0.93$; $P < 0.001$) in all ash taxa except the Manchurian × black ash hybrid ($r = 0.67$; $P = 0.100$) (Table 2). SLA and leaf N were not correlated with diameter growth in most taxa. The exception was that diameter growth was correlated with leaf N in Manchurian ash ($r = 0.74$; $P = 0.038$) (Table 2).

There was a significant interaction between the effects of taxon and date on A ($F = 2.88$; $df = 15,124$; $P < 0.001$), which was greater for green ash than some other species on 22 Jun, all other species on 27 Jul and 7 Sep, and only blue ash on 24 Aug (Figure 3a). A of blue ash was lower than all the other ash taxa on 24 Aug. There was a significant interaction between the effect of taxon and date on g_s ($F = 5.10$; $df = 15,124$; $P < 0.001$); g_s of green ash was greater than the other species on 22 Jun and 27 Jul, did not differ from other taxa on 24 Aug, and was greater than blue, black, and the Manchurian × black ash hybrid on 7 Sep (Figure 3b). There also was a significant interaction between taxon and date for PNUE ($F = 2.08$; $df = 15,124$; $P = 0.015$). PNUE of green ash was greater than that of black ash on 22 Jun (Figure 3c). On 27 Jul, however, PNUE of green and blue ash did not differ, but both were greater than that of Manchurian ash, and PNUE of blue ash was greater

than that of white ash (Figure 3c). On 24 Aug, there were no differences in PNUE among the ash taxa (Figure 3c). On 7 Sep, PNUE of green ash was greater than that of Manchurian, but no other comparisons were different (Figure 3c). Taxon and date had significant but not interacting effects on ϕ_{PSII} (species: $F = 16.20$; $df = 15,124$; $P < 0.001$, date: $F = 22.14$; $df = 15,124$; $P < 0.001$). ϕ_{PSII} of green ash was greater than the other taxa on all dates, which was largely influenced by the difference between green ash (mean = 0.20) and the other taxa on 7 Sep (Figure 3d). ϕ_{PSII} was lower on 24 Aug than on 22 Jun and 27 Jul (means ≤ 0.14). ϕ_{PSII} on 7 Sep was not different than on the other sampling dates.

Correlations between measures of growth and physiology were not consistently significant, either by date or by ash taxa (Tables 2–5). Diameter growth was not significantly correlated with physiological measures on 22 June (soil moisture high) (Table 2), but was significantly correlated with some leaf variables for some taxa on 27 July (soil moisture still high). For example, Fv'/Fm' was significantly correlated with growth for white ash ($r = 0.79$; $P = 0.019$) and Manchurian ash ($r = 0.77$; $P = 0.024$) (Table 3). On 24 Aug (precipitation was low), C_i was correlated with growth for green ash ($r = 0.77$; $P = 0.025$), and A and PNUE were both correlated with growth for Manchurian ash ($r = 0.71$; $P = 0.050$ and $r = 0.86$; $P = 0.001$ for A and PNUE, respectively) (Table 4). On 7 Sep (precipitation was low), A was correlated with growth for green ash ($r = 0.73$; $P = 0.040$); ϕ_{PSII} was correlated with growth ($r = -0.78$; $P = 0.022$) for white ash; and A, C_i , and ϕ_{PSII} were all correlated with growth for Manchurian ash ($r = 0.72$; $P = 0.046$, $r = -0.72$; $P = 0.047$, $r = 0.73$; $P = 0.041$ for A, C_i , and ϕ_{PSII} , respectively) (Table 5).

Some measures of physiology were generally correlated with one another. Among all sampling dates, PNUE was often negatively correlated with leaf N and SLA, and g_s was often correlated positively with C_i . On most sampling dates, A was positively correlated with g_s and PNUE, and PNUE was positively correlated with g_s , especially for black, Manchurian, and Manchurian × black ash. On 7 Sep when precipitation was low, more frequently among taxa than on the other sampling dates, ϕ_{PSII} was correlated with A, PNUE, and g_s (if significant, $r \geq 0.71$; $P \leq 0.050$) (Table 5).

Table 2. Pearson's correlation coefficients for leaf traits, growth, photosynthesis, stomatal conductance, and fluorescence among all trees on June 22, 2015 (=wet).

Blue	SLA	dia gr	A	PNUE	g_s	C_i	Fv'/Fm'	ϕPSII
N	0.93***	0.46	-0.45	-0.92**	-0.24	-0.04	-0.56	-0.69
SLA		0.31	-0.63	-0.95***	-0.54	-0.28	-0.77*	-0.66
dia gr			-0.14	-0.48	-0.11	-0.18	0.33	-0.40
A				0.72*	0.75*	0.16	0.57	0.77*
PNUE					0.53	0.20	0.60	0.79*
g _s						0.74*	0.60	0.27
C _i							0.30	-0.28
Fv'/Fm'								0.31
White								
N	0.99***	-0.58	-0.57	-0.82*	0.16	0.46	-0.64	-0.37
SLA		-0.54	-0.61	-0.84**	0.16	0.51	-0.67	-0.44
dia gr			0.12	0.36	0.07	0.11	0.20	-0.03
A				0.78*	0.21	-0.60	0.50	0.71*
PNUE					0.31	-0.30	0.77*	0.41
g _s						0.63	0.36	-0.22
C _i							-0.06	-0.78*
Fv'/Fm'								0.04
Green								
N	0.99***	-0.12	-0.55	-0.88**	-0.57	0.24	-0.05	-0.01
SLA		-0.20	-0.56	-0.85**	-0.57	0.25	-0.06	0.02
dia gr			-0.07	-0.56	0.19	0.02	-0.47	-0.43
A				0.82*	0.67	-0.75*	0.08	0.71*
PNUE					0.73*	-0.46	0.02	0.41
g _s						-0.04	0.38	0.41
C _i							0.20	-0.59
Fv'/Fm'								0.35
Black								
N	0.98***	-0.40	0.26	-0.60	0.23	-0.05	0.37	0.31
SLA		-0.31	0.08	-0.73*	0.06	-0.21	0.21	0.15
dia gr			-0.14	0.29	-0.41	-0.23	-0.14	0.08
A				0.54	0.85**	0.63	0.93***	0.80*
PNUE					0.44	0.50	0.40	0.31
g _s						0.87**	0.91**	0.42
C _i							0.74*	0.27
Fv'/Fm'								0.65
Man × Black								
N	0.67	-0.31	-0.28	-0.72	0.01	0.36	0.09	0.05
SLA		-0.09	-0.59	-0.76*	-0.25	0.43	-0.38	-0.27
dia gr			-0.01	-0.01	-0.15	-0.24	-0.27	-0.45
A				0.85*	0.77*	-0.13	0.63	0.81*
PNUE					0.54	-0.27	0.42	0.60
g _s						0.53	0.91**	0.85**
C _i							0.54	0.23
Fv'/Fm'								0.77*
Manchurian								
N	0.83**	0.74*	0.44	-0.21	0.23	0.11	0.69	-0.18
SLA		0.43	0.01	-0.57	-0.01	-0.05	0.48	-0.43
dia gr			0.52	0.06	0.15	-0.10	0.52	-0.18
A				0.78*	0.79*	0.57	0.53	0.55
PNUE					0.74*	0.60	0.14	0.71*
g _s						0.94***	0.66	0.48
C _i							0.63	0.41
Fv'/Fm'								-0.20

*P < 0.05, **P < 0.01, ***P < 0.001; N = leaf nitrogen ($\mu\text{mol mol}^{-2} \text{s}^{-1}$); SLA = specific leaf area ($\text{m}^2 \text{g}^{-1}$); dia gr = diameter growth in 2015 (cm); A = net assimilation rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$); g_s = stomatal conductance ($\text{mol m}^{-2} \text{s}^{-1}$); PNUE = photosynthetic nitrogen use efficiency ($\mu\text{mol mol}^{-2} \text{s}^{-1}$); C_i = intercellular CO₂ ($\mu\text{mol mol}^{-1}$); Fv'/Fm' = light-adapted variable fluorescence; ϕPSII = fraction of absorbed photons used by photosystem II.

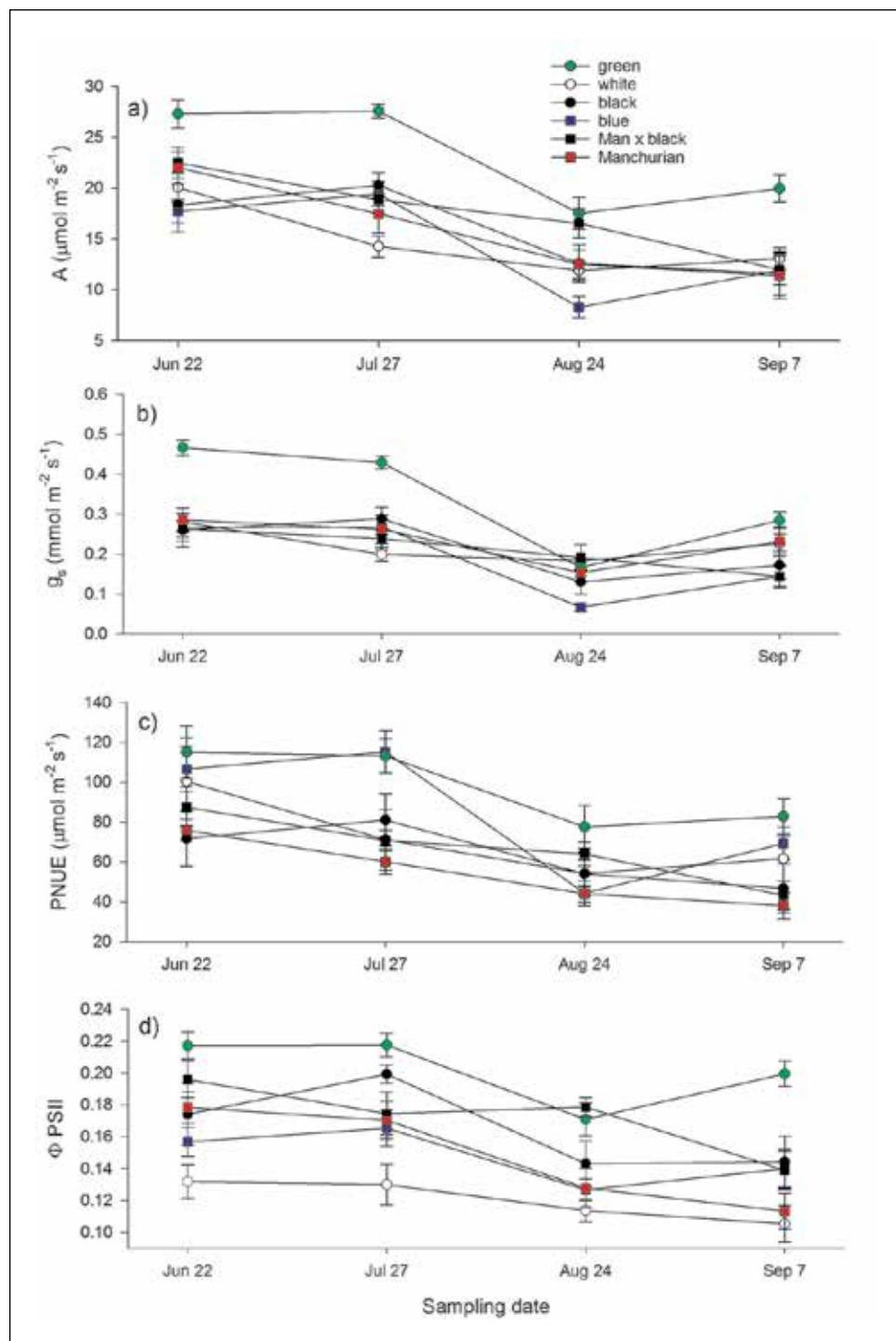


Figure 3. Mean (a) CO_2 assimilation rate (A), (b) stomatal conductance (g_s), (c) photosynthetic nitrogen use efficiency (PNUE), and (d) efficiency of photosystem II (ΦPSII) for six ash taxa by sampling date. Key for taxa is located in (b). Dots represent means of eight trees, and error bars are one standard error from the mean. Man x black = Manchurian x black ash.

Table 3. Pearson's correlation coefficients for leaf traits, growth, photosynthesis, stomatal conductance, and fluorescence among all trees on July 27, 2015 (=wet).

Blue	SLA	dia gr	A	PNUE	g _s	C _i	Fv'/Fm'	φPSII
N	0.93***	0.46	0.05	-0.79*	-0.03	-0.11	-0.48	-0.09
SLA		0.31	-0.14	-0.83**	-0.35	-0.29	-0.48	0.09
dia gr			-0.19	-0.57	0.16	0.29	-0.28	0.04
A				0.55	0.63	-0.33	0.60	0.91**
PNUE					0.34	-0.15	0.72*	0.46
g _s						0.52	0.86**	0.46
C _i							0.42	-0.45
Fv'/Fm'								0.37
White								
N	0.99***	-0.58	-0.56	-0.84**	0.43	0.77*	-0.51	-0.35
SLA		-0.54	-0.54	-0.84**	0.48	0.80*	-0.44	-0.32
dia gr			0.44	0.45	0.06	-0.25	0.79*	0.42
A				0.76*	0.20	-0.62	0.69	0.83*
PNUE					-0.21	-0.77*	0.61	0.67
g _s						0.64	0.19	0.54
C _i							-0.35	-0.23
Fv'/Fm'								0.59
Green								
N	0.99***	-0.12	0.49	-0.97***	0.42	0.02	0.44	0.42
SLA		-0.20	0.42	-0.95***	0.37	0.01	0.45	0.45
dia gr			-0.17	0.04	0.36	0.52	-0.58	-0.39
A				-0.40	0.27	-0.43	0.75*	0.51
PNUE					-0.39	-0.06	-0.37	-0.29
g _s						0.74*	-0.03	0.32
C _i							-0.62	-0.13
Fv'/Fm'								0.62
Black								
N	0.98***	-0.40	0.19	-0.77*	0.08	-0.05	0.21	-0.20
SLA		-0.31	0.08	-0.83*	-0.06	-0.21	0.03	-0.31
dia gr			-0.05	0.33	-0.30	-0.55	0.04	0.31
A				0.38	0.91**	0.63	0.76*	0.71*
PNUE					0.50	0.48	0.28	0.54
g _s						0.88**	0.68	0.62
C _i							0.56	0.50
Fv'/Fm'								0.82*
Man × Black								
N	0.67	-0.31	0.38	-0.30	0.19	-0.11	0.67	0.61
SLA		-0.09	0.29	-0.16	-0.09	-0.43	0.48	0.69
dia gr			0.54	0.80*	0.52	0.29	0.27	0.17
A				0.76*	0.79*	0.38	0.77*	0.56
PNUE					0.68	0.44	0.31	0.24
g _s						0.86**	0.46	-0.03
C _i							0.06	-0.52
Fv'/Fm'								0.72*
Manchurian								
N	0.83**	0.74*	0.40	-0.08	-0.10	-0.45	0.44	0.25
SLA		0.43	0.21	-0.22	-0.36	-0.50	0.12	0.18
dia gr			0.41	0.09	0.34	0.14	0.77*	0.03
A				0.88**	0.76*	0.11	0.60	0.75*
PNUE					0.88**	0.34	0.42	0.70
g _s						0.65	0.63	0.47
C _i							0.46	-0.16
Fv'/Fm'								0.01

*P < 0.05, **P < 0.01, ***P < 0.001; N = leaf nitrogen ($\mu\text{mol mol}^{-2}$ s^{-1}); SLA = specific leaf area (m^2g^{-1}); dia gr = diameter growth in 2015 (cm); A = net assimilation rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$); g_s = stomatal conductance ($\text{mol m}^{-2} \text{s}^{-1}$); PNUE = photosynthetic nitrogen use efficiency ($\mu\text{mol mol}^{-2} \text{s}^{-1}$); C_i = intercellular CO₂ ($\mu\text{mol mol}^{-1}$); Fv'/Fm' = light-adapted variable fluorescence; φPSII = fraction of absorbed photons used by photosystem II.

Table 4. Pearson's correlation coefficients for leaf traits, growth, photosynthesis, stomatal conductance, and fluorescence among all trees on August 24, 2015 (=dry).

Blue	SLA	dia gr	A	PNUE	g_s	C_i	Fv'/Fm'	ϕ_{PSII}
N	0.93***	0.46	0.25	0.62	0.34	0.52	-0.31	0.28
SLA		0.31	-0.04	0.23	0.17	0.71	-0.40	-0.08
dia gr			-0.31	0.25	-0.39	-0.10	-0.62	0.33
A				0.60	0.92**	0.21	0.60	0.60
PNUE					0.40	-0.10	-0.19	0.66
g_s						0.56	0.70	0.30
C_i							0.29	-0.31
Fv'/Fm'								-0.06
White								
N	0.99***	-0.58	0.06	0.14	-0.31	-0.25	0.24	-0.15
SLA		-0.54	0.12	0.13	-0.23	-0.28	0.32	-0.14
dia gr			0.52	0.47	0.70	-0.29	0.30	0.51
A				0.15	0.53	-0.92**	0.33	0.63
PNUE					0.29	-0.04	0.08	0.15
g_s						-0.17	0.47	0.07
C_i							-0.24	-0.68
Fv'/Fm'								-0.10
Green								
N	0.99***	-0.12	-0.39	0.06	-0.26	0.06	0.32	0.16
SLA		-0.20	-0.39	0.03	-0.31	-0.03	0.29	0.21
dia gr			-0.09	-0.01	0.46	0.77*	-0.19	-0.66
A				0.84**	0.73*	0.12	0.61	0.47
PNUE					0.75*	0.29	0.80*	0.43
g_s						0.75*	0.44	-0.08
C_i							0.07	-0.46
Fv'/Fm'								0.32
Black								
N	0.98***	-0.40	-0.50	-0.33	-0.59	-0.17	-0.68	-0.57
SLA		-0.31	-0.73	-0.59	-0.77*	-0.39	-0.67	-0.78*
dia gr			-0.60	-0.42	-0.47	-0.36	0.48	-0.51
A				0.84*	0.97***	0.75	0.31	0.91**
PNUE					0.85*	0.86*	0.56	0.58
g_s						0.87*	0.39	0.88**
C_i							0.28	0.44
Fv'/Fm'								0.15
Man × Black								
N	0.67	-0.31	-0.48	-0.21	-0.34	-0.60	0.04	-0.02
SLA		-0.09	0.03	0.17	-0.10	-0.43	0.43	0.57
dia gr			0.65	0.41	0.61	0.67	-0.30	0.36
A				0.78*	0.88**	0.77*	0.47	0.59
PNUE					0.93**	0.78*	0.72	0.31
g_s						0.90**	0.50	0.30
C_i							0.21	0.12
Fv'/Fm'								0.20
Manchurian								
N	0.83**	0.74*	0.65	0.80*	0.34	-0.23	-0.20	0.67
SLA		0.43	0.27	0.61	0.01	-0.30	0.12	0.28
dia gr			0.71*	0.79*	0.64	0.10	0.13	0.48
A				0.86**	0.61	-0.19	-0.40	0.70
PNUE					0.68	-0.04	-0.08	0.51
g_s						0.63	-0.10	0.40
C_i							0.22	-0.09
Fv'/Fm'								-0.74*

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; N = leaf nitrogen ($\mu\text{mol mol}^{-2} \text{s}^{-1}$); SLA = specific leaf area (m^2g^{-1}); dia gr = diameter growth in 2015 (cm); A = net assimilation rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$); g_s = stomatal conductance ($\text{mol m}^{-2} \text{s}^{-1}$); PNUE = photosynthetic nitrogen use efficiency ($\mu\text{mol mol}^{-2} \text{s}^{-1}$); C_i = intercellular CO_2 ($\mu\text{mol mol}^{-1}$); Fv'/Fm' = light-adapted variable fluorescence; ϕ_{PSII} = fraction of absorbed photons used by photosystem II.

Table 5. Pearson's correlation coefficients for leaf traits, growth, photosynthesis, stomatal conductance, and fluorescence among all trees on September 7, 2015 (=dry).

Blue	SLA	dia gr	A	PNUE	g_s	C_i	Fv'/Fm'	ϕ_{PSII}
N	0.93***	0.46	0.31	-0.34	0.24	-0.07	0.03	-0.02
SLA		0.31	-0.01	-0.58	-0.08	-0.30	-0.27	-0.21
dia gr			0.64	0.33	0.39	-0.11	0.50	0.68
A				0.76*	0.92**	0.62	0.93***	0.74*
PNUE					0.68	0.54	0.88**	0.81*
g_s						0.85**	0.87**	0.48
C_i							0.66	0.13
Fv'/Fm'								0.71*
White								
N	0.99***	-0.58	0.16	-0.77*	0.62	0.45	0.59	0.50
SLA		-0.54	0.12	-0.79*	0.63	0.48	0.64	0.45
dia gr			-0.54	0.10	-0.48	-0.15	-0.32	-0.78*
A				0.39	0.49	-0.17	0.03	0.80*
PNUE					-0.31	-0.48	-0.63	0.10
g_s						0.74*	0.56	0.40
C_i							0.42	-0.19
Fv'/Fm'								0.18
Green								
N	0.99***	-0.12	-0.18	-0.78*	-0.03	0.24	-0.11	0.14
SLA		-0.20	-0.26	-0.81*	-0.06	0.33	-0.15	0.06
dia gr			0.73*	0.57	0.35	-0.53	0.22	0.64
A				0.70	0.79*	-0.22	0.80*	0.80*
PNUE					0.52	-0.20	0.50	0.38
g_s						0.40	0.76*	0.48
C_i							0.07	-0.38
Fv'/Fm'								0.65
Black								
N	0.98***	-0.40	0.12	-0.50	0.20	0.29	-0.16	0.08
SLA		-0.31	0.03	-0.57	0.10	0.22	-0.16	-0.07
dia gr			0.08	0.30	0.11	0.28	0.08	0.12
A				0.75*	0.99***	-0.03	0.09	0.92**
PNUE					0.69	-0.22	0.20	0.71*
g_s						0.13	0.11	0.91**
C_i							0.14	0.03
Fv'/Fm'								-0.20
Man × Black								
N	0.67	-0.31	-0.43	-0.67	-0.19	0.21	-0.02	-0.14
SLA		-0.09	-0.16	-0.39	0.44	0.68	-0.17	0.11
dia gr			-0.19	-0.14	-0.09	-0.08	-0.35	-0.58
A				0.94**	0.85**	0.13	0.26	0.74*
PNUE					0.57	-0.29	0.14	0.70
g_s						0.58	0.23	0.55
C_i							-0.14	0.18
Fv'/Fm'								-0.04
Manchurian								
N	0.83**	0.74*	0.64	0.51	0.47	-0.72*	0.56	0.62
SLA		0.43	0.50	0.40	0.36	-0.67	0.71*	0.26
dia gr			0.72*	0.62	0.51	-0.71*	0.47	0.73*
A				0.98***	0.95***	-0.75*	0.70	0.88**
PNUE					0.96***	-0.70	0.67	0.87**
g_s						-0.52	0.65	0.82*
C_i							-0.57	-0.66
Fv'/Fm'								0.38

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; N = leaf nitrogen ($\mu\text{mol mol}^{-2} \text{s}^{-1}$); SLA = specific leaf area ($\text{m}^2 \text{g}^{-1}$); dia gr = diameter growth in 2015 (cm); A = net assimilation rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$); g_s = stomatal conductance ($\text{mol m}^{-2} \text{s}^{-1}$); PNUE = photosynthetic nitrogen use efficiency ($\mu\text{mol mol}^{-2} \text{s}^{-1}$); C_i = intercellular CO₂ ($\mu\text{mol mol}^{-1}$); Fv'/Fm' = light-adapted variable fluorescence; ϕ_{PSII} = fraction of absorbed photons used by photosystem II.

DISCUSSION

There was little variation in ecophysiology among the six ash taxa during the 2015 growing season in central Ohio, U.S.A. Ash that were not adapted to the study site were similar in physiological performance to those that were native (white and green ash). Weather during the 2015 growing season was typical for northeast Ohio with precipitation decreasing in the latter part of the summer. Our results suggest that the EAB-resistant Manchurian ash and the Manchurian × black ash hybrid 'Northern Treasure' are likely just as well-suited physiologically to growing conditions in the Midwestern United States as the formerly commonly planted 'Autumn Purple' white ash and 'Patmore' green ash. However, further testing at other locations and in more years is needed to thoroughly evaluate the suitability of EAB-resistant ash cultivars across the range of potential planting.

Measures of growth and leaf physiology revealed key interspecific differences between 'Patmore' green ash and the other ash taxa, and blue ash and the other ash taxa, both of which could be explained by eco-physiological performance. Green ash grew faster and generally had higher photosynthesis than the other taxa, which is consistent with its tolerance to a wide variety of environmental conditions (MacFarlane and Meyer 2005). In addition, Schutzki and Fernandez (1998) found that green ash seedlings subjected to drought maintained higher growth rates than either black or white ash. Relative to many deciduous trees, green ash has a high photosynthetic capacity (average A of 20 to 25 $\mu\text{mol m}^{-2} \text{s}^{-1}$) (Larcher 2003). Over the growing season, A for green ash ranged from 18 to 28 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Different populations of green ash are known to have different hydraulic architecture, which was especially apparent under experimental drought conditions (Shumway et al. 1991). Hence, the eco-physiology for 'Patmore' green ash that we studied may not be representative of other green ash cultivars or populations. Intraspecific differences in net photosynthesis are not unusual among deciduous trees (Pallardy 2008).

When there was adequate precipitation during the first half of the growing season, A and g_s were greater in green ash than in some of the other ash taxa. All ash responded similarly to dry conditions in the latter part of the growing season by decreasing stomatal conductance (g_s on 24 Aug and 7 Sep vs. 27 Jul and 22 Jun), which is an initial plant response to water

deficit and a typical drought-avoidant response (Lambers et al. 1998; Larcher 2003). A similar declining pattern was observed for PNUE and ϕ_{PSII} , which suggests that photosynthetic efficiency declined with stomatal closure. The greater efficiency of photosystem II in green ash relative to the other taxa on 7 Sep may simply be reflective of differences in the timing of the onset of dormancy, as a few white and black ash trees already possessed senescing foliage.

Studies that explicitly tested white, green, and European (*F. excelsior*) ash response to drought found that ash are generally drought-tolerant, but also exhibit some drought-avoidant responses. In response to experimentally induced drought, ash species maintained cell turgor through osmotic adjustments or cell-wall elasticity and exhibited higher photosynthetic rates than drought-intolerant species (Davies and Kozlowski 1977; Abrams et al. 1990; Carlier et al. 1992; Peltier and Marigo 1999). Green ash also exhibited reduced leaf area during drought (Shumway et al. 1991) and stomatal conductance declined when precipitation was low, as was the case for all taxa in our study. When precipitation was adequate, g_s of green ash was similar to that observed in other studies for well-watered European ash seedlings (0.4 vs. 0.6 to 0.4 $\text{mmol m}^{-2} \text{s}^{-1}$ in European ash) (Patonnier et al. 1999; Peltier and Marigo 1999). When precipitation was low, g_s that we observed in the other ash taxa was similar to that of European ash subjected to experimental drought (0.1 to 0.2 in our study vs. 0.1 $\text{mmol m}^{-2} \text{s}^{-1}$ in European ash) (Patonnier et al. 1999; Peltier and Marigo 1999).

Differences in ecophysiology of blue ash relative to the other ash species likely reflect its adaptations to more xeric growing conditions. Blue ash had lower leaf N concentration than the other ash species, which suggests less investment in photosynthetic machinery (Lambers et al. 1998). Consistent with that, blue ash had lower CO_2 assimilation rates, g_s , and PNUE relative to some of the other ash taxa when precipitation was low. Yet these physiological differences did not translate to reduced diameter growth in blue ash relative to the other taxa. Plants that are adapted to favorable environments generally have higher maximum relative growth rates than those adapted to poor environments (Lambers et al. 1998; Poorter and De Jong 1999), which may explain why blue ash grew slower than green ash, but not why there were few differences in growth among blue ash and the other taxa.

Although leaf N varied significantly among ash species, SLA did not, which is also consistent with low variation in growth rates. SLA is a function of leaf thickness and density and is a key character that determines capacity for growth; a high leaf area relative to leaf mass allows plants to grow fast (Lambers et al. 1998; Poorter and De Jong 1999). Within species, SLA was not significantly correlated with growth but was highly correlated with leaf N ($r \geq 0.93$) in all ash except Manchurian × black ($r = 0.67$). This suggests that leaves with a higher SLA would also have a greater photosynthetic capacity (Lambers et al. 1998), although this was not reflected in any of our measurements (i.e., A was not correlated with SLA on an intraspecific basis).

Many measures of ash physiology were not significantly correlated with growth, perhaps because (1) environmental conditions in 2015 were not limiting for growth, and (2) instantaneous measurements were not representative of season-length physiological status. Chlorophyll fluorescence increases in response to excess light, drought, or other stressors that decrease intercellular CO₂ supply and thus negatively affect phytochemical reactions (Krause and Weis 1991; Lambers et al. 1998). Lack of a relationship between variable fluorescence or the efficiency of photosystem II and growth may indicate that the degree of stress experienced by ash in our study was not appreciable enough to affect growth rate. Other studies also reported high, low, negative, or no correlations between CO₂ uptake and growth rate (Lambers et al. 1998; Poorter and De Jong 1999; Larcher 2003). Short-term (instantaneous in our case) measurements do not reliably reflect seasonal patterns in photosynthesis (Pallardy 2008). Also, the relationship between photosynthesis and respiration, partitioning of photosynthate within the tree, and total leaf area were not measured and all contribute to variation in growth rate (Pallardy 2008). Although A on particular sampling dates did not correlate with growth among individual trees, high rates of A in green ash may have contributed to its greater diameter growth relative to other ash taxa.

Within a species, measures of physiology that are known to be tightly linked were often significantly correlated. For example, stomata regulate the rate at which CO₂ diffuses into the leaf (Lambers et al. 1998; Larcher 2003; Pallardy 2008), and A and g_s were often significantly positively correlated for most species on most sampling dates. ϕ PSII was more

frequently correlated with A, g_s, and PNUE on the last sampling date of the growing season, relative to other sampling dates. Low precipitation and the onset of dormancy on the final sampling date probably represented the most stressful conditions experienced by trees over the course of the growing season.

CONCLUSIONS

The lack of significant variation in growth and physiology among ash species, both when environmental conditions were favorable and during dry, late summer conditions, suggests that all taxa that we tested are generally adapted to environmental conditions in central Ohio. Notably, the Asian ash species Manchurian ash and the Manchurian × black ash hybrid ‘Northern Treasure’ are both EAB-resistant (Herms 2015) and performed physiologically just as well as North American species native to Ohio. These results indicate that Manchurian ash and the Manchurian × black ash hybrid ‘Northern Treasure’ are both sufficiently adapted to growing conditions in the Midwestern United States. We suggest that either could be planted in Midwestern urban forests in place of ash species that are susceptible to EAB.

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Résumé. L'invasion nord-américaine de l'agile du frêne (EAB) (*Agrilus planipennis* Fairmaire) a accru l'intérêt de la phylogénie, de l'écologie et de la physiologie des frênes (*Fraxinus*, Oleaceae). Dans un jardin commun du centre de l'Ohio, les performances de trois cultivars nord-américains de frêne très sensibles à l'agile du frêne (*F. pennsylvanica* 'Patmore,' *F. americana* 'Autumn Purple,' et *F. nigra* 'Fall Gold'), d'une espèce nord-américaine moins susceptible (*F. quadrangulata*) et de deux taxons réputés résistants (*F. mandshurica* et *F. mandshurica* × *F. nigra* 'Northern Treasure') furent comparées. Au cours de la saison de croissance 2015, furent mesurés la croissance en diamètre, la concentration foliaire en azote, la surface foliaire spécifique et à quatre périodes (dont deux avec une précipitation adéquate et deux avec une faible précipitation), nous mesurâmes le taux d'assimilation du gaz carbonique CO₂ (A), la conductance stomatique (g_s), la concentration intercellulaire du CO₂ (C_i), l'efficacité photosynthétique de l'azote (PNUE), la variation de la fluorescence (Fv'/Fm': l'efficacité de l'énergie récoltée via les centres ouverts de réaction du photosystème II), et la fraction des photons absorbés par le photosystème II utilisés pour la photosynthèse (φPSII). *F. pennsylvanica* montra la croissance la plus rapide et lors de la plupart des périodes d'échantillonnage il s'est avéré supérieur pour la performance physiologique (A, g_s, and φPSII). De manière générale cependant, il y eut peu de variation interspécifique en croissance et en physiologie parmi les différents taxons de frêne testés, puisque tous performaient bien. Ceci suggère que les hybrides résistants à l'agile du frêne, *F. mandshurica* et *F. mandshurica* × *F. nigra* 'Northern Treasure', ainsi que le *F. quadrangulata* modérément résistant, sont tout autant physiologiquement bien adaptés aux conditions de croissance du Midwest américain que les cultivars de frêne de Pennsylvanie ou de frêne américain, qui étaient largement plantés avant l'invasion de l'agile.

Zusammenfassung. Die Invasion des Asiatischen Eschenprachtkäfers (EAB) in Nordamerika hat das Interesse an der Phylogenie, Ökologie und Physiologie des Asiatischen Eschenprachtkäfers verstärkt. In einem gewöhnlichen Garten in Zentral-Ohio verglichen wir die Erscheinung/Leistung von drei nordamerikanischen Eschenkultivaren (*Fraxinus*, Oleaceae), die hochgradig anfällig auf EAB reagieren (*F. pennsylvanica* 'Patmore,' *F. americana* 'Autumn Purple,' und *F. nigra* 'Fall Gold'), eine nordamerikanische Art, die weniger anfällig gegenüber EAB reagiert (*F. quadrangulata*) und zwei Arten, die gegenüber EAB resistent sind (*F. mandshurica* und *F. mandshurica* × *F. nigra* 'Northern Treasure'). Während der Wachstumsperiode in 2015 haben wir Durchmesserzuwachs, Stickstoffkonzentration im Blatt und spezifische Blattfläche gemessen, sowie an vier Daten (zwei mit adäquater und zwei mit niedriger Ausfällung) die CO₂ Assimulationsrate (A), Leitfähigkeit der Stomata (g_s), interzellulare CO₂ Konzentration (C_i), photosynthetische Effizienz bei der Stickstoffaufnahme (PNUE), variable Fluoreszenz (Fv'/Fm': Effizienz der gewonnenen Energie aus einer offenen Photosyntheseesystem II Reaktion) und die Fraktion der durch das Photosyntheseesystem II absorbierten Photonen, die für die Photosynthese verwendet werden (φPSII). *F. pennsylvanica* wuchs am schnellsten und an den meisten Standorten war die physiologische Performance überragend (A, g_s, und φPSII). Generell gab es nur kleine interspezifische Variatio-

nen in Wachstum und Physiologie zwischen den getesteten Eschenarten, weil sich alle gut entwickelten. Das bedeutet, dass die EAB-resistenten *F. mandshurica* und *F. mandshurica* × *F. nigra* Hybride, sowie die moderat resistente Blaue Esche genauso physiologisch gut geeignet sind für die Wachstumsbedingungen im Mittleren Westen der Vereinigten Staaten wie die Grünen und Weißen Eschenkultivare, die weitläufig bereits vor der EAB-Invasion gepflanzt wurden.

Resumen. La invasión del barrenador esmeralda del fresno (EAB, por sus siglas en inglés) (*Agrilus planipennis* Fairmaire) en América del Norte ha aumentado el interés en la filogenia, la ecología y la fisiología del fresno (*Fraxinus*, Oleaceae). En un jardín comunitario en el centro de Ohio, se comparó el rendimiento de tres cultivares de fresno de América del Norte que son altamente susceptibles a la EAB (*F. pennsylvanica* 'Patmore,' *F. americana* 'Autumn Purple,' y *F. nigra* 'Fall Gold'), una especie de América del Norte que es menos susceptible a la EAB (*F. quadrangulata*) y dos taxones que son resistentes a la EAB (*F. mandshurica* y *F. mandshurica* × *F. nigra* 'Northern Treasure'). Durante la temporada de crecimiento de 2015 se midió el diámetro de crecimiento, la concentración foliar de N, el área foliar específica y en cuatro fechas (dos con una adecuada y dos con baja precipitación) se midió la tasa de asimilación de CO₂ (A), la conductancia estomática (g_s), la concentración de CO₂ intercelular (C_i), la eficiencia en el uso de nitrógeno fotosintético (PNUE), la fluorescencia variable (Fv'/ Fm': eficiencia de la energía recolectada por los centros de reacción abiertos del fotosistema II), y la fracción de fotones absorbidos por el fotosistema II que se usaron para la fotosíntesis (φPSII). *F. pennsylvanica* creció más rápido y en la mayoría de las fechas de muestreo fue superior en rendimiento fisiológico (A, g_s, y φPSII). En general, sin embargo, hubo poca variación interspecífica en el crecimiento y la fisiología entre los diferentes taxones de fresno, ya que todos se desempeñaron bien. Esto sugiere que el híbrido de *F. mandshurica* y *F. mandshurica* × *F. nigra* resistentes a EAB, así como el fresno azul moderadamente resistente, son fisiológicamente adecuados para las condiciones de crecimiento en el medio oeste de los Estados Unidos como variedades de fresno blanco y verde que se habían plantado ampliamente antes de la invasión de EAB.