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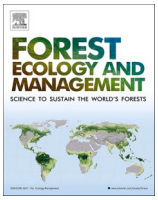

Rapid growth in clonal *Juglans nigra* L. is most closely associated with early foliation, robust branch architecture, and protandry

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ABSTRACT

The advantages of clonal forestry have been well described, but little progress has been made in the identification of phenotypes best suited to this method in high-value hardwood species. The genetic variation within, clonal repeatability (broad-sense heritability) of, and Pearson's correlations among phenological, morphological, physiological, and growth traits (N = 22) of black walnut (*Juglans nigra* L.) were investigated using 25 grafted clonal genotypes. The trees were grown at wide spacing (4.6 m × 6.1 m) in an intensively managed plantation in north-central Indiana, USA. Clonal effect was significant ($p < 0.05$) for most traits except gas exchange variables. Many phenological traits showed high clonal repeatability ($R_c^2 > 0.70$), including foliation dates, first female bloom, first pollen shed, and crown retention rate (autumnal defoliation). Some traits showed moderate repeatability ($0.35 < R_c^2 < 0.7$), such as branch angle, branch frequency, tree diameter, height, anthracnose severity, and foliar carbon and nitrogen concentration. Net CO_2 assimilation rate and stomatal conductance had low repeatability ($R_c^2 < 0.35$). We observed a previously unreported association between sexual morph and tree stem growth, i.e., protandrous trees generally grew faster than protogynous trees. This association between sexual morph and stem growth may be an evolutionary consequence of differences in reproductive costs in protandrous versus protogynous trees, and needs to be tested in other monoecious woody species. Overall, our analyses indicated that the following traits are associated with rapid stem growth: 1) early foliation; 2) early male flowering or late female flowering, i.e., more likely a protandrous variety; 3) large average branch diameter; 4) high branch frequency; 5) small (more vertical) average branch angle; 6) early leaf fall; 7) low later-season foliar carbon concentration; and 8) large number of small fruits and seeds. These traits may be used, with further testing, to define a biomass ideotype for *J. nigra*.

1. Introduction

Ideotype breeding, which has been applied to many agronomic crops, some fruit tree crops, and a few conifer species (Dickmann et al., 1994), may be a key to the success of clonal forestry. An ideotype was proposed as a biological model that has predictable yield or quality of end products in a defined environment (Donald, 1968). This approach to breeding requires quantification of the effects of numerous phenological, morphological, and physiological traits, as well as the interactions among these traits on the dynamics of plant structure and productivity (Ford, 1992). Thus, definition of a timber ideotype requires examination of the amount of variation in plant traits that affect yield and/or quality, and estimates of the heritability and correlations among these traits (Campbell, 1961; Weber et al., 1985; Dunlap and Stettler, 1998). Although ideotypes are generally defined based on end product traits, i.e., at rotation age or harvest, ideotypes based on early-growth or mid-rotation characteristics may be useful to improve breeding efforts, particularly for tree species that can take multiple decades to mature.

Established tree crop ideotypes in conifers and hardwoods aiming for biomass production have included traits in crown architecture, photosynthetic rate, growth rate, disease resistance, tolerance to extreme climates, root system, fruiting, leaf phenology, and other traits

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Table 1
Origin and sexual morph of the 25 black walnut (*Juglans nigra* L.) clones in this study.

Clone	Mother	Origin[1]	Sexual morph[2]
C55	Unknown	Darlington, IN	PG
C130	Unknown	West Lafayette, IN	PG
C715	'Tippecanoe-1'	West Lafayette, IN	PT
C720	'Fayette-1'	West Lafayette, IN	PG
C702	BW95	West Lafayette, IN	PT
C703	BW249	South Raub, IN	PT
C707	BW95	South Raub, IN	PG
C710	'Purdue-1'	South Raub, IN	PG
C714	'Purdue-1'	South Raub, IN	PT
C705	BW205	West Lafayette, IN	PG
C701	BW41	West Lafayette, IN	PG
C717	BW36	West Lafayette, IN	PT
C718	'Purdue-1'	Breeding selection	PT
C730	'Purdue-1'	Breeding selection	PT
C700	Unknown	wild	PT
C708	Unknown	wild	PG
C709	Unknown	West Lafayette, IN	PG
C712	Unknown	wild	PT
C713	Unknown	wild	PG
C716[3]	Unknown	wild	HM
C719	Unknown	wild	PG
C726	Unknown	wild	PG
C728	Unknown	wild	PT
C729	Unknown	wild	PG
C777	Unknown	wild	PG

[1] The location of the ortet, usually a progeny test of a selected *J. nigra*, but some were from wild populations.
[2] PT: protandrous; PG: protogynous; HM: homogamous.
[3] C716 was observed as PT in 2010, but HM in 2011. It was considered HM because the records in 2011 were more accurate than those of 2010.
Adapted from Pang et al. 2017

(Dickmann et al., 1994; Koski and Dickmann, 1992; Pöykkö and Pulkkinen, 1990; Pulkkinen and Poykko, 1990). Among those traits, late leafing was usually preferred to avoid frost damage; however, the phenology of flowering has not been considered as a component of an ideotype. Dichogamy, the temporal separation of the maturity of male and female flowers within a plant (Lloyd and Webb, 1986), is usually considered a reproductive mechanism for monoecious plants to avoid self-fertilization, but it may have implications for vegetative and reproductive growth and, thus, be a potential component of ideotypes. Heterodichogamy in non-dioecious species refers to two sexual morphs (or flowering types) that flower in opposite but complementary sequence. The staminate flowers of protandrous (PT) trees shed pollen before receptivity of the pistillate bloom, whereas in protogynous (PG) genotypes, pistillate flowers are receptive before pollen is shed from catkins (Warmund and Coggeshall, 2009). Homogamous (HM) genotypes, which are rare in *Juglans*, have flowers of both sexes blooming at about the same time (Kumar and Sharma, 2013). The complete separation of the two sexes in dioecious species provides excellent models to study reproductive cost, but analysis of the fitness costs of sexual morph are rare in monoecious species (Obeso, 2002).

Black walnut (*Juglans nigra* L.), a monoecious forest tree species native to eastern North America, is renowned for its highly valuable timber, with prices ranging from US$200 to >$4000 m^{-3} for delivered logs (Settle et al., 2018). Its wood is used for veneer, flooring, furniture, and gunstocks. *J. nigra* also produces edible nuts for wildlife and humans, provides habitat for wildlife, and stabilizes soil (McKenna and Coggeshall, 2018). Although *J. nigra* timber is mostly obtained from naturally regenerated forests, thousands of hectares have been planted to *J. nigra* in monospecific or mixed-species plantations in the Central Hardwood Forest Region over the past several decades. Most planted trees are from open-pollinated sources, although some are from seed orchards of parents selected in progeny trials based on growth and form characteristics (Woeste and McKenna, 2004; McKenna and Coggeshall, 2018). In recent decades, landowners have shown increasing interest in planting grafted ramets of selected genotypes, replicating the clonal forestry practices that have been applied to species within *Salicaceae*, such as willow (*Salix* spp.) and poplar (*Populus* spp.), and conifers such as loblolly pine (*Pinus taeda* L.) (Stovall et al., 2011; Tharakan et al., 2005). The goal of clonal forestry with *J. nigra* is to improve the value of logs at harvest, rather than to improve yield of fiber or biomass. Clonal production of *J. nigra* for timber is still in its infancy, in part because traits associated with wood quality and wood color must be assessed at a more mature growth stage than growth traits associated with biomass production (i.e., *J. nigra* can take 60–80 years or more to reach merchantable size).

For *Juglans*, in particular, dichogamy has been analyzed from the perspective of morph-specific mating patterns in Japanese walnut (*J. ailantifola*) (Kimura et al., 2012), frequency of self-pollination and intolerance of inbreeding in *J. nigra* (Beineke, 1983; Rink et al., 1994; Ebrahimi et al., 2018), and the equal frequency of PG and PT in natural populations of Persian walnut (*J. regia* L.), northern California black walnut (*J. hindsii* Jeps.), and *J. nigra* (Gleeson, 1982; McKenna and Coggeshall, 2018). Solar et al. (2001) reported negative correlations between flowering phenology and trunk diameter in a cohort of eight to twelve-year-old *J. regia*, but no studies have explored that relationship in *J. nigra*. Additionally, relatively few studies have examined correlations across multiple developmental traits in tree ideotypes, which can be good predictors for plant functional strategies (Kafuti et al., 2019).

As an initial effort toward the development of timber-based ideotypes in *J. nigra*, we assessed the variance components and broad-sensed heritability of 22 phenological, physiological, morphological, and growth traits in a population of 25 select *J. nigra* clones. We calculated the Pearson's correlations among these traits to identify morpho-physiological features associated with rapid stem growth in an intensively cultivated and nutrition-rich environment. We hypothesized that traits associated with crown architecture and phenology would most significantly influence the rate of stem growth, and expected no differences between PT and PG clones (i.e., no effect of dichogamy) on these associations.

2. Material and methods

2.1. Study area

This study was conducted in a 40.5 ha *J. nigra* plantation in Tippecanoe County, Indiana, US (40.4° N, 87° W) and managed by Arbor-America, Inc. The local average annual low temperature is 4.7 °C, high 11.1 °C, and the average annual precipitation is 97 cm (U.S. Climate Data, 2020). The soil type is a well-drained Elston loam (Web Soil Survey, 2020); site index is approximately 29 m on a 50 year basis (Zellers et al., 2012). The site is relatively flat (slopes < 5%) and was previously used for corn (*Zea mays*) production.

Scions from 25 *J. nigra* clones were grafted onto seedling rootstocks in a nearby nursery per methodology in Salifu et al. (2006), and later transplanted to the site as one-year-old grafted trees in 2002. For the convenience of management, trees were planted in clonal blocks with an among-tree spacing of 4.6 m × 6.1 m (356 trees ha^{-1}), and trees that did not survive in 2002 were replanted in 2003. Cultural treatments for the plantation were consistently applied from plantation establishment through the end of this study. An automated drip fertigation system supplied water and nutrients every two days throughout each growing season (for a detailed description of the fertilization treatment see Goodman et al. (2013; 2014). Pre- and post-emergent herbicides were applied during the first three years after planting to enhance the establishment of *J. nigra* ramets, and continued periodically as needed to suppress understory herbaceous competition and ensure higher nutrient uptake from fertigation. Azoxystrobin was sprayed, usually in late July or August, to suppress walnut leaf anthracnose, caused by *Gnomonia leptostyla* (Fr.) Ces. and de N. (Zellers et al., 2012), and narrow range oil

Table 2
Abbreviations for the traits measured in black walnut (*Juglans nigra* L).

Abbreviation	Trait
Ang	average angle of all branches
Ang_{BDmax}	average angle of the thickest branch in each one-meter stem segment
Anth	score of anthracnose severity
BBA	branch basal area (the sum of cross-sectional area of all branches per meter of stem)
BD	average diameter of all branches
BD_{max}	average diameter of the thickest branch in each one-meter stem segment
BF	branch frequency (number of branches per meter of stem, pruning scars included)
FD	foliation dates
FF	first female flowering dates, i.e., the dates of first pistillate bloom being receptive
[C]	foliar carbon concentration ($[C]_{low}$ for lower crown, and $[C]_{up}$ for mid-upper crown)
CR	crown radius
CrRT	crown retention rate (autumnal defoliation)
DBH	diameter at breast height (1.37 m)
Ht	tree height
ILA	average individual leaf area (ILA_{low} for lower crown, and ILA_{up} for mid-upper crown)
ILM	average individual leaf mass (ILM_{low} for lower crown, and ILM_{up} for mid-upper crown)
MF	first male flowering dates, i.e., the dates of first pollen shed
[N]	foliar nitrogen concentration ($[N]_{low}$ for lower crown, and $[N]_{up}$ for mid-upper crown)
NAR	net CO_2 assimilation rate (NAR_{1st} for the first measurement, and NAR_{2nd} for the second measurement)
SC	stomatal conductance (SC_{1st} for the first measurement, and SC_{2nd} for the second measurement)
SLA	specific leaf area
SVI	stem volume index

was applied at a rate of 0.2 lb Ai/acre (US EPA Pesticide Product Label, 2016) to treat walnut scale (*Quadraspidiotus juglansregiae*) on individual trees. Trees were pruned every winter after 2003 to encourage formation of a single straight stem.

2.2. Juglans nigra clones

This study originally included 212 grafted ramets, five to ten per clone, of 25 *J. nigra* clones selected from wild populations and from ArborAmerica, Inc., as well as a walnut tree improvement program managed by the Hardwood Tree Improvement and Regeneration Center (HTIRC) at Purdue University (Table 1; Pang et al. 2017). Some trees were excluded from the analysis of particular traits because of wind damage to the stem that occurred in summer 2009, 2010, and 2011. The final number of trees analyzed ranged from 152 to 172, depending on the traits evaluated. The clonal identity of each tree was verified by microsatellite markers in 2013, and mislabeled trees were corrected (Pang et al., 2017). Based on our observation of the flowering phenology, 14 clones were PG, 10 PT, and one HM (Table 1).

2.3. Data collection

We collected data on 22 traits, with one or more measurement for each trait, related to phenology, morphology, physiology, and growth of *J. nigra* from 2009 − 2011 (Table 2).

2.3.1. Phenology

Foliation, i.e., when leaf buds break dormancy, was monitored every two or three days in April and May in 2009, 2010, and 2011 using five stages: dormant (1), bud swell (2), green tip (3), leaf burst (4), and leaf expansion (5) (Fig. A.1). The foliation date (FD) of a tree was defined as the Julian day when 50% of the terminal buds in a tree were at stage 4. Anthesis, which usually started shortly after foliation, was observed every three days in May and June in 2010 and 2011 to determine the first female flowering date (FF), i.e., the Julian day of pistillate flowers became receptive, as shown in stage 2 of Figure 16.8 in Polito (1998). The date of first male flowering (MF) was determined as the Julian day of pollen shed, i.e., when yellow pollen became visible when catkins were flipped by finger or blown by wind. In autumn, we visually observed crown retention rate (CrRT), i.e., the percentage of crown retaining leaves on Sep 15th, 2010 and Sep 30th, 2011 (the growing season started about two weeks later in 2011 than in 2010).

2.3.2. Tree growth

We measured diameter at breast height (DBH, 1.37 m from the ground), tree height (Ht), and crown radius (CR) at the end of each growing season from 2008 to 2011. DBH was estimated to the nearest 0.25 cm from the average of caliper readings on north–south and west-east axes, while CR was the average of the four cardinal directions. Ht was measured using an Impulse 200 rangefinder (Laser Technology Inc., Colorado). Stem volume index (SVI; dm^{-3}) was calculated by using the paraboloid equation: $V_{st} = 1/2^* A_b{}^*Ht$ (Husch et al., 2002), where A_b is the cross-sectional area at 1.37 m of tree height including bark, and Ht is tree height.

2.3.3. Crown architecture

We measured branch attributes using a lift (Altec Inc., Alabama) with a vertical reach of 13.7 m. Branch diameter was measured in two perpendicular directions at the base of each branch. Branch angle (the adaxial angle), was measured for all branches throughout the stem except those smaller than 1.3 cm in diameter in the lower crown that were often dead. The average angle (Ang) and average branch diameter (BD) were calculated for each tree for analysis. Due to the proportionally much higher contribution of large branches to overall tree growth, the thickest branch in each one–meter stem segment of tree height for every tree was identified in the dataset; the mean large branch angle (Ang_{BDmax}) and mean large branch diameter (BD_{max}) was calculated from these branches for each tree.

Branch frequency (BF; branches m^{-1}) was defined as the number of branches per meter of stem, while branch basal area (BBA; cm^{-2} m^{-1}) was the sum of branch cross-sectional area (calculated by using measured branch diameter) at each branch collar per meter of stem. BF and BBA were based on the branched portion of the bole, i.e., to the height of the highest measured branch in each tree, and not total tree height. Scars from pruned branches were measured and included in all trait values except branch angle variables.

2.3.4. Leaf morphology and physiology

Individual leaf area (ILA) and mass (ILM) were determined in July 2010. We selected leaves from the two eastern quadrants of the crown; five leaves were selected each from lower and mid-upper crown positions from five random trees per clone. Collected leaves were first stored at 4 °C and then scanned using an Epson Expression™ 10,000 XL scanner. Images were processed with WinFolia™ (Régent Instruments, Québec, Canada) to determine ILA to the nearest 0.0001 cm^2. Leaves were then oven dried at 65 °C for 72 h and weighed to the nearest 0.01 g. Specific leaf area (SLA) was determined as the ratio of ILA to ILM. Finally, dried leaves were mechanically ground and about 2 mg leaf powder was randomly subsampled for foliar nitrogen and carbon concentration analysis (to the nearest 0.01%) using LECO® Elemental Analysis System. Although anthracnose was treated with foliar sprays, anthracnose occurred throughout the plantation and many trees showed anthracnose symptoms: sunken spots on leaves and early defoliation. Therefore, anthracnose severity was rated at the end of July 2011 by visually inspecting the entire lower crown (up to 2 m high). We used a three-level evaluation system (Fig. A.2): level 1 = almost all leaves have no anthracnose; level 2 = half or more leaves have light anthracnose, with less than 30% of leaf area showing symptoms; and level 3 = half or more leaves have severe anthracnose, with more than 30% of leaf area from a leaf displaying symptoms.

Table 3
Mean and range in phenological, physiological, and morphological traits of 25 black walnut (*Juglans nigra* L.) clones.

[1]Trait	[2]N_c	[3]N_t	Tree level		Clone level		Unit
			Mean ± SE	Range	Mean ± SE	Range	
FD2009	24	/	/	/	122 ± 1	115–133	day
FD2010	23	81	110 ± 1	100–121	111 ± 2	100–122	day
FD2011	25	197	123 ± 0	113–132	124 ± 1	113–132	day
FF2010	25	113	128 ± 0	122–144	129 ± 1	122–144	day
FF2011	25	175	136 ± 0	131–145	136 ± 1	130–144	day
MF2010	25	122	128 ± 1	116–140	128 ± 1	117–139	day
MF2011	25	182	140 ± 1	130–153	140 ± 1	130–152	day
CrRT2010	25	172	55 ± 2	25–100	60 ± 0	30–100	%
CrRT2011	25	169	54 ± 1	13–95	60 ± 0	20–100	%
Anth2011	25	169	1.5 ± 0.1	1.0–3.0	1.4 ± 0.1	1.0–3.0	/
SLA_{low}	25	120	148.8 ± 1.4	111.2–202.7	148.0 ± 2.2	127.8–183.7	$cm^2 \cdot g^{-1}$
SLA_{up}	25	125	122.4 ± 1.2	99.7–164.0	122.2 ± 2.2	99.7–147.0	$cm^2 \cdot g^{-1}$
ILA_{low}	25	120	416.9 ± 7.6	193.3–754.6	421.6 ± 12.0	322.4–554.6	cm^2
ILA_{up}	25	128	449.1 ± 7.2	259.9–635.2	452.9 ± 10.7	337.2–554.2	cm^2
ILM_{low}	25	120	2.8 ± 0.1	1.4–5.0	2.9 ± 0.1	2.2–3.8	g
ILM_{up}	25	128	3.7 ± 0.1	1.9–5.8	3.7 ± 0.1	2.7–5.6	g
$[C]_{low}$	25	120	46.21 ± 0.16	42.17–49.76	46.32 ± 0.27	43.87–48.81	%
$[C]_{up}$	25	126	48.04 ± 0.16	43.67–52.24	48.12 ± 0.29	45.52–50.50	%
$[N]_{low}$	25	122	2.57 ± 0.03	1.57–3.64	2.59 ± 0.05	2.14–3.08	%
$[N]_{up}$	25	127	2.82 ± 0.03	2.08–3.68	2.82 ± 0.05	2.47–3.46	%
NAR_{1st}	12	36	15.9 ± 0.2	9.4–20.5	15.9 ± 0.3	14.3–17.2	$\mu molCO_2 \cdot m^{-2} \cdot s^{-1}$
NAR_{2nd}	12	35	11.9 ± 0.3	3.4–19.0	11.9 ± 0.4	8.6–14.0	$\mu molCO_2 \cdot m^{-2} \cdot s^{-1}$
SC_{1st}	12	36	0.62 ± 0.03	0.26–2.17	0.61 ± 0.05	0.42–0.98	$molH_2O \cdot m^{-2} \cdot s^{-1}$
SC_{2nd}	12	35	0.43 ± 0.02	0.03–1.25	0.43 ± 0.03	0.24–0.58	$molH_2O \cdot m^{-2} \cdot s^{-1}$
Ang	25	172	63.8 ± 0.5	47.9–79.6	65.5 ± 1.1	53.2–79.6	Degree ()
Ang_{BDmax}	25	168	54.9 ± 0.7	29.5–73.3	57.5 ± 1.3	45.1–68.0	Degree ()
BD	25	172	2.79 ± 0.02	1.82–3.69	2.77 ± 0.04	2.18–3.19	cm
BD_{max}	25	168	4.33 ± 0.04	2.97–5.65	4.3 ± 0.07	3.33–4.83	cm
BF	25	172	14.6 ± 0.2	7.8–20.4	14.1 ± 0.4	8.9–18.4	m^{-1}
BBA	25	172	71.6 ± 1.1	41.7–112.1	70.5 ± 2.1	54.3–94.6	$cm^2 \cdot m^{-1}$
DBH2009	25	172	12.4 ± 0.1	8.5–16.9	12.0 ± 0.2	8.5–14.1	cm
DBH2010	25	172	14.6 ± 0.1	9.9–18.7	14.2 ± 0.3	9.9–16.4	cm
DBH2011	25	169	16.2 ± 0.1	11.1–19.9	15.8 ± 0.3	11.0–18.1	cm
Ht2009	25	172	8.1 ± 0.1	5.8–10.1	8.0 ± 0.1	5.8–9.4	m
Ht2010	25	172	9.5 ± 0.1	7.2–11.3	9.3 ± 0.2	7.3–11.0	m
Ht2011	24	152	10.8 ± 0.1	7.7–13.2	10.5 ± 0.2	7.7–12.3	m
CR2009	25	172	2.9 ± 0.0	2.4–3.5	2.9 ± 0.0	2.6–3.1	m
CR2010	25	172	2.7 ± 0.0	2.0–3.5	2.7 ± 0.0	2.5–3.2	m
CR2011	25	169	2.6 ± 0.0	1.4–3.2	2.5 ± 0.0	2.0–3.2	m
SVI2009	25	171	49.9 ± 1.0	16.6–90.4	46.2 ± 2.2	16.6–74.2	dm^3
SVI2010	25	171	81.0 ± 1.4	28.1–130.8	75.1 ± 3.6	28.1–116.5	dm^3
SVI2011	24	152	111.9 ± 2.0	37.0–183.4	104.6 ± 4.8	37.0–159.4	dm^3

[1] See Table 2 for the meaning of the abbreviations.
[2] Number of clones.
[3] Number of trees.

Net CO_2 assimilation rate (NAR) and stomatal conductance (SC) were monitored twice: first on July 27th, 28th, and Aug 2nd; and second on Aug 31st, Sep 1st, and Sep 2nd in 2011. Twelve clones that represented the range in distribution of both DBH and crown densities (i.e., branch frequencies) observed throughout all 25 clones were selected. Three trees per clone (i.e., 36 trees total) were randomly chosen. Sampling occurred during three mostly or fully sunny days each time. During each sampling day, we measured one tree in each clone (12 trees per day), randomizing the sequence of clones, as measurement of all 36 trees was not possible due to the logistical challenges of the use of the lift in such a large plantation. Measurements were made on three fully expanded, undamaged, sun-exposed leaves in the upper third crown of each tree using a LiCOR-6400 infrared gas-exchange system (LI-COR Biosciences, Lincoln, Nebraska, US) between 10 AM and 2 PM. The detailed settings and operations of LiCOR-6400 followed Gauthier and Jacobs (2009).

2.4. Data analysis

Variance analysis was conducted using a mixed-effects approach (PROC MIXED) in SAS 9.4 (SAS Institute, Inc., Cary, NC). We used restricted maximum likelihood (REML) to determine the amount and significance of clonal (genotypic) effect and the variance components of residual effects (Holland, 2006). All traits were analyzed with the following model (Eq. [1]):

$$X_{ij} = \mu + C_i + \varepsilon_{ij} \quad (1)$$

where X_{ij} is the observation on the jth ramet of ith clone; μ is the overall mean of a trait; C_i is the random effect of ith clone; and ε_{ij} the residual effect. Models for each trait were tested for normality and variance homogeneity using PROC MIXED and PROC UNIVARIATE. All variables except Anth, CrRT2010, and SC_{1st} met the normality assumption of residuals for Eq. [1]. These three variables were still analyzed using original data, however, because no techniques of data transformation could achieve normal distribution of their residuals. Mixed effect models were also used to conduct joint analyses of pooled data from different times or locations so that the fixed effects of time or crown position could be estimated (see Appendices for details).

Clonal repeatability (R_c^2), usually interpreted as an upper bound for broad-sense heritability (Falconer and Mackay, 1996), was expressed as Eq. [2] (Becker 1984):

$$R_c^2 = \frac{\sigma_c^2}{(\sigma_c^2 + \sigma_e^2)} \quad (2)$$

Table 4
Analysis of variance for phenological traits and susceptibility to anthracnose of 25 black walnut (*Juglans nigra* L.) clones: variance components and their probabilities, clonal repeatability estimates, and genetic, environmental, and phenotypic coefficients of variation from model [1][1].

[2]Trait	Clone		Random error		[3]CV_G(%)	[3]CV_e(%)	[3]CV_p(%)	R_c^2 ± SE
	σ^2_c	P-value	σ^2_e	P-value				
[4]FD2010	45.77	<0.001	0.47	<0.001	6.1	0.6	6.7	0.99 ± 0.01
FD2011	32.15	<0.001	0.26	<0.001	4.6	0.4	5.0	0.99 ± 0.00
FF2010	19.89	<0.001	0.31	<0.001	3.5	0.4	3.9	0.98 ± 0.01
FF2011	21.65	<0.001	0.51	<0.001	3.4	0.5	3.9	0.98 ± 0.01
MF2010	43.14	<0.001	0.43	<0.001	5.2	0.5	5.7	0.99 ± 0.01
MF2011	45.69	<0.001	0.07	<0.001	4.8	0.2	5.0	1.00 ± 0.00
CrRT2010	0.05	<0.001	0.02	<0.001	36.7	20.7	57.5	0.76 ± 0.09
CrRT2011	0.04	<0.001	0.01	<0.001	31.7	14.9	46.6	0.82 ± 0.08
Anth2011	0.33	0.001	0.21	<0.001	39.7	31.3	71.0	0.62 ± 0.11
SLA_{low}	80.08	0.011	174.94	<0.001	6.0	8.9	14.9	0.31 ± 0.09
SLA_{up}	79.89	0.006	113.43	<0.001	7.3	8.7	16.0	0.41 ± 0.10
ILA_{low}	2493.36	0.008	4520.72	<0.001	11.9	16.0	27.9	0.36 ± 0.10
ILA_{up}	1480.94	0.027	5209.13	<0.001	8.6	16.0	24.6	0.22 ± 0.08
ILM_{low}	0.11	0.020	0.30	<0.001	11.7	19.2	30.9	0.27 ± 0.09
ILM_{up}	0.21	0.019	0.57	<0.001	12.4	20.4	32.8	0.27 ± 0.09
$[C]_{low}$	1.48	0.003	1.63	<0.001	2.6	2.8	5.4	0.48 ± 0.10
$[C]_{up}$	1.73	0.002	1.70	<0.001	2.7	2.7	5.4	0.50 ± 0.10
$[N]_{low}$	0.04	0.007	0.08	<0.001	8.1	10.7	18.8	0.37 ± 0.10
$[N]_{up}$	0.05	0.003	0.06	<0.001	7.9	8.9	16.8	0.45 ± 0.10
NAR_{1st}	0.72	0.059	3.32	<0.001	5.3	11.5	16.8	0.18 ± 0.06
NAR_{2nd}	1.62	0.049	6.85	<0.001	10.7	22.0	32.7	0.19 ± 0.06
SC_{1st}	1.46×10^{-2}	0.109	0.12	<0.001	19.7	56.9	76.5	0.11 ± 0.05
SC_{2nd}	5.88×10^{-3}	0.088	0.04	<0.001	18.1	49.3	67.4	0.12 ± 0.05
Ang	26.24	0.001	18.54	<0.001	7.9	6.6	14.5	0.59 ± 0.11
Ang_{BDmax}	31.29	0.004	49.09	<0.001	9.9	12.4	22.2	0.39 ± 0.10
BD	0.03	0.007	0.07	<0.001	6.6	9.2	15.8	0.34 ± 0.10
BD_{max}	0.07	0.019	0.24	<0.001	6.3	11.4	17.7	0.24 ± 0.09
BF	3.50	0.001	2.45	<0.001	13.2	11.1	24.3	0.59 ± 0.11
BBA	64.48	0.007	142.32	<0.001	11.4	16.9	28.3	0.31 ± 0.09
DBH2009	1.03	0.003	0.89	<0.001	8.4	7.8	16.2	0.54 ± 0.11
DBH2010	1.22	0.003	0.82	<0.001	7.8	6.4	14.1	0.60 ± 0.11
DBH2011	1.28	0.003	0.89	<0.001	7.2	5.9	13.1	0.59 ± 0.11
Ht2009	3051.00	0.004	3017.79	<0.001	6.9	6.9	13.8	0.50 ± 0.10
Ht2010	5941.27	0.002	2694.15	<0.001	8.3	5.6	13.8	0.69 ± 0.10
Ht2011	6212.04	0.002	2512.80	<0.001	7.5	4.7	12.2	0.71 ± 0.10
CR2009	52.12	0.066	458.00	<0.001	2.5	7.3	9.8	0.10 ± 0.08
CR2010	178.35	0.014	590.79	<0.001	4.9	8.9	13.8	0.23 ± 0.09
CR2011	267.95	0.011	731.70	<0.001	6.5	10.7	17.1	0.27 ± 0.09
SVI2009	8.74×10^7	0.003	8.90×10^7	<0.001	19.8	20	39.8	0.50 ± 0.10
SVI2010	2.46×10^8	0.002	1.58×10^8	<0.001	20.6	16.5	37.0	0.61 ± 0.11
SVI2011	4.26×10^8	0.002	2.45×10^8	<0.001	19.5	14.8	34.2	0.63 ± 0.11

[1] The details of the model are available in materials and methods.
[2] See Table 2 for the meaning of the abbreviations.
[3] CV_G: genotypic (clonal) coefficients of variation; CV_e: coefficients of variation for error; CV_P: phenotypic coefficients of variation.
[4] The repeatability of foliation dates in 2009 could not be determined due to small sample sizes for each clone.

where σ_c^2 is the variance among clones; and σ_e^2 is the residual variance. The standard error for clonal repeatability was estimated as Eq. [3] (Becker, 1984):

$$S.E.\left(R_c^2\right) = \sqrt{\frac{2(n-1)\left(1-R_c^2\right)^2\left[1+(k-1)R_c^2\right]^2}{k^2(n-N)(N-1)}} \quad (3)$$

where N is the number of clones in this test; n is the number of individual trees; and k is the harmonic mean number of trees per clone.

Genotypic coefficients of variation (CV_G) and residual coefficients of variation (CV_e) were estimated using Eq. [4] and Eq. [5], respectively:

$$CV_G = \frac{100\sqrt{\sigma_c^2}}{\mu} \quad (4)$$

$$CV_e = \frac{100\sqrt{\sigma_e^2}}{\mu} \quad (5)$$

where μ is the clonal mean for each trait estimated by Eq. [1]. The phenotypic coefficients of variation (CV_P) were calculated as the sum of CV_G and CV_e.

Pearson's product-moment correlations (r_G) among the traits were calculated following Eq. [6] using clonal means of each trait.

$$r_G = \frac{\sigma_{C(xy)}}{\sqrt{\sigma_{c(x)}^2\sigma_{c(y)}^2}} \quad (6)$$

where $\sigma_{c(xy)}$ is the clonal covariance component between trait x and y; and $\sigma_{c(x)}^2$ and $\sigma_{c(y)}^2$ are the clonal variance component for trait x and y, respectively. An absolute value of r_G lower than 0.35 was considered weak correlation, between 0.35 and 0.70 as moderate correlation, and greater than 0.70 as strong correlation. The equation for genetic correlation (Becker, 1984) was identical with eq. [6], so Pearson's correlations are also the upper-bound of genetic correlations. Pearson's correlations were also analyzed by sexual morphs (PT vs. PG; Appendices). Standard errors (S_r) for r_G were calculated following Eq. [7]:

$$S_r = \sqrt{\frac{1-r_G{}^2}{n-2}} \quad (7)$$

Where n is the number of clones corresponding to each r_G.

Table 5
Pearson's correlations among phenological, physiological, and morphological traits of black walnut (*Juglans nigra* L.). Colors are indicative of correlation coefficients: dark red means 1, white means 0, and dark blue means −1. ***: P < 0.001; **: P < 0.01; *: P < 0.05.

Trait[1]	FD2009	FD2010	FD2011	FF2010	FF2011	MF2010	MF2011	CrRT2010	CrRT2011	Anth2011	SLA_{up}	SLA_{low}	ILA_{up}	ILA_{low}	ILM_{up}	ILM_{low}	
FD2009																	FD2009
FD2010	0.84***																FD2010
FD2011	0.84***	0.83***															FD2011
FF2010	0.07	0.01	-0.06														FF2010
FF2011	0.03	-0.11	0.14	0.4*													FF2011
MF2010	0.49*	0.65***	0.37	0.24	-0.48*												MF2010
MF2011	0.74***	0.82***	0.77***	-0.05	-0.37	0.76***											MF2011
CrRT2010	0.36	0.38	0.58**	-0.09	0.25	0.01	0.35										CrRT2010
CrRT2011	0.17	0.16	0.25	-0.18	0.19	-0.06	0.07	0.64***									CrRT2011
Anth2011	-0.13	-0.06	-0.17	0.3	0.1	0.02	-0.2	0.11	-0.15								Anth2011
SLA_{up}	-0.32	-0.45*	-0.39	-0.16	0.07	-0.4*	-0.41*	0.2	0.06	0.45*							SLA_{up}
SLA_{low}	-0.31	-0.49*	-0.44*	-0.07	0.16	-0.37	-0.45*	0.1	0.01	0.41*	0.76***						SLA_{low}
ILA_{up}	-0.14	-0.05	0.02	-0.17	0.05	-0.05	-0.04	-0.05	0.21	-0.08	-0.39	-0.07					ILA_{up}
ILA_{low}	0.23	0.18	0.14	0.02	0.32	-0.08	-0.06	0.23	0.57**	0.12	0.04	0.07	0.34				ILA_{low}
ILM_{up}	0.08	0.2	0.21	-0.07	-0.02	0.14	0.2	-0.13	0.16	-0.3	-0.76***	-0.47*	0.86***	0.27			ILM_{up}
ILM_{low}	0.36	0.4	0.34	0.06	0.23	0.09	0.16	0.18	0.54**	-0.08	-0.33	-0.41*	0.36	0.88***	0.48*		ILM_{low}
$[N]_{up}$	0.01	-0.19	-0.04	0.12	0.18	-0.1	-0.2	0.23	0.09	0.31	0.39	0.40*	-0.24	-0.17	-0.44*	-0.35	$[N]_{up}$
$[N]_{low}$	-0.07	-0.32	-0.23	-0.06	0.03	-0.19	-0.32	0.13	0.12	0.28	0.55**	0.48*	-0.36	-0.15	-0.57**	-0.36	$[N]_{low}$
$[C]_{up}$	0.31	0.18	0.42*	0.07	0.04	0.2	0.27	0.59**	0.37	0.45*	0.13	0.11	-0.05	0.11	-0.13	0.05	$[C]_{up}$
$[C]_{low}$	0.18	-0.03	0.27	0.12	0.17	0.05	0.14	0.58**	0.53**	0.35	0.24	0.13	-0.08	0.18	-0.16	0.13	$[C]_{low}$
NAR_{1st}	-0.46	-0.40	-0.44	0.31	-0.17	0.25	-0.34	-0.17	-0.03	0.10	0.17	0.36	0.39	0.01	0.06	-0.13	NAR_{1st}
NAR_{2nd}	0.19	0.14	0.21	0.05	0.10	-0.33	0.19	0.20	-0.23	0.45	0.22	0.15	-0.68*	-0.50	-0.66*	-0.54	NAR_{2nd}
SC_{1st}	-0.13	-0.07	-0.09	0.53	-0.15	0.25	-0.03	0.06	-0.40	0.18	-0.13	-0.04	-0.49	-0.30	-0.19	-0.24	SC_{1st}
SC_{2nd}	0.17	0.09	0.13	0.24	0.03	-0.20	0.10	0.20	-0.40	0.67*	0.28	0.15	-0.74**	-0.30	-0.71**	-0.37	SC_{2nd}
BF	-0.28	-0.18	-0.17	0.07	0.08	-0.36	-0.22	-0.28	-0.22	-0.32	-0.32	-0.22	0.01	-0.3	0.18	-0.15	BF
Ang	0.27	0.12	0.43*	-0.21	0.19	-0.04	0.15	0.56**	0.48*	-0.05	0.05	0.23	0.27	0.25	0.12	0.11	Ang
Ang_{BDmax}	0.07	-0.06	0.26	-0.28	0.12	-0.15	0.01	0.57**	0.59**	-0.05	0.14	0.17	0.2	0.27	0.04	0.16	Ang_{BDmax}
BD	-0.17	-0.08	-0.11	-0.15	0	-0.11	-0.1	-0.04	0.12	-0.07	0.12	0.01	0.39	0.1	0.22	0.09	BD
BD_{max}	-0.31	-0.19	-0.23	-0.17	-0.1	-0.07	-0.14	-0.13	0.2	-0.26	-0.04	-0.09	0.51*	0.08	0.33	0.12	BD_{max}
BBA	-0.39	-0.22	-0.36	0.1	-0.06	-0.02	-0.22	-0.07	0.22	0.1	-0.12	0	0.42*	0.14	0.33	0.16	BBA
DBH2009	-0.57**	-0.45*	-0.58**	0.24	0.11	-0.2	-0.51**	-0.61**	-0.28	-0.04	-0.16	-0.07	0.17	-0.21	0.19	-0.15	DBH2009
DBH2010	-0.54**	-0.37	-0.52**	0.22	0.09	-0.18	-0.46*	-0.59**	-0.27	-0.06	-0.22	-0.14	0.23	-0.22	0.25	-0.12	DBH2010
DBH2011	-0.53**	-0.37	-0.5*	0.2	0.1	-0.19	-0.45*	-0.58**	-0.24	-0.05	-0.2	-0.16	0.24	-0.2	0.26	-0.09	DBH2011
Ht2009	-0.33	-0.17	-0.24	-0.24	-0.04	-0.19	-0.23	-0.51**	-0.29	-0.19	-0.03	-0.16	0.11	-0.2	0.14	-0.11	Ht2009
Ht2010	-0.22	-0.04	-0.19	-0.14	-0.03	-0.04	-0.13	-0.56**	-0.33	-0.27	-0.19	-0.26	0.08	-0.27	0.17	-0.14	Ht2010
Ht2011	-0.29	-0.09	-0.28	-0.13	-0.03	-0.06	-0.25	-0.61**	-0.3	-0.21	-0.24	-0.3	0.25	-0.18	0.33	-0.04	Ht2011
CR2009	-0.46*	-0.27	-0.46*	-0.08	-0.24	-0.14	-0.31	-0.32	-0.04	0.25	-0.03	-0.05	0.45*	0.2	0.36	0.23	CR2009
CR2010	-0.24	-0.06	-0.18	0.01	-0.14	0.13	0.04	0.02	0.36	0.24	0.04	0.06	0.39	0.25	0.31	0.24	CR2010
CR2011	-0.23	-0.15	-0.08	0.02	-0.03	0.05	0.06	-0.24	0.12	-0.46*	-0.54**	-0.34	0.49*	0.06	0.64***	0.24	CR2011
SVI2009	-0.51*	-0.38	-0.52**	0.07	0.07	-0.21	-0.47*	-0.64***	-0.28	-0.15	-0.15	-0.07	0.18	-0.21	0.21	-0.15	SVI2009
SVI2010	-0.43*	-0.27	-0.43*	0.07	0.05	-0.14	-0.37	-0.62***	-0.28	-0.2	-0.24	-0.16	0.21	-0.23	0.26	-0.13	SVI2010
SVI2011	-0.42*	-0.26	-0.45*	0.08	0.09	-0.15	-0.43*	-0.63***	-0.27	-0.18	-0.22	-0.17	0.25	-0.18	0.31	-0.09	SVI2011

	$[N]_{up}$	$[N]_{low}$	$[C]_{up}$	$[C]_{low}$	NAR_{1st}	NAR_{2nd}	SC_{1st}	SC_{2nd}	BF	Ang	Ang_{BDmax}	BD	BD_{max}	BBA	
$[N]_{low}$	0.86***														$[N]_{low}$
$[C]_{up}$	0.55**	0.37													$[C]_{up}$
$[C]_{low}$	0.58**	0.52**	0.79***												$[C]_{low}$
NAR_{1st}	0.18	0.05	-0.21	-0.03											NAR_{1st}
NAR_{2nd}	0.76	0.65	0.47	0.50	0										NAR_{2nd}
SC_{1st}	-0.01	-0.08	-0.21	-0.08	0.10	0.33									SC_{1st}
SC_{2nd}	0.71	0.56	0.51	0.48	-0.14	0.87	0.53								SC_{2nd}
BF	-0.26	-0.31	-0.55**	-0.43*	0.21	0.15	0.53	0.05							BF
Ang	0.35	0.15	0.7***	0.54**	-0.15	0.15	-0.27	0.13	-0.37						Ang
Ang_{BDmax}	0.35	0.26	0.76***	0.61**	-0.04	0.10	-0.35	0.07	-0.44*	0.89***					Ang_{BDmax}
BD	-0.16	-0.29	-0.24	-0.17	0.25	-0.40	-0.33	-0.51	-0.07	0.05	0.01				BD
BD_{max}	-0.18	-0.25	-0.34	-0.17	0.38	-0.50	-0.39	-0.71	0.13	-0.03	-0.01	0.8***			BD_{max}
BBA	-0.17	-0.21	-0.32	-0.13	0.39	-0.29	-0.01	-0.25	0.21	-0.28	-0.19	0.4*	0.66***		BBA
DBH2009	-0.12	-0.19	-0.63***	-0.41*	0.43	-0.20	0.14	-0.27	0.51**	-0.53**	-0.53**	0.41*	0.51**	0.57**	DBH2009
DBH2010	-0.18	-0.26	-0.64***	-0.45*	0.46	-0.22	0.12	-0.30	0.52**	-0.54**	-0.52**	0.45*	0.54**	0.59**	DBH2010
DBH2011	-0.19	-0.28	-0.62**	-0.43*	0.45	-0.23	0.09	-0.30	0.5*	-0.52**	-0.49*	0.47*	0.55**	0.59**	DBH2011
Ht2009	-0.39	-0.33	-0.59**	-0.4*	0.06	-0.30	-0.14	-0.45	0.31	-0.4*	-0.44*	0.45*	0.36	0.11	Ht2009
Ht2010	-0.31	-0.37	-0.66***	-0.54**	0.08	-0.31	-0.15	-0.48	0.42*	-0.4*	-0.53**	0.42*	0.38	0.12	Ht2010
Ht2011	-0.31	-0.34	-0.64***	-0.52**	0.25	-0.34	-0.21	-0.51	0.37	-0.46*	-0.5*	0.46*	0.47*	0.3	Ht2011
CR2009	-0.34	-0.27	-0.31	-0.28	0.23	-0.26	0.05	-0.13	0.12	-0.43*	-0.23	0.4*	0.46*	0.69***	CR2009
CR2010	-0.26	-0.26	-0.11	0.07	0.38	-0.09	-0.12	-0.25	-0.04	-0.11	-0.06	0.43*	0.46*	0.66***	CR2010
CR2011	-0.64***	-0.6**	-0.4*	-0.22	-0.07	-0.56	-0.03	-0.65	0.33	-0.18	-0.19	0.26	0.51**	0.58**	CR2011
SVI2009	-0.22	-0.25	-0.67***	-0.48*	0.28	-0.26	0.01	-0.38	0.49*	-0.49*	-0.53**	0.47*	0.52**	0.45*	SVI2009
SVI2010	-0.24	-0.32	-0.69***	-0.54**	0.30	-0.28	0.00	-0.42	0.52**	-0.47*	-0.54**	0.48*	0.52**	0.44*	SVI2010
SVI2011	-0.26	-0.32	-0.69***	-0.56**	0.35	-0.34	-0.05	-0.47	0.47*	-0.49*	-0.53**	0.51*	0.55**	0.5*	SVI2011

[1]See Table 2 for the meaning of the abbreviations, and Table A.5 for standard errors.

[1]See Table 2 for the meaning of the abbreviations, and Table A.5 for standard errors.

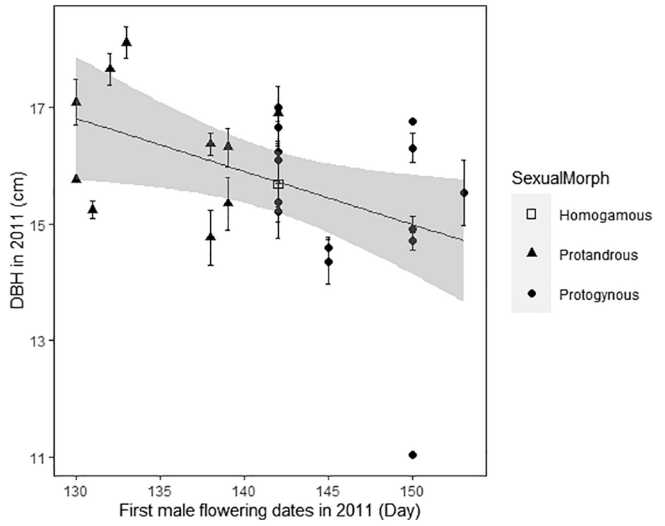

Fig. 1. Pearson's correlation between DBH and timing of male flowering (MF) in 2011, r_G = -0.45 (S_r=±0.19), p < 0.05.

3. Results

3.1. Clonal variation and repeatability

3.1.1. Phenology

Juglans nigra clones showed large variation in phenological traits (Table 3). FD of the clones spanned 18 days in 2009, 22 days in 2010, and 19 days in 2011, an average of 20 days. PT clones always leafed out three to seven days earlier than PG clones (Table A.1). FF ranged from Julian day (hereafter, Day) 122 to Day 144 in 2010 (22 days), and Day 130 to Day 144 in 2011 (14 days). MF spanned 22 days both in 2010 and 2011. On average, female flowers of PG clones were receptive two to seven days earlier than PT clones, but PT clones shed pollen about 11 days earlier than PG clones (Table A.1). Near the end of the growing season (Day 258 in 2010, and Day 273 in 2011), CrRT varied from 30 to 100% in 2010, and 20 to 100% in 2011.

Phenological traits generally had high repeatability (Table 4). Repeatability of FD, FF, and MF ranged from 0.89 ± 0.09 (mean ± standard error) to 1 ± 0. CrRT also showed high repeatability, 0.76 ± 0.09 to 0.82 ± 0.08.

3.1.2. Tree growth

The *J. nigra* clones in our study population varied greatly in growth traits (Table 3). On average, DBH increased 1.6 cm yr^{-1}, Ht increased 1.4 m yr^{-1}, and SVI increased 31 dm^3 yr^{-1} across all clones. The largest clone had a mean DBH of 14.1 cm in 2009, 16.4 cm in 2010, and 18.1 cm in 2011, and was 66.0%, 65.5%, and 63.8% larger than the DBH of the smallest clone in the three years, respectively. The tallest clone was, on average, 60.6%, 50.6%, and 59.9% taller than the shortest clone in 2009, 2010, and 2011, respectively. CR of the widest clone was 20.5%, 29.3%, and 58.2% wider than the narrowest clone in 2009, 2010, and 2011, respectively. As for SVI, the largest clone was 347%, 315%, and 332% greater than the smallest clone in 2009, 2010, and 2011, respectively. Genotypic coefficient of variation among clones (CV_G, Table 4) for tree growth traits was <10% for most traits except for SVI (19.5% to 20.6%). PT clones were 8.6%, 7.3%, and 7.2% larger in average DBH and 18.0%, 15.6%, and 17.1% larger in average SVI than PG clones in 2009, 2010, and 2011, respectively (Table A.1).

Clonal repeatability (R_c^2) of tree growth traits was fairly stable from 2009 to 2011 (Table 4). Moderate to high R_c^2 was observed across years for DBH (0.54 ± 0.11 to 0.60 ± 0.11), Ht (0.50 ± 0.10 to 0.71 ± 0.10), and SVI (0.50 ± 0.10 to 0.63 ± 0.11). The R_c^2 of CR was relatively low, with the highest value 0.27 ± 0.09 in 2011.

3.1.3. Leaf morphological and physiological traits

Juglans nigra clones in the study population displayed great variation in leaf morphological and physiological traits within and across crown positions (Tables 3 and A2). At the tree-level, leaves in the mid-upper crown had larger area (ILA_{up}: 449.1 ± 7.2 cm^2 versus ILA_{low}: 416.9 ± 7.6 cm^2; p = 0.031) and heavier weight (ILM_{up}: 3.7 ± 0.1 g versus ILM_{low}: 2.8 ± 0.1 g; p < 0.001) than those in the lower crown across all clones. The interactions between crown position and clone for ILA and ILM (Table A.2) were due to eight clones expressing higher mean ILA_{low} than ILA_{up}, and three clones having higher mean ILM_{low} than ILM_{up}. Leaves in the lower crown had higher SLA than leaves in the mid-upper crown (SLA_{low}: 148.8 ± 1.4 $cm^2 \cdot g^{-1}$versus SLA_{up}: 122.4 ± 1.2 $cm^2 \cdot g^{-1}$; p < 0.001). Leaves in the mid-upper crown also had higher nitrogen ($[N]_{up}$: 2.82 ± 0.03% versus $[N]_{low}$: 2.57 ± 0.03%; p < 0.001) and carbon concentration ($[C]_{up}$: 48.04 ± 0.16% versus $[C]_{low}$: 46.21 ± 0.16%; p < 0.001) than leaves in the lower crown. The average of tree-level NAR was 15.9 ± 0.2 and 11.9 ± 0.3 μmol s^{-1} m^{-2} in the two rounds of measurement, respectively. The SC was 0.62 ± 0.03 and 0.42 ± 0.02 $molH_2O \cdot m^{-2} \cdot s^{-1}$ in the two rounds of measurement, respectively. Clonal effect was marginally significant for NAR and insignificant for SC at $\alpha = 0.05$.

Although we observed differences in mean values of leaf traits between the mid-upper and lower crown, the CV_G of the two crown positions were similar across most traits (Table 4). Among all traits, foliar [C] showed smallest CV_G (lower crown: 2.6%, mid-upper crown: 2.7%), smaller than that of foliar [N] (lower crown: 8.1%, mid-upper crown: 7.9%). For traits that were only measured in one crown position, NAR had CV_G of 5.3 and 10.7 for the 1st and 2nd measurement, respectively; SC had CV_G of 19.5 and 19.7 for the 1st and 2nd measurement, respectively; and anthracnose severity was 39.7%.

Leaf traits displayed weak to moderate R_c^2 (Table 4). SC had the lowest R_c^2 among all leaf traits (0.11 ± 0.05 and 0.12 ± 0.05). NAR had R_c^2 of 0.18 ± 0.06 and 0.19 ± 0.06. ILAs and ILMs had R_c^2 ranging from 0.22 ± 0.08 to 0.41 ± 0.10, while foliar [C] and [N] showed moderate R_c^2 (0.37 ± 0.10 to 0.50 ± 0.10). Anthracnose scores also had moderate R_c^2 (0.62 ± 0.11).

3.1.4. Crown architecture

Juglans nigra clones varied considerably in crown architectural traits (Table 3). Ang ranged from 47.9° to 79.6°, and Ang_{BDmax} varied between 29.5° and 73.3°. BD ranged from 1.82 cm to 3.69 cm, and BD_{max} ranged from 2.97 cm to 5.65 cm. BF extended from 7.8 m^{-1} to 20.4 m^{-1}, and BBA was between 41.7 cm^2 m^{-1} and 112.1 $cm^2 \cdot m^{-1}$. PT clones on average had one more branch per meter than PG clones (Table A.1).

Crown architecture traits had low to moderate R_c^2 (Table 4). The CV_G of most crown architectural traits was below 10%, except BF and BBA. Diameter-related variables BD, BD_{max}, and BBA, showed low R_c^2 (0.24 ± 0.09 to 0.34 ± 0.10). BF, Ang, and Ang_{BDmax} showed moderate R_c^2, from 0.39 ± 0.10 to 0.59 ± 0.11.

3.2. Pearson's correlations

Correlations among traits were calculated in two parallel analyses; sex morphs were 1) combined and 2) kept separate. In general, the two analyses confirmed each other, although combined correlations were often stronger than those correlations for morphs analyzed separately. Results from the combined analysis will generally be presented, although some discrepancies between the two analyses will be also discussed. Standard errors for Pearson's correlation coefficients in Table 5, A.3, and A.4 were presented in Table A.5.

All phenological traits were positively correlated in the combined (Table 5) and morph-specific (Table A.3 and A.4) analyses. For example, FD of all three years were moderately to strongly correlated with MF (For MF2011, r_G= 0.74 to 0.82 (all three p < 0.001); for MF2010, r_G= 0.37 to 0.65 (two of three p < 0.05). FF was moderately to strongly

positively correlated with FD (FF2011 vs FD in all three years, r_G= 0.66 to 0.79 for PG clones, all three $p < 0.05$, Table A.3; r_G= 0.51 to 0.60 for PT clones, all three $p > 0.05$, Table A.4). The correlations differed by sexual morph for between FF and MF, being strongly and positively correlated in PG clones ($r_G = 0.84$ in 2010, and$r_G = 0.89$ in 2011, both $p < 0.001$, Table A.3), but insignificantly and positively correlated in PT clones ($r_G = 0.36$ in 2010 and$r_G = 0.62$ in 2011; Table A.4).

Most phenological traits were also correlated with growth traits (Table 5). FD were moderately and negatively correlated with DBH (r_G = -0.37 to −0.58, seven of nine $p < 0.05$ in the three-year × three-year matrix of correlation coefficients) and SVI (r_G = -0.26 to −0.52, six of nine $p < 0.05$ in the three-year × three-year matrix of correlation coefficients). Ht and CR were also negatively correlated with FD, though most correlations were non-significant. FF showed weak positive correlations with DBH and SVI. But the correlations between MF2011 and DBH were moderately negative (r_G = -0.45 to −0.51, all three $p < 0.05$; Fig. 1), as was the correlation between MF2011 and SVI (r_G = -0.37 to −0.47, two of three $p < 0.05$). CrRT2010 showed moderate negative correlations with DBH, Ht, and SVI across three years (r_G = -0.51 to −0.64, all $p < 0.05$).

FD in all three years, FF and MF in 2011, and CrRT in both 2010 and 2011 were moderately to strongly and positively correlated with ILA_{low} and ILM_{low} for PG clones ($r_G = 0.42$ to 0.76, eight of 14; $p < 0.05$ in the two-variable × seven-variable correlation coefficient matrix, Table A.3), but these correlations in PT clones were weak and mixed (having both positive and negative correlations, Table A.4). FDs were negatively correlated with SLA_{up} and SLA_{low}, ($r_G = -0.31$ to −0.49, three of six $p <$ 0.05 in the two-position × three-year correlation coefficient matrix), so were MF ($r_G = -0.37$ to −0.45, three of four $p < 0.05$ in the two-position × two-year correlation coefficient matrix). The CrRT in 2010 and 2011 were moderately positively correlated with foliar [C] in both mid-upper crown and lower crown ($r_G = 0.37$ to 0.59, three of four $p < 0.01$ in the two-year × two-position correlation coefficient matrix, Table 5), and the same correlations were especially strong in PT clones ($r_G = 0.75$ to 0.90, all four $p < 0.05$, in the two-year × two-position correlation coefficient matrix, Table A.4). Susceptibility to anthracnose was found to have inconsistent and weak correlations with all phenological traits.

On the other hand, most correlations between phenological traits and crown architectural traits were weak and insignificant (Table 5). The most notable strong correlations were between CrRT and Ang and Ang_{BDmax}, (r_G= 0.48 to 0.59, all four $p < 0.05$, in the two-year × two-variable correlation coefficient matrix).

Correlations among leaf traits often, but not always, depended on crown position. ILA was significantly and positively correlated with ILM in both crown positions ($r_G = 0.86$ and 0.88, both $p < 0.001$) (Table 5). ILA and ILM were negatively correlated with $[N]_{up}$ and $[N]_{low}$, especially ILM_{up} (r_G = -0.44 and −0.57, both $p < 0.05$). $[N]_{up}$ and $[N]_{low}$ were moderately and positively correlated with $[C]_{up}$ and $[C]_{low}$, (r_G = 0.37 to 0.58, three of four $p < 0.01$ in the two-position × two-position correlation coefficient matrix). SLA_{up} and SLA_{low} were moderately and positively correlated with $[N]_{up}$ and $[N]_{low}$ ($r_G = 0.39$ to 0.55, three of four $p < 0.05$ in the two-position × two-position correlation coefficient matrix). Anthracnose severity was moderately correlated with SLA_{up} and SLA_{low} ($r_G = 0.41$ and 0.45, respectively, and both $p < 0.05$).

Among all leaf traits, only foliar [C] and ILA were significantly correlated with crown architectural traits (Table 5). Notably, foliar $[C]_{up}$ and $[C]_{low}$ were moderately and negatively correlated with BF (r_G = −0.43 and −0.55, both $p < 0.05$), but moderately to strongly positively correlated with Ang and Ang_{BDmax}, (r_G= 0.54 to 0.76, all four $p < 0.05$ in the two-position × two-variable correlation coefficient matrix). ILA_{up} was moderately correlated with BD_{max} and BBA, (r_G= 0.42 and 0.51, both $p < 0.05$). No significant correlations between net CO_2 assimilation, or stomatal conductance and other traits, especially growth traits were found.

Foliar [C] was the most strongly correlated leaf trait with stem growth traits (Table 5). $[C]_{up}$ and $[C]_{low}$ were moderately negatively correlated with DBH, Ht, and SVI (r_G = -0.40 to −0.69, all 18$p < 0.05$ in the two-position × three-variable × three-year correlation coefficient matrix). $[N]_{up}$ and $[N]_{low}$ were also negatively correlated with DBH, Ht, and SVI (Table 5), but the correlations were stronger in PT clones than in PG clones (Table A.3 and A.4). ILA_{up} and ILM_{up} were positively and moderately correlated with CR ($r_G = 0.39$ to 0.49 for ILA_{up}, two of three $p < 0.05$).

Crown architectural traits were moderately correlated with each other and moderately correlated with tree growth traits (Table 5). BF was negatively correlated with Ang and Ang_{BDmax} (r_G = -0.37 and −0.44, $p < 0.05$ for BF and Ang_{BDmax}), though the correlations were stronger in PT clones (r_G = -0.64 and −0.66, both $p < 0.05$, Table A.3 and A.4). BF was weakly correlated with BD and BD_{max}. BD, BD_{max}, and BBA were moderately positively correlated with DBH, Ht, CR, and SVI (most $r_G = 0.4$ to 0.69 with $p < 0.05$ in the three-variable × four-variable × three-year correlation coefficient matrix). BF was also moderately positively correlated with growth traits, especially DBH and SVI ($r_G = 0.47$ to 0.52, all six $p < 0.05$). Ang and Ang_{BDmax} were negatively correlated with DBH, Ht, and SVI (r_G = -0.40 to −0.54, all 18$p < 0.05$ in the two-variable × three- variable × three-year correlation coefficient matrix).

4. Discussion

4.1. Broad-sense heritability

Estimates of heritability for traits measured in this study (Table 4) were higher than those from other studies of *J. nigra* and other tree species. Previous estimates of narrow-sense heritability for DBH based on half-sib families ranged from 0.25 to 0.40, and estimates for height ranged from 0.33 to 0.45 (Beineke and Masters, 1973; Rink and Stelzer, 1981). This result was unsurprising because broad-sense heritability is always greater or equal to narrow-sense heritability (Otto, 2001). Our estimate of heritability of Ang (0.59 ± 0.11) was considerably higher than the previous estimate of 0.20 for *J. nigra* (Beineke and Masters, 1973), which was based on trees that were only four years old, but within the range reported in Scots pine, from 0.12 to 0.76 (Haapanen et al., 1997). The heritability for branch diameter was low (0.24) in Scots pine (Haapanen et al., 1997); our result was similar ($R_c^2 = 0.34 \pm 0.10$). An R_c^2 of 0.41 for branch number was reported by Beineke and Masters (1973), lower than the estimates for the equivalent metric, BF (0.59 ± 0.11), used in this study. McKown et al. (2014) reported heritabilities of 0.18 ± 0.03 and 0.45 ± 0.03 for maximum photosynthetic rate and stomatal conductance in *Populus trichocarpa*, respectively, similar to that of NAR (0.18 ± 0.06 and 0.19 ± 0.06), but higher than SC (0.11 ± 0.05 and 0.12 ± 0.05) in this study.

Heritability estimates for tree traits can, however, vary over years (McKenna and Coggeshall, 2018), an observation supported by our results. The unusually high level of environmental uniformity maintained within our study area probably contributed to the generally high heritability estimates and low coefficients of variability observed overall.

In general, traits with moderate to high R_c^2 and that are moderately to strongly correlated with stem growth were considered for inclusion in the ideotype. Despite low R_c^2 (0.34 ± 0.10), BD was significantly correlated with stem growth (Table 5). In addition, BD affects timber quality. Therefore, BD was included as an ideotype component.

4.2. Correlations among phenological traits and stem growth traits

The correlation between date of MF and FF was negative when data from sexual morphs was combined (Table 5), but positive when morphs were analyzed separately (Table A.3 and A.4). We believe that this is an example of an analytical artifact caused by a phenomenon called “Simpson’s paradox” (Good and Mittal, 1987) and that the morph-specific correlations, i.e., positive correlations, are more accurate.

The generally positive correlations between phenological traits

probably indicated that various *J. nigra* phenological traits are regulated by a common set of genes with strong influence, which was also reflected by those traits' high broad-sense heritabilities. Positive correlations among FD, MF, and FF dates were also found in the *J. nigra* studies of Morrissey and Gustafson (1989) in Nebraska, Warmund and Coggeshall (2009) in Missouri, and in Persian walnut (*J. regia* L.) (Solar et al., 2001) in Slovenia. Bud break and flowering phenology in breeding populations of *Corylus avellane* (Yao and Mehlenbacher, 2000) were also strongly correlated.

Foliation is an essential annual event for temperate woody plants, and it is sensitive to shifting climate. If foliation starts too early, trees are in danger of exposure to late frost, which can significantly damage or kill the vegetative and reproductive buds, slowing growth and degrading form over time (Beineke et al., 1991). *Juglans nigra* is susceptible to frost once buds break (Tryon and True, 1964), so late flushing selections have been preferred by breeders, even though Beineke (1975) reported the association between FD and growth in *J. nigra* was near zero ($r = 0.02$). Conversely, our analysis showed that earlier leafing clones tended to have faster growth (Table 5), although late spring frosts did not occur in any of the three years of our study. Early foliating genotypes of *J. regia* had larger trunk diameter than later leafing ones (Solar et al., 2001), in accordance with our findings in *J. nigra*.

Foliation date changes year to year depending on chilling and rates of spring warming, but relative foliation date within a population is highly consistent (Zhao et al., 2017). Thus, genotypes that leaf out earlier are always at higher risk of frost injury in the spring than those that leaf out later. Spring frost injury is associated with growth reduction in *J. nigra* (Leites et al., 2019). The best age to assess phenology and other traits of *J. nigra* has not been determined empirically. Phenological traits have high heritability in general, but there is evidence that in some temperate deciduous species juvenile trees show an earlier phenology than co-occurring adults (Augspurger and Bartlett, 2003). These results may not be relevant to our study as all trees in our study were the same age and at sexual maturity, and much of the difference in phenology observed by Augspurger and Bartlett (2003) was attributed to temperature differences caused by atmospheric effects interacting with canopy structure. The effects of ontogeny and development on trait correlations remains an open question in *J. nigra*, but it is helpful to assess phenological traits as soon as the trees become sexually mature, because it is easier to observe leaves and flowers when the trees are short.

4.3. Correlations among physiological traits and stem growth

Foliar nitrogen and carbon concentrations are important for tree growth. The negative correlations that we observed between foliar [C] and [N] and stem growth, and between CrRT and stem growth, may indicate that fruits were a stronger sink than the stem (Smith and Samach, 2013), at least at the time when the leaf samples were collected (between the end of July and middle of August). Approaching the end of the growing season, the carbon sink strength toward stem growth generally weakens as sink strength increases toward both root and fruit development (Oliver and Larson, 1990; Pinney et al., 1998). *Juglans nigra* has particularly large and oily fruits and seeds that are energy-dense. In late-summer and fall, the carbon uptake in Persian walnut depends mostly on the availability of fruits as effective sinks where photosynthates can be stored (Moscatello et al., 2017). Corroboration of this sink shift is indicated by the strong positive correlation between foliar [C] at both crown positions and size of fruits and seeds, and also possibly by the positive correlation between CrRT and size of fruits and seeds (Pang, 2014). Strong correlations, whether negative, such as those between foliar [C] and BF and between foliar [C] and BD and BD_{max}, or positive, such as the correlations between foliar [C] and Ang and Ang_{BDmax}, may have been the result of genetic linkage, epistatic interaction, or the presence of pleiotropy among these traits. It is also likely that some correlations we observed may change in other populations under different environmental conditions (Falconer and Mackay, 1996).

Clonal effect for NAR was marginally significant, and SC insignificant (Table 4). The low clonal effect of these two traits was probably due to high variation among leaves within trees versus low variations among clones. For instance, we observed about 50% within-tree variation versus about 7% clonal variation for NAR. Todhunter (1981) also reported insignificant clonal effect of photosynthetic rate in seedlings of 12 *J. nigra* clones. In addition, no correlations were found by Todhunter (1981) between gas exchange variables and growth traits. Photosynthetic rate was also weakly related to growth rate in seedlings in provenance tests of *Pinus contorta* (Sweet and Wareing, 1968) and *Picea sitchensis* (Ludlow and Jarvis, 1971). It is possible that the display of leaf area, i.e., the surface of light interception, played a more important role in tree growth than photosynthesis itself (Todhunter, 1981). A negative, but insignificant, correlations between SLA and growth traits was also seen in Todhunter's study (1981) of seedlings of *J. nigra* clones.

4.4. Correlations among crown architectural traits and stem growth

Crown architectural traits are commonly related to stem growth. Solar et al. (2001) reported that branch density (frequency) was positively correlated with stem diameter and tree height in *J. regia*; our results were similar (Table 5). The amount of stemwood produced in *Pinus contorta* and *Picea sitchensis* was controlled by annual height growth and number of lateral branches produced per unit shoot length (Cannell, 1974). Larger Douglas–fir trees had higher branch densities per unit length of annual segment (Weiskittel et al., 2007). In these examples, the authors suggested that branch frequency was positively correlated with stem growth. In our study, positive correlations between branch diameter variables (BD, BD_{max}, and BBA) and tree growth (DBH, Ht, and SVI) indicated that larger branches and higher branch frequency led to faster growth, likely because of higher leaf biomass and area (Zellers et al., 2012). Positive correlations between branch attributes and stemwood production have also been reported in Sitka spruce (*Pinus sitchensis*) (Cannell et al., 1983) and lodgepole pine (*Pinus contorta*) (Thompson, 1985).

Correlations among crown architectural traits and tree growth have important implications for crown ideotypes. Acute branch angle is associated with fast stem growth (Table 5), thus narrow crowns and rapid growth may be combined. Yet acute branch angles self-prune poorly, lead to larger wounds that occlude slowly when silviculturally pruned, and may eventually result in more defects in the wood at maturity (McKenna and Coggeshall, 2018). Large branches with acute angles also tend to have a greater risk of breakage from strong winds than branches with flatter (more horizontal) angles in *J. nigra* (Dr. William Reid, Pecan Experiment Field, Chetopa, KS 67336, USA, personal communication). Furthermore, death or breakage of large branches are more likely than small branches to provide infection courts and allow decay to spread into the center of the trunk (Shortle and Dudzik, 2012), causing concerns for timber quality. Overall, a crown architecture of many small branches with more horizontal angles would be favored for wood quality, although that crown architecture may sacrifice juvenile growth due to the associations among large branch size, acute branch angle, and fast stem growth. Genetics, stand density management, optimal pruning regimes and other silvicultural methods may help mitigate these trade-offs.

4.5. Association between dichogamy and vegetative growth

The positive association between protandry and faster growth (versus protogyny) in *J. nigra* (Fig. 1) may be an evolutionary consequence of dichogamy in monoecious woody species, i.e., the reproductive costs for the two sexual morphs may be unequal. Life history traits related to sexual dimorphism is largely determined by cost of reproduction (Delph, 1999). The sizes of male woody dioecious species are usually larger than that of females (Cipollini and Whigham, 1994; Krischik and Denno, 1990; Obeso, 2002; Fang et al., 2021), probably because males invest proportionally fewer resources in reproduction, but more in maintenance and growth than females (Delph, 1999; Obeso, 1997). On average, PG clones grew larger fruits and seeds than PT clones (Pang, 2014), and the majority of varieties in the nut breeding programs of *J. nigra* are PG (Warmund and Coggeshall, 2009), indicating that in *J. nigra* PT trees may allocate more resources to vegetative growth, but less resources to reproduction than PG ones. Solar et al. (2001) reported a similar trend in *J. regia*; genotypes with larger trunk diameters also tended to be PT. Unfortunately, Solar's result was not age-specific, but reflected a cohort ranging from eight to twelve years old, so the effect of sexual morphs on tree growth could not be confidently determined. Although our sample size was small, our study may be the first to document an association between protandry and faster stem growth in *J. nigra.* Aside from differences in reproductive effort, the association between PT clones and faster stem growth may arise partly because PT genotypes initiate vegetative growth earlier, but start filling seeds later than PG genotypes during the period of leaf display. Genotypes with longer leaf display were associated with faster stem growth in *Populus trichocarpa* (McKown et al., 2014). The effects of phenology and sexual morph on *J. nigra* stem growth are undoubtedly complex and worthy of additional research.

It should be noted that MF was used as a predictor rather than FF because male flowering could be more reliably assessed in the field. Catkins were conspicuous and turned yellow when shedding pollen, but female blooms were small and green, thus were difficult to tell from the leaves at times. Higher accuracy with MF observations may also be why MF is more significant correlated to stem growth than FF.

The expression of sexual morph begins at about age 10 in *J. nigra*, by which time other traits of direct value, such as growth rate, straightness, and branch habit, can be evaluated. Thus, sexual morph has not been used as a primary selection criterion, but could be used as a deciding factor when thinning or making within-family selections. Although it is possible that selection for sexual morph in a breeding program could lead to poor pollination or a reduction in seed crop diversity, in practice this is not a concern because wild pollen is ubiquitous, the production of a population of offspring having a highly biased ratio of sexual morphs has never been observed, there is wide variation in flowering phenology within sexual morphs, and if controlled pollination is desired, pollen can be stored (Ebrahimi et al., 2018; McKenna and Coggeshall, 2018).

5. Conclusions

We found that the following traits are associated with greater early stem growth for *J. nigra* under an intensive management regime (i.e., a biomass ideotype): 1) early foliation; 2) early male flowering, i.e., usually protandry; 3) large average branch diameter; 4) high branch frequency; 5) small branch angle; 6) early leaf fall (low crown retention rate near the end of the season); 7) low foliar carbon concentration at the mid-end of the growing season; and 8) a large number of small fruits and seeds. This work, however, should be considered preliminary in the context of fine hardwood management. Development of ideotypes associated with fine timber production will require both long-term assessment of these biomass-associated traits, both at mid- and full rotation, and measurement of additional traits specific to wood quality, such as timber form, heartwood percentage, and wood color, that may only be evaluated through destructive sampling at mature tree sizes.

Likewise, the effect of dichogamy on vegetative growth of monoecious hardwood trees needs further verification. For example, our sample of *J. nigra* genotypes were previously selected for growth rate and stem form, potentially limiting the applicability of the genetic parameter estimates that were reported. While most of our estimates agreed with previous studies of *J. nigra* and other woody species, few studies have discovered or noted differences in stem growth between sexual morphs within a species. Future studies of reproductive and growth traits in other monoecious woody species should enhance our understanding of the evolutionary costs of dichogamy and potentially lead to changes in our approach to tree improvement.

CRediT authorship contribution statement

Kejia Pang: Methodology, Formal analysis, Investigation, Writing - original draft, Writing - review & editing. **Keith E. Woeste:** Methodology, Resources, Writing - review & editing, Project administration. **Michael R. Saunders:** Methodology, Investigation, Resources, Writing - review & editing. **James R. McKenna:** Methodology, Investigation, Resources. **Michael V. Mickelbart:** Methodology, Resources, Writing - review & editing. **Douglass F. Jacobs:** Methodology, Resources, Writing - review & editing. **Charles H. Michler:** Conceptualization, Resources, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A

See Figs. A1 and A2 and Tables A1-A5.

Fig. A1. Foliation stages of black walnut (*Juglans nigra* L.). From left: 1. Dormant; 2. Bud swell; 3. Green tip; 4. Leaf burst; 5. Leaf expansion. (Photo credit: Dr. William Reid, Pecan Experiment Field, Chetopa, KS 67336, USA).

Fig. A2. The severity of anthracnose in black walnut (*Juglans nigra* L.) leaves (clockwise): level 1 - no anthracnose; level 2 - light anthracnose; level 3 - severe anthracnose.

Table A1
Mean and range in phenological, physiological, morphological, and growth traits of 25 black walnut *(Juglans nigra* L.*)* clones.

Trait[1]	Sexual morph[2]	[3]N_c	[4]N_t	Tree level		Clone level		Unit
				Mean ± SE	Range	Mean ± SE	Range	
FD2009	PT	10	68	/	/	119 ± 1	115–127	day
	PG	13	97	/	/	123 ± 1	116–133	
	HM	1	6	/	/			
FD2010	PT	10	36	105 ± 1	100–118	106 ± 2	100–118	day
	PG	12	42	114 ± 1	106–121	113 ± 2	106–120	
	HM	1	3	117 ± 1	116–118			
FD2011	PT	10	75	120 ± 1	113–130	122 ± 2	113–129	day
	PG	14	113	125 ± 1	118–132	125 ± 1	120–132	
	HM	1	8	131 ± 0	131–132			
FF2010	PT	10	29	129 ± 1	126–144	130 ± 2	126–144	day
	PG	14	82	128 ± 0	122–137	128 ± 1	122–136	
	HM	1	2	129 ± 2	127–130			
FF2011	PT	10	61	141 ± 0	136–145	141 ± 1	138–145	day
	PG	14	110	133 ± 0	131–140	134 ± 1	131–140	
	HM	1	4	141 ± 1	140–142	141		
MF2010	PT	10	40	122 ± 1	116–129	121 ± 1	116–129	day
	PG	14	79	132 ± 1	127–140	132 ± 1	127–139	
	HM	1	3	123 ± 0	123–124			
MF2011	PT	10	85	134 ± 0	130–142	135 ± 1	130–142	day
	PG	14	91	146 ± 0	142–153	146 ± 1	142–153	
	HM	1	5	142 ± 0	142–142			
CrRT2010	PT	10	68	51 ± 3	25–100	61 ± 9	26–100	%
	PG	14	98	60 ± 2	25–100	63 ± 6	28–100	
	HM	1	6	42 ± 8	25–75			
CrRT2011	PT	10	67	53 ± 3	13–95	62 ± 7	18–95	%
	PG	14	96	54 ± 2	18–95	59 ± 5	38–95	
	HM	1	6	53 ± 4	40–68			
DBH2009	PT	10	68	13.1 ± 0.2	9.9–16.9	12.6 ± 0.3	10.9–14.1	cm
	PG	14	98	12 ± 0.1	8.5–15.6	11.6 ± 0.3	8.5–13.1	
	HM	1	6	11.9 ± 0.3	10.9–12.8			
DBH2010	PT	10	68	15.2 ± 0.2	12.2–18.7	14.8 ± 0.3	13–16.4	cm
	PG	14	98	14.2 ± 0.1	9.9–17.9	13.8 ± 0.4	9.9–15.4	
	HM	1	6	14.2 ± 0.4	13.1–15.2			
DBH2011	PT	10	67	16.8 ± 0.2	13.6–19.9	16.4 ± 0.4	14.8–18.1	cm
	PG	14	96	15.7 ± 0.1	11.1–19.7	15.3 ± 0.4	11.1–17	
	HM	1	6	15.7 ± 0.4	14.4–16.9			
Ht2009	PT	10	68	8.1 ± 0.1	6.5–10.1	8 ± 0.2	7.4–9.4	m
	PG	14	98	8.1 ± 0.1	5.8–9.7	7.8 ± 0.2	5.8–8.8	
	HM	1	6	8.6 ± 0.1	8.1–9			
Ht2010	PT	10	68	9.6 ± 0.1	7.2–11.3	9.4 ± 0.3	7.8–11	m
	PG	14	98	9.5 ± 0.1	7.2–10.9	9.2 ± 0.2	7.3–10.2	
	HM	1	6	9.6 ± 0.3	8.2–10			
Ht2011	PT	10	63	10.8 ± 0.1	8.1–13.2	10.7 ± 0.3	9.5–12.3	m
	PG	13	83	10.7 ± 0.1	7.7–12.2	10.4 ± 0.3	7.7–11.3	
	HM	1	6	11 ± 0.3	10.2–12			
CR2009	PT	10	68	3 ± 0	2.5–3.4	2.9 ± 0	2.7–3.1	m
	PG	14	98	2.9 ± 0	2.4–3.5	2.9 ± 0	2.6–3.1	
	HM	1	6	3 ± 0.1	2.7–3.5			
CR2010	PT	10	68	2.7 ± 0	2.1–3.4	2.7 ± 0	2.5–2.9	m
	PG	14	98	2.7 ± 0	2–3.5	2.8 ± 0.1	2.5–3.2	
	HM	1	6	2.7 ± 0.1	2.3–3.1			
CR2011	PT	10	67	2.6 ± 0	1.4–3.2	2.5 ± 0.1	2.2–2.8	m
	PG	14	96	2.5 ± 0	1.7–3.2	2.5 ± 0.1	2–3.2	
	HM	1	6	2.7 ± 0.1	2.3–3.2			
SVI2009	PT	10	67	54.4 ± 1.7	30.2–90.4	50.6 ± 3.5	37.6–74.2	dm^3
	PG	14	98	46.8 ± 1.1	16.6–84.1	42.9 ± 2.9	16.6–55.4	
	HM	1	6	48.4 ± 2.9	37.9–57.5			
SVI2010	PT	10	67	87.8 ± 2.5	51.3–130.8	81.5 ± 5.8	58.6–116.5	dm^3
	PG	14	98	76.7 ± 1.7	28.1–130.5	70.5 ± 4.7	28.1–91.1	
	HM	1	6	76.1 ± 5.4	55.3–90.9			
SVI2011	PT	10	63	121.6 ± 3.3	70.1–183.4	113.8 ± 7.3	84–159.4	dm^3
	PG	13	83	105 ± 2.3	37–177.9	97.2 ± 6.5	37–126.1	
	HM	1	6	107.3 ± 8.1	82.5–134			

Trait[1]	Sexual morph[2]	[3]N_c	[4]N_t	Tree level		Clone level		Unit
				Mean±SE	Range	Mean±SE	Range	
Anth2011	PT	10	67	1.6±0.1	1–3	1.5±0.2	1–2.4	/
	PG	14	96	1.4±0.1	1–3	1.4±0.2	1–3	
	HM	1	6	1.3±0.2	1–2			
ILA_{low}	PT	10	40	422.3±11.3	321.3–585.8	425.1±14.6	359.9–501	cm^2
	PG	14	56	399.3±10.8	193.3–553.6	409.6±16.1	322.4–485.7	
	HM	1	4	554.7±80.9	363.6–754.7			

(*continued on next page*)

Table A1 (*continued*)

Trait[1]	Sexual morph[2]	[3]N_c	[4]N_t	Tree level		Clone level		Unit
				Mean±SE	Range	Mean±SE	Range	
ILA_{up}	PT	10	43	446.8±13.3	305.1–635.2	451.7±17.1	386.1–553.3	cm^2
	PG	14	59	444±11	259.9–619.9	448.8±14.4	337.2–554.2	
	HM	1	4	521.5±28.4	478–603.3			
ILM_{low}	PT	10	40	2.8±0.1	2–4.2	2.8±0.1	2.3–3.4	g
	PG	14	56	2.8±0.1	1.4–4.3	2.8±0.1	2.2–3.7	
	HM	1	4	3.9±0.6	2.4–5			
ILM_{Up}	PT	10	43	3.6±0.1	1.9–5.8	3.6±0.2	2.7–4.5	g
	PG	14	59	3.7±0.1	2–5.6	3.8±0.2	2.8–5.6	
	HM	1	4	4.7±0.3	4–5.3			
SLA_{low}	PT	10	41	151.6±2.5	120–202.7	151.8±4.3	138.7–183.7	$cm^2 \cdot g^{-1}$
	PG	14	56	146.4±2	111.2–179.6	145.6±2.5	127.9–160.7	
	HM	1	4	144.5±4.6	134.3–153.8			
SLA_{up}	PT	10	43	125.8±3.2	100.1–214.9	125.5±3.9	110.7–147	$cm^2 \cdot g^{-1}$
	PG	14	59	123.5±2	99.7–191.1	120.6±2.6	99.7–139	
	HM	1	4	111.3±4	100.7–119.9			
$[C]_{low}$	PT	10	40	45.77±0.26	42.77–49.76	46.27±0.54	43.87–48.81	%
	PG	14	56	45.95±0.29	39.57–49.62	46.41±0.32	44.27–47.93	
	HM	1	4	45.58±0.77	43.57–46.86			
$[C]_{up}$	PT	10	42	47.47±0.2	45.09–50.73	47.91±0.35	45.93–49.51	%
	PG	14	59	47.99±0.29	41–52.24	48.37±0.44	45.52–50.5	
	HM	1	4	46.69±0.24	46.24–47.17			
$N_{[low]}$	PT	10	40	2.56±0.05	2–3.64	2.65±0.09	2.34–3.08	%
	PG	14	56	2.52±0.05	1.87–3.37	2.56±0.07	2.14–2.93	
	HM	1	4	2.29±0.24	1.57–2.57			
$N_{[up]}$	PT	10	42	2.83±0.04	2.24–3.49	2.9±0.06	2.67–3.14	%
	PG	14	59	2.77±0.05	2.08–3.68	2.79±0.08	2.47–3.46	
	HM	1	4	2.5±0.1	2.2–2.63			
NAR_{1st}	PT	4	12	16.3±0.4	13.7–17.9	16.4±0.4	15.5–17.2	$\mu mol \cdot s^{-1} \cdot m^{-2}$
	PG	8	24	15.6±0.4	10.8–17.5	15.7±0.4	14.3–17.1	
NAR_{2nd}	PT	4	12	11.1±0.5	6.0–16.8	11.1±0.9	8.6–12.7	$\mu mol \cdot s^{-1} \cdot m^{-2}$
	PG	8	23	12.2±0.5	7.0–16.1	12.3±0.5	10.5–14	
SC_{1st}	PT	4	12	0.61±0.12	0.34–1.86	0.63±0.13	0.44–0.98	$molH_2O \cdot m^{-2} \cdot s^{-1}$
	PG	8	24	0.61±0.06	0.29–1.37	0.6±0.05	0.42–0.79	
SC_{2nd}	PT	4	12	0.37±0.06	0.03–0.66	0.38±0.06	0.24–0.51	$molH_2O \cdot m^{-2} \cdot s^{-1}$
	PG	8	23	0.43±0.05	0.10–0.90	0.44±0.03	0.30–0.58	
Ang	PT	10	68	63.5±0.9	47.9–75	65.4±1.8	55.3–70.3	Degree ()
	PG	14	98	63.8±0.6	49.2–79.6	65.4±1.6	53.2–79.6	
	HM	1	6	67.7±3.1	60.7–78.6			
Ang_{BDmax}	PT	10	68	54.8±1.2	29.5–73.3	58.2±2.2	46.1–68	Degree ()
	PG	14	94	55±0.8	38.4–72.3	57.2±1.8	45.1–68	
	HM	1	6	55.3±4.1	42.3–71.4			
BD	PT	10	68	2.79±0.04	1.88–3.36	2.79±0.09	2.18–3.19	cm
	PG	14	98	2.79±0.03	1.82–3.69	2.76±0.05	2.36–2.98	
	HM	1	6	2.8±0.09	2.59–3.16			
BD_{max}	PT	10	68	4.31±0.07	2.97–5.59	4.32±0.15	3.33–4.83	cm
	PG	14	94	4.34±0.05	3.3–5.65	4.29±0.09	3.69–4.73	
	HM	1	6	4.24±0.21	3.69–4.92			
BF	PT	10	68	15.2±0.3	9.5–20.4	14.7±0.5	13.1–16.9	m^{-1}
	PG	14	98	14.1±0.3	7.8–20.1	13.7±0.6	8.9–18.4	
	HM	1	6	15.3±0.6	13.1–17.3			
BBA	PT	10	68	74.2±1.7	46.7–112.1	71.7±2.7	55.1–81.9	$cm^2 \cdot m^{-1}$
	PG	14	98	70.1±1.5	41.7–105.7	69.9±3.2	54.3–94.6	
	HM	1	6	65.5±4.8	48.9–77.9			

[1] See Table 2 for the meaning of the abbreviations.
[2] PT: protandrous; PG: protogynous; HM: homogamous.
[3] Number of clones.
[4] Number of trees.

Table A2
Analysis of variance components of traits of black walnut (*Juglans nigra* L.) clones measured at multiple times or at multiple crown positions from joint analysis model [SE1][1] or [SE2][2]: F-test and probability of fixed effects, and variance components of random effects.

Traits[3]	Fixed effects		Random effects						
	Year (Age)		Clone		Clone × Year		Random error	AR(1)	
	F	P	σ^2_c	P	σ^2_{cy}	P	σ^2_e*	ρ	P
DBH	4.27×10^3	<0.001	1.14	0.003	0.01	0.010	0.89	0.96	<0.001
Ht	676.36	<0.001	4.69×10^3	0.002	314.15	0.006	2.81×10^3	0.63	<0.001
CR	46.58	<0.001	58.13	0.097	104.22	0.002	594.27	0.34	<0.001
SVI	643.77	<0.001	2.16×10^8	0.003	2.71×10^7	<0.001	1.78×10^8	0.91	<0.001
FD	305.41	<0.001	30.93	0.001	6.97	<0.001	0.31	0.29	0.003
MF	246.89	<0.001	33.83	0.002	10.62	<0.001	0.21	1.31×10^{-3}	0.993
FF	65.49	<0.001	8.29	0.035	12.43	<0.001	0.43	-4.25×10^{-3}	0.976
CrRT	0.15	0.707	0.03	0.006	0.01	0.001	0.01	0.14	0.090
	Day		Clone		Clone × Day		Random error	AR(1)	
	F	P	σ^2_c	P	σ^2_{cy}	P	σ^2_e*	ρ	P
NAR	16.16	<0.001	0.22	0.298	2.99	<0.001	2.99	0.14	0.250
SC	12.22	<0.001	1.72×10^{-3}	0.367	0.03	<0.001	0.03	0.47	<0.001
	Crown position		Clone		Clone × Position		Random error	AR(1)	
	F	P	σ^2_c	P	σ^2_{cp}	P	σ^2_e*	ρ	P
SLA	306.02	<0.001	75.67	0.007	8.12	0.186	143.24	0.38	<0.001
ILA	5.22	0.031	778.51	0.119	1.23×10^3	0.024	4867.25	0.08	0.418
ILM	51.39	<0.001	0.07	0.130	0.10	0.024	0.44	0.22	0.026
[C]	125.36	<0.001	1.53	0.002	0.05	0.310	1.69	0.20	0.052
[N]	75.07	<0.001	0.05	0.002	0.00	.	0.07	0.30	<0.001

[1] For traits measured at multiple times, we used (Eq. SE1): $X_{ijk} = \mu + C_i + T_k + C_iT_k + \varepsilon_{ijk}$ [SE1], where X_{ijk} is the observation on the jth ramet of ith clone in kth year or day; μ is the overall mean of a trait; C_i is the random effect of ith clone; T_k is the fixed time effect of the kth year (age) or day; C_iT_k is the random interaction between clone and time (year or day); and ε_{ijk} the residual effect with autonomic correlation structure - AR(1) assumed for the random effect.

[2] For traits measured at different crown positions, we used (Eq. SE2): $X_{ijl} = \mu + C_i + P_l + C_iP_l + \varepsilon_{ijl}$ [SE2], where X_{ijl} is the observation on the jth ramet of ith clone in *l*th location; μ is the overall mean; C_i is the random effect of ith clone; P_l is the fixed effect of the *l*th crown position; C_iP_l is the random interaction between clone and crown position; and ε_{ijl} the residual effect with autonomic correlation structure - AR(1) assumed for the random effect.

[3] See Table 2 for the meaning of the abbreviations.

* P-values for σ^2_e are all < 0.001.

Table A3

Pearson's correlations among phenological, physiological, and morphological traits of protogynous black walnut (*Juglans nigra* L.) clones. Colors are indicative of correlation coefficients: dark red means 1, white means 0, and dark blue means −1. ***: P < 0.001; **: P < 0.01; *: P < 0.05.

Traits[1]	FD2009	FD2010	FD2011	FF2010	FF2011	MF2010	MF2011	CrRT2010	CrRT2011	Anth2011	SLA_{up}	SLA_{low}	ILA_{up}	ILA_{low}	ILM_{up}	ILM_{low}	
FD2009	FD2009																
FD2010	0.79**	FD2010															
FD2011	0.79**	0.81**	FD2011														
FF2010	0.39	0.24	0.24	FF2010													
FF2011	0.67*	0.66*	0.79***	0.51	FF2011												
MF2010	0.32	0.32	0.27	0.84***	0.66*	MF2010											
MF2011	0.73**	0.79**	0.93***	0.38	0.89***	0.43	MF2011										
CrRT2010	0.48	0.72**	0.76**	-0.14	0.52	0.02	0.68**	CrRT2010									
CrRT2011	0.43	0.53	0.41	-0.04	0.47	0.07	0.54*	0.68**	CrRT2011								
Anth2011	-0.11	0.01	-0.1	-0.01	-0.1	0.12	-0.28	0.01	-0.22	Anth2011							
SLA_{up}	-0.09	-0.04	-0.36	-0.28	-0.31	-0.07	-0.48	-0.1	-0.27	0.58*	SLA_{up}						
SLA_{low}	-0.11	-0.24	-0.3	-0.23	-0.22	-0.09	-0.4	0.08	-0.01	0.39	0.62*	SLA_{low}					
ILA_{up}	-0.14	0.08	0.29	-0.18	0.25	-0.12	0.31	0.35	0.41	0.06	-0.29	-0.06	ILA_{up}				
ILA_{low}	0.51	0.66*	0.42	0.08	0.54*	0.28	0.46	0.6*	0.76**	0.14	0.29	0.18	0.03	ILA_{low}			
ILM_{up}	-0.04	0.12	0.36	-0.07	0.29	-0.13	0.43	0.29	0.44	-0.27	-0.67*	-0.37	0.89***	-0.1	ILM_{up}		
ILM_{low}	0.54	0.75**	0.5	0.17	0.58*	0.28	0.59*	0.52	0.72**	-0.05	0.03	-0.21	0.09	0.92***	0.08	ILM_{low}	
$[N]_{up}$	0.15	-0.12	0.01	0.3	0.05	0.25	-0.15	-0.05	-0.19	0.58*	0.13	0.5	0.12	-0.06	-0.09	-0.26	$[N]_{up}$
$[N]_{low}$	0.08	-0.35	-0.27	0.07	-0.18	0.07	-0.43	-0.31	-0.33	0.4	0.26	0.58*	-0.01	-0.14	-0.21	-0.38	$[N]_{low}$
$[C]_{up}$	0.43	0.26	0.59*	0.27	0.4	0.26	0.39	0.45	0.1	0.37	-0.11	0.18	0.11	0.21	0.05	0.12	$[C]_{up}$
$[C]_{low}$	0.37	0.11	0.55*	0.36	0.57*	0.41	0.5	0.33	0.25	0.26	-0.1	0.22	0.11	0.12	0.03	0.02	$[C]_{low}$
NAR_{1st}	-0.36	-0.11	-0.28	0.74*	0.04	0.41	-0.04	-0.27	-0.13	0.04	-0.53	-0.17	0.36	-0.22	0.37	-0.12	NAR_{1st}
NAR_{2nd}	-0.19	-0.33	-0.36	0.03	-0.53	-0.39	-0.58	-0.24	-0.41	0.48	0.39	0.60	-0.47	-0.33	-0.63	-0.51	NAR_{2nd}
SC_{1st}	-0.06	0.12	0.12	-0.24	-0.01	-0.38	0.14	0.13	-0.06	-0.33	-0.44	0.00	0.08	-0.31	0.36	-0.27	SC_{1st}
SC_{2nd}	0.00	-0.15	-0.15	-0.17	-0.42	-0.42	-0.48	-0.05	-0.34	0.62	0.64	0.62	-0.45	-0.09	-0.73*	-0.30	SC_{2nd}
BF	-0.26	-0.2	-0.19	-0.13	-0.34	-0.46	-0.1	-0.14	-0.04	-0.44	-0.16	-0.04	-0.23	-0.59*	-0.07	-0.55	BF
Ang	0.29	0.14	0.52	-0.05	0.4	0.02	0.37	0.62*	0.35	0.14	-0.06	0.5	0.23	0.24	0.16	0.04	Ang
Ang_{BDmax}	0.16	0.08	0.41	-0.1	0.25	-0.04	0.27	0.54*	0.36	0.14	-0.06	0.42	0.19	0.25	0.12	0.07	Ang_{BDmax}
BD	-0.29	0.21	-0.1	-0.11	-0.01	0.11	0	0.18	0.23	0.37	0.25	-0.05	0.54	0.27	0.31	0.33	BD
BD_{max}	-0.39	-0.02	-0.24	-0.06	0	0.13	-0.02	0.01	0.41	0.06	0.17	0.03	0.36	0.17	0.19	0.2	BD_{max}
BBA	-0.36	-0.07	-0.27	-0.1	-0.2	-0.05	-0.1	0.02	0.49	0.07	0.35	0.17	0.07	0.14	-0.13	0.08	BBA
DBH2009	-0.63*	-0.48	-0.61*	0.14	-0.37	0.09	-0.39	-0.58*	-0.23	-0.02	-0.03	-0.19	-0.05	-0.46	-0.06	-0.35	DBH2009
DBH2010	-0.62*	-0.4	-0.56*	0.12	-0.38	0.05	-0.35	-0.54*	-0.21	-0.02	-0.05	-0.26	0.01	-0.46	0.01	-0.33	DBH2010
DBH2011	-0.59*	-0.37	-0.54*	0.12	-0.36	0.04	-0.33	-0.55*	-0.2	0.03	0.01	-0.26	-0.02	-0.45	-0.04	-0.32	DBH2011
Ht2009	-0.55	-0.36	-0.44	-0.22	-0.35	-0.14	-0.32	-0.54*	-0.49	-0.04	0.1	-0.4	-0.09	-0.51	-0.06	-0.34	Ht2009
Ht2010	-0.47	-0.38	-0.46	-0.08	-0.25	-0.05	-0.29	-0.55*	-0.42	-0.03	0.13	-0.26	-0.12	-0.46	-0.12	-0.33	Ht2010
Ht2011	-0.5	-0.3	-0.49	0.01	-0.29	0.03	-0.32	-0.61*	-0.53	0.05	0.07	-0.39	-0.02	-0.46	-0.02	-0.27	Ht2011
CR2009	-0.4	0.02	-0.25	-0.33	-0.41	-0.29	-0.24	-0.05	0.1	0.3	0.36	-0.15	0.19	0.01	0	0.07	CR2009
CR2010	-0.26	0	-0.15	-0.12	0.05	-0.04	0.05	0.05	0.52	0.2	0.57*	0.29	0.17	0.26	-0.12	0.17	CR2010
CR2011	-0.3	-0.25	0	-0.1	0.1	-0.06	0.24	0.02	0.48	-0.58*	-0.35	-0.28	0.09	-0.15	0.28	-0.02	CR2011
SVI2009	-0.63*	-0.5	-0.62*	0.01	-0.41	-0.01	-0.42	-0.61*	-0.3	-0.08	0.02	-0.22	-0.09	-0.5	-0.09	-0.39	SVI2009
SVI2010	-0.58*	-0.42	-0.57*	0.05	-0.36	0	-0.36	-0.57*	-0.25	-0.07	0.01	-0.22	-0.05	-0.48	-0.05	-0.36	SVI2010
SVI2011	-0.52	-0.32	-0.58*	0.1	-0.34	0.08	-0.37	-0.62*	-0.4	-0.01	0.04	-0.29	-0.04	-0.42	-0.04	-0.27	SVI2011

	$[N]_{up}$	$[N]_{low}$	$[C]_{up}$	$[C]_{low}$	NAR_{1st}	NAR_{2nd}	SC_{1st}	SC_{2nd}	BF	Ang	Ang_{BDmax}	BD	BD_{max}	BBA	
$[N]_{up}$	$[N]_{up}$														
$[N]_{low}$	0.85***	$[N]_{low}$													
$[C]_{up}$	0.58*	0.3	$[C]_{up}$												
$[C]_{low}$	0.66*	0.41	0.85***	$[C]_{low}$											
NAR_{1st}	0.17	-0.15	-0.24	-0.20	NAR_{1st}										
NAR_{2nd}	0.88**	0.73*	0.37	0.22	0.32	NAR_{2nd}									
SC_{1st}	0.03	-0.09	-0.18	-0.36	0.35	0.33	SC_{1st}								
SC_{2nd}	0.88**	0.74*	0.61	0.38	0.02	0.92	0.24	SC_{2nd}							
BF	-0.16	-0.17	-0.52	-0.46	0.38	0.30	0.60	0.02	BF						
Ang	0.48	0.3	0.81***	0.72**	-0.27	0.29	0.15	0.46	-0.33	Ang					
Ang_{BDmax}	0.34	0.2	0.81***	0.59*	-0.24	0.26	0.07	0.46	-0.47	0.91***	Ang_{BDmax}				
BD	-0.21	-0.35	-0.35	-0.32	0.42	-0.36	-0.19	-0.40	-0.09	-0.36	-0.31	BD			
BD_{max}	-0.14	-0.16	-0.58*	-0.35	0.48	-0.46	-0.14	-0.61	0.06	-0.49	-0.5	0.83***	BD_{max}		
BBA	-0.06	-0.03	-0.47	-0.36	0.27	-0.23	-0.42	-0.35	0.05	-0.51	-0.43	0.69**	0.85***	BBA	
DBH2009	-0.05	-0.05	-0.64*	-0.38	0.62	0.08	0.08	-0.20	0.45	-0.72**	-0.7**	0.39	0.67*	0.63*	DBH2009
DBH2010	-0.11	-0.12	-0.65*	-0.44	0.65	0.05	0.11	-0.23	0.45	-0.75**	-0.7**	0.47	0.68*	0.63*	DBH2010
DBH2011	-0.09	-0.1	-0.63*	-0.43	0.64	0.06	0.10	-0.20	0.41	-0.77**	-0.71**	0.48	0.66*	0.62*	DBH2011
Ht2009	-0.4	-0.31	-0.67*	-0.45	0.15	-0.23	0.15	-0.33	0.38	-0.73**	-0.71**	0.3	0.41	0.26	Ht2009
Ht2010	-0.25	-0.18	-0.73**	-0.41	0.35	-0.12	0.23	-0.32	0.51	-0.71**	-0.81***	0.3	0.49	0.3	Ht2010
Ht2011	-0.26	-0.22	-0.7**	-0.45	0.43	-0.12	0.13	-0.30	0.4	-0.81***	-0.81***	0.44	0.56*	0.41	Ht2011
CR2009	-0.25	-0.23	-0.32	-0.51	0.12	-0.07	-0.16	0.00	-0.1	-0.53	-0.28	0.71**	0.5	0.64*	CR2009
CR2010	-0.13	-0.09	-0.36	-0.21	0.56	-0.32	-0.42	-0.46	-0.16	-0.3	-0.23	0.75**	0.67*	0.61*	CR2010
CR2011	-0.64*	-0.46	-0.49	-0.25	-0.05	-0.78*	-0.23	-0.92**	0.09	-0.31	-0.26	0.14	0.37	0.26	CR2011
SVI2009	-0.16	-0.1	-0.74**	-0.46	0.48	-0.02	0.12	-0.28	0.51	-0.77**	-0.78**	0.36	0.64*	0.56*	SVI2009
SVI2010	-0.14	-0.1	-0.75**	-0.47	0.58	0.01	0.18	-0.27	0.55	-0.77**	-0.8**	0.41	0.67*	0.57*	SVI2010
SVI2011	-0.2	-0.16	-0.75**	-0.5	0.59	-0.05	0.14	-0.31	0.47	-0.83***	-0.82***	0.47	0.68*	0.57*	SVI2011

[1]See Table 2 for the meaning of the abbreviations, and Table A.5 for standard errors.

[1]See Table 2 for the meaning of the abbreviations, and Table A.5 for standard errors.

Table A4

Pearson's correlations among phenological, physiological, and morphological traits of protandrous black walnut (*Juglans nigra* L.) clones. Colors are indicative of correlation coefficients: dark red means 1, white means 0, and dark blue means −1. ***: P < 0.001; **: P < 0.01; *: P < 0.05.

Traits[1]	FD2009	FD2010	FD2011	FF2010	FF2011	MF2010	MF2011	CrRT2010	CrRT2011	Anth2011	SLA_{up}	SLA_{low}	ILA_{up}	ILA_{low}	ILM_{up}	ILM_{low}	
FD2009																	
FD2010	0.86**																
FD2011	0.88***	0.84**															
FF2010	-0.13	-0.01	-0.21														
FF2011	0.57	0.51	0.6	0.47													
MF2010	0.48	0.73*	0.25	0.36	0.24												
MF2011	0.85**	0.77**	0.9***	-0.1	0.62	0.31											
CrRT2010	0.49	0.34	0.63	-0.06	0.67*	-0.17	0.38										
CrRT2011	0.16	0.14	0.25	-0.35	0	-0.14	-0.15	0.62									
Anth2011	-0.17	-0.14	-0.24	0.69*	0.53	0.08	-0.2	0.25	-0.07								
SLA_{up}	-0.38	-0.65*	-0.25	-0.16	0.08	-0.85**	-0.33	0.43	0.3	0.31							
SLA_{low}	-0.4	-0.59	-0.46	-0.04	0.08	-0.47	-0.42	0.12	-0.02	0.47	0.76*						
ILA_{up}	-0.37	-0.18	-0.44	-0.18	-0.51	0.19	-0.52	-0.38	0.05	-0.3	-0.18	0.2					
ILA_{low}	-0.43	-0.34	-0.44	-0.09	-0.34	-0.09	-0.63	0.04	0.62	0.17	0.31	0.24	0.35				
ILM_{up}	-0.09	0.2	-0.25	-0.01	-0.47	0.63	-0.24	-0.62	-0.11	-0.38	-0.7*	-0.31	0.78**	0.19			
ILM_{low}	-0.11	0.11	-0.07	-0.03	-0.34	0.24	-0.28	-0.02	0.59	-0.12	-0.24	-0.48	0.13	0.73*	0.34		
$[N]_{up}$	0.38	0.04	0.31	-0.27	0.22	-0.32	0.15	0.69*	0.51	0.17	0.46	0.16	-0.49	0.05	-0.67*	-0.01	$[N]_{up}$
$[N]_{low}$	0.07	-0.18	0.02	-0.28	-0.01	-0.4	-0.17	0.52	0.55	0.27	0.53	0.26	-0.37	0.26	-0.6	0.12	$[N]_{low}$
$[C]_{up}$	0.22	0.12	0.35	-0.18	0.33	-0.27	-0.01	0.86**	0.9***	0.21	0.52	0.18	-0.19	0.45	-0.46	0.31	$[C]_{up}$
$[C]_{low}$	0.11	-0.13	0.14	-0.06	0.24	-0.4	-0.14	0.75*	0.76*	0.32	0.63	0.23	-0.36	0.4	-0.62	0.25	$[C]_{low}$
NAR_{1st}	-0.27	-0.82	-0.43	-0.37	-0.09	-0.75	-0.80	0.54	0.28	0.15	0.80	0.85	0.31	0.55	-0.38	-0.28	NAR_{1st}
NAR_{2nd}	0.55	0.20	0.57	0.29	0.85	-0.41	0.60	0.68	0.03	0.64	0.39	0.29	-0.80	-0.93	-0.76	-0.86	NAR_{2nd}
SC_{1st}	-0.44	-0.25	-0.34	0.98	0.81	0.21	0.04	0.07	-0.87	0.84	-0.03	-0.15	-0.90	-0.61	-0.49	-0.28	SC_{1st}
SC_{2nd}	-0.07	-0.17	-0.01	0.80	0.98	-0.13	0.23	0.44	-0.58	0.93	0.25	0.12	-1.00	-0.83	-0.76	-0.65	SC_{2nd}
BF	-0.21	0.1	-0.05	0.31	-0.13	0.2	0.09	-0.52	-0.61	-0.1	-0.55	-0.5	-0.06	-0.53	0.22	-0.12	BF
Ang	0.31	0.16	0.37	-0.41	0.11	-0.15	0.1	0.58	0.69*	-0.39	0.27	0.09	0.32	0.27	0.03	0.14	Ang
Ang_{BDmax}	0.14	0	0.27	-0.53	-0.09	-0.35	-0.08	0.61	0.86**	-0.36	0.4	0.05	0.2	0.45	-0.13	0.36	Ang_{BDmax}
BD	-0.03	-0.25	-0.1	-0.21	-0.27	-0.26	-0.13	-0.19	0.03	-0.57	0.09	0.04	0.33	-0.13	0.22	-0.21	BD
BD_{max}	-0.25	-0.31	-0.23	-0.28	-0.52	-0.27	-0.33	-0.25	0.02	-0.65*	-0.01	-0.04	0.59	-0.11	0.36	-0.11	BD_{max}
BBA	-0.31	-0.18	-0.48	0.39	-0.17	0.28	-0.51	-0.27	-0.21	0.17	-0.2	0.2	0.67*	-0.02	0.49	-0.15	BBA
DBH2009	-0.25	-0.14	-0.48	0.28	-0.4	0.35	-0.32	-0.82**	-0.5	-0.16	-0.5	-0.14	0.41	-0.2	0.66*	-0.12	DBH2009
DBH2010	-0.17	-0.04	-0.39	0.26	-0.37	0.43	-0.24	-0.79**	-0.48	-0.24	-0.58	-0.21	0.46	-0.21	0.74*	-0.08	DBH2010
DBH2011	-0.17	-0.03	-0.36	0.21	-0.37	0.41	-0.22	-0.78**	-0.46	-0.31	-0.58	-0.23	0.51	-0.19	0.77**	-0.06	DBH2011
Ht2009	0	-0.02	-0.05	-0.37	-0.34	0	-0.02	-0.46	-0.04	-0.53	-0.16	-0.04	0.28	-0.06	0.42	-0.09	Ht2009
Ht2010	0.2	0.28	0.12	-0.26	-0.29	0.35	0.25	-0.57	-0.27	-0.66*	-0.57	-0.39	0.29	-0.23	0.64*	0	Ht2010
Ht2011	0.11	0.22	-0.04	-0.37	-0.51	0.4	0.02	-0.63	-0.13	-0.68*	-0.6	-0.34	0.51	-0.05	0.8**	0.13	Ht2011
CR2009	-0.77**	-0.6	-0.89***	0.24	-0.61	-0.02	-0.88***	-0.67*	-0.21	0.17	-0.03	0.25	0.57	0.29	0.46	0.1	CR2009
CR2010	-0.42	-0.3	-0.45	0.32	0.02	-0.02	-0.6	-0.08	0.19	0.39	0.24	0.49	0.43	0.31	0.22	-0.06	CR2010
CR2011	-0.33	-0.13	-0.41	0.26	-0.34	0.24	-0.37	-0.63	-0.42	-0.18	-0.42	-0.09	0.57	-0.28	0.63	-0.21	CR2011
SVI2009	-0.17	-0.08	-0.34	0.03	-0.42	0.26	-0.24	-0.75*	-0.34	-0.33	-0.43	-0.11	0.43	-0.16	0.66*	-0.11	SVI2009
SVI2010	-0.02	0.1	-0.19	0	-0.38	0.41	-0.06	-0.74*	-0.38	-0.46	-0.6	-0.28	0.44	-0.21	0.76*	-0.05	SVI2010
SVI2011	-0.06	0.08	-0.23	-0.05	-0.44	0.41	-0.13	-0.74*	-0.31	-0.48	-0.59	-0.26	0.54	-0.13	0.82**	0.01	SVI2011

	$[N]_{up}$	$[N]_{low}$	$[C]_{up}$	$[C]_{low}$	NAR_{1st}	NAR_{2nd}	SC_{1st}	SC_{2nd}	BF	Ang	Ang_{BDmax}	BD	BD_{max}	BBA	
$[N]_{up}$	$[N]_{up}$														
$[N]_{low}$	0.92***	$[N]_{low}$													
$[C]_{up}$	0.67*	0.65*	$[C]_{up}$												
$[C]_{low}$	0.84**	0.84**	0.9***	$[C]_{low}$											
NAR_{1st}	0.69	0.68	0.49	0.60	NAR_{1st}										
NAR_{2nd}	0.53	0.53	0.57	0.63	-0.24	NAR_{2nd}									
SC_{1st}	0.00	-0.06	-0.30	0.15	-0.29	0.46	SC_{1st}								
SC_{2nd}	0.32	0.29	0.11	0.48	-0.22	0.78	0.90	SC_{2nd}							
BF	-0.56	-0.5	-0.65*	-0.65*	-0.93	0.29	0.61	0.47	BF						
Ang	0.28	0.11	0.64*	0.43	0.52	-0.36	-0.96	-0.80	-0.66*	Ang					
Ang_{BDmax}	0.48	0.42	0.78**	0.65*	0.62	-0.25	-0.90	-0.70	-0.64*	0.89***	Ang_{BDmax}				
BD	-0.17	-0.29	-0.1	-0.08	-0.52	-0.37	-0.65	-0.70	-0.16	0.49	0.3	BD			
BD_{max}	-0.21	-0.24	-0.16	-0.16	-0.13	-0.50	-0.90	-0.90	0.09	0.43	0.36	0.81**	BD_{max}		
BBA	-0.28	-0.2	-0.25	-0.21	0.24	0.45	0.85	0.85	0.18	-0.03	-0.14	0.17	0.48	BBA	
DBH2009	-0.63*	-0.56	-0.71*	-0.62	-0.92	-0.14	0.22	-0.01	0.45	-0.36	-0.54	0.46	0.42	0.53	DBH2009
DBH2010	-0.67*	-0.63*	-0.71*	-0.67*	-0.87	-0.26	0.11	-0.14	0.44	-0.28	-0.49	0.49	0.44	0.52	DBH2010
DBH2011	-0.73*	-0.71*	-0.7*	-0.7*	-0.82	-0.35	0.01	-0.25	0.43	-0.2	-0.44	0.54	0.48	0.49	DBH2011
Ht2009	-0.43	-0.43	-0.27	-0.38	-0.57	-0.24	-0.62	-0.62	0	0.17	-0.01	0.69*	0.39	-0.14	Ht2009
Ht2010	-0.6	-0.69*	-0.54	-0.68*	-0.58	-0.51	-0.49	-0.66	0.23	0.05	-0.19	0.53	0.32	-0.12	Ht2010
Ht2011	-0.53	-0.53	-0.48	-0.62	-0.44	-0.55	-0.66	-0.78	0.15	0.08	-0.09	0.5	0.41	0.08	Ht2011
CR2009	-0.4	-0.1	-0.37	-0.24	-0.72	-0.04	0.70	0.40	0.28	-0.38	-0.29	0.12	0.35	0.69*	CR2009
CR2010	-0.27	-0.1	0.18	0.1	-0.63	0.83	0.17	0.46	-0.11	0.11	0.01	0.27	0.2	0.51	CR2010
CR2011	-0.65*	-0.56	-0.57	-0.59	-1.00	0.22	0.25	0.17	0.57	-0.2	-0.36	0.45	0.62	0.74*	CR2011
SVI2009	-0.63	-0.57	-0.59	-0.6	-0.85	-0.17	-0.21	-0.33	0.32	-0.17	-0.37	0.59	0.45	0.33	SVI2009
SVI2010	-0.69*	-0.69*	-0.65*	-0.71*	-0.75	-0.38	-0.27	-0.46	0.35	-0.12	-0.36	0.56	0.43	0.27	SVI2010
SVI2011	-0.69*	-0.67*	-0.61	-0.69*	-0.69	-0.44	-0.37	-0.55	0.31	-0.06	-0.29	0.56	0.48	0.32	SVI2011

[1]See Table 2 for the meaning of the abbreviations, and Table A.5 for standard errors.

[1]See Table 2 for the meaning of the abbreviations, and Table A.5 for standard errors.

Table A5
Standard errors (S_r, ±) for Pearson's correlation coefficients.

[1]r_G (±)	Standard errors (S_r, ±) associated with r_Gs in different tables					
	all clones	protogynous clones	protandrous clones	gas exchange variables: NAR_{1st}, NAR_{2nd}, SC_{1st}, and SC_{2nd}		
	Table 5 [2]n = 25	Table A.3 n = 14	Table A.4 n = 10	Table 5 n = 12	Table A.3 n = 8	Table A.4 n = 4
0.30	0.20	0.28	0.34	0.30	0.39	0.67
0.33	0.20	0.27	0.33	0.30	0.39	0.67
0.35	0.20	0.27	0.33	0.30	0.38	0.66
0.38	0.19	0.27	0.33	0.29	0.38	0.65
0.40	0.19	0.26	0.32	0.29	0.37	0.65
0.43	0.19	0.26	0.32	0.29	0.37	0.64
0.45	0.19	0.26	0.32	0.28	0.36	0.63
0.48	0.18	0.25	0.31	0.28	0.36	0.62
0.50	0.18	0.25	0.31	0.27	0.35	0.61
0.53	0.18	0.24	0.30	0.27	0.35	0.60
0.55	0.17	0.24	0.30	0.26	0.34	0.59
0.58	0.17	0.24	0.29	0.26	0.33	0.58
0.60	0.17	0.23	0.28	0.25	0.33	0.57
0.63	0.16	0.22	0.27	0.25	0.32	0.55
0.65	0.16	0.22	0.27	0.24	0.31	0.54
0.68	0.15	0.21	0.26	0.23	0.30	0.52
0.70	0.15	0.21	0.25	0.23	0.29	0.50
0.73	0.14	0.20	0.24	0.22	0.28	0.48
0.75	0.14	0.19	0.23	0.21	0.27	0.47
0.78	0.13	0.18	0.22	0.20	0.26	0.44
0.80	0.13	0.17	0.21	0.19	0.24	0.42
0.83	0.12	0.16	0.20	0.18	0.23	0.39
0.85	0.11	0.15	0.19	0.17	0.22	0.37
0.88	0.10	0.14	0.17	0.15	0.19	0.34
0.90	0.09	0.13	0.15	0.14	0.18	0.31

[1] Only standard errors for $|r_G| >= 0.30$ were shown.
[2] Number of clones corresponding to each r_G.

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