

Short-Term Physiological Responses of Black Walnut (*Juglans nigra* L.) to Plantation Thinning

Martin-Michel Gauthier and Douglass F. Jacobs

Abstract: We studied physiological responses of mature black walnut (*Juglans nigra* L.) trees to determine the time necessary for photosynthetic adaptation to plantation thinning. Measurements were taken before treatment (July 25, 2007) and for the first 3 days after thinning (July 29, 30, and 31, 2007). Measurements did not continue in August because trees had developed leaf anthracnose and senescence was occurring, but measurements resumed on May 29, 2008 and July 29, 2008. Repeated measures of net photosynthetic rates (A) showed that thinned trees did not respond immediately to partial release, but nearly doubled in A compared with a 35% increase in control trees 1 year after thinning. Significant increases in light, leaf water status, relative humidity of the air, and nitrogen content per unit leaf area were also found in thinned trees 1 year after treatment. From these variables, light ($r^2 = 0.79$) showed the strongest relationship with A . Results suggest that black walnut requires a full growing season before it responds to treatment when thinned late in the growing season. Thinning earlier, such as in June, may trigger a more rapid adaptation in A of thinned trees that was not detected in our study. FOR. SCI. 55(3):221–229.

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EFFECTIVE SILVICULTURAL MANAGEMENT requires knowledge of the biology of individual trees, the environment in which they grow, and their reaction to disturbance. In this regard, thinning is an important silvicultural practice that can have a long-term impact on stand development (Larsen and Johnson 1998). Thinning is generally applied at the beginning of the stem-exclusion stage, when trees start to compete actively for growing space (Oliver and Larson 1996), but can also be applied at regular intervals until overstory removal. Without this intervention, tree growth and log quality may diminish over time. Thinning provides an opportunity for managers to select for species composition, density, and tree quality. Increases in diameter growth of residual trees were shown after thinning (Simard et al. 2004, Schuler 2006). Few thinning studies have been conducted with broadleaf species at the physiological level. Thinning has been shown to increase available light and photosynthesis in paper birch (*Betula papyrifera* Marsh.) (Wang et al. 1995) and improve water relations through higher predawn leaf water potential (Ψ_{pd}) in sessile oak (*Quercus petraea* [Matt.] Liebl.) (Bréda et al. 1995). Of particular interest to this study is black walnut (*Juglans nigra* L.), currently one of the most economically valuable species in North America. Ecophysiological traits of walnut species, such as photosynthetic adaptations to light and water stress, are still poorly documented (Le Roux et al. 1999a). Studies examining such adaptations in mature trees are especially scarce because of the difficulty of accessing leaves in mature canopies and

the time-consuming nature of physiological measurements (Loewenstein and Pallardy 1998, Koike et al. 2001).

The goal of this experiment was to investigate physiological responses in plantation-grown black walnut after thinning to identify factors responsible for changes in photosynthetic adaptation, such as light, water, and nutrients. The objective was to answer three basic questions: How much time is necessary for black walnut trees to increase photosynthetic rate per unit leaf area after thinning? What factors are responsible for the increase? How much variability is explained by each factor? Environmental and plant physiological variables were measured, as well as some leaf morphological parameters. To investigate the time necessary for photosynthetic adaptation, thinning has to be performed during the summer or fall. The effects of performing such treatments during the growing season have not been investigated in deciduous angiosperms. There is some evidence of thinning shock in the literature, i.e., sunscald, chlorotic foliage, and reductions in height or diameter growth for the first few years, in Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) stands as influenced by thinning intensity, site quality, vigor, and age (Staebler 1956, Harrington and Reukema 1983). Similar effects may occur by thinning black walnut during the summer in hot, dry weather. Investigating short-term physiological responses to thinning provides an opportunity to examine this potential occurrence.

Black walnut diameter growth response to thinning is already well known (Clark 1967, Phares and Williams 1971,

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Bohanek and Groninger 2003, Tokár and Krekulová 2005) and detecting such a response was not our intent. Rather, the purpose of this study was to gain a better understanding of the means by which black walnut trees increase their photosynthetic capacity that eventually leads to increases in diameter growth.

Materials and Methods

Site Description

A black walnut plantation located near Lafayette, IN, USA (40°19'44 N, 86°42'35 W) was selected for study. Mean annual temperature, precipitation, and frost-free days for this area are 10.1°C, 937 mm, and 233 days, respectively. Elevation is 211 m above mean sea level. The 48-ha area was established in 1989 with 1-year-old bareroot stock at a spacing of 6.8 m between rows and 1.5 m between trees. Thinning of lower-quality trees was performed yearly from 1990 until 2005. The landowner's objective was to maintain the crown competition factor near 100 based on guidelines for managing black walnut (Schlesinger and Funk 1977). Crown competition factor is a measure of competition that integrates tree size and stand density. Values greater than 100 show crowding; values less than 100 indicate room for expansion. Corn (*Zea mays* L.) was grown between rows for the first 6 years after planting. Measurement trees were located on deep, well-drained Ockley silt loam on less than 2% slope. Estimated site index was 24 m at age 50, favorable for black walnut growth (Schlesinger and Funk 1977).

Experimental Design and Thinning Treatment

Mowing was performed before initiation of the experiment, and 1 week before each set of gas-exchange measurements during the second growing season to facilitate access and provide uniform understory conditions for soil water content and temperature measurements. Our intent was to avoid the confounding effects of debris from cut trees and potential negative effects of herbicide translocation to root systems of measurement trees. A completely randomized design was established for this study. The number of experimental units was based on preliminary gas-exchange measurements taken on black walnut trees in July 2006 for a similar study. We used the sample size equation (Equation 1) to determine how many trees were needed to have a 95% degree of confidence that the sample mean is within $1 \mu\text{mol m}^{-2} \text{s}^{-1}$ of the population mean,

$$n = \left[\frac{z_{\alpha/2} \times \sigma}{E} \right]^2, \quad (1)$$

where n is sample size, $z_{\alpha/2}$ is the critical z value, the positive value at the vertical boundary for the area of $\sigma/2$ in

the right tail of the standard normal distribution (1.96), σ is SD (1.4855), and E is margin of error (1). The data set of photosynthetic rates was 7.25, 11.17, 8.91, 10.93, 8.20, 10.58, 10.91, and $10.57 \mu\text{mol m}^{-2} \text{s}^{-1}$.

Based on these calculations, eight black walnut trees were selected ($n = 8$), and one treatment (thinned or control) was randomly applied to each tree. Four trees were left untouched to serve as controls, and four were released on northern and southern orientations because the within-row spacing was most dense. The thinning treatment can be classified as a partial release. Before thinning, the distance between neighboring trees within a row was 2.4 m for both treatments. Measurement trees were selected based on similarity in height, dbh, form, and crown length (Table 1). Felled trees were in a codominant position, 16.2 ± 0.2 m in height and 22.8 ± 0.7 cm in dbh on average. A radius of at least one tree length (20 m) was left between measurement trees. For plantations of irregular spacing, Schlesinger and Funk (1977) recommend thinning when crown width is greater than twice the distance between trees (4.86 m). Crown widths for both control (6.4 m) and thinned (6.0 m) measurement trees were greater, indicating that thinning was necessary.

Gas Exchange

Gas-exchange measurements were performed on clear days to minimize the effects of increased diffuse radiation. Prethinning measurements were recorded on July 25, 2007. Thinning was performed on July 28, and post-thinning measurements were assessed on July 29, 30, and 31. Measurements did not continue in August because walnut trees had developed leaf anthracnose and senescence was occurring, but measurements resumed after leaf expansion on May 29, 2008 and again on July 29, 2008. Gas exchange was measured between 10:00 am and 2:00 pm using a portable photosynthesis system (LI-6400; Li-Cor, Inc., Lincoln, NE). Measurements were taken on the southern orientation to avoid confounding effects of spatial heterogeneity in leaf morphology. Le Roux et al. (1999b) reported large variations in leaf mass per unit area (LMA) and leaf nitrogen content per unit area (N_a) along a south-north horizontal transect in a mature walnut tree. Two fully expanded, attached leaves from the same branch at the middle canopy position of each tree (~ 11.5 m) were sampled, and the average was used for statistical analyses. The second or third set of leaflets from the apex of the compound leaf was sampled; the first set of leaflets was generally not large enough to fit inside the infrared gas exchange analyzer chamber. A mobile lift (Altec 37-GR; Altec Industries, Inc., Birmingham, AL) was used to reach the leaves. The LI-6400 main console was mounted inside the bucket, and

Table 1. Mean ($n = 4 \pm$ SE) dbh, height, and crown characteristics of thinned and unthinned black walnut trees before thinning

Treatment	No. of trees	dbh (cm)	Height	Crown length	Middle canopy position
Control	4	23.5 \pm 1.1	16.6 \pm 0.5	9.3 \pm 0.2	11.9 \pm 0.4
Thinned	4	22.7 \pm 1.1	15.7 \pm 0.4	8.8 \pm 0.4	11.3 \pm 0.4

the infrared gas exchange analyzer was attached to the bucket edge to provide an in situ measure of gas exchange. A near-ambient $[\text{CO}_2]$ of $380 \mu\text{mol mol}^{-1}$ and relative humidity (RH) between 50 and 75% were used in the chamber to maintain a similar humidity gradient between the leaf and the air under ambient conditions. Light and temperature inside the chamber were set according to ambient conditions based on external sensors attached to the chamber. Other gas exchange parameters measured by the LI-6400, such as stomatal conductance (g), transpiration (E), vapor pressure deficit (D), and intrinsic water-use efficiency (WUE), were also used to explain potential treatment effects. WUE was calculated as $A g^{-1}$ and expressed as $\mu\text{mol of CO}_2 (\text{mol of H}_2\text{O})^{-1}$ (de Souza et al. 2005).

Leaf Water Potential and Leaf Morphology

Leaves sampled for gas exchange were also measured for midday leaf water potential (Ψ_{md}) with a pressure chamber (PMS Instruments Company, Corvallis, OR). After Ψ_{md} was measured, leaves were placed between two moistened paper towels and inserted in a plastic bag and then placed in a large cooler with ice. Leaves were brought back to the laboratory and stored in a refrigerator at 5°C . Leaf area was measured using a leaf area meter (LI-3100; Li-Cor, Inc.). Leaves were dried at 65°C for at least 48 h, ground, and weighed for determination of LMA. A sample of the ground product of the entire leaf was used to determine leaf N using a LECO CNS-2000 Analyzer (LECO Corporation, St. Joseph, MI). Leaf N_a was computed by multiplying N concentration (g g^{-1}) and LMA (g m^{-2}) (Wilson et al. 2000).

Soil Parameters

Soil temperature and water content were monitored by installing one soil moisture sensor (ECH₂O dielectric aquameter; Decagon Devices, Inc., Pullman, WA) and one 12-bit soil temperature sensor (Onset Computers, Bourne, MA) within a 2-m radius on the southern orientation of each measurement tree. Soil temperature sensors were inserted to a depth of 3 cm of the soil profile. Soil water content sensors were inserted to vertically monitor average water content in the top 20 cm of the soil profile. Sensors were connected to HOBO data loggers (Onset Computers). Measurements were taken at the beginning of every hour and averaged daily. Three soil samples were collected from the upper 10 cm of the mineral soil layer within a radius of 2 m from measurement trees on July 3, 2007 and May 1, 2008 to determine soil N, P, K, Mg, cation exchange capacity (CEC), and soil pH. Samples were sent to a professional laboratory for analysis (A&L Great Lakes Laboratories, Fort Wayne, IN). Test procedures followed standards of the US Forest Service, North Central Region of the United States (Brown 1998). Soil NO_3^- and NH_4^+ were extracted by the cadmium reduction method (Huffman and Barbarick 1981), and soil P was extracted by the Bray and Kurtz (1945) procedure. Soil K and Mg were extracted by the Mehlich 3 method (Mehlich 1984). Content after extraction was determined by inductively coupled plasma spectrometry (Soltanpour and Workman 1981).

Statistical Analyses

One-way analysis of variance was used to test for thinning effects on mean A and other physiological variables at each sampling event. A repeated-measures statement was used to test for change from prethinning conditions. Linear regression and correlations were used to model A as a function of all environmental and plant physiological variables on July 29, 2008. Normality was assessed both visually and with use of the Kolmogorov-Smirnov test. Homogeneity of variance was assessed both visually and with Levene's test. With small sample sizes and repeated measures, SE bars can be misleading when statistical differences with figures are interpreted (Cumming et al. 2007). Hence, both differences at $P < 0.10$ (*) and at $P < 0.05$ (**) are indicated. All analyses were performed using SAS (SAS Institute, Cary, NC).

Results

Mean A did not differ between treatments except for the third day after thinning when control trees had higher A ($P = 0.04$) (Figure 1). The change in A from the prethin conditions was not statistically significant either, although thinned trees nearly doubled in A with an increase of $7.2 \pm 2.6 \mu\text{mol m}^{-2} \text{s}^{-1}$ 1 year after treatment as opposed to an increase of $2.8 \pm 2.0 \mu\text{mol m}^{-2} \text{s}^{-1}$ in control trees. Repeated-measures analysis indicated a time \times treatment interaction with light ($P = 0.06$) (Figure 2). Compared with prethin conditions, contrasts showed that ambient light decreased over the 1-year period under control trees but increased under thinned trees ($P = 0.04$). Relative humidity was also higher in thinned trees on July 29, 2008 ($P = 0.04$). Other variables such as g , E , and D did not differ between treatments over time (Figure 3). On the second day after thinning, WUE was higher ($P = 0.04$) in control trees. Thinned trees had higher leaf Ψ_{md} before thinning ($P = 0.02$) and on the third day after thinning compared with control trees ($P = 0.09$) (Figure 3). The comparison with prethin conditions showed a thinning effect ($P = 0.09$); the increase in water stress was greater in control trees than in thinned trees on July 29, 2008.

Control trees had higher LMA before thinning ($P = 0.04$) and for the first 2 days after thinning ($P = 0.03$ and 0.09) (Figure 4). A decrease was observed shortly after full leaf expansion on May 29, 2008. The time \times treatment interaction ($P = 0.02$) and contrasts showed that the decrease was greater in control trees than in thinned trees ($P = 0.09$). A different trend was found with N_a ; thinned trees had higher N_a than control trees ($P = 0.06$) 1 year after treatment (Figure 4).

Soil temperature showed a steeper increase near thinned trees for all 3 days after thinning ($P = 0.07$, 0.07 , and 0.05 , respectively). The increase averaged $2.6 \pm 0.2^\circ\text{C}$ near thinned trees compared with $1.8 \pm 0.1^\circ\text{C}$ near control trees. The effect dissipated 1 year after treatment (Figure 5). No differences were found in soil water content. Increased precipitation provided almost twice the amount of soil moisture during the 2008 growing season compared with 2007

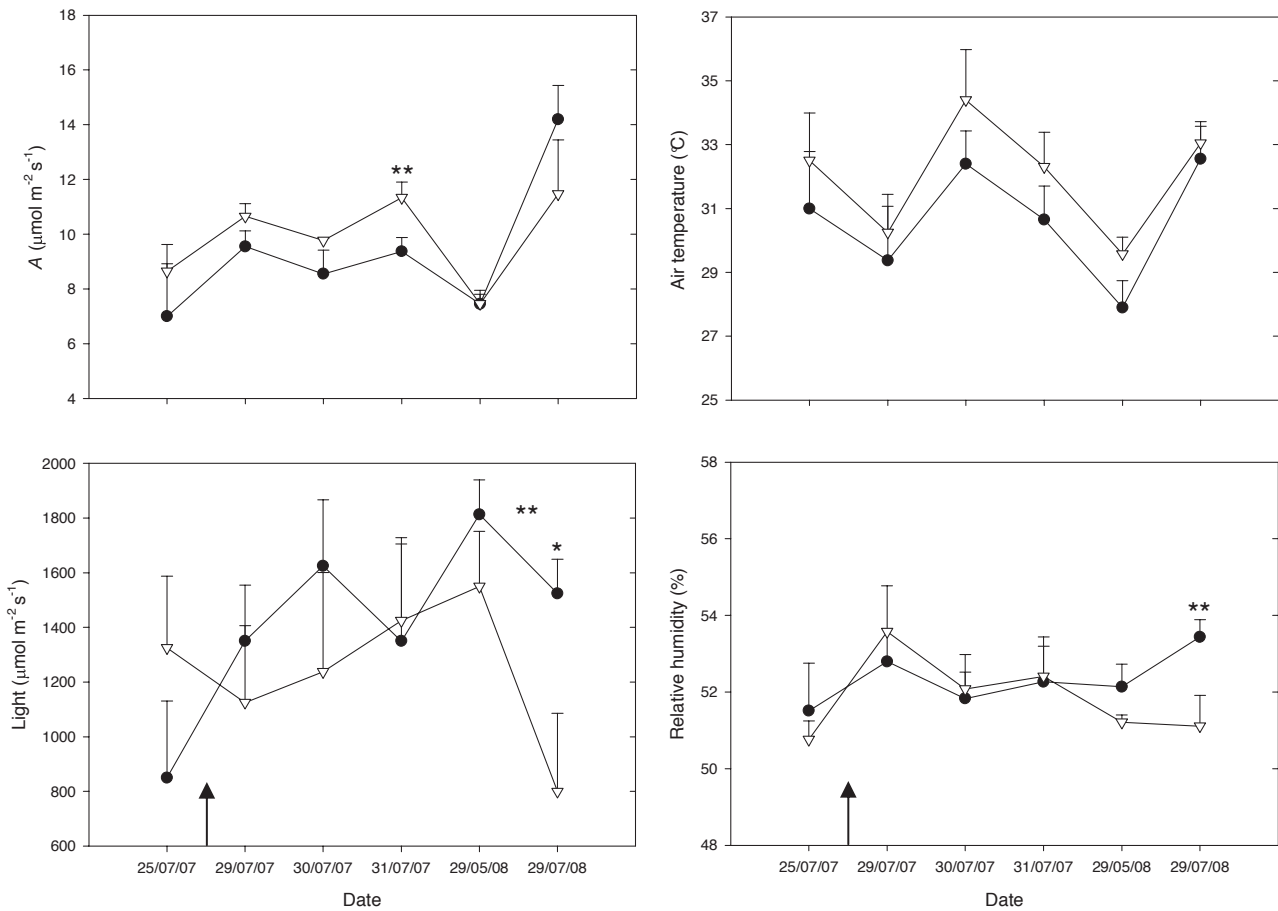


Figure 1. Mean ($n = 4 \pm \text{SE}$) photosynthetic and environmental parameters for each sampling date of control (∇) and thinned (\bullet) black walnut. Timing of thinning treatment indicated by arrow (July 28, 2007). From top left to bottom right: net photosynthesis (A), air temperature, light, and relative humidity. Statistical differences: * $P < 0.10$, ** $P < 0.05$; those located between dates indicate a time \times treatment interaction.

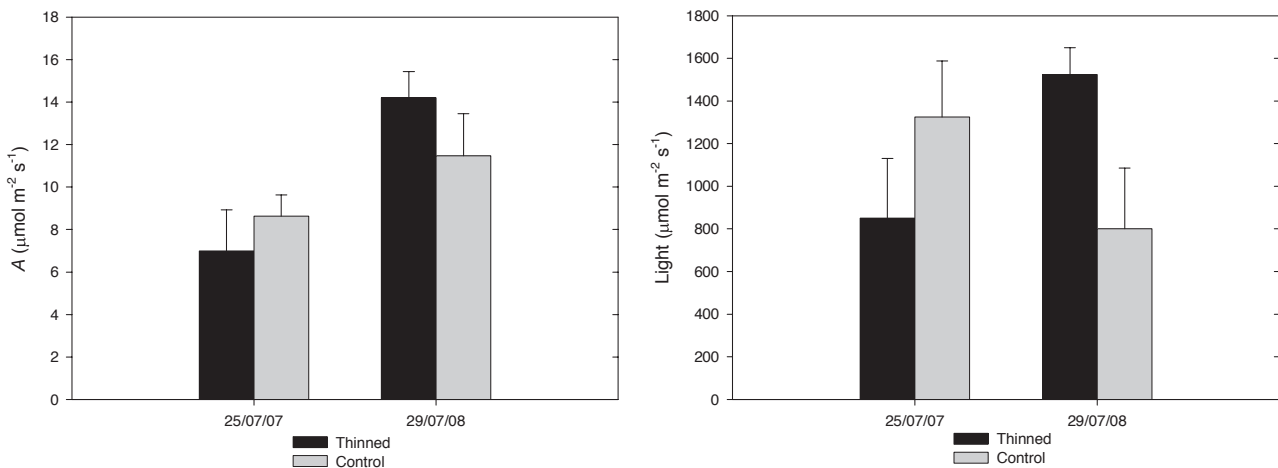


Figure 2. Mean ($n = 4 \pm \text{SE}$) change in A and light from prethinning conditions (July 25, 2007) to 1 year after treatment (July 29, 2008) of control and thinned black walnut. The time \times treatment interaction was significant for light ($P = 0.04$), but not for A ($P = 0.28$).

(Figure 5). No treatment differences were found with regard to soil NO_3^- , NH_4^+ , P, K, Mg, pH, and CEC for either July 2007 or May 2008 (Table 2).

Relationships between physiological parameters and A were analyzed for measurements taken 1 year after thinning (July 29, 2008), the only date for which mean A was higher

in thinned trees. Light, E , and g were all positively related to A . Soil water content, soil temperature, LMA, N_a , leaf Ψ_{md} , D , and RH were not significantly related to A . Light had the strongest relationship with A ($r^2 = 0.79$) (Figure 6). All explanatory variables were correlated with each other ($r > 0.45$).

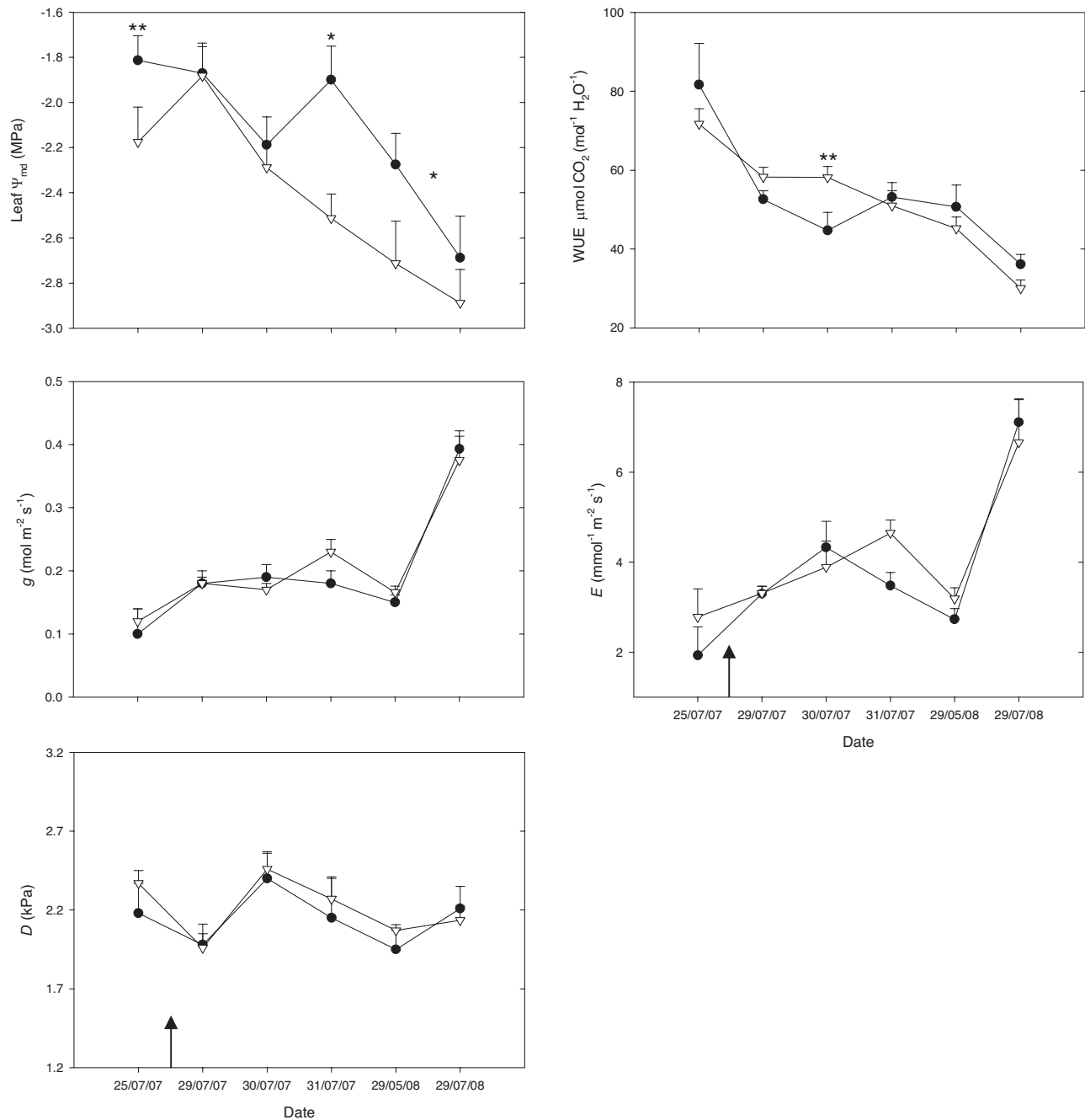


Figure 3. Mean ($n = 4 \pm \text{SE}$) leaf physiological parameters for each sampling date of control (∇) and thinned (\bullet) black walnut. From top left to bottom right: midday leaf water potential (Ψ_{md}), water-use efficiency (WUE), stomatal conductance (g), leaf transpiration (E), and vapor pressure deficit (D). Timing of treatment and statistical differences are indicated as in the legend to Figure 1.

Discussion

The near doubling of A in thinned black walnut 1 year after treatment compared with a 35% increase in control trees, although not statistically significant, has biological significance, considering that most physiological studies of mature trees usually have small sample sizes (Loewenstein and Pallardy 1998, Le Roux et al. 1999b, Koike et al. 2001, Piel et al. 2002) and large variability (Bréda et al. 1995, Wang et al. 1995, Tang et al. 2005). This increase in A is also supported by favorable changes in environmental conditions and plant physiological variables. When compared

with control trees, thinned trees had higher light, Ψ_{md} , ρ , and N_a 1 year after treatment. Other species and similar treatments such as gap openings and controlled light transfers with seedlings were used for comparison with our study because no other published article investigating immediate responses in mature trees was found. Wang et al. (1995) studied precommercial thinning of 9- to 13-year-old paper birch stands in British Columbia, Canada. They found that A increased with increasing thinning intensity and attributed the change to increases in light and foliar N concentration. These results corroborate our findings with black walnut.

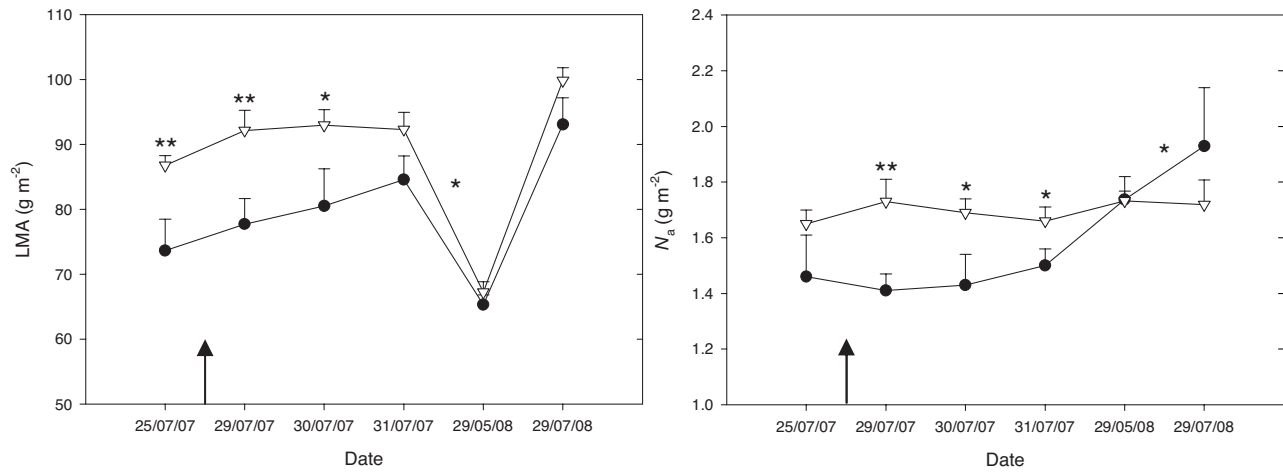


Figure 4. Mean ($n = 4 \pm SE$) leaf mass (LMA) and nitrogen content (N_a) per unit area for each sampling date of control (∇) and thinned (\bullet) black walnut. Timing of treatment and statistical differences are indicated as in the legend to Figure 1.

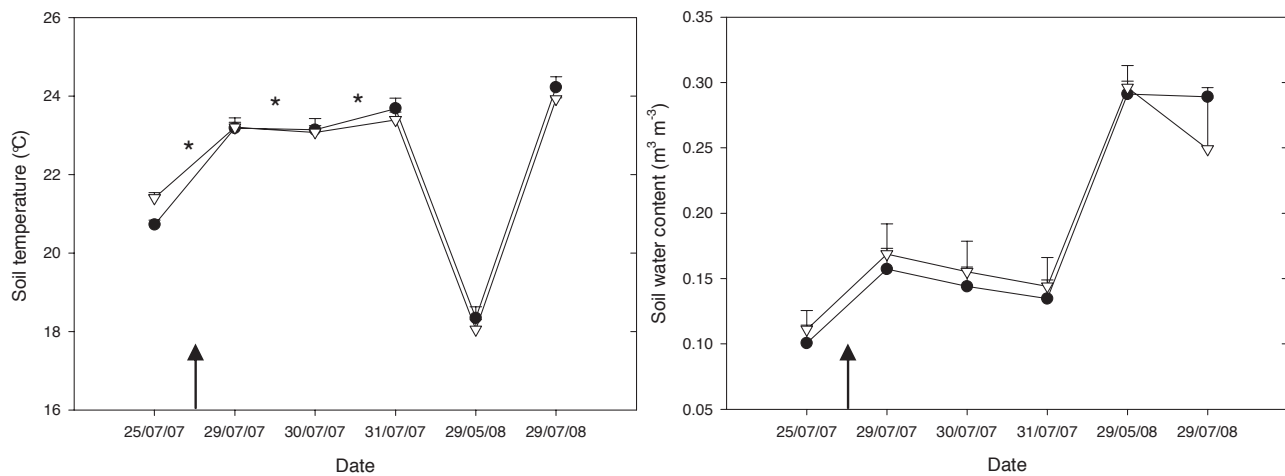


Figure 5. Mean ($n = 4 \pm SE$) soil temperature and soil water content for each sampling date of control (∇) and thinned (\bullet) black walnut. Timing of treatment and statistical differences are indicated as in the legend to Figure 1.

Table 2. Mean ($n = 4 \pm SE$) soil nutrients, pH, and cation exchange capacity (CEC) for thinned and unthinned black walnut trees before (2007) and after (2008) plantation thinning

Treatment	NO_3^-	NH_4^+	P	K	Mg	pH	CEC (mEq 100 g $^{-1}$)
.....(mg l $^{-1}$).....							
2007							
Control	4.1 \pm 0.3	4.2 \pm 0.3	58 \pm 1	240 \pm 11	243 \pm 19	7.2 \pm 0.0	8.4 \pm 0.2
Thinned	4.8 \pm 0.7	3.6 \pm 0.2	60 \pm 4	241 \pm 6	242 \pm 27	7.1 \pm 0.1	8.6 \pm 0.6
2008							
Control	2.8 \pm 0.3	3.8 \pm 0.2	40 \pm 5	195 \pm 11	210 \pm 13	7.0 \pm 0.1	6.6 \pm 0.3
Thinned	2.7 \pm 0.5	3.5 \pm 0.4	54 \pm 4	215 \pm 11	206 \pm 11	7.1 \pm 0.1	7.2 \pm 0.2

Because Wang et al. (1995) did not measure gas exchange before thinning or during the first few months after thinning, time comparisons cannot be made. Frak et al. (2001) showed that photosynthetic capacity of 1-year-old hybrid walnut (*J. nigra* \times *regia*) seedlings increased 25–45% within 20 days of transfer from low to high light conditions. However, maximal carboxylation rate (V_{cmax}) and light-saturated electron transport (J_{max}) to the new light regime were not attained 50 days after transfer. Determinate growth of walnut species is probably responsible for the lack of immediate response, i.e., 3 days, in our study. Le Roux et al.

(1999b) noted that only 1% of all shoots from a 20-year-old walnut tree exhibited a second flush of growth. Naidu and DeLucia (1997) have also shown a lack of full adaptation of photosynthetic capacity in sugar maple (*Acer saccharum* Marsh.) seedlings 1 month after low- to high-light transfer. Four weeks after light transfer, adaptation in sugar maple was approximately 50%, but northern red oak (*Quercus rubra* L.) seedlings showed a more rapid adaptation, with increasing A 2 weeks after transfer. Full adaptation of sun foliage to shade in Pacific silver fir (*Abies amabilis* Dougl.) was detected within a few months (Brooks et al. 1994).

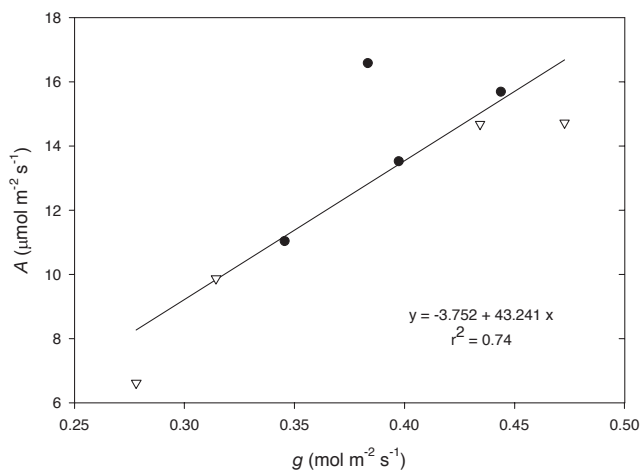
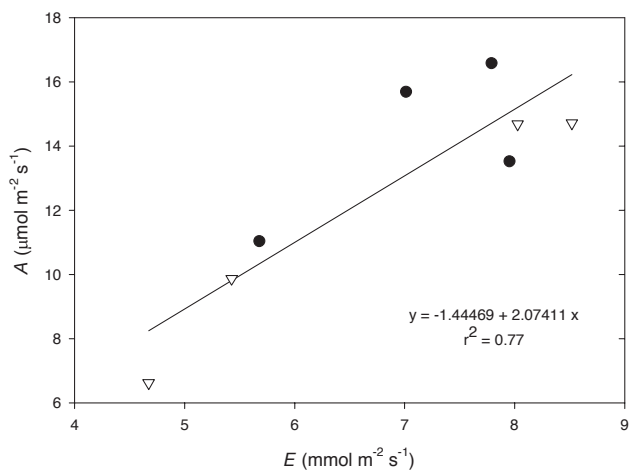
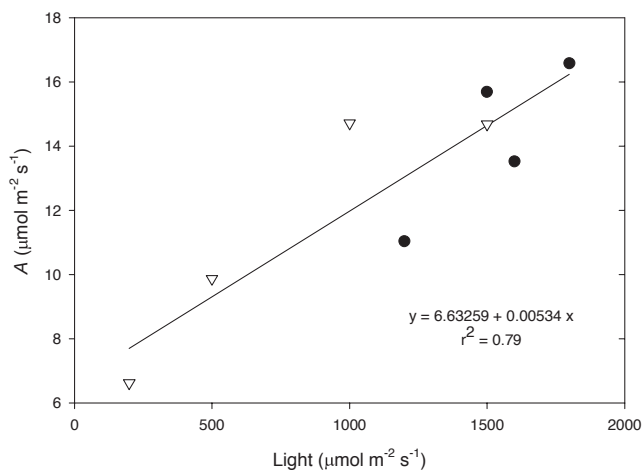


Figure 6. Regression of A as influenced by light ($P = 0.003$), E ($P = 0.004$), and g ($P = 0.006$) 1 year after treatment in control (∇) and thinned (\bullet) black walnut.

Timing of the thinning treatment may have played a role in the lack of response for the first 3 days after thinning. Frak et al. (2001) demonstrated that fully developed walnut leaves exhibited a weak ability for photosynthetic adaptation when light transfer was made 91 days after bud burst in 1 year but were able to acclimate when light transfer was made 58 days after bud burst during the next year. Thinning was carried out approximately 80 days after bud burst in this

study, which may have been too late in the growing season. Lack of response in 2007 was exacerbated by leaf anthracnose that developed in early August, resulting in leaf senescence.

The photosynthetic response of thinned trees was influenced by light conditions before and after thinning. Light levels found in control trees before thinning ($1,300 \mu\text{mol m}^{-2} \text{s}^{-1}$) were near the light saturation point for walnut (Dean et al. 1982, Koike et al. 2001), probably because measurement trees were in a codominant position. One year after treatment, however, light levels near control trees decreased by $525 \pm 275 \mu\text{mol m}^{-2} \text{s}^{-1}$ whereas those near thinned trees increased by $675 \pm 372 \mu\text{mol m}^{-2} \text{s}^{-1}$. This finding suggests that crowns of control trees are beginning to compete for light resources with neighboring trees whereas thinned trees have additional space to grow, at least in the southern orientation where gas exchange was measured. Regressions showed that light had a strong positive relationship with A . Thus, the light increase in thinned trees provided additional photons to drive photosynthesis.

Thinned trees showed a steady increase in N_a after thinning, whereas N_a in control trees remained fairly constant throughout the measurement period. The relationship between A and N_a has been shown previously with many tree species at all stages of development, including mature walnut (Koike et al. 2001, Kenzo et al. 2006). The amount of photosynthesis carried out per unit leaf area is generally related to the quantity of leaf N supplied to photosynthetic functions because more than half of total leaf N is allocated to the photosynthetic apparatus (Evans and Seemann 1989). Frak et al. (2001) found that N_a and leaf N partitioning were critical to photosynthetic adaptation of walnut seedlings to different light treatments. Naidu and DeLucia (1997) also found increased N_a after transfer of northern red oak and sugar maple seedlings from low to high light. Thus, increased N_a may play a complementary role in the increased A of thinned trees.

Soil water content was very stable between treatments for the first few days after thinning, and a treatment effect was not expected after such a short time. In 2008, however, soil water content nearly tripled from prethin levels ($0.10 \text{ m}^3 \text{ m}^{-3}$), because of higher precipitation during the 2008 growing season. Measurements 1 year after treatment indicated that thinned trees had an average daily soil water content of $0.29 \pm 0.01 \text{ m}^3 \text{ m}^{-3}$ compared with $0.25 \pm 0.04 \text{ m}^3 \text{ m}^{-3}$ in control trees. Although not statistically different because of the high variability among control trees, this increase may have helped improve leaf water status of thinned trees. Thinning has been shown to enhance water relations in oak through higher leaf Ψ_{pd} (Bréda et al. 1995). Improved leaf water status is generally one of the main effects of thinning and has been shown for many gymnosperms (Aussenac 2000). Soil temperature increased after thinning, probably due to increased irradiance of the ground, but this effect dissipated 1 year after treatment. Soil nutrients did not differ with thinning over the first growing season. This result was expected; soil sampling was done primarily to characterize nutrient status, not to detect a treatment effect. Such an effect, if any, would have required more intensive sampling in more than one soil horizon. It is

possible that the increase in leaf N_a may have been caused by increased soil N availability for thinned trees, but that was not detectable by our sampling design.

Overall, we did not see any evidence of thinning shock even though thinning was carried out late in the growing season under hot, dry weather. It may be of interest to further investigate the timing of thinning treatments in black walnut. Thinning shortly after leaf expansion, provided that weather and site conditions are favorable, may allow trees more time to adjust to changes in environmental conditions before they set buds for the next growing season.

Conclusions

The first objective of this experiment was to determine the time necessary for physiological responses of plantation-grown black walnut trees after thinning. Results showed that 1 year was needed for thinned trees to increase A compared with control trees when thinned late in the growing season. Significant increases in light, leaf Ψ_{md} , RH, and N_a were also found in thinned trees 1 year after treatment. High light levels before thinning (codominant tree position) and leaf age at time of treatment were probably responsible for the lack of immediate response. Thinning earlier in the growing season, such as in June, may trigger a more rapid adaptation in photosynthesis of thinned trees that was not detected in our study. The second and third objectives were to determine which factors were responsible for the increase in A and how much variability could be explained by each factor. Light showed the strongest relationship with A and explained the most variation (79%). Improved leaf Ψ_{md} and higher N_a probably also contributed to increased A . Our results suggest that codominant, 19-year-old black walnut growing on fertile sites that are thinned late in the growing season and are susceptible to anthracnose require a full year before they respond to changes in environmental conditions triggered by plantation thinning.

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