Gibberellic Acid 4+7 Influences Shoot Growth of Seedling Pecan and Bitternut Hickory[1]

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Abstract

Shoot development of seedling hickories is slow, limiting their success as viable crops using standard growing techniques. Because hickories are predominantly propagated by seed, we questioned whether gibberellic acid (GA) could be used on seedlings to overcome slow shoot development during juvenility. Treatments of one-year-old seedlings of bitternut hickory [*Carya cordiformis* (Wangenh.) K. Koch], pignut hickory [*C. glabra* (Mill.) Sweet], pecan [*C. illinoinensis* (Wangenh.) K. Koch], kingnut hickory [*C. laciniosa* (F. Michx.) Loud.], shagbark hickory [*C. ovata* (Mill.) K. Koch], and mockernut hickory [*C. tomentosa* (Lam.) Nutt.] began at bud break by applying a solution of 500 ppm GA_{4+7} dissolved in 95% ethanol directly to apical buds or stem tissue at three-day intervals for 27 days. After 160 days, neither treatment affected caliper of any taxon, although species differences were observed. Compared to nontreated control plants, treatment of buds resulted in a 234% and 144% increase in shoot height of bitternut hickory and pecan, respectively. In a second experiment, the same treatments were implemented on seedlings of bitternut hickory shortly after germination. Only shoot height and dry weight were affected (increased) by application of GA_{4+7}. This study indicates plant growth regulators could be effective at increasing shoot extension of some hickories.

Chemicals used in this study: Gibberellic acid 4+7 (GA_{4+7}).

Species used in this study: bitternut hickory [*Carya cordiformis* (Wangenh.) K. Koch]; pignut hickory [*C. glabra* (Mill.) Sweet]; pecan [*C. illinoinensis* (Wangenh.) K. Koch]; kingnut hickory [*C. laciniosa* (F. Michx.) Loudon]; shagbark hickory [*C. ovata* (Mill.) K. Koch]; and mockernut hickory [*C. tomentosa* (Lam.) Nutt.].

Index words: Species diversity, nursery production, *Carya*, plant growth regulators.

Significance to the Horticulture Industry

Current trends in nursery production have led to the repetitive use of easily grown, closely related taxa, resulting in increased species homogeneity in the landscape. This lack of diversity reduces landscape resiliency by increasing the susceptibility of managed landscapes to exotic pests and extreme weather events (Ma et al. 2020). Increased crop diversity in the nursery industry not only lends to increased diversity in managed landscapes but creates new opportunities for profit by nursery growers. Unfortunately, many desirable species remain nonviable due to production bottlenecks. For example, immense interest exists in effectively producing hickories; however, their slow shoot development and strong episodic growth require prolonged time investments, which reduce their viability as options for many nursery growers. An understanding of how certain plant growth regulators can be used to manipulate growth may bolster their potential. While hickories of section Carya were not responsive to gibberellic acid in our study, growers pursuing the production of pecan and bitternut hickory (in the section Apocarya) could apply solutions of 500 ppm GA_{4+7} on seedlings to maximize shoot growth within the growing season. Additional research is needed to determine which cues promote additional shoot growth on hickory species of section Carya.

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Introduction

Some underutilized native trees offer superior ornamental features and adaptability traits that merit use in managed landscapes. However, these species are rarely available in nurseries due to production bottlenecks. Hickories (*Carya* Nutt.) are one such group of trees that are frequently sought after by horticulturists and urban foresters but are infrequently available in commerce (Dirr 2009). Current availabilities reflect their adoption by specialty nurseries that market container-grown plants and forestry nurseries selling bare-root whips. One limiting factor that restricts the acceptance of hickories on a commercial scale is their propensity for slow shoot development as seedlings (Miller and Graves 2019). *Carya* species are typically regarded as exhibiting a lag-phase shoot development period where energy is focused on the development of a taproot during their initial formative years and shoot development is neglected (Holch 1931, Sparks 2005, Toumey 1929). It is not uncommon for growers with experience producing hickories to report twelve-year crop cycles to achieve saleable-sized plants for balled and burlapped production (Ben French, Johnson's Nursery, Menomonee Falls, WI, personal communication). Subsequently, this lag-phase development is blamed as one

of the leading reasons for their negligible representation in the green industry. It is unclear, however, if all species of *Carya* are similarly restricted by the same patterns of shoot development and if plant growth regulators could be used to hasten their growth to a saleable size.

Pecan, a major nut crop in the United States and around the globe, is an example of a species of the genus *Carya* that is produced commercially. Along with its congeners, it is typically considered difficult to transplant (Dirr 2009), another trait of hickories that limits their use. This taxon belongs to the section Apocarya, which comprises taxa collectively referred to as the "pecan hickories." It is accompanied in this subgrouping by water hickory [*C. aquatica* (F. Michx.) Nutt.], bitternut hickory, and the Mexican hickory (*C. palmeri* Manning). Morphologically and taxonomically, the taxa belonging to this section differ from the ten species comprising section Carya, collectively referred to as the "true hickories," and the five species comprising section Sinocarya, the "Asian hickories" (Thompson and Grauke 1991).

Overall, an understanding of shoot extension and development of different species known to exhibit slow growth has been neglected in horticulture. Limited research has been conducted to explore how hickories respond to plant growth regulators that could alter their growth, with some work exploring how plant growth regulators can influence root morphology (Miller and Graves 2019). However, gibberellins, the family of plant growth regulators responsible for imparting control over cellular growth and shoot expansion, are known to have potential for modifying shoot growth of pecan (Brison 1974, Nasr and Hassan 1975, Shreve 1967, Wiggans and Martin 1961). For example, a report of the application of gibberellin (GA_3) on the stem of pecan seedlings indicated it yielded increases in size, so much so that seedlings were large enough to patch bud in their first year (Taylor 1973). Similarly, for layered shoots of hybrids in the genus *Quercus* L., Denig et al. 2014 observed improved shoot growth when the terminal bud was treated with 500 ppm of GA_{4+7}. Due to the overall lack of available information and the potential promise of the use of gibberellins to modify growth of hickories, we questioned if species in the genus *Carya* exhibit analogous growth and responses to gibberellins and whether the location and timing of application is a key factor in seedling development. Our objectives were to characterize species differences and assess responses of seedlings to application placement and growth stage when treated with GA_{4+7}.

Materials and Methods

Experiment 1: Effects of GA_{4+7} on one-year-old seedlings of six species of Carya. In fall of 2017, fresh seeds of bitternut hickory, pignut hickory, pecan, kingnut hickory, shagbark hickory, and mockernut hickory were obtained. All taxa except pecan and mockernut hickory were collected from wild populations growing near Ithaca, NY. Pecan and mockernut hickory seeds were acquired from wild populations in Springfield, IL and Greensboro, NC, respectively. Seeds were surface sterilized with an ethanol solution, and cold-moist stratified in moistened peat at 4 C (39.2 F) for 120 days to overcome embryo dormancy (Dirr 2009). After stratification, seeds were sown singly ≈5 cm (≈2 in) deep (Wood 2003) in nursery containers measuring 16.5 cm (6.5 in) in diameter and 17.8 cm (7 in) deep, filled with a peat and perlite based (LM-111) potting substrate (Lambert Peat Moss, Inc., Riviere-Ouelle, Quebec, Canada). Plants were grown in a glass-covered greenhouse maintained at 26.7 C (80 F) in Ithaca, NY through the 2018 growing season and subsequently stored in a cooler at 4 C (39.2 F) for 125 days. In spring of 2019, plants were removed from the cooler and placed on a greenhouse bench in a completely randomized design. Beginning at budbreak, plants were either left nontreated (control) or treated with a solution of 500 ppm GA_{4+7} dissolved in 95% ethanol applied directly to the most proximal 5 cm (2 in) of stem tissue (stem) or the distal-most position on the apical bud or extending shoot (bud) by coating the entire surface via dabbing with a cotton swab. Treatments continued at three-day intervals for 27 days for a total of nine applications. The experiment comprised 11-single plant replicates/species/treatment (N=198).

Supplemental lighting was provided with high pressure sodium lights set to a 16-hour diurnal pattern which provided a photosynthetic photon flux of ≈206 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at plant height as measured with a quantum sensor (SQ-520 Apogee Instruments, Logan, UT). Temperature and relative humidity were logged every 15 minutes by a HOBO MX2302 data logger (Onset Computer Corporation, Bourne, MA). Mean temperature and relative humidity were 24.4 C (76 F) with a range of 17.2 C to 36.5 C (63 F to 98 F) and 68.1% with a range of 22.7% to 94%, respectively. Plants were irrigated as needed with municipal tap water and fertilized twice weekly with a 21N–7P–7K water-soluble fertilizer (JR Peters, Allentown, PA) applied via fertigation at a rate of 150 $mg \cdot L^{-1}$. After 160 days in the greenhouse, shoot extension and caliper data were recorded. Shoot extension was measured as the length of the stem from where the bud broke in the spring to the distal-most end of the apical bud. Shoot caliper was measured as the diameter of the stem at 2.5cm above the surface of the potting substrate using a digital micrometer. Plants were not destructively harvested due to an intended evaluation to determine if treatments imposed in 2019 effected growth of plants the following season. However, due to an unforeseen nutrient deficiency, plant growth and survival was erratic in 2020 across treatments, including controls, and further data collection ceased. These symptoms, which did not manifest during the 2019 growing season, aligned well with Mouse Ear Disorder and were later determined to be caused by nickel deficiency (Miller and Bassuk 2022).

Data were subject to a two-way analysis of variance assessing species and treatment. When interaction terms were not significant, data were pooled across significant main effects. Post-hoc comparisons were made using Tukey's honestly significant difference test. All data were analyzed using JMP Pro 15 software (JMP Version 15, SAS Institute Inc., Cary, NC).

Experiment 2: Effects of GA_{4+7} on seedlings of bitternut hickory shortly after germination. Seeds of bitternut

Table 1. Significance of species and treatment main effects and their interactions on shoot extension and caliper responses to GA_{4+7} treatments applied to seedlings of *Carya cordiformis*, *C. glabra*, *C. illinoinensis*, *C. laciniosa*, *C. ovata*, and *C. tomentosa*.

Response	Effects [z]	DF	F ratio	*P*-value [y]
Shoot Extension	Species	5	11.91	< 0.0001
	Treatment	2	22.92	< 0.0001
	Species*Treatment	10	5.22	< 0.0001
Caliper	Species	5	19.71	< 0.0001
	Treatment	2	1.09	0.3403
	Species*Treatment	10	1.31	0.2327

[z]Main effects and interactions.

[y]Significance at $P \leq 0.05$.

hickory were harvested fresh from wild plants in Ithaca, NY in fall of 2020. Seeds were treated identically to those in Experiment 1. After cold-moist stratification, seeds were removed from the cooler and sown just below the surface of the LM-111 potting substrate (Lambert Peat Moss, Inc., Riviere-Ouelle, Quebec, Canada) in nursery containers that measured 10 cm (3.9 in) diameter and 9 cm (3.5 in) deep. Irrigation and fertigation were conducted the same as Experiment 1. Once hypocotyls of 21 seedlings attained a minimum height of 3.5 cm (1.4 in), treatments were implemented. Similar to Experiment 1, seedlings were either left nontreated (control) or treated with 500 ppm GA_{4+7} dissolved in a solution of 95% ethanol applied directly to the most proximal 3 cm (1.2 in) of stem tissue (stem) or the distal-most position on the extending shoot (bud) by dabbing with a cotton swab. Treatment intervals and duration were identical to Experiment 1. Plants were grown in the greenhouse for a total of 90 days where mean temperature and relative humidity were 19.8 C (67.6 F) with a range of 15.9 C to 38.8 C (60.6 F to 101.8 F) and 44.4% with a range of 6.02% to 88.5%, respectively. Supplemental lighting was provided with high pressure sodium lights set to a 16-hour diurnal pattern which provided a photosynthetic photon flux of ≈247 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at plant height as measured with a quantum sensor (SQ-520 Apogee Instruments, Logan, UT). At the conclusion of the growing period, plants were carefully removed from their nursery containers and roots were separated from the potting substrate by careful washing. Plants were destructively harvested to record final growth data. Responses measured included: shoot height and stem caliper, number of nodes, leaf surface area, as well as dry weights of leaves, shoots, and roots. Shoot height was measured from the cotyledon scar to the distal-most end of the terminal bud. Caliper was measured using a digital micrometer at 2.5 cm (1 in) above the surface of the potting substrate. Roots and shoots were separated at the cotyledon scar by completely severing with a hand pruner. A LI-COR 3100 leaf area meter (LI-COR Biosciences Inc., Lincoln, NE) was used to measure leaf surface area, after which all tissues were packaged separately in paper bags and dried in an oven at 65 C (149 F) for three days. Once dried, leaf, shoot, and root tissues were weighed separately.

Data were subject to a one-way analysis of variance. Post-hoc comparisons were made using Tukey's honestly significant difference test. All responses except caliper were either log (shoot height and shoot dry weight) or square root (number of nodes, leaf surface area, leaf dry weight, and root dry weight) transformed to meet the assumptions of the ANOVA model. All data were analyzed using JMP Pro 15 software (JMP Version 15, SAS Institute Inc., Cary, NC).

Results and Discussion

Experiment 1. There was no interaction between species and treatment for shoot caliper. However, there was a main effect of species ($P < 0.0001$) (Table 1). Data for this response were pooled across treatments to demonstrate species differences (Fig. 1). The interaction and main effects were each significant for shoot extension ($P < 0.0001$) (Table 1). Compared to nontreated control plants, treatment of buds resulted in a 234% and 144% increase in shoot extension of bitternut hickory and pecan, respectively (Fig. 2).

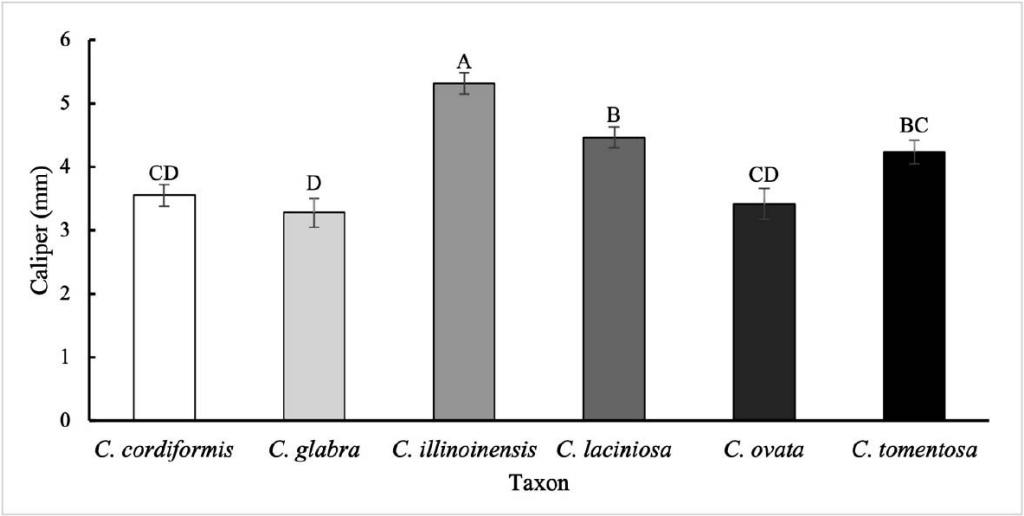

Fig. 1. Mean caliper of six species of *Carya*. Error bars indicate standard error. Data were pooled across treatments to reflect main effect of species. Means with same letter are not different according to Tukey's honestly significant difference test ($P \leq 0.05$).

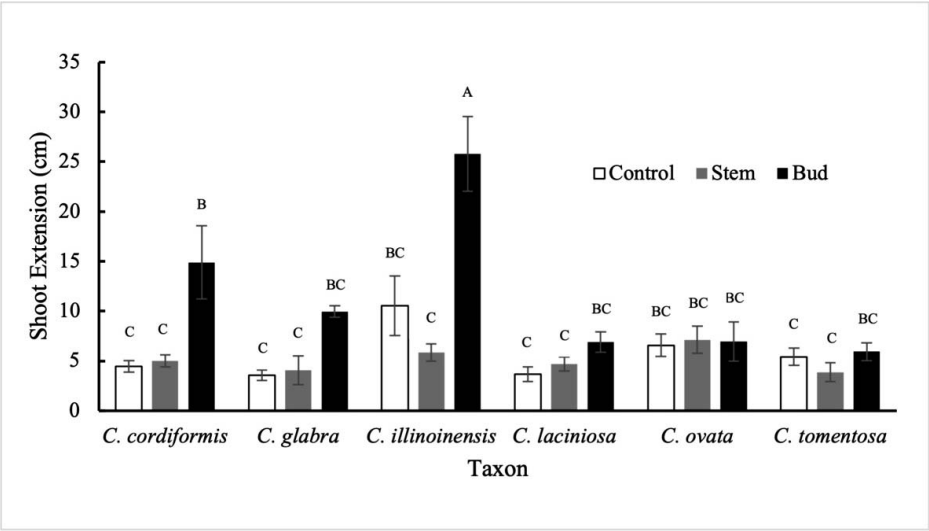

Fig. 2. Mean shoot extension of six species of *Carya* in response to treatment with GA_{4+7} at the stem or terminal bud in Experiment 1. Error bars indicate standard error. Means across species and treatments with same letter are not different according to Tukey's honestly significant difference test ($P \leq 0.05$).

Experiment 2. No responses except for shoot height ($P < 0.0001$) and shoot dry weight ($P = 0.0277$) were affected by the treatments (Table 2). Compared to controls, stem and bud treatments resulted in 43% and 209% increases in shoot height, respectively (Table 2). In the case of shoot dry weight, the stem treatment was not different from the controls, however, the bud treatment resulted in an 129% increase over the controls (Table 2). Caliper, number of nodes, leaf surface area, leaf dry weight, and root dry weight were not affected by either treatment involving GA_{4+7}.

Determinate, preformed, and monopodial growth patterns are characteristic of hickories and pecan (Pallardy 2008). Seedlings and juvenile plants exhibit these traits while also diverting energy to the growth of a taproot, instead of shoot development (Sparks 2005). While pecans typically exhibit this lag-phase shoot development during the first four years following germination (Sparks 2005), it is unclear how long this period lasts with other hickories. Annual shoot growth primarily originates from the terminal buds, which develop in the previous year and expand rapidly. Shoot extension is concluded with the development of the next terminal bud, thereby qualifying the growth of hickories as monopodial (Pallardy 2008). Buds of species that exhibit these types of growth patterns typically enter a quiescent state and inhibitory control is only released once certain environmental cues take place (Pallardy 2008). Because the shoot is pre-formed within the developing terminal buds of the previous season, shoot growth is largely pre-determined by the conditions of the previous year. As such, growth potentials and manipulation of growth beyond the preformed development for a given season are somewhat limited. In Experiment 1, the pre-determined nature of shoot development was unaffected by application of GA_{4+7} to the stem but was modified in bitternut hickory and pecan (Fig. 3) by treatments of GA_{4+7} to the apical meristem (terminal bud) (Fig. 2). In Experiment 2, the pre-determined nature of shoot development and how it can be manipulated was made clear by the number of nodes and the responses of shoot height and dry weight in seedlings that were grown from germinated seeds (Fig. 4). The number of nodes was not different across treatments; however, application of GA_{4+7} was capable of increasing not only shoot extension for both stem and bud treatments, but also shoot dry weight for treatments to the apical meristem (Table 2). The increased dry weight of the apical treatments indicate carbon allocation to the shoot was increased and that shoots were

Table 2. Effects of GA_{4+7} applications to seedlings of *Carya cordiformis* on height, caliper, and number of nodes of shoots, leaf surface area, and dry weight of leaves, shoots, and roots. All responses except caliper were transformed to meet the assumptions of the model; non-transformed means (±SE) are presented.

Treatment	Shoot height (cm)[w]	Caliper (mm)[v]	Number of nodes	Leaf surface area (cm^2)	Leaf dry weight (g)	Shoot dry weight (g)	Root dry weight (g)
Control[z]	8.8 ± 1.6 b	1.96 ± 0.12	8.9 ± 0.4	65.7 ± 13.2	0.32 ± 0.07	0.21 ± 0.05 b	1.96 ± 0.32
Bud[y]	27.2 ± 1.8 a	1.94 ± 0.13	9.5 ± 0.5	62.1 ± 15.3	0.31 ± 0.08	0.48 ± 0.06 a	1.31 ± 0.37
Stem[x]	12.6 ± 1.7 c	1.90 ± 0.12	9.9 ± 0.5	42.1 ± 14.1	0.21 ± 0.07	0.22 ± 0.06 b	1.39 ± 0.34

[z]Nontreated plants.

[y]Treated by applying 500 ppm GA_{4+7} dissolved in 95% ETOH to the most apical 1 cm (0.4 in) of the extending shoot.

[x]Treated by applying 500 ppm GA_{4+7} dissolved in 95% ETOH to the most proximal 3 cm (1.2 in) of stem tissue.

[w]Means (within column) with the same letter are not significantly different according to Tukey's honestly significant difference test ($P \leq 0.05$).

[v]Caliper of plants was measured at 2.5 cm (1 in) above the surface of the potting substrate.

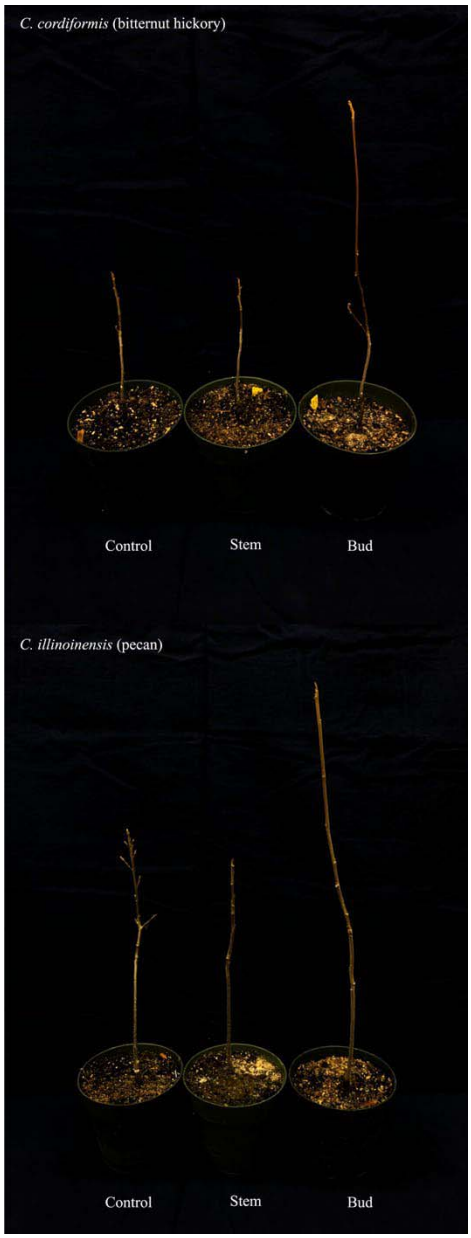

Fig. 3. Representative seedlings of bitternut hickory (top row) and pecan (bottom row) at the end of their second growing season after treatment in Experiment 1. From left to right within each row: nontreated (control), treated with 500 ppm GA_{4+7} to the proximal 5 cm (2 in) of the stem (stem), or the distal most position on the apical meristem (bud). Gibberellic acid solution was dissolved in 95% ethanol and applied by coating the entire surface of treated tissue via dabbing with a cotton swab. Treatments initiated after budbreak and continued at three-day intervals for 27 days. Images depict seedlings at the time of data collection after 160 days in a greenhouse.

not simply extended without affecting secondary development. While not significant, there was a trend of decreased root dry weight of bitternut hickory in Experiment 2 with the plants treated with GA_{4+7} compared to the controls. We question whether this trend could become a significant factor if plants were repeatedly treated over multiple growing seasons. If so, it may suggest that the application of GA_{4+7} to stems skews carbon allocation to shoots rather than roots. Similarly, bitternut hickory in Experiment 2

Fig. 4. Representative seedlings of bitternut hickory (*C. cordiformis*) from Experiment 2. Pictured are plants at the time of data collection, 90 days into their first growing season following germination. From left to right: nontreated (control), treated with 500 ppm GA_{4+7} dissolved in a solution of 95% ethanol applied directly to the most proximal 3 cm (1.2 in) of stem tissue (stem), or the distal-most position on the extending shoot (bud). Treatments initiated shortly after germination and continued at three-day intervals for 27 days.

exhibited a trend of decreased leaf surface area and leaf dry weight, but only with plants treated with GA_{4+7} on the stem. This pattern may also suggest variation in carbon allocation pending application locale. Further studies should explore these trends to determine if gibberellins could effectively reverse the lag-phase shoot development of some hickories as seedlings without negatively impacting crop quality.

While gibberellins have been utilized in modifying shoot growth (Amissah and Bassuk 2004, Eshed et al. 1996, Ranwala et al. 2003), flowering (Evans et al. 1992, Harkess and Lyons 1994), fruit development (Knoche et al. 2011, McArtney et al. 2014, Schmidt et al. 2008), or combinations of these features (Sarmiento and Kuehny 2003, Lordan et al. 2017) of many horticultural crops, few attempts have been made to manipulate the determinate nature of shoots of hickories. Taylor (1973) imposed treatments of sprays of gibberellic acid on seedlings of pecan which resulted in tall, spindly growth. The details of the treatments of that study are unclear. However, in a separate experiment, Taylor (1973) applied a mixture of one-part GA_3 (0.5% GA_3 via Gibrell®) to two-parts anhydrous lanum (lanolin) to the base of the shoot of seedlings of pecan 7-10 days after germination. The author reported seedlings treated with this mixture exhibited cambial growth, resulting in increased shoot caliper (Taylor 1973). In addition, Taylor (1973) reported that repeating the treatment three additional times at 10–14-day intervals resulted in seedlings of 46-61 cm (18.1-24 in) tall after six months. In Experiment 1, treatment to the apical meristem did increase shoot extension for bitternut hickory and pecan (Fig. 2) but did not affect growth of the other four species. Interestingly, Taylor (1973) treated the stems with GA_3 to achieve increased caliper of pecan whereas in Experiment 1, neither treatment of the apical meristem or

the base of the stem resulted in changes to the caliper of any of the six species studied, including pecan. However, our experiment was conducted on seedlings in their second growing season. More aligned with the phenological stage of the study conducted by Taylor (1973), in Experiment 2 we treated bitternut hickory seedlings with GA_{4+7} shortly after germination. Again, these treatments did not influence caliper (Table 2). We question if the differences in results are due to the differing form of gibberellins used in the two studies or if the mode in which the compounds were implemented plays a larger role. Other research involving treatment of young pecans with gibberellic acid report a range of responses from limited growth of treated plants (Wiggans and Martin 1961) to more profound differences in plant height of treated seedlings (Nasr and Hassan 1975, Shreve 1967). These results indicate variability of growth responses due to differing forms and modes of application of gibberellins and future studies should compare these methodologies to determine which factors influence this variation.

Some species of *Carya* are reported to occasionally exhibit flushes of growth late in the season (Pallardy 2008). The reason for this pattern is not well understood and has not been explored. However, this pattern inspired a replication of Experiment 1 using GA_3 once terminal buds had set after shoot extension in early summer. The goal of this study was to determine if a second flush of growth could be induced by application of GA_3. The results of that replication indicated those treatments were not effective at promoting a second flush of growth for any of those taxa (data not shown).

Based on the findings and this research as well as the findings of other studies (Miller and Graves 2019), generalizing all species of *Carya* based on observations of the most familiar taxon unnecessarily limits the popularity of hickories in the green industry. Other studies have shown that each taxon belonging to this genus should likely be considered on a case-by-case basis (Miller and Graves 2019). Our results provide further evidence to support this argument. While caliper was not affected by treatments with gibberellins, the six species differed in caliper (stem diameter) at the same stage in development (Fig. 1). To that effect, growers should continue to evaluate and grow hickories, and likely other taxa, on a species-by-species basis.

Interestingly, only species belonging to section Apocarya appeared responsive to gibberellic acid compared to those of section Carya (Fig. 1). This pattern may help illuminate which cues control lag-phase shoot development in the different hickories. Dirr (2009) states that, of the taxa represented in North America, bitternut hickory is considered one of the fastest growing species of the genus. The fact that some taxa grow more quickly than others likely implies variation in the patterns of plant development as well as the cues and controls which determine those patterns. Additional studies should explore further which factors control lag-phase shoot development of different species of hickory to find solutions for nursery growers. Given the extensive native ranges of some hickories, the role of intra-genetic variation within each taxon should be strongly considered (Peterson 1990).

This study indicates plant growth regulators could be effective at positively altering growth of some hickories for nursery production. Not all hickories should be treated identically with the goal of achieving uniform results. Instead, production of hickories should be evaluated on a case-by-case basis. The application of GA_{4+7} to the apical meristem is effective at promoting increased shoot development of bitternut hickory shortly after germination as well as during the subsequent growing season. Pecan seedlings in their second year of growth can also be treated with GA_{4+7} to increase shoot extension. For specialty nurseries that sell small container hickories such as standard #1 containers, this technique may reduce production time to saleable-sized plants by one or more growing seasons.

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