

RESPONSE OF CAMBIAL AND SHOOT GROWTH IN TREES TREATED WITH PACLOBUTRAZOL

by Shuju Bai¹, William Chaney², and Yadong Qi³

Abstract. Three experiments were conducted to investigate the effect of paclobutrazol on shoot and cambial growth of nine tree species located in Indiana and Louisiana, U.S. In Experiment I, white oak (*Quercus alba* L.) and red oak (*Q. rubra* L.) in Indiana were treated in April 1995 with paclobutrazol using the soil drench method. In Experiment II, paclobutrazol was applied in April 1996, using the soil injection method, to eight species growing in Indiana: white oak, red oak, sweetgum (*Liquidambar styraciflua* L.), black walnut (*Juglans nigra* L.), European black alder (*Alnus glutinosa* L.), yellow poplar (*Liriodendron tulipifera* L.), white ash (*Fraxinus americana* L.), and white pine (*Pinus strobus* L.). In Experiment III, two species, sweetgum and cherrybark oak (*Q. falcata* var. *pagodaefolia* L.) in Louisiana, were treated with paclobutrazol by the soil drench method in March 1997. At the end of the 1998 growing season, annual shoot growth and annual xylem ring increment were measured for each of the two to four growing seasons after treatment in the three experiments. The effects of paclobutrazol on cambial growth and annual shoot growth at various positions along the trunk and in the canopy varied with species and treatment duration. Paclobutrazol reduced cambial growth in white oak, red oak, cherrybark oak, sweetgum, European black alder, and white pine with the amount varying among species, vertical location in the tree, and year after treatment.

Key Words. Paclobutrazol (PBZ); growth retardant; cambial growth; annual shoot growth; xylem ring increment.

Paclobutrazol (PBZ), which inhibits gibberellin synthesis and consequently cell elongation (Kimball 1990; Grossmann 1992; Rademacher 2000), is known to reduce the growth of woody plants and has been used successfully for this purpose by horticulturists and utility arborists (Keever et al. 1990; Werblow 1998; Fletcher et al. 2000). The use of PBZ by utility arborists lengthens the time between trimming cycles, reduces the amount of time at the job site, and lowers the amount of biomass removed during trimming for many tree species (Redding et al. 1994; Burch et al. 1996). Shoot growth reduction along with other benefits to tree health reported in recent years has led to the expansion of PBZ use solely by utility foresters to its use by commercial arborists for management of other trees in the urban landscape (Chaney 2003).

Although PBZ is known to suppress shoot growth of most tree species (Davis and Curry 1991) and to increase

tolerance to drought conditions and resistance to fungal organisms (Chaney et al. 1996; Fletcher et al. 2000), the response of cambial growth in PBZ-treated trees has not been clearly elucidated. Because the principal focus of research with growth retardants such as PBZ has been on growth in height, only a few observations have been recorded concerning growth in diameter. Previous research, although limited in scope, has generally indicated a suppression of cambial growth (Gilliam et al. 1988; Estabrooks 1993; Schnurr et al. 1996). Growth in diameter of trees is a major cause of damage to hardscape in urban areas, accounting for a significant portion of annual tree program expenditures by municipalities (McPherson and Peper 1995). Hence, the main objective of this study was to determine the effect of the tree growth regulator PBZ on cambial growth of several tree species growing in the different environmental conditions of Indiana and Louisiana, U.S. Growth in length of terminal and lateral shoots also was measured to relate the acknowledged reduction of primary growth to any effect on secondary or cambial growth.

MATERIALS AND METHODS

Trees used in this study were in two locations; one at the Horticulture Farm at Southern University and A&M College in Baton Rouge, Louisiana, U.S., and the other at Martell Experimental Forest near Purdue University in West Lafayette, Indiana, U.S. Three experiments were designed, two at the Indiana and one at the Louisiana site, using a combination of nine tree species. For Experiment I conducted in Indiana, two species, red oak (*Quercus rubra* L.) and white oak (*Q. alba* L. [10 cm (4 in.) average caliper]) were treated by the soil drench method in April 1995. Experiment II, also in Indiana, involved eight species ranging from 4 to 8 cm [1.6 to 3.2 in.] caliper treated in April 1996 using the soil injection method: black walnut (*Juglans nigra* L.), European black alder (*Alnus glutinosa* L.), red oak, sweetgum (*Liquidambar styraciflua* L.), white ash (*Fraxinus americana* L.), white oak, white pine (*Pinus strobus* L.), and yellow poplar (*Liriodendron tulipifera* L.). Experiment III, conducted in Louisiana, involved two species treated in March 1997 using the soil drench method: cherrybark oak (*Q. falcata* var. *pagodaefolia* Elliott) and sweetgum [4 cm (1.6 in.) average caliper].

Twenty (Experiment I), 12 (Experiment II), and 14 (Experiment III) plantation trees of each species growing at 2 × 2 m [6.6 × 6.6 ft] spacing were selected based on their size and condition in 1995, 1996, and 1997, respectively. Adjacent trees were not selected for the studies to avoid root interaction and the unintended exposure to PBZ treatment. Half of the trees for each species used in the three experiments was randomly assigned to each of two different treatment groups. The treatments were basal drench or soil injection with PBZ formulated as Profile 2SC or water as a control in complete random experimental designs. The dose of PBZ applied was 9.6 g active ingredient (g a.i.) (0.34 oz) per tree in all the experiments except the sweetgum trees in Louisiana, which were treated with 4.8 g a.i. (0.17 oz.) per tree.

For Experiment I, the annual shoot growth for the 1995, 1996, 1997, and 1998 growing seasons was measured on the main stem, on four lateral shoots in the upper crown, and on four lateral shoots in the lower crown of each tree. For Experiment II, annual shoot growth for the 1996, 1997, and 1998 growing seasons was measured on the main stem and four lateral shoots of each tree. For Experiment III, the annual shoot growth for the 1997 and 1998 growing seasons was measured as in Experiment II. The amount of annual growth was apparent by locating the terminal bud scale scars on branches. All of the species used normally produce only one flush of growth each growing season. Shoot growth for European black alder is not reported because it was impossible to locate with certainty the bud scale scars on this species.

Cross-sections of the trunk were removed approximately 50 cm (20 in.) from the base of each tree for observations of annual xylem ring width in Experiment I. In Experiment II, three cross-sections were removed from each selected tree. One was approximately 10 cm (4 in.) from the base; the second was either 2 or 4 m (6.6 or 13.2 ft) from the base (determined by the height of the tree), and the third was from wherever the cross-section would include the annual rings of xylem for the 1995 through 1998 growing seasons. In Experiment III, an increment borer was used to obtain a wood sample for determining the ring width at a height of 10 cm (4 in.) from the base of each tree. An increment core also was taken from the highest point in the trees that would include the annual rings of xylem for the 1996 through 1998 growing seasons. Increment core samples were taken from only two heights in the trees in Louisiana because the trees were not tall enough to allow for additional sampling.

Each cross-section was sanded smooth with a handheld orbital sander, and each increment core was cut with a sharp blade to make a flat surface to facilitate microscopic viewing of the annual rings of xylem. Xylem ring widths for the year before PBZ treatment through the 1998 growing season were measured along four radii at approximately right angles for each cross-section using an Acu-rite III (Jamestown, NY) digital measuring system. Wood sections were placed on the table of the manually mobilized scale assembly and viewed through a lens with 10× magnification. The console was set for incremental measurement mode, and it gave a digital readout of the distance across each xylem ring with an accuracy of 0.001 mm (0.00004 in.).

Data were analyzed using analysis of variance and differences between means were determined using Tukey's Studentized Range (HSD) test, $P \leq 0.05$.

RESULTS

Annual Shoot Growth

Annual growth was not affected the first growing season after PBZ treatment in either red or white oak grown in Indiana (Experiment I), but it was markedly reduced in the central leader and in shoots of the upper and lower crown of white oak for the next three growing seasons (Table 1). Significant

Table 1. Annual and total shoot growth (cm) for 4 years and total reduction expressed as a percentage of untreated controls for white and red oak in Indiana untreated and treated in April 1995 with paclobutrazol using the soil drench method.

Treatment	Year				4-year total	Percentage reduction
	1995	1996	1997	1998		
White oak						
<i>Central leader</i>						
Control	42.9 a	46.6 a	41.1 a	40.9 a	170.5 a	
Treated	39.0 a	20.0 b	6.6 b	10.5 b	76.1 b	55
<i>Shoots in upper crown</i>						
Control	38.5 a	36.9 a	39.6 a	31.3 a	146.3 a	
Treated	31.2 a	14.6 b	7.0 b	8.1 b	60.9 b	58
<i>Shoots in lower crown</i>						
Control	28.2 a	34.1 a	32.8 a	26.6 a	121.7 a	
Treated	20.2 a	9.3 b	3.4 b	5.8 b	38.7 b	68
Red oak						
<i>Central leader</i>						
Control	91.0 a	51.3 a	62.4 a	45.4 a	250.1 a	
Treated	76.9 a	26.3 b	12.5 b	14.9 b	130.6 b	48
<i>Shoots in upper crown</i>						
Control	72.5 a	42.3 a	40.6 a	37.4 a	192.8 a	
Treated	67.4 a	18.6 b	8.9 b	12.3 b	107.2 b	44
<i>Shoots in lower crown</i>						
Control	44.0 a	35.1 a	31.6 a	20.1 a	130.8 a	
Treated	51.5 a	20.0 a	5.2 b	7.2 b	83.9 b	36

Pairs of values followed by the same lowercase letter are not significantly different at the $P \leq 0.05$ level.

reduction in annual shoot growth also was observed in the central leader and the upper crown of red oak for the second and the next two growing seasons. However, in the lower crown of red oak, significant reduction in annual shoot growth occurred only in the third and fourth years after PBZ treatment. Nevertheless, the total growth in shoot length was reduced throughout the crown in both species by as much as 36% to 68% compared to the untreated controls (Table 1).

Annual shoot growth of the central leader of the seven species investigated in Experiment II in Indiana showed large variations among species and years in response to soil injection of PBZ (Table 2). Annual growth of the central leader of sweetgum and white pine was reduced for the three growing seasons after PBZ treatment. Reduction of annual growth of the central leader of red oak, white ash, and white oak occurred in the first and second growing seasons after treatment, but in the third season, growth suppression disappeared (Table 2). In yellow poplar, inhibition occurred

only in the first season after treatment. No inhibition of shoot growth was observed through the three growing seasons in black walnut. Total growth of the central leader over the 3-year study period was significantly suppressed in only sweetgum (99%), white oak (46%), and white pine (30%) (Table 2).

For growth in length of the lateral shoots in the seven species in Experiment II in Indiana, only PBZ-treated sweetgum and white oak trees were suppressed for the three growing seasons after treatment, resulting in a total reduction in three growing seasons of 99% and 66%, respectively. Shoot growth of lateral branches of white pine was inhibited only in the second and third growing seasons, but this growth suppression was adequate to result in 19% less growth of PBZ-treated trees during the 3-year study period (Table 2). Growth reduction in red oak and yellow poplar occurred only the first growing season after treatment. No growth suppression was found in black walnut (Table 2).

Table 2. Annual and total shoot growth (cm) for 3 years and total reduction expressed as a percentage of untreated controls of seven species of trees in Indiana untreated and treated in April 1996 with paclobutrazol using the soil injection method.

Treatment	Year			3-year total	Percentage reduction	Treatment	Year			3-year total	Percentage reduction
	1996	1997	1998				1996	1997	1998		
Black walnut						White oak					
<i>Central leader</i>						<i>Central leader</i>					
Control	27.5 a	13.5 a	7.5 a	48.5 a		Control	37.3 a	32.0 a	28.7 a	98.0 a	
Treated	12.5 a	8.9 a	6.8 a	28.2 a	42	Treated	18.2 b	13.7 b	20.7 a	52.6 b	46
<i>Lateral shoots</i>						<i>Lateral shoots</i>					
Control	10.0 a	10.5 a	8.2 a	28.7 a		Control	41.7 a	28.7 a	32.8 a	103.2 a	
Treated	7.0 a	5.6 a	4.8 a	17.4 a	39	Treated	14.7 b	10.0 b	10.2 b	34.9 b	66
Red oak						White pine					
<i>Central leader</i>						<i>Central leader</i>					
Control	71.7 a	45.7 a	31.2 a	148.6 a		Control	95.3 a	82.3 a	89.8 a	267.4 a	
Treated	64.3 b	31.3 b	28.1 a	123.7 a	17	Treated	84.0 b	48.0 b	55.7 b	187.7 b	30
<i>Lateral shoots</i>						<i>Lateral shoots</i>					
Control	55.4 a	23.4 a	21.5 a	100.3 a		Control	55.4 a	46.5 a	37.2 a	139.1 a	
Treated	40.1 b	17.5 a	16.2 a	73.8 a	26	Treated	50.0 a	34.7 b	28.6 b	113.3 b	19
Sweetgum						Yellow poplar					
<i>Central leader</i>						<i>Central leader</i>					
Control	51.5 a	54.7 a	67.0 a	173.2 a		Control	53.7 a	43.0 a	63.3 a	160.0 a	
Treated	0.8 b	0.3 b	0.3 b	1.4 b	99	Treated	37.0 b	44.1 a	59.5 a	140.6 a	12
<i>Lateral shoots</i>						<i>Lateral shoots</i>					
Control	34.0 a	27.7 a	21.7 a	83.4 a		Control	32.3 a	28.3 a	24.7 a	85.3 a	
Treated	0.7 b	0.3 b	0.2 b	1.2 b	99	Treated	21.8 b	22.4 a	18.6 a	62.8 a	26
White ash											
<i>Central leader</i>											
Control	44.8 a	37.5 a	37.5 a	119.8 a							
Treated	31.3 b	26.3 b	35.0 a	92.6 a	23						
<i>Lateral shoots</i>											
Control	31.0 a	20.5 a	15.2 a	66.7 a							
Treated	24.0 a	17.5 a	13.9 a	55.4 a	17						

Pairs of values followed by the same lowercase letter are not significantly different at the $P \leq 0.05$ level.

Table 3. Annual and total shoot growth (cm) for 2 years and total reduction expressed as a percentage of untreated controls of sweetgum and cherrybark oak in Louisiana untreated and treated in March 1997 with paclobutrazol using the soil drench method.

Treatment	Year		2-year total	Percentage reduction
	1997	1998		
Sweetgum				
<i>Central leader</i>				
Control	83.5 a	89.3 a	172.8 a	95
Treated	6.5 b	1.4 b	7.9 b	
<i>Lateral shoots</i>				
Control	33.3 a	28.0 a	61.3 a	96
Treated	1.4 b	1.1 b	2.5 b	
Cherrybark oak				
<i>Central leader</i>				
Control	36.1 a	30.0 a	66.1 a	46
Treated	31.2 a	4.2 b	35.4 b	
<i>Lateral shoots</i>				
Control	24.8 a	25.0 a	49.8 a	42
Treated	23.9 a	4.8 b	28.7 b	

Pairs of values followed by the same lowercase letter are not significantly different at the $P \leq 0.05$ level.

Table 4. Annual xylem ring increment (mm) 50 cm from the ground line for white and red oak for the year prior to treatment and for 4 years after treatment with paclobutrazol in April 1995 using the soil drench method, with total reduction expressed as a percentage of untreated controls.

Treatment	Prior 1994	Year				Total 1995–98	Percentage reduction
		1995	1996	1997	1998		
White oak							
Control	4.95 a	4.43 a	5.06 a	4.50 a	6.11 a	20.10 a	80
Treated	5.30 a	1.60 b	0.99 b	0.70 b	0.71 b	4.00 b	
Red oak							
Control	6.19 a	4.65 a	4.65 a	4.03 a	5.57 a	18.90 a	60
Treated	6.24 a	2.68 b	1.78 b	1.37 b	1.81 b	7.64 b	

Pairs of values followed by the same lowercase letter are not significantly different at the $P \leq 0.05$ level.

In Louisiana, annual shoot growth of sweetgum was markedly inhibited in both the central leader and the lateral shoots for the two growing seasons after PBZ treatment, resulting in total growth suppression of 95% and 96%, respectively (Table 3). For cherrybark oak, inhibition occurred only in the second growing season after treatment, and the total reduction in growth in 2 years was significant, but less than in sweetgum.

Annual Xylem Ring Increment

In Experiment I, the width of the annual ring of xylem produced 50 cm (20 in.) up from the base of trees was significantly reduced in both white and red oak during the first growing season after PBZ treatment by the soil drench method. This suppression of cambial activity in treated trees persisted for the four growing seasons of the study, resulting in a total reduction of cambial growth in white and red oak of 80% and 60%, respectively (Table 4).

Xylem accumulation at the base of the trunk of trees treated in spring 1996 using the soil injection method (Experiment II) showed that PBZ suppressed annual ring increment in sweetgum for the first and second growing seasons after treatment, and in white oak for the second and third seasons (Table 5). Reduction of xylem accumulation occurred in white pine in only the first growing season after treatment and in European black alder in the third growing season after treatment. No growth suppression near the base of the trunk was observed in the other species (Table 5).

A similar pattern of xylem growth reduction in sweetgum and white oak also occurred in the cross-sections 2 or 4 m (6.6 or 13.2 ft) above the ground line (Table 5). Treated European black alder had significantly reduced annual ring growth for the three growing seasons after PBZ treatment. In addition, PBZ suppressed annual ring increment of white pine in the second growing season. No growth reduction 2 or 4 m high was found in the other species investigated (Table 5).

Annual ring increment in the upper crown in the cross sections of the trunk that included four years of xylem growth of the eight species treated in 1996 using the soil injection method (Experiment II) also are shown in Table 5. PBZ-treated sweetgum trees had less xylem increment than control trees for the three growing seasons after treatment. Growth suppression also occurred in white oak and white pine during the second and the third growing seasons. Annual ring increment in the upper crown in the other species was not affected by PBZ (Table 5).

Total cambial growth for the three years following PBZ treatment was significantly reduced ($P \leq 0.05$) only for sweetgum and white oak. There also was a 3-year reduction in the mid-trunk section of European black alder and in the cross-section within the crown of white pine (Table 5).

In Louisiana (Experiment III), the annual ring increment of cherrybark oak was reduced by PBZ at both the base and within the crown for the two growing seasons after PBZ

Table 5. Annual xylem ring increment (mm) for the year prior to treatment and for 3 years after treatment with paclobutrazol in April 1996 using the soil injection method on eight tree species growing in Indiana, with total reduction expressed as a percentage of untreated controls.

Treatment	Year				Total 1996–98	Percentage reduction	Treatment	Year				Total 1996–98	Percentage reduction
	Prior 1995	After treatment						Prior 1995	After treatment				
Black walnut							White ash						
<i>Within crown</i>							<i>Within crown</i>						
Control	1.36 a	1.38 a	1.06 a	1.08 a	3.52 a		Control	1.55 a	1.63 a	1.95 a	2.07 a	5.65 a	
Treated	0.82 a	1.28 a	0.99 a	0.94 a	3.21 a	9	Treated	1.09 a	1.27 a	1.32 a	1.48 a	4.07 a	28
<i>Mid-trunk (2–4 m high)</i>							<i>Mid-trunk (2–4 m high)</i>						
Control	2.05 a	2.44 a	1.46 a	1.67 a	5.57 a		Control	2.21 a	2.11 a	2.21 a	2.15 a	6.47 a	
Treated	1.74 a	1.54 a	1.14 a	1.40 a	4.08 a	27	Treated	1.39 a	1.62 a	1.55 a	1.66 a	4.83 a	25
<i>Base of trunk (10 cm above ground line)</i>							<i>Base of trunk (10 cm above ground line)</i>						
Control	1.86 a	1.42 a	1.25 a	1.66 a	4.33 a		Control	2.03 a	2.25 a	1.92 a	2.25 a	6.42 a	
Treated	2.06 a	1.61 a	1.05 a	1.04 a	3.70 a	15	Treated	1.67 a	1.57 a	1.30 a	1.71 a	4.58 a	29
European black alder							White oak						
<i>Within crown</i>							<i>Within crown</i>						
Control	2.06 a	1.84 a	1.46 a	1.50 a	4.80 a		Control	2.42 a	2.17 a	1.84 a	2.68 a	6.69 a	
Treated	2.59 a	1.20 a	1.11 a	1.29 a	3.60 a	25	Treated	2.46 a	1.08 a	0.80 b	0.97 b	2.85 b	57
<i>Mid-trunk (2–4 m high)</i>							<i>Mid-trunk (2–4 m high)</i>						
Control	5.80 a	5.00 a	3.90 a	6.27 a	15.17 a		Control	3.02 a	2.98 a	2.69 a	3.26 a	8.93 a	
Treated	3.15 a	2.16 b	1.27 b	2.40 b	5.83 b	62	Treated	2.30 a	1.04 a	0.90 b	1.11 b	3.05 b	66
<i>Base of trunk (10 cm above ground line)</i>							<i>Base of trunk (10 cm above ground line)</i>						
Control	5.19 a	3.85 a	3.30 a	4.45 a	11.60 a		Control	4.11 a	2.94 a	2.91 a	4.36 a	10.21 a	
Treated	5.00 a	3.25 a	2.73 a	2.25 b	8.23 a	29	Treated	3.63 a	1.40 a	0.95 b	1.16 b	3.51 b	66
Red oak							White pine						
<i>Within crown</i>							<i>Within crown</i>						
Control	3.14 a	2.16 a	2.07 a	3.36 a	7.59 a		Control	4.71 a	4.95 a	8.67 a	10.50 a	24.12 a	
Treated	4.54 a	2.38 a	1.80 a	2.85 a	7.03 a	7	Treated	5.35 a	5.67 a	4.42 b	5.29 b	15.38 b	36
<i>Mid-trunk (2–4 m high)</i>							<i>Mid-trunk (2–4 m high)</i>						
Control	4.32 a	2.82 a	2.37 a	3.38 a	8.57 a		Control	9.77 a	9.05 a	10.39 a	10.77 a	30.21 a	
Treated	4.17 a	2.23 a	1.79 a	2.60 a	6.62 a	23	Treated	8.48 a	8.79 a	8.42 b	10.17 a	27.38 a	9
<i>Base of trunk (10 cm above ground line)</i>							<i>Base of trunk (10 cm above ground line)</i>						
Control	5.87 a	4.39 a	3.39 a	4.91 a	12.69 a		Control	9.17 a	11.32 a	9.84 a	12.08 a	33.24 a	
Treated	5.97 a	3.19 b	2.04 a	3.57 a	8.80 a	31	Treated	8.95 a	9.33 b	8.22 a	11.46 a	29.01 a	13
Sweetgum							Yellow poplar						
<i>Within crown</i>							<i>Within crown</i>						
Control	4.68 a	4.23 a	3.78 a	4.26 a	12.27 a		Control	2.83 a	2.64 a	2.98 a	3.65 a	9.27 a	
Treated	4.18 a	1.99 b	1.66 b	1.54 b	5.19 b	58	Treated	2.74 a	1.92 a	2.57 a	3.83 a	8.32 a	10
<i>Mid-trunk (2–4 m high)</i>							<i>Mid-trunk (2–4 m high)</i>						
Control	4.50 a	4.42 a	3.51 a	3.58 a	11.51 a		Control	3.28 a	2.55 a	2.71 a	3.99 a	9.25 a	
Treated	3.54 a	2.46 b	2.17 b	2.07 a	6.70 b	42	Treated	2.68 a	1.88 a	2.33 a	3.62 a	7.83 a	15
<i>Base of trunk (10 cm above ground line)</i>							<i>Base of trunk (10 cm above ground line)</i>						
Control	4.10 a	4.44 a	4.97 a	4.93 a	14.34 a		Control	2.47 a	2.25 a	2.20 a	3.90 a	8.35 a	
Treated	3.78 a	3.37 b	3.45 b	4.13 a	10.95 b	24	Treated	2.25 a	2.16 a	2.63 a	4.16 a	8.95 a	(–7)

Pairs of values for each set of control and treated trees followed by the same lowercase letter are not significantly different at the $P \leq 0.05$ level.

treatment, resulting in a total reduction compared to untreated controls of 56% and 53%, respectively. However, reduction of cambial growth in sweetgum occurred only in the first growing season after PBZ treatment, but this was sufficient to cause a 29% reduction at the base of trees during the two year period of the study (Table 6).

DISCUSSION

The principal focus of research with tree growth retardants has been on shoot length and growth in height. Reductions in shoot growth reported range from a low of 20% to a high of 90% among a broad spectrum of species including hardwoods, conifers, shrubs, and palms (Wheeler 1987;

Table 6. Annual xylem ring increment (mm) for the year prior to treatment and for 2 years after treatment with paclobutrazol in March 1997 using the soil drench method for cherrybark oak and sweetgum growing in Louisiana, with total reduction expressed as a percentage of untreated controls.

Treatment	Year			Total 1997–98	Percentage reduction
	Prior 1996	After treatment 1997	1998		
Cherrybark oak					
<i>Within crown (2–4 m high)</i>					
Control	2.00 a	2.22 a	1.82 a	4.04 a	
Treated	1.60 a	1.06 b	0.82 b	1.88 b	53
<i>At base of tree (10 cm above ground line)</i>					
Control	4.63 a	5.86 a	5.74 a	11.60 a	
Treated	4.21 a	3.19 b	1.89 b	5.08 b	56
Sweetgum					
<i>Within crown (2–4 m high)</i>					
Control	1.75 a	1.85 a	0.99 a	2.84 a	
Treated	1.29 a	1.52 b	0.88 a	2.40 a	15
<i>At base of tree (10 cm above ground line)</i>					
Control	2.91 a	1.83 a	1.76 a	3.59 a	
Treated	2.01 a	1.21 b	1.34 a	2.55 b	29

Pairs of values followed by the same lowercase letter are not significantly different at the $P \leq 0.05$ level.

Ruter 1994; Burch et al. 1996; Hensley and Yogi 1996; Arron et al. 1997).

Of the nine species investigated in this study, only European black alder and cherrybark oak have not previously been reported to show reduction in shoot growth when treated with a gibberellin synthesis inhibitor like PBZ. Although shoot growth of European black alder was reduced by PBZ treatment, we could not quantify the amount because the terminal bud scale scars, which indicate the beginning and ending point of annual shoot growth, were not visible.

Our data demonstrate the wide variability among species in sensitivity to PBZ mentioned above. With the exception of sweetgum in Louisiana, only one dose rate was used for all nine species investigated. For example, shoot growth of black walnut was not affected by PBZ either in the main stem or in the lateral branches at the 9.6 g a.i. (0.34 oz.) dose rate. However, shoot growth in sweetgum at this dose rate was markedly reduced during the three growing seasons after treatment, whereas other species showed reductions in shoot growth in only some growing seasons (Tables 1, 2, and 3).

The differences in response among species found in this study are consistent with the dose rate charts provided by distributors of commercial formulations of PBZ that recommend six rates categories, A through F [1.25 to 4 g

a.i. (0.04 to 0.14 oz) per inch dbh] reflecting different sensitivities among species to PBZ. Black walnut, white ash, white pine, and yellow poplar are recognized as the least sensitive and are in category F for the highest dose rate. Sweetgum is quite sensitive to paclobutrazol and is in category B. Both red and white oak are intermediate and are in category D. Cherrybark oak, although not yet assigned to a category, probably should be in D based on the response found in this study. The majority of oaks are in category E, with a few in F. The dose rate applied in this study was that for category D or E depending on the diameter of the tree treated. Because of the small caliper [4 cm (0.16 in.)] of the sweetgum trees used in Louisiana, the 4.8 g a.i. (0.17 oz) dose rate also was that for category E.

Although the preponderance of research has focused on shoot growth, a few observations have been recorded concerning growth in diameter. Schnurr et al. (1996) found that both PBZ and flurprimidol (another growth retardant with the same mode of action as PBZ) reduced height and stem caliper of Jack pine (*Pinus banksiana*) seedlings. Reduction in trunk diameter also was observed in apple (*Malus* spp.) (Estabrooks 1993), peach (*Prunus* spp.) (Liyembani and Taylor 1989), Colt cherry (*Prunus avium* × *P. pseudocerasus*) (Asamoah and Atkinson 1985), and red maple (*Acer rubrum*) (Gilliam et al. 1988) with the suppression continuing for 2 to 3 years after treatment. The different responses in cambial growth we found among the species to the same dose of PBZ is consistent with the varied effects expected from a single dose rate on shoot growth.

Cambial activity at different vertical positions in a tree may respond to PBZ differently. For example, in white pine, reduction in xylem ring width occurred in the cross-section 10 cm (4 in.) above the ground line in the year of treatment. In the second year after treatment, reduction shifted to the cross-sections 2 m (6.6 ft) above the ground line, as well as within the canopy, and in the third year after treatment, xylem accumulation only in the uppermost cross-section was reduced.

This raises the question concerning the mode of action of PBZ on cambial growth. It was suggested by Elfving (1984) that the reduction in trunk growth in apple (*Malus* spp.) is due either to reduced shoot growth and associated leaf area or to direct effect of PBZ on cambial growth itself. Because gibberellins are not known to be produced in the cambium, but rather in leaf primordia and root tips, any effect on cell growth in the cambial region would rely on a disruption of the quantity of gibberellins translocated via the phloem or xylem (Leopold and Kriedemann 1975). The varied length of the translocation conduit between the gibberellin source and the cambial location in the trunk or tree crown, as well as the relative importance of leaf primordia or root tip produced gibberellins, could account for the differences reported.

The climatic differences between Indiana and Louisiana seemed to have little influence on the efficacy of PBZ with respect to shoot growth (Tables 1, 2, and 3). However, there was a marked difference between the two experimental sites in cambial growth of sweetgum. At both locations, cambial growth was reduced in the year of treatment with PBZ, but in Louisiana the effect did not continue into the second growing season and the percent reduction was much less, both in the lower trunk and within the canopy in particular (Tables 5 and 6). This difference may be due to the application method, which was soil injection in Indiana and soil drench in Louisiana, rather than to climatic differences.

To provide a perspective of the potential impact of the reduction in shoot and cambial growth reported here on trees in the landscape, the total green aboveground weight of an untreated and PBZ treated white oak is estimated. The estimate is based on the average height [750 cm (25 ft)] and trunk diameter [14 cm (5.6 in.)] of the control white oaks at the termination of this study. These average measurements were reduced by the 4-year reductions in height and diameter determined for white oak growing in Indiana (Tables 1 and 4). A nonlinear regression equation specific to white oak was used (Total green weight = $1.3426 \times D^{2.2409} \times H^{0.4275}$ where D is tree diameter and H is height) (Myers and Polak 1976). Using this equation, the total weight of an average 16-year-old untreated white oak used in this study was found to be 109.3 kg (240 lb), whereas the total weight of a white oak treated with PBZ 4 years earlier was calculated to be 78.6 kg (173 lb), a 30.7 kg (67.6 lb) reduction in total weight.

Whether the reduction in cambial growth by PBZ was a function of a direct effect on meristematic activity and cell development through gibberellin synthesis inhibition or an indirect effect caused by reduced shoot growth with consequent reduced photosynthesis and carbohydrate partitioning was not determined and needs to be investigated. Additional studies also are needed to determine if there are any effects on cell structure, cell composition, or other micro aspects of xylem anatomy that could affect wood strength and susceptibility of trees to failure under wind or ice loading.

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¹Department of Computer Science
Southern University and A&M College
P.O. Box 9221
Baton Rouge, LA 70813, U.S.

²Department of Forestry and Natural Resources
715 West State Street
Purdue University
West Lafayette, IN 47907, U.S.

³Urban Forestry Program
Southern University and A&M College
P.O. Box 11288
Baton Rouge, LA 70813, U.S.

*Corresponding author.

Résumé. Trois expériences ont été menées afin de vérifier l'effet du paclobutrazol sur la croissance des pousses et du cambium de neuf espèces d'arbres localisées en Indiana et en Louisiane. Dans l'Expérience I, le chêne blanc (*Quercus alba* L.) et le chêne rouge (*Quercus rubra* L.) en Indiana ont été traités en avril 1995 avec du paclobutrazol au moyen de la méthode par trempage du sol. Dans l'Expérience II, le paclobutrazol a été appliqué en avril 1996 au moyen de la méthode par injection dans le sol sur huit espèces poussant en Indiana, soient le chêne blanc, le chêne rouge, le liquidambar styracifère (*Liquidambar styraciflua* L.), le noyer noir (*Juglans nigra* L.), l'aulne européen (*Alnus glutinosa* L.), le tulipier de Virginie (*Liriodendron tulipifera* L.), le frêne blanc (*Fraxinus americana* L.) et le pin blanc (*Pinus strobus* L.). Dans l'Expérience III, deux espèces en Louisiane—liquidambar et chêne rouge du Sud (*Quercus falcata* var. *pagodaefolia* L.)—ont été traités par la méthode de trempage du sol en mars 1997. À la fin de la saison de croissance 1998, le taux de croissance de la pousse et l'épaisseur des anneaux de xylème ont été mesurés pour chacune des deux à quatre années de croissance qui se sont écoulées depuis le traitement avec les trois expériences. Les effets du paclobutrazol sur la croissance du cambium et des pousses annuelles, et ce à différentes positions sur le tronc et dans la cime, ont varié selon les espèces et la durée du traitement. Le paclobutrazol a diminué la croissance cambiale chez le chêne blanc, le chêne rouge, le chêne rouge du Sud, le liquidambar, l'aulne européen et le pin blanc de manière variable selon l'espèce, l'élévation dans l'arbre et le nombre d'Années après le traitement.

Zusammenfassung. Es wurden drei Experimente durchgeführt, um die Wirkung von Paclobutrazol auf das Trieb- und Kambiumwachstum von neun Baumarten in Indiana und Louisiana zu erforschen. In Experiment I wurden *Quercus alba* und *Q. rubra* in Indiana im April 1995 mit Paclobutrazol über den Boden durch Tränken behandelt. Im Experiment II wurde Paclobutrazol im April

1996 durch Bodeninjektion an 8 Arten (*Q. alba*, *Q. rubra*, *Liquidamber styraciflua*, *Juglans nigra*, *Alnus glutinosa*, *Liriodendron tulipifera*, *Fraxinus americana* und *Pinus strobus*) in Indiana behandelt. Im Experiment III wurden im März 1997 in Louisiana 2 Baumarten (*Liquidamber styraciflua* und *Q. falcata*) durch eine Tränkung des Bodens behandelt. Am Ende der Wachstumsperiode 1998 wurden das jährliche Triebwachstum und der Jahresringzuwachs für jede der 2 bis 4 Wachstumsperioden nach der Behandlung gemessen. Die Auswirkungen von Paclobutrazol auf das sekundäre Dickenwachstum und die jährliche Triebblänge an verschiedenen Positionen entlang des Stammes und in der Krone variierte mit der Baumart und der Dauer der Behandlung. Paclobutrazol reduzierte das Dickenwachstum bei *Q. alba*, *Q. rubra*, *Q. falcata*, *Liquidamber styraciflua*, *Alnus glutinosa* und *Pinus strobus* in unterschiedlichem Ausmaß je nach Art, vertikaler Lage im Baum und dem Zeitraum nach der Behandlung.

Resumen. Se condujeron tres experimentos para investigar el efecto del paclobutrazol en el crecimiento cambial y de brotes de nueve especies de árboles localizados en Indiana y Louisiana. En el experimento I, el encino blanco (*Quercus alba* L.) y encino rojo (*Q. rubra* L.), en Indiana, fueron tratados en Abril de 1995 con

paclobutrazol usando el método de zanjas en el suelo. En el experimento II, se aplicó paclobutrazol en Abril de 1996, usando el método de inyección al suelo, a ocho especies en Indiana: encino blanco, encino rojo, liquidámbar (*Liquidamber styraciflua* L.), nogal negro (*Juglans nigra* L.), aile negro europeo (*Alnus glutinosa* L.), chopo amarillo (*Liriodendron tulipifera* L.), fresno blanco (*Fraxinus americana* L.) y pino blanco (*Pinus strobus* L.). En el experimento III, dos especies de liquidámbar y encino (*Q. falcata* var. *pagodaefolia* L.), en Louisiana, fueron tratadas con paclobutrazol por el método de zanjas en el suelo en Marzo de 1997. A finales de la estación de crecimiento de 1998 se midió el crecimiento de los brotes y el incremento de los anillos anuales del xilema para las cuatro estaciones de crecimiento después de los tratamientos en los tres experimentos. Los efectos del paclobutrazol en el crecimiento cambial y en los brotes, en diferentes localizaciones a lo largo del tronco y en la copa, variaron con las especies y la duración de los tratamientos. Paclobutrazol redujo el crecimiento cambial en encino blanco, encino rojo, liquidámbar, aile y pino blanco, en una cantidad variable de acuerdo a las especies, la localización vertical en el árbol y el año después del tratamiento.