Effects of Timing and Intensity of Summer Pruning on Reproductive Traits of Two Southern Highbush Blueberry Cultivars

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Abstract. Blueberry (*Vaccinium* spp.) summer pruning can increase yield by promoting healthy fall foliage to support the reproductive development. However, there has been little research to examine the effects of timing and intensity of summer pruning in subtropical conditions. The objective of this study was to determine the effects of summer pruning timing and intensity on reproductive traits of mature ‘Jewel’ and ‘Emerald’ southern highbush blueberry (SHB) plants (*V. corymbosum* L. interspecific hybrid) in subtropical Florida. The effect of pruning time was evaluated by removing 30% of the canopy in June or July. The effect of intensity was evaluated by pruning either 30% or 60% of the canopy in June, followed by removal of the upper 5 cm of regrowth (“tipping”) in July. Both timing and intensity used nonpruned plants as a control. The same plants were evaluated over three consecutive seasons (June 2011–May 2014). Main effects of pruning time, intensity, and tipping were evaluated. Tipping did not affect the reproductive traits evaluated. ‘Emerald’ reproductive traits were unaffected by either summer pruning time or intensity over the 3-year study. ‘Jewel’ yield was unaffected in the first year, but was increased by 48% and 65% in years 2 and 3, respectively, in the 30% pruning treatment compared with the nonpruned control. Lack of pruning in ‘Jewel’ decreased inflorescence bud number compared with moderate pruning likely due to more diseased foliage that increased defoliation. Thus, pruning effects on reproductive traits were cultivar dependent. Leaving ‘Jewel’ plants unpruned for two or more seasons reduced inflorescence bud number and yield.

Pruning blueberry (*Vaccinium* spp.) bushes is an important cultural practice (Mainland, 1989; Shutak and Marucci, 1966; Williamson et al., 2004) that, if done properly, results in a balance between plant vigor and cropping, and ensures new growth for the following season’s crop (Yarborough, 2006). The overall objectives of pruning are to obtain optimal and stable yields of high-quality fruit and to increase the plant life span (Pescie et al., 2011). Pruning renews the canopy and increases productivity of blueberry bushes by stimulating vegetative and reproductive growth.

Pruning practices vary in different production regions based on climate, growing conditions, and blueberry species. SHB (*V. corymbosum* interspecific hybrid) is the major species of blueberry grown in Florida and other mild winter areas. High temperatures and a long-growing season characterize the

climate where SHB are typically grown, and summer pruning after fruit harvest stimulates healthy vegetative growth through the end of the growing season by removing older foliage that would otherwise serve as source of inoculum for leaf diseases (Kovaleski et al., 2015a; Patten et al., 1991; Williamson et al., 2004). This is important as the fall foliage supports inflorescence bud development and increases carbohydrate reserve accumulation to support early fruit development the following growing season (Lyrene, 1992; Swain and Darnell, 2001, 2002; Williamson and Miller, 2002).

Although summer pruning is an important commercial practice for SHB production, there has been little research examining the effects of timing and intensity of summer pruning on reproductive growth of this species. Bañados et al. (2009) compared no pruning and both early and late summer pruning in southern and northern (*V. corymbosum*) highbush blueberry cultivars. Early summer pruning increased inflorescence bud number in ‘O’Neal’ and ‘Star’ SHB compared with late summer pruning, whereas the nonpruned control had an intermediate inflorescence bud number. However, both summer pruning times decreased inflorescence

bud number in ‘Elliott’, a northern highbush cultivar, compared with no pruning.

Summer pruning effects on blueberry yield are also inconsistent. Williamson and Darnell (1996) found that no pruning and early summer pruning in ‘Sharpblue’ SHB increased the yield compared with late summer pruning in Florida. However, Pescie et al. (2011) found that summer pruning alone reduced yield of ‘O’Neal’ SHB compared with summer followed by winter pruning or compared with nonpruned plants in Argentina. Summer followed by winter pruning also increased fruit size in ‘O’Neal’ compared with no pruning (Pescie et al., 2011). Yield and fruit size in rabbiteye blueberry (*Vaccinium virgatum*) were increased by summer followed by winter pruning compared with winter pruning alone in North Carolina (Mainland, 1989). However, in Georgia, yield decreased in summer or winter pruned rabbiteye blueberries compared with nonpruned plants, although fruit size was greater in the pruned treatments compared with nonpruned (Austin, 1997). Krewer et al. (2004) found no differences in yield or fruit size between summer pruned and nonpruned rabbiteye blueberry in Georgia.

The intensity of pruning plays a role in yield of blueberry bushes. Heavy summer pruning decreased yield of rabbiteye blueberry compared with moderate and no pruning in Louisiana, but had no effect on fruit size (Spiers et al., 2002). Davies (1983) found moderate pruning, regardless of season, produced the highest yields compared with heavy and nonpruned rabbiteye blueberries in Florida. Austin and Bondari (1989) reported that yield and fruit size of ‘Tifblue’ rabbiteye blueberry were similar among light, moderate, and heavy pruning intensities over a 5-year period in Georgia.

Most summer pruning studies in blueberries have been carried out in climates far different from those found in subtropical blueberry production regions, and few studies have been done with SHB, which is expanding in acreage in the southeast United States and California, and warmer regions of Argentina and Chile (Bañados, 2004, 2009). The hypothesis tested in this research was that summer pruning increases reproductive growth and yield in SHB compared with no pruning. The objectives of this study were to determine the effects of timing and intensity of summer pruning on inflorescence bud number, number of fruits set per inflorescence bud, yield, and quality of berries in SHB.

Materials and Methods

‘Emerald’ and ‘Jewel’ SHB plants, field planted at the UF-IFAS Plant Science Research and Education Unit in Citra, FL in 2006, were used in this experiment. ‘Emerald’ bushes are high yielding, with large, firm, flavorful berries that ripen from mid-April to mid-May in north-central Florida (Lyrene, 2001a, 2008). ‘Jewel’ produces smaller, more tart berries, and generally

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yields less than ‘Emerald’ (Lyrene, 2001a, 2001b; Williamson and Lyrene, 2004). The planting was on raised pine bark beds and the plants were spaced 0.9 m by 2.7 m in-row and between rows, respectively. Fertilizer was applied at an annual rate of 2000 kg·ha⁻¹ of 12N–1.7P–6.6K, evenly distributed every 20 d from March through October. The plants received irrigation through microsprinklers at a rate of 9.5 mm·d⁻¹ from mid-February through mid-October and 7.1 mm·d⁻¹ from mid-October through mid-February; and overhead irrigation provided frost protection. Hydrogen cyanamide (1.5% v/v) was applied in late December to defoliate plants and aid in fulfilling the chilling requirement.

Pruning treatments to assess effects of timing, intensity, and shoot tipping were imposed after fruit harvest in Spring 2011. To determine effects of pruning time, 30% of the canopy was removed in June (early) or July (late). To determine pruning intensity effects, either 30% (moderate) or 60% (heavy) of the canopy was removed in June, both followed by shoot tipping in July. Both timing and intensity treatments were compared with a nonpruned control. The effect of shoot tipping was assessed by comparing tipping vs. no tipping in July on plants that received moderate pruning in June. Pruning treatments, as well as tipping, were done mechanically, pruning the top and sides of plants with a hand-held hedge trimmer PP2822 (Poulan PRO; Charlotte, NC.). Tipping consisted of removal of about the top 4 cm of regrowth. In 2012 and 2013, the treatments were pruned 5 cm above the cut from the previous year (followed by tipping when appropriate), therefore, achieving about the same initial pruned plant size for each treatment. The experiment was a randomized complete block design (RCBD), with four plant plots (one guard plant on each side and two central data plants) and six replications per cultivar. Because the field consisted of alternating rows of ‘Emerald’ and ‘Jewel’, each cultivar was evaluated independently for pruning intensity, timing, and tipping and direct comparisons between the two cultivars were not made. Data were collected for three seasons starting with the first pruning in 2011, using different seasons as repeated measures. Pairwise comparisons were made to test the main effects of timing, intensity, and tipping.

Following shoot growth cessation in the fall, five shoots per plant originating from regrowth after the pruning treatments—or in the case of the nonpruned control, the entire year’s shoot growth—were randomly selected for assessment of the total number of inflorescence buds per shoot, inflorescence bud density (number of inflorescence buds per centimeter), and number of fruits per inflorescence bud. For inflorescence bud density, the total length of the regrowth shoot was used for the pruned treatments, whereas for the nonpruned control the entire year’s shoot growth was used. The number of fruits per inflorescence bud was assessed the week before first harvest to assure only fruits that

set were included, and was done by counting the number of fruits on the selected shoots and dividing by the number of inflorescence buds.

Berries were harvested on individual plants twice a week starting in late March to avoid berry loss. For ‘Jewel’, two data plants were harvested per treatment per replication, whereas only one plant was harvested for ‘Emerald’. In 2012, the last harvest dates were 10 and 21 May for ‘Jewel’ and ‘Emerald’, respectively, whereas in 2013 and 2014, the last harvest dates for both cultivars were 31 and 29 May, respectively. Total yield and yield distribution in 2-week periods were calculated. Average berry weight was measured at each harvest by selecting representative samples consisting of 25 commercially acceptable fruits per data plant. The total number of inflorescence buds per plant was estimated using yield, average berry weight, and number of fruits per inflorescence bud to evaluate the contribution of inflorescence bud number to total yield. The total number of buds per plant was estimated by the equation:

$$\text{Total number of inflorescence buds} = \frac{\text{Yield}}{\text{Berry weight} \times (\text{number of fruit/inflorescence bud})}$$

Fruit quality was determined in 2012 and 2013 using 25 fruit samples at “early” (12 Apr. 2012 and 8 Apr. 2013 for ‘Emerald’, and 5 Apr. 2012 and 15 Apr. 2013 for ‘Jewel’), “mid” (23 Apr. 2012 and 25 Apr. 2013 for ‘Emerald’, and 16 Apr. 2012 and 29 Apr. 2013 for ‘Jewel’), and “late” (30 Apr. 2012 and 13 May 2013 for ‘Emerald’, and 23 Apr. 2012 and 9 May 2013 for ‘Jewel’) fruit harvests. Berries were stored overnight at 10 °C, then removed and returned to room temperature before firmness measurements using a Firmtech 2 fruit firmness tester (BioWorks, Inc., Wamego, KS). Berries were stored at –30 °C until fruit quality analysis was performed. For quality analysis, total soluble solids (TSS), titratable acidity (TA), and anthocyanin content were measured. Berries were thawed, homogenized, and centrifuged at 14,623 g for 20 min (Legend XTR Centrifuge; Thermo Scientific, Waltham, MA). The supernatant was collected and filtered through cheesecloth. Total soluble solids were determined using a portable refractometer model AR200 (Reichert, Depew, NY). Total TA was determined as the percentage of citric acid by titrating 6 mL of juice diluted in 50 mL of deionized water with 0.1 M NaOH to a pH of 8.2 using an automated Titrator 719 S Tritino (Metrohm, Riverview, FL). Initial pH of the juice was recorded and the TSS:TA ratio was calculated.

For anthocyanin content, 0.5 g of juice from “mid” fruit harvest was diluted in 18 mL of 0.5% HCl in methanol solution. Samples were incubated for 1 h at 4 °C and absorbance was read spectrophotometrically at 520 nm using a PowerWave XS2 Microplate Spectrophotometer (BioTek Instruments, Inc., Winooski, VT). Anthocyanin was calculated

as cyanidin-3-glucoside (CND) content [(total anthocyanins × molar mass of CND) ÷ molar extinction coefficient] (adapted from Siegelman and Hendricks, 1958).

Based on the RCBD, data were analyzed using PROC GLIMMIX on SAS 9.2 (SAS Institute Inc., Cary, NC), and pairwise comparisons of treatment means were used to compare individual treatments for main effect differences. Errors in *P* values caused by multiple comparisons were adjusted using Tukey’s honestly significant difference at *P* ≤ 0.05. Whenever interactions between treatments (timing, intensity, and tipping) and years were significant, data were analyzed within years across treatments and within treatments across years.

Results

Pruning in June or July decreased the number of inflorescence buds per shoot in both cultivars in 2011 compared with the nonpruned control (Table 1). However, inflorescence bud number per shoot decreased significantly from 2011 to 2013 in the nonpruned control plants of both cultivars, and was not different from June pruned ‘Emerald’ or June and July pruned ‘Jewel’ in 2012 or 2013. Inflorescence bud density increased in the July pruned plants compared with nonpruned control and June pruned (Table 1). June pruning increased number of fruits per inflorescence bud compared with the nonpruned control in ‘Emerald’ (Table 2), whereas in ‘Jewel’, differences in number of fruits per inflorescence bud were only present in 2014 (as a result of 2013 pruning), when both June and July pruning increased the number of fruits per inflorescence bud compared with the control.

Pruning intensity also affected inflorescence bud number per shoot, which was greater in the nonpruned control compared with the 30% and 60% pruning treatments in 2011 for both cultivars (Table 1). However, the significant decrease in number of inflorescence buds in the nonpruned control from 2011 to 2012 resulted in similar inflorescence buds per shoot between the nonpruned control and the 30% and 60% pruned plants. The only exception was in the heavily pruned (60% removal) ‘Jewel’ plants, where inflorescence bud number per shoot increased in 2013. There were no differences in inflorescence bud density or number of fruits per inflorescence bud among pruning intensities (Tables 1 and 2). Tipping had no effect on the number of inflorescence buds per shoot, inflorescence bud density, or number of inflorescence buds per plant for either cultivar (Tables 1 and 2).

Timing of pruning affected number of inflorescence buds per plant in ‘Jewel’, but not in ‘Emerald’. The nonpruned ‘Jewel’ plants had more inflorescence buds per plant in 2012 compared with June and July pruned plants (Table 2); however, the significant reduction in inflorescence buds per plant in the nonpruned control from 2012 to 2013 resulted in similar numbers of inflorescence

Table 1. Effect of pruning intensity and timing on number of inflorescence buds per regrowth shoot and inflorescence bud density in 'Emerald' and 'Jewel' southern highbush blueberry.

Treatment ^z	Inflorescence buds per shoot (no.)			Inflorescence bud density (buds/cm) ^y
	2011	2012	2013	
'Emerald'				
Timing				
Nonpruned control ^x	15.0 aA ^w	8.5 aB	6.7 aB	0.28 b
June	6.5 bAB	7.7 abA	5.3 abB	0.27 b
July	5.4 bA	5.5 bA	4.8 bA	0.40 a
Intensity				
0% ^y	15.0 aA	8.5 aB	6.7 aB	0.28 a
30%	5.3 bA	6.8 aA	5.9 aA	0.30 a
60%	8.3 bA	8.5 aA	7.4 aA	0.24 a
Tipping				
Tipped	5.3 aA	6.8 aA	5.9 aA	0.30 a
Not tipped	6.5 aAB	7.7 aA	5.3 aB	0.27 a
	2011	2012	2013	
'Jewel'				
Timing				
Nonpruned control	15.7 aA	9.5 aB	3.9 aC	0.21 b
June	6.5 bB	9.2 aA	6.2 aB	0.24 b
July	7.8 bA	7.3 aA	5.1 aB	0.32 a
Intensity				
0%	15.7 aA	9.5 aB	3.9 bC	0.21 a
30%	7.6 bA	7.9 aA	6.7 bA	0.22 a
60%	10.9 bA	10.9 aA	11.3 aA	0.22 a
Tipping				
Tipped	7.6 aA	7.9 aA	6.7 aA	0.22 a
Not tipped	6.5 aB	9.2 aA	6.2 aB	0.24 a

^z"Timing," "Intensity," and "Tipping" are main effects. "0%," "30%," and "60%" refer to the percentages of canopy volume removed during pruning in June. "Tipped" refers to the removal of the upper 5 cm of regrowth in July.

^yInflorescence bud density was averaged over 3 years due to no significant interaction between treatment and year.

^xEntire year's shoot growth was used for nonpruned control.

^wMeans followed by the same lowercase letter within a column for each main effect and cultivar or uppercase letter within a row for each variable are not significantly different by Tukey at $P \leq 0.05$.

Table 2. Effect of pruning intensity and timing on number of fruits per inflorescence bud and total number of inflorescence buds per plant in 'Emerald' and 'Jewel' southern highbush blueberry.

Treatment ^x	Fruits/inflorescence bud				Inflorescence buds per plant (no.) ^z			
	‘Emerald’ ^y	‘Jewel’			‘Emerald’ ^z	‘Jewel’		
		2012	2013	2014		2012	2013	2014
Timing								
Nonpruned control	3.0 b ^w	1.2 a	3.1 a	3.0 b	1,329 a	2,070 aA	1,142 aB	869 aB
June	3.7 a	2.1 a	2.8 a	4.1 a	1,002 a	1,158 bB	1,455 aA	922 aB
July	3.3 ab	2.0 a	3.0 a	4.3 a	1,063 a	1,127 bA	1,449 aA	1,096 aA
Intensity								
0%	3.0 a	1.2 a	3.1 a	3.0 a	1,329 a	2,070 aA	1,142 bB	869 aB
30%	3.5 a	2.0 a	3.2 a	3.5 a	1,137 ab	1,364 abB	1,950 aA	1,208 aB
60%	3.6 a	1.8 a	3.7 a	3.6 a	912 b	1,197 bB	1,593 abA	1,315 aB
Tipping								
Tipped	3.5 a	2.0 a	3.2 a	3.5 a	1,137 a	1,364 aB	1,950 aA	1,208 aB
Not tipped	3.7 a	2.1 a	2.8 a	4.1 a	1,002 a	1,158 aB	1,455 aA	922 aB

^zTotal number of inflorescence buds = yield/[berry weight $\times$ (no. of fruits/inflorescence bud)].

^yFruits/inflorescence bud and inflorescence buds per plant means were averaged over 3 years for 'Emerald' due to no significant interaction between treatment and year.

^x"Timing," "Intensity," and "Tipping" are main effects. "0%," "30%," and "60%" refer to the percentages of canopy volume removed during pruning in June. "Tipped" refers to the removal of the upper 5 cm of regrowth in July.

^wMeans followed by the same lowercase letter within a column for each main effect or uppercase letter within a row and cultivar for each variable are not significantly different by Tukey at $P \leq 0.05$.

buds per plant among timing treatments in 2013 and in 2014. In 2012, more intense pruning (60% removal) decreased inflorescence buds per plant in 'Jewel' compared with the nonpruned control (Table 2). In 2013, however, 60% pruning and the control were similar, but 30% pruning had more inflorescence buds per plant than the control.

There were no significant effects of timing, intensity, or tipping treatments on yield (averaging 6.63 kg/plant) or yield per harvest period in 'Emerald' in any of the years (data not shown). In 'Jewel', neither timing nor tipping affected yield or yield per harvest period (Table 3). However, 30% pruning increased yield compared with the nonpruned control in 2013 and 2014. In 2013, 60%

pruning yielded significantly less in April than the nonpruned control and 30% removal. Similarly, in 2014, 60% pruning yielded less than the nonpruned control in the first half of April, and less than the 30% pruning in the second half of April. In 2013 and 2014, both 60% and 30% removal yielded more than the control in the first half of May, but yield during the latter half of May was significantly greater in heavily pruned plants compared with other intensities.

In 'Jewel', the more intense pruning (60%) increased berry weight in 2012 compared with the nonpruned control (Table 4). However, in 2013 and 2014, heavy pruning resulted in the smallest berry weight compared with other intensities. For 'Jewel', the July pruning increased berry weight compared with the nonpruned control in 2012, and with June pruning in 2013 and 2014. There were no differences among treatments for season average berry weight (averaging 1.83 g) for 'Emerald' (data not shown). There was no negative correlation between yield and berry weight ($R^2 = 0.003$ and 0.101 for 'Jewel' and 'Emerald', respectively) in this study.

There were few differences in berry weight through the first half of April or the first half of May in 'Jewel' (Table 4). The nonpruned control and June pruned plants had smaller berries compared with July pruned plants in the second half of April, while only June pruned plants had smaller berries compared with July in May. Pruning intensity had no effect on berry weight through May 15. By the end of the harvest season (second half of May), however, heavy (60%) pruning significantly reduced berry weight compared with the nonpruned control. This period was also when heavily pruned plants yielded more than other intensities in 2013 and 2014 (Table 3).

There were no differences in berry firmness for 'Emerald' among treatments in any year, nor was there an effect of treatment on 'Jewel' berry firmness in 2012 (data not shown). In 2013, however, 60% and 30% pruning significantly increased the berry firmness compared with the nonpruned control (219 and 206 vs. 190 g·mm⁻¹ for 60%, 30%, and control, respectively, $P \leq 0.05$). Pruning had no effect on berry internal quality in 'Emerald', while effects on berry quality of 'Jewel' were slight. Compared with the nonpruned control, heavy pruning reduced TSS from 11.2 to 10.2 °Brix ($P \leq 0.001$) and anthocyanin content from 103.1 to 70.4 mg·L⁻¹ ($P \leq 0.005$) in 'Jewel'. Total soluble solids were also reduced by June pruning compared with the nonpruned control (10.5 vs. 11.2 °Brix, respectively, $P \leq 0.05$). Titratable acidity ranged from 0.77 to 0.79 for 'Emerald' and 0.94 to 0.98 for 'Jewel', with no differences among pruning treatments. There was also no difference in the TSS:TA ratio among treatments for either cultivar, averaging 13.7 and 11.4 for 'Emerald' and 'Jewel', respectively.

Discussion

The cultivars studied responded differently to pruning treatments, possibly due to

Table 3. Effect of pruning intensity and timing on yield and yield distribution in each harvest period in 'Jewel' southern highbush blueberry.

Treatment ^y	Yield (kg/plant)				
	Total	Period ^z			
		1–15 Apr.	16–30 Apr.	1–15 May	16–30 May
2012					
Timing					
Nonpruned control	3.19 a ^x	1.89 a	1.19 a	0.12 a	—
June	3.62 a	1.85 a	1.62 a	0.15 a	—
July	3.79 a	2.21 a	1.45 a	0.13 a	—
Intensity					
0%	3.19 a	1.89 a	1.19 a	0.12 a	—
30%	4.39 a	2.20 a	1.95 a	0.23 a	—
60%	3.12 a	1.47 a	1.52 a	0.12 a	—
Tipping					
Tipped	4.39 a	2.20 a	1.95 a	0.23 a	—
Not tipped	3.62 a	1.85 a	1.62 a	0.15 a	—
2013					
Timing					
Nonpruned control	4.95 a	0.77 a	2.94 a	1.10 a	0.15 a
June	6.22 a	0.46 a	2.83 a	2.31 a	0.61 a
July	6.40 a	0.66 a	3.30 a	2.06 a	0.40 a
Intensity					
0%	4.95 b	0.77 a	2.94 a	1.10 b	0.15 b
30%	7.31 a	0.62 a	3.52 a	2.71 a	0.47 b
60%	5.80 ab	0.17 b	1.60 b	2.97 a	1.06 a
Tipping					
Tipped	7.31 a	0.62 a	3.52 a	2.71 a	0.47 a
Not tipped	6.22 a	0.46 a	2.83 a	2.31 a	0.61 a
2014					
Timing					
Nonpruned control	3.78 a	0.27 a	2.08 a	1.31 b	0.12 a
June	5.17 a	0.16 a	2.46 a	2.18 ab	0.37 a
July	6.19 a	0.25 a	2.78 a	2.74 a	0.47 a
Intensity					
0%	3.78 b	0.27 a	2.08 ab	1.31 b	0.12 b
30%	6.22 a	0.14 ab	2.89 a	2.73 a	0.45 b
60%	5.58 ab	0.02 b	1.26 b	3.07 a	1.26 a
Tipping					
Tipped	6.22 a	0.14 a	2.89 a	2.73 a	0.45 a
Not tipped	5.17 a	0.16 a	2.46 a	2.18 a	0.37 a

^zAverage yields for 2-week harvest periods.

^y"Timing," "Intensity," and "Tipping" are main effects. "0%," "30%," and "60%" refer to the percentages of canopy volume removed during pruning in June. "Tipped" refers to the removal of the upper 5 cm of regrowth in July.

^xMeans followed by the same letter within a column and main effect are not significantly different by Tukey at $P \leq 0.05$.

different plant architectures, phenology, and vigor. Pruning had little effect on reproductive traits of 'Emerald', a highly productive cultivar (J.G. Williamson, personal communication) exhibiting semierect canes (Lyrene, 2008), with short, thick horizontal shoots distributed throughout the canopy. On the other hand, 'Jewel', which was more affected by pruning treatments, has upright canes (Lyrene, 2001b), with long, thin, vertical shoots and is less productive than 'Emerald'. Thus, mechanical pruning that reduces plant height would affect 'Jewel' to a greater extent compared with 'Emerald', because the fruiting shoots in 'Emerald' are more evenly distributed in the canopy.

Moderate (30%) pruning increased inflorescence bud number per plant in 'Jewel' in 2013 compared with the nonpruned control, likely due to healthier foliage and decreased defoliation from leaf diseases—such as blueberry leaf rust [*Pucciniastrum vaccinii* (G. Wint.)]—in response to the pruning treatment (Kovaleski et al., 2015a). Ojiambo et al.

(2006) found that leaf spots and defoliation decreased inflorescence bud formation and yield in rabbiteye and SHB, as did Williamson and Miller (2002) for SHB. However, other factors are also involved in inflorescence bud initiation, as the 60% pruning treatment in 'Jewel' had similar levels of leaf disease and defoliation as the 30% pruning treatment (Kovaleski et al., 2015a), but inflorescence bud number per plant was not different from the nonpruned control. This may be an effect of the decreased canopy volume in the heavy pruned plants compared with moderate and nonpruned plants (Kovaleski et al., 2015a).

Although Salvo et al. (2012) concluded that the number of inflorescence buds per plant is the most important component of blueberry yield, in our study, there was not a strong correlation between inflorescence bud number and yield ($R^2 = 0.11$ and 0.38 for 'Jewel' and 'Emerald', respectively). Heavy pruning (60% canopy removal) of 'Emerald' did not reduce yield compared with the

nonpruned control, although inflorescence number per plant in the 60% pruning was significantly reduced. Similarly, heavy pruning of 'Jewel' in 2012 did not reduce yield compared with the nonpruned control or moderately pruned treatment, although inflorescence buds per plant was reduced. This implies a compensatory mechanism among inflorescence bud number, number of fruits per inflorescence bud, and fruit size as components of blueberry yield, as suggested by Hancock et al. (2000). In 2012, the number of fruits per inflorescence bud was especially low possibly due to two consecutive convective freeze events in 13 and 14 Feb., resulting in great damage and drop of blooming flowers and early-formed fruits. In 2013 and 2014, the number of fruits per inflorescence bud was higher than in 2012, and similar to those reported by others (Hancock et al., 2000; Salvo et al., 2012; Smagula, 1993). Hancock et al. (2000) also demonstrated that bud position in the plant affects the number of fruits per inflorescence bud, for which we sought to control by selecting shoots in different parts of the canopy. Further, it is possible that, due to the nature of the mechanically summer pruning, the majority of the fruiting shoots were located at a similar height, and these are more uniform compared with winter hand-pruned bushes.

In 2014, inflorescence bud number, number of fruits per inflorescence bud, and average berry weight were similar between moderately pruned 'Jewel' and nonpruned controls. However, moderate pruning significantly increased yield compared with the control, demonstrating the cumulative effect of slight, nonsignificant increases in individual yield components. The lack of effect of heavy pruning on yield in our study contrasts with previous work on 'Sharpblue' SHB (Williamson and Darnell, 1996) and rabbiteye blueberry (Austin and Bondari, 1989; Davies, 1983; Souza et al., 2014), where heavy pruning resulted in yield reduction. Our results may differ from previous work due to differences in the amount and location of canopy pruning and/or differences in pruning season.

Spiers et al. (2002) found that heavy pruning increased early yield of rabbiteye blueberry compared with moderate pruning; however, our data clearly demonstrate the tendency of heavy pruning to significantly delay fruit harvest in 'Jewel'. Spiers et al. (2002), however, hedged only portions of the canopy, and therefore the half of the plant that remained unpruned would not be affected by pruning and may have contributed to earlier yields. Souza et al. (2014) found that winter hand pruning, regardless of intensity, resulted in earlier yields for rabbiteye blueberry compared with no pruning. Krewer et al. (2004) showed that hedging resulted in delayed inflorescence bud development during the spring, which is linked to the time of inflorescence bud initiation (Kovaleski et al., 2015b). Bañados et al. (2009) also shows that summer pruning delayed fruit harvest as a result of delayed flower bud development,

Table 4. Effect of pruning intensity and timing on average berry weight per season and average berry weight in each harvest period in 'Jewel' southern highbush blueberry.

Treatment ^y	Berry wt (g)						
	Season avg			Period ^z			
	2012	2013	2014	1–15 Apr. ^x	16–30 Apr.	1–15 May	16–30 May
Timing							
Nonpruned control	1.55 b ^x	1.74 ab	1.62 ab	1.74 a	1.59 b	1.51 ab	1.34 a
June	1.59 ab	1.60 b	1.45 b	1.78 a	1.58 b	1.40 b	1.16 b
July	1.82 a	1.79 a	1.68 a	1.92 a	1.76 a	1.61 a	1.38 a
Intensity							
0%	1.55 b	1.74 a	1.62 a	1.74 a	1.59 a	1.51 a	1.34 a
30%	1.68 ab	1.70 a	1.55 a	1.87 a	1.66 a	1.44 a	1.21 ab
60%	1.89 a	1.43 b	1.23 b	1.77 a	1.64 a	1.36 a	1.01 b
Tipping							
Tipped	1.68 a	1.70 a	1.55 a	1.87 a	1.66 a	1.44 a	1.21 a
Not tipped	1.59 a	1.60 a	1.45 a	1.78 a	1.58 a	1.40 a	1.16 a

^zAverage berry weights for 2-week harvest periods.

^x“Timing,” “Intensity,” and “Tipping” are main effects. “0%,” “30%,” and “60%” refer to the percentages of canopy volume removed during pruning in June. “Tipped” refers to the removal of the upper 5 cm of regrowth in July.

^yMeans followed by the same letter within a column and main effect are not significantly different by Tukey at $P \leq 0.05$.

which could also be the case in heavily summer-pruned plants having reduced early yields in the study by Pescie et al. (2011).

In our study, fruit from the later harvest in heavily pruned 'Jewel' plants were smaller than late harvested fruit in moderate and the nonpruned control. Continuous heavy pruning may have reduced carbon availability for fruits by decreasing canopy volume (Kovaleski et al., 2015a) and therefore current photosynthate production and/or by depleting the plants' reserves (McFadyen et al., 2011), decreasing fruit size. The season average berry weight was also decreased by the heavy pruning treatment compared with other pruning intensities in 2013 and 2014, likely because much of the fruit ripened later in the season, when fruit size was smaller. In contrast to our results where heavy pruning decreased fruit size, Strik et al. (2003) and Jorquera-Fontena et al. (2014) found that heavy winter hand pruning increased berry weight compared with moderate hand pruning and no pruning in highbush blueberry. However, the removal of inflorescence buds during winter pruning would decrease inflorescence bud number and therefore berry number the following growing season, potentially increasing berry weight. Spiers et al. (2002) also found no differences in berry weight between severities of pruning, even though there were differences in yield. The authors speculated that the already high vigor of the cultivar studied was not increased by pruning, which may also explain the lack of pruning effects on berry weight in the highly vigorous 'Emerald'.

The impact of pruning severity on fruit quality was negligible. Although berry firmness of 'Jewel' increased in the 30% and 60% pruning treatments, this did not appear to be related to smaller berry size, since size was unaffected in the 30% pruning treatment. This suggests that size is not the only factor influencing berry firmness.

Pruning time had little effect on any reproductive traits in either cultivar. Although Bañados et al. (2009) found a reduction in the number of inflorescence buds per

shoot in late pruning compared with early pruning in both northern and SHB, this effect was not observed in the present study. The lack of pruning time effect on inflorescence bud number in our study may be due to the high temperatures and a long growing season, which may delay (Spann et al., 2004) and/or extend the period of inflorescence bud initiation. This would have reduced the effect of pruning time on the initiation of inflorescence buds, and subsequently, the number of inflorescence buds per shoot.

Timing of summer pruning did not affect total yield in either cultivar, supporting work by Krewer et al. (2004), who also found no effect of time of summer pruning on total yield in rabbiteye blueberries. In contrast, Williamson and Darnell (1996) found late pruning of 'Sharpblue' SHB reduced yield compared with early pruning and no pruning. 'Sharpblue' generally ripens later in the season (Williamson and Lyrene, 2004) than either 'Jewel' or 'Emerald', and since plants were pruned 9 weeks after peak of harvest, the pruning treatment in the Williamson and Darnell study would have occurred much later than the July pruning treatment used in the present study. This would have decreased the time between pruning and inflorescence bud initiation, when shoot growth ceases, which can be as early as late August for 'Emerald' (Kovaleski et al., 2015b), and likely accounts for the differences found between the two studies. Although Bañados et al. (2009) found late summer pruning delayed fruit harvest in 'O'Neal' and 'Star' SHB, timing of fruit harvest was unaffected by time of summer pruning in our study. However, the authors speculated that in other regions with higher temperatures during the fall, such as in our case, the rate of inflorescence bud formation would increase, eliminating any delay in bloom or harvest of late pruned treatments the following spring.

Late pruning increased berry size over the season compared with the nonpruned control for 'Jewel' in 2012, which was similar to results from Bañados et al. (2009). However, in 2013 and 2014, seasonal average fruit size

in late pruned plants and the nonpruned control were similar and generally larger compared with early-pruned plants. This was probably a result of the trend toward lower yield in the control treatment, and the trend toward higher yields in April—when fruit were larger—in the late pruned compared with the early-pruned plants.

Although there were TSS differences among treatments in 'Jewel', these were not large enough to impact the TSS:TA ratio. Maust et al. (1999) found that increasing inflorescence bud density resulted in decreased fruit size and quality, as well as delayed ripening in 'Misty' SHB. In the present study, the late pruning treatment increased the inflorescence bud density in both cultivars compared with other timings, but neither berry weight nor yield distribution were affected. However, the increased inflorescence bud density was primarily due to reduced regrowth in this treatment (Kovaleski et al., 2015a), while the number of inflorescence buds per shoot was among the lowest. Maust et al. (1999) speculated that effects of inflorescence bud density on fruit size and quality were more pronounced in cultivars that break floral buds much earlier than vegetative buds, and therefore may experience carbohydrate limitations to fruit growth (such as 'Misty' SHB). The cultivars used in the present study exhibited a relatively synchronous floral and vegetative budbreak, and likely would not experience such limitations to growth, especially considering the use of hydrogen cyanamide, which typically results in earlier vegetative budbreak (Williamson et al., 2002).

Although blueberry fruit are known for their high content of antioxidants (Qureshi et al., 2014), to our knowledge, the present study is the first to evaluate the effect of multiple years of a management practice on anthocyanin content in blueberry. The reduction in anthocyanin content due to heavy pruning compared with the nonpruned control in 'Jewel' may be due to the vigorous growth early in the spring in the heavy pruning treatment (data not shown), which likely increased fruit shading compared with the nonpruned control. However, in 'Emerald', the more horizontal growth typical of this variety would decrease fruit shading, allowing more exposure to full sun and resulting in no decrease of anthocyanin content in the heavy pruning treatment.

Pruning effects on reproductive traits in SHB were cultivar dependent. Neither summer pruning time, intensity, nor shoot tipping affected yield, yield distribution, or season average berry weight in 'Emerald' over the 3-year study, whereas moderate (30%) pruning in years 2 and 3 increased yield in 'Jewel' compared with the nonpruned control. The differences in the cultivar responses are likely due to differences in plant architecture. 'Jewel' exhibits a more upright canopy, with most of the fruiting shoots located on the periphery, whereas 'Emerald' exhibits a dense canopy with fruiting shoots throughout the canopy. Thus, many of the fruiting shoots in 'Emerald' would not have been affected by

the pruning treatments. The lack of response in 'Jewel' to the first year of pruning suggests that leaving plants of 'Jewel' unpruned for 1 year may not be detrimental, but two or more seasons without pruning reduces inflorescence bud number and yield.

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