

Collection of wood quality data by X-ray densitometry: a case study with three southern pines

Thomas L. Eberhardt^{1,3} · Lisa J. Samuelson²

Received: 16 June 2014 / Published online: 29 May 2015
© Springer-Verlag Berlin Heidelberg (outside the USA) 2015

Abstract X-ray densitometry is a technique often used in tree growth and wood quality studies to incrementally measure density (specific gravity) along a radial strip of wood. Protocols for this technique vary between laboratories because of differences in species, equipment, tree age, and other factors. Here, the application of X-ray densitometry is discussed in terms of a case study specific to the southern pines, whereby loblolly (*Pinus taeda* L), longleaf (*Pinus palustris* Mill.), and slash (*Pinus elliottii* Engelm.) pine wood cores were analyzed using an automated system. Objectives of this study included an assessment of the potential impacts on whole-core wood quality data from wood core extraction and use of two different demarcation methods (threshold and inflection point) for the earlywood–latewood transition. Wood core extraction before X-ray densitometry showed minimal impact on the shapes of individual ring profiles, and whole-core wood quality data were essentially unchanged. An assessment of the inflection point method employed for determining the earlywood–latewood transition point in the X-ray densitometry data demonstrated that the growth ring profiles for the southern pines are not amenable to polynomial fitting. Indeed, in the southern pines, the earlywood–latewood transitions are as equally abrupt as the latewood–earlywood transitions. Accordingly, a threshold density deemed appropriate to define the onset of a growth ring would be equally appropriate to define the onset of latewood formation.

✉ Thomas L. Eberhardt
teberhardt@fs.fed.us

¹ Southern Research Station, USDA Forest Service, 2500 Shreveport Highway, Pineville, LA 71360, USA

² School of Forestry and Wildlife Sciences, Auburn University, 3301 SFWS Building, Auburn, AL 36849, USA

³ Present Address: Forest Products Laboratory, USDA Forest Service, One Gifford Pinchot Drive, Madison, WI 53726, USA

Introduction

Wood formation begins at the cambium, a sheath of meristematic tissue between the bark and wood that encircles the branches, stem, and roots of trees (Chaffey 1999). For the conifers, particularly the pines (*Pinus* sp.), annual rings are readily distinguished by the formation of lower specific gravity (SG) earlywood (springwood) at the beginning of the growing season, transitioning into higher SG latewood (summerwood) that continues to form until radial growth all but ceases at the end of the growing season. Wood from pines in the southeastern USA readily displays this feature with usually abrupt SG transitions between years and characteristically wide latewood bands (Kubler 1980; Eberhardt et al. 2011). Commonalities between southern pine species prevent their differentiation by traditional wood identification techniques (Panshin and de Zeeuw 1980); however, in situations where the entire stem cross section is available, pith and second annual ring diameter measurements can be used to separate longleaf pine (*Pinus palustris* Mill.) from the other southern pine species (Eberhardt et al. 2011). An anomaly to the aforementioned abrupt SG transitions between years has been reported for loblolly pine (*Pinus taeda* L.) grown outside its native range in the milder climate of Hawaii (Samuelson et al. 2013). The observed gradual decrease in SG through the latewood–earlywood transition, particularly evident in the juvenile wood zone, could have resulted from growth throughout the year given milder climate conditions not found on the mainland (Harms et al. 2000; Samuelson et al. 2010, 2013).

Studies on tree growth patterns by dendrochronologists have long involved the visual demarcation of the onset and termination of annual rings accompanied by careful measurements of ring widths. Matching of overlapping growth patterns between trees has been a mainstay of climate records built by dendrochronology. Attempts at morphometric analyses of individual rings in response to stress factors (e.g., climate events, silvicultural treatments) focused on the proportions of earlywood and latewood (Jagels and Telewski 1990). Recent studies suggest that within-ring density patterns, not just proportions of earlywood and latewood, can be attributed to climate parameters for a given growing season (Ivković and Rozenberg 2004; Rozenberg et al. 2004; Franceschini et al. 2013; Gonzalez-Benecke et al. 2015). The most common application for X-ray densitometry is the collection of wood quality data (ring SG, latewood percent, etc.) which have been used to determine the transition age from juvenile wood to mature wood (Koubaa et al. 2005; Clark et al. 2006; Gapare et al. 2006; Mora et al. 2007; Guller et al. 2012) as well as differences imparted by site quality (Adamopoulos et al. 2009) and physiographic region (Tasissa and Burkhart 1998; Clark et al. 2006; Jordan et al. 2008; Samuelson et al. 2013). For the benefit of foresters and ecologists, determination of the SG of a wood core taken from bark to pith can be weighted to give a value for SG reflecting that for a tree (Williamson and Wiemann 2010).

It is generally accepted that extractives do not contribute significantly to the physical/mechanical properties of wood (Panshin and de Zeeuw 1980) and so standard determinations of wood physical/mechanical properties (ASTM 1993; Forest Products Laboratory 2010) are not adjusted to compensate for extractives

content. For X-ray densitometry, wood cores may be scanned as either received (Park et al. 2006; Guller et al. 2012) or following extraction. For example, the heartwood of *Larix* sp. was reported to have an exceptionally high extractives content, and thus, extraction prior to X-ray densitometry was recommended (Grabner et al. 2005). Solvents used for extraction vary widely between laboratories and include pentane (Bouffier et al. 2008), benzene–ethanol in the ratio of 2:1 (Fujimoto and Koga 2010), cyclohexane–ethanol in a ratio of 2:1 (Koubaa et al. 2005), and acetone (Grabner et al. 2005; Gapare et al. 2006; Kantavichai et al. 2010). Identifying the solvent used is essential since the extractive yields are dependent on solvent selection (Pettersen 1984). In a study by Bergsten et al. (2001), extractive contents were found to impact X-ray densitometry data both by adding to the mass of the specimen and by affecting the mass attenuation coefficient (Bergsten et al. 2001); a specific caveat to specimen extraction before X-ray densitometry was that lower shrinkage and greater checking/cracking in thicker specimens following extraction may result in SG underestimations. Maximum and minimum SG values along ring number were shown to be impacted by extraction; however, this dendrochronological study did not provide any demarcation of earlywood–latewood transition, nor were any wood quality data determined (Helama et al. 2010).

In addition to SG values for individual growth rings, X-ray densitometry also affords the ability to determine the proportions of earlywood and latewood, and the corresponding SG values. This allows the study of intra-ring wood density variation that is becoming increasingly of interest to assess physiologically imparted variations in wood (Koubaa et al. 2002; Park et al. 2006; Franceschini et al. 2012). It is therefore necessary to have confidence in the method by which the earlywood–latewood and latewood–earlywood transition points are identified. The seemingly most-cited definition for what constitutes latewood is that put forth by Mork (1928) wherein a latewood tracheid is one in which the width of the common cell wall for two adjacent tracheids, when multiplied by two, is equal or greater than the width of the lumen (Larson 1969). A second interpretation of this anatomically based definition, as noted by others (Koubaa et al. 2002; Antony et al. 2012), does not include the multiplier (i.e., twice the width of the common cell wall). The first definition (with multiplier) appears to be preferred (Larson 1969; Antony et al. 2012). Although commonly used as the gold standard by which other methods are judged, Larson (1969) clearly states that Mork’s definition fails in juvenile wood and in growth rings with diffuse transition zones. Indeed, Mork’s index is an arbitrarily set “threshold” (Park et al. 2006), albeit not based on SG values, but tracheid cross-sectional dimensions. Herein, the term “threshold method” is used to describe the operation of using a set value for SG that, when crossed along the density profile, marks the earlywood–latewood transition and, equally important, the latewood–earlywood transition. The computational ease in applying the threshold method has undoubtedly contributed to its ubiquitous use with X-ray densitometry data (Koubaa et al. 2002), particularly for the southern pines (Clark et al. 2006; Jordan et al. 2008; Love-Myers et al. 2009; Samuelson et al. 2010; Antony et al. 2012).

For other conifers, primarily *Picea* sp., various curve-fitting/modeling operations have been proposed to define earlywood–latewood transitions; the latewood–earlywood transitions are largely overlooked. Some of the more recently reported methods can be denoted as follows: inflection points of polynomials fitted to density profiles of individual/modeled rings (Koubaa et al. 2002; Antony et al. 2012), models based on the generalized lambda distribution (Ivković and Rozenberg 2004), and intra-ring wood density profile modeling based on the work of Mothe et al. (1998) as widely reported by Franceschini et al. (2012, 2013). These curve-fitting/modeling operations have been focused on tree species having gradual earlywood–latewood transitions. An issue identified during the application of some models has been noncompliant false rings observed as transient spikes in wood SG within an actual (not modeled) annual ring (Pernestål et al. 1995; Franceschini et al. 2013).

Paramount in any X-ray densitometry study is the consistent application of protocols for specimen preparation and robust demarcation of the earlywood–latewood and latewood–earlywood transition points, together allowing the generating of data that can be compared across the length of the wood core and between wood core sample sets. Several alternative methods have been employed for demarcation of the earlywood–latewood transition for other conifers (e.g., *Picea* sp., *Abies* sp.), but only a couple of studies have addressed the merits and pitfalls of the threshold method applied to the X-ray densitometry data of pines (Antony et al. 2012; Kumar 2002); justification for the continued use of the threshold method with the southern pines is warranted. In the present study, wood cores were taken from mature (age 50 years) loblolly, longleaf, and slash (*Pinus elliottii* Engelm.) pines from a common site with the objectives of (1) providing a long-overdue assessment of the impacts of wood core extraction on whole-core wood quality data and (2) testing the suitability of two ring demarcation methods (threshold and inflection point) for ring density profiles that are characteristic of the southern pines.

Materials and methods

Study tree sampling

Fifty-year-old loblolly, longleaf, and slash pine trees used in this study were located in the USDA Forest Service Harrison Experimental Forest (30.65 N, 89.04 W) near Saucier, Mississippi, USA. Plantations were established in 1960 for growth and genetics studies on longleaf, loblolly, and slash pines (Schmidting 1973). Nine trees were sampled for each species as reported by Samuelson et al. (2012). The diameter ranges at breast height (1.37 m) were as follows: loblolly pine, 31.5–40.2 cm; longleaf pine, 31.1–39.1 cm; slash pine, 30.5–35.4 cm. An increment borer was used to remove wood cores (12 mm diameter) at breast height. These were stored under refrigeration to prevent deterioration prior to processing.

Wood core processing and scanning

At the laboratory, cores were placed in wooden core holders, dried (50 °C, 24 h), and then permanently glued (Gorilla Glue, Cincinnati, Ohio) into the wooden core holders. Mounted cores were sawn into 2.3-mm-thick strips, from bark to pith, ensuring that the transverse surface of the core, bordered by adhering wood strips remaining from the core holders, would be orthogonal to the X-ray beam. Densitometry was performed using a Quintek Measurement Systems (Knoxville, TN) X-ray densitometer. Density measurements were determined using a 0.06-mm X-ray slit width and step size to afford SG values at 0.06-mm intervals. Cores were scanned along the radial direction from bark to pith, with the data transformed to afford plots along ring number (cambial age). A SG of 0.48 was used to differentiate between earlywood and latewood zones (Koubaa et al. 2002; Clark et al. 2006; Antony et al. 2012). Densitometer calibration was on a green volume and oven-dried mass basis. Given concerns that the solvent extraction would soften the glue used to prepare the core specimens, thin stainless-steel wire was used to secure each core to its adhering wood strips. Core specimens were then extracted with acetone in a Soxhlet apparatus, using 3 daytime cycles. The cores were allowed to steep in solvent overnight by terminating the daytime cycle when the core specimens were submerged in freshly distilled solvent. Extracted cores were then dried in a fume hood before removing the wires. The cores were conditioned in the laboratory and then analyzed again by X-ray densitometry.

Statistical analyses and curve fitting

Wood quality measures (e.g., ring SG, latewood SG) were weighted by ring basal area to obtain mean basal area weighted whole-core values for each tree. The effects of extraction on whole-core (bark to pith) wood quality data were tested using analysis of variance (PROC GLM, SAS/STAT[®] 9.3). A determination of nonsignificance was made for all tests with a $P > 0.05$. Three X-ray densitometry traces were randomly selected from each of the southern pine species from which one core was selected to illustrate representative density profiles; differences in wood core lengths and individual ring alignments preclude calculations of a single density profile representing the “average” of multiple wood cores. Densitometry traces for individual rings were plotted as a percent of ring width from pith to bark before fitting with polynomial equations in Microsoft Excel; inflection points were determined by second derivative calculations.

Results and discussion

Wood core extraction

Wood quality data plotted across ring number for loblolly, longleaf, and slash pines followed generally similar patterns in unextracted and extracted wood cores (Figs. 1, 2). Since the trees were at the upper rotation age (50 years) for sawtimber

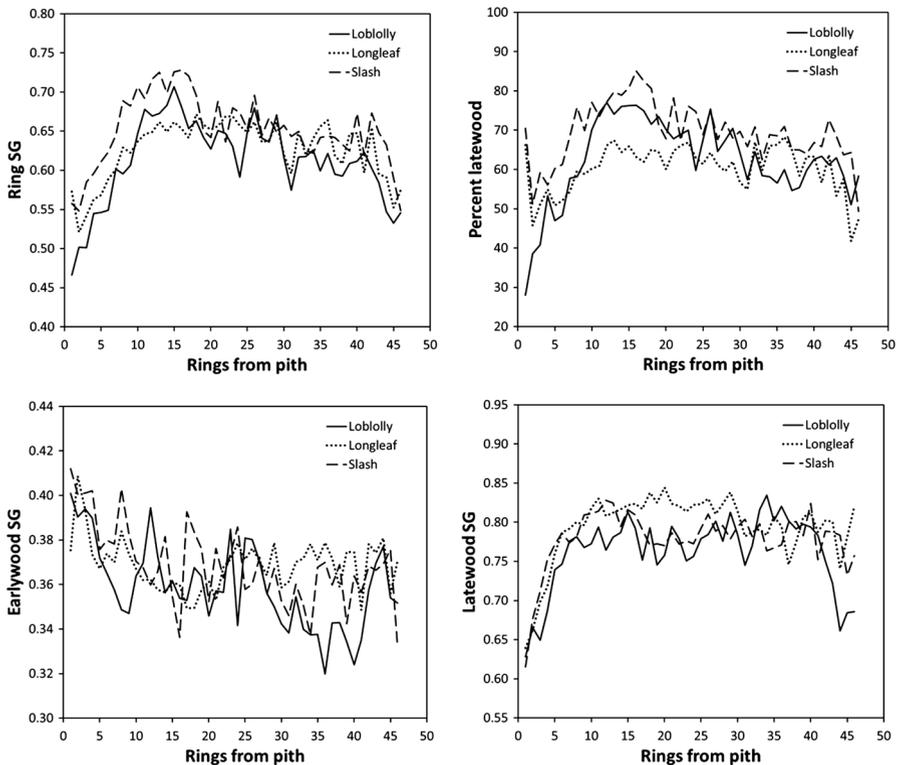


Fig. 1 Plots of mean ring SG, earlywood SG, latewood SG, and percent latewood for loblolly, longleaf, and slash pine wood cores before extraction

(Biblis et al. 1998), the observed decrease in ring SG in the mature wood (Spurr and Hsiung 1954) was anticipated; this feature would be absent in the densitometry of trees used for pulpwood, often being harvested at 20 years (Biblis et al. 1998), if not earlier. Plots for percent latewood showed similar trends to those for ring SG given that the latter is a direct reflection of the proportions of latewood and earlywood (Clark and Saucier 1989; Tasissa and Burkhart 1998). Plots of latewood SG and earlywood SG paralleled those in the literature (Jordan et al. 2008). Similar ring SG values across each ring number for the extracted wood cores were reflected by similar whole-core ring SG values, with a probability for loblolly pine ($P = 0.058$) missing the cutoff for statistical significance (Table 1). Cole et al. (1966) showed some seemingly lower SG values for southern pines following extraction; however, statistics were not conducted to determine significance. Dips in ring SG and latewood percent near the pith for the unextracted longleaf and slash pine wood cores (Fig. 1) were absent in the corresponding extracted wood cores (Fig. 2); this is highlighted by the ovals drawn on each plot in Fig. 2. High ring SG values near the pith can be attributed to extractives deposited at the onset of heartwood formation. It should be noted that highly resinous wood specimens can give SG values that are

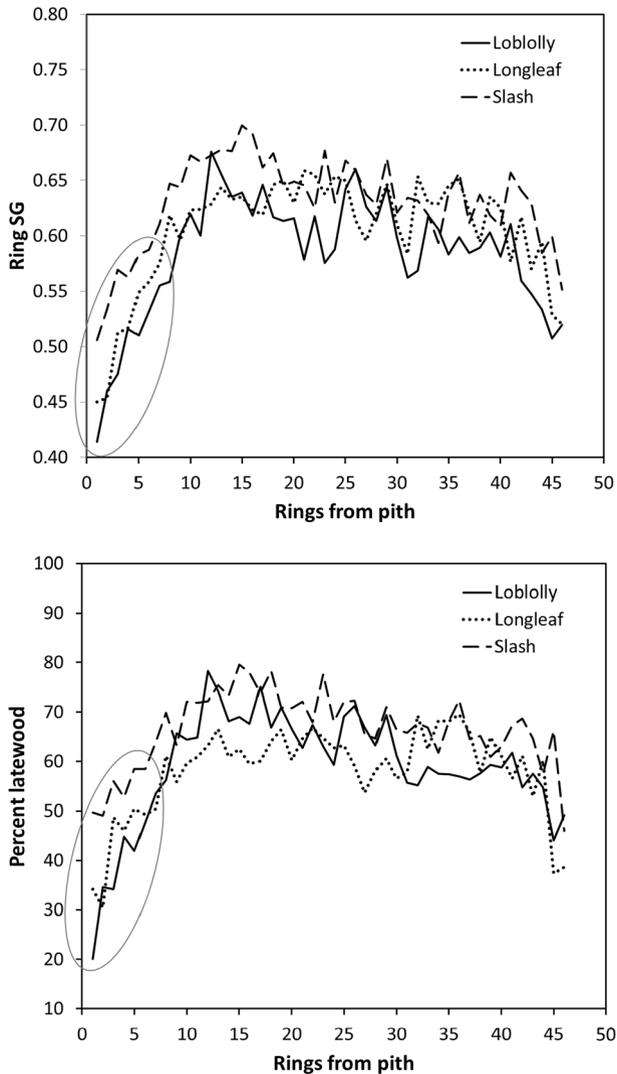


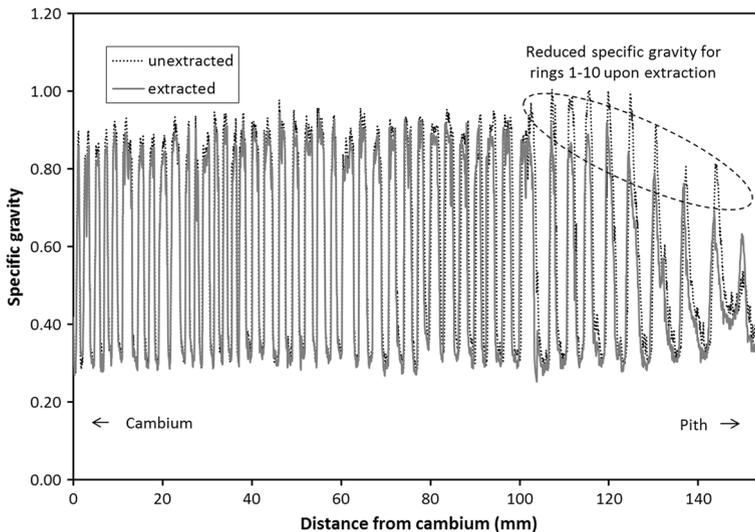
Fig. 2 Plots of mean ring SG and percent latewood for loblolly, longleaf, and slash pine wood cores after extraction

much higher than those typically reported. For example, a lightened southern pine stump wood gave a SG value of 0.94 that was lowered to 0.58 following extraction with dichloromethane (Eberhardt et al. 2007). While wood core extraction is commonly practiced before X-ray densitometry, often overlooked are the possibilities of specimen shrinkage and checking/cracking leading to SG values deviating from the true SG (Bergsten et al. 2001).

Wood cores were scanned on the X-ray densitometer from the cambium (bark) to the pith with the SG values plotted along an increasing distance value from the

Table 1 Whole-core wood quality data ANOVA for effect of wood core extraction including mean values, standard deviations (in parentheses), and probabilities (*P*) for significant differences

Wood quality measure	Sample core condition	Loblolly pine	Longleaf pine	Slash pine
Ring SG	Not extracted	0.61 (0.02)	0.63 (0.04)	0.65 (0.02)
	Extracted	0.58 (0.02)	0.61 (0.04)	0.63 (0.02)
	<i>P</i>	0.058	0.416	0.343
Latewood SG	Not extracted	0.77 (0.02)	0.80 (0.03)	0.78 (0.02)
	Extracted	0.75 (0.02)	0.78 (0.03)	0.77 (0.02)
	<i>P</i>	0.228	0.386	0.614
Earlywood SG	Not extracted	0.35 (0.01)	0.36 (0.01)	0.36 (0.02)
	Extracted	0.34 (0.01)	0.35 (0.00)	0.36 (0.02)
	<i>P</i>	0.174	0.228	0.377
Percent latewood	Not extracted	61.1 (4.8)	60.9 (5.2)	68.2 (4.1)
	Extracted	57.6 (3.9)	59.1 (4.8)	65.2 (3.3)
	<i>P</i>	0.267	0.609	0.396
Ring width (mm)	Not extracted	4.30 (0.28)	3.77 (0.40)	3.99 (0.55)
	Extracted	4.19 (0.48)	3.84 (0.33)	3.72 (0.49)
	<i>P</i>	0.757	0.884	0.549

**Fig. 3** X-ray densitometry traces from longleaf pine wood core before and after extraction

cambium, left to right. Generally, it was possible to overlay the two densitometry traces (unextracted and extracted) for a given core; however, the alignments were not perfect in that there were both vertical and horizontal deviations in the plots, especially when progressing toward the pith. This observation is illustrated in Fig. 3

which shows the densitometry traces for a longleaf pine wood core before and after extraction. An oval drawn on this figure highlights the aforementioned observation in the juvenile wood zone. Vertically, the maximum SG recorded for each of the rings appeared to be slightly higher for the unextracted core. Horizontally, the alignments of the rings along the length of the cores were not perfect with the unextracted core showing slightly greater distances from the cambium in the juvenile wood zone. Thus, wood core lengths were slightly shorter following extraction.

The SG profiles for individual rings along a representative wood core for each species, before and after extraction, are shown in Fig. 4. The plot for each ring (numbers 5, 20, and 35 from the cambium) shows generally good agreement in

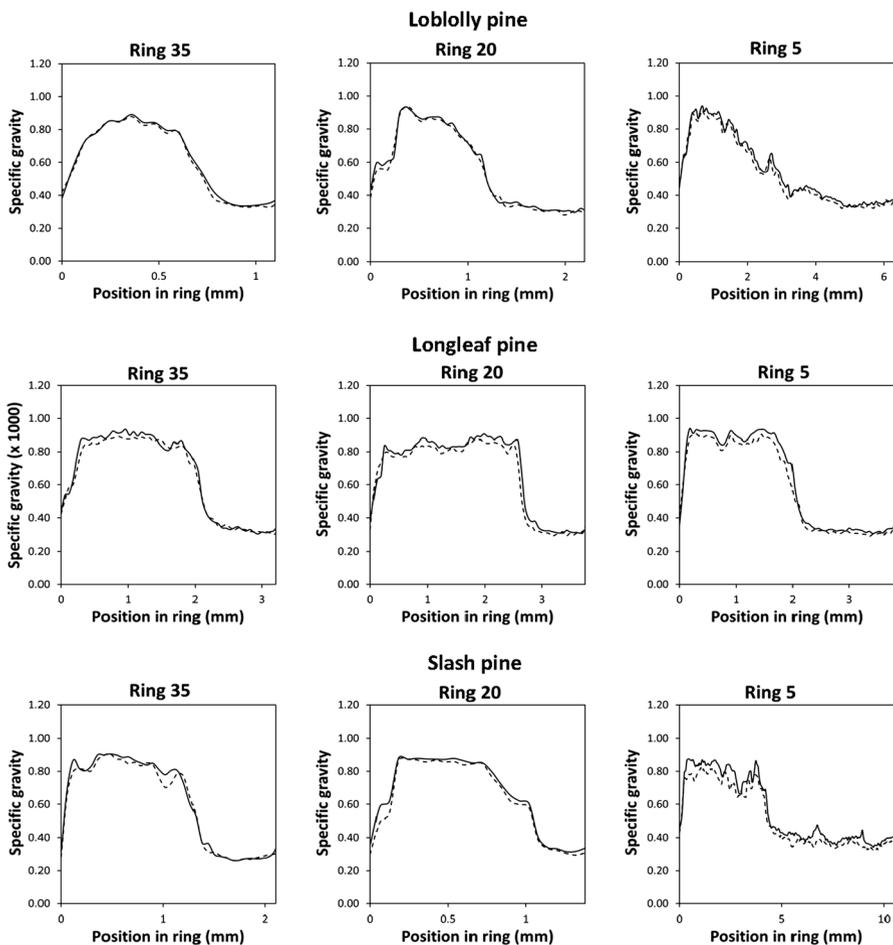


Fig. 4 X-ray densitometry profiles for individual growth rings in the mature (ring numbers 35 and 20) and juvenile (ring number 5) wood zones for loblolly, longleaf, and slash pine wood cores before (*solid line*) and after (*dashed line*) extraction

shape of each profile between the extracted and unextracted cores. The SG values at each position within an individual ring profile were observed to be equivalent or slightly lower for the extracted core, consistent with the whole-core values in Table 1. This result parallels that of Helama et al. (2010) where the maximum and minimum ring SG values, each as highest or lowest single point for a given ring, appeared lower after extraction. The data in the present study do not provide evidence for variability in the mass of extractives between the earlywood and latewood; the extractive content of loblolly pine earlywood was shown to be only slightly higher than that for the corresponding latewood (Ifju and Labosky 1972). It should be noted that subtle deviations in the densitometry traces are not unexpected given that placement of the specimen in the instrument core holder would result in similar paths, but not identical paths, for the X-ray beam along the length of the core. The plots shown in the present study demonstrate the robustness (i.e., high degree of reproducibility) for X-ray densitometry as a technique. Thus, the early pursuit of X-ray densitometry for its sensitivity and objectivity during within-ring measurements (Jagels and Telewski 1990) is herein substantiated.

It is generally accepted that extractives do not contribute significantly to the physical/mechanical properties of wood (Panshin and de Zeeuw 1980; Forest Products Laboratory 2010). Unusually, high extractive contents may result in unusually high values for SG that would not correlate well with mechanical properties. In these occasional instances, extraction may be warranted. For example, the extractive contents in the heartwood of *Larix* sp. are reported to be exceptionally high, leading to the recommendation of solvent extraction prior to X-ray densitometry (Grabner et al. 2005). The caveat is that extractive yields are dependent on solvent selection (Pettersen 1984). Studies utilizing different solvents may not be directly comparable, especially where the solvent system is not commonly applied. Acetone was selected for extractions in the present study given its common use for extractives determinations. Similar results before and after extraction (Table 1) suggest that SG values determined on extracted southern pine specimens are generally no more representative than those from the corresponding unextracted specimens. Greater similarity in results from younger trees (e.g., 20 years) would be expected given even lower extractive contents.

The earlywood and latewood boundaries

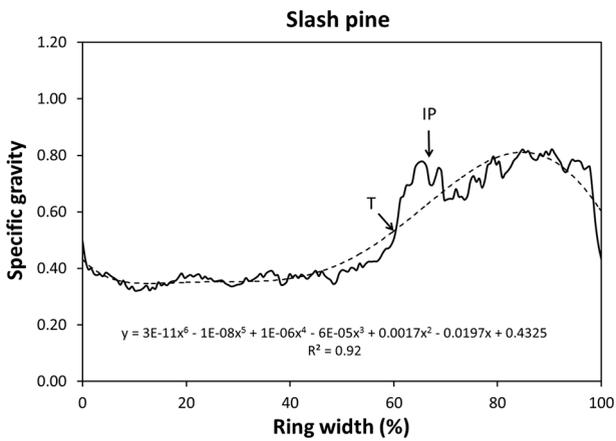
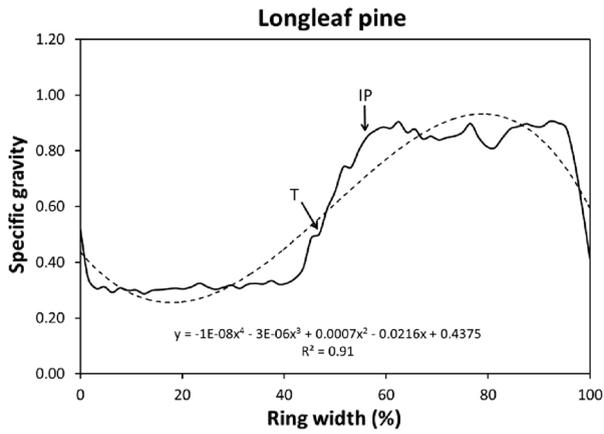
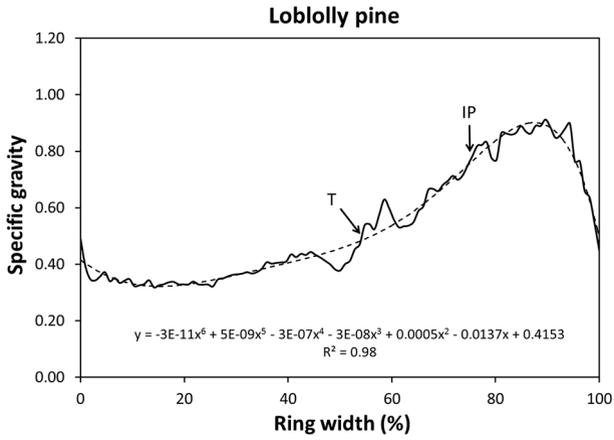
Latewood formation was defined by Mork (1928) as when the tracheids are such that the width of the common cell wall for two adjacent tracheids, when multiplied by two, is equal or greater than the width of the lumen (Larson 1969). Mork's index is thus an arbitrarily set "threshold" (Park et al. 2006), based not on SG values, but tracheid cross-sectional dimensions. The term "threshold method" describes the operation of using a set value for SG that, when crossed along the density profile, marks the earlywood–latewood transition and, equally important, the latewood–earlywood transition. A SG of 0.48 was selected as the threshold in the present study on the basis of the exclusive use of this value in prior studies with loblolly (Clark

et al. 2006; Jordan et al. 2008; Love-Myers et al. 2009; Samuelson et al. 2010; Antony et al. 2012) and slash (Hodge and Purnell 1993) pines. For mature southern pine wood (ring numbers 20 and 35 in Fig. 4), the earlywood–latewood transition is equally abrupt as the latewood–earlywood transition; thus, a threshold density deemed appropriate to define the onset of a growth ring is equally appropriate to define the onset of latewood formation within that growth ring.

Abrupt earlywood–latewood transitions were also observed in the juvenile wood (ring number 5 in Fig. 4) in the longleaf and slash pine wood cores, but not loblolly pine wood core. Thus, in the juvenile wood zone for the longleaf and slash pine wood cores, a threshold density deemed appropriate to define the onset of a growth ring should again be equally appropriate to define the onset of latewood formation within that growth ring. It could be argued that the gradual earlywood–latewood transition illustrated for the loblolly pine juvenile wood growth ring may be more amenable to the curve fitting and modeling applied to other species (e.g., *Picea*) with gradual earlywood–latewood transitions. In a comparative study by Antony et al. (2012), agreement among earlywood–latewood transition points determined by three different methods (Mork’s index, threshold method, inflection point along fitted smooth splines) was greater in the mature wood than the juvenile wood of loblolly pine; it was stated that both Mork’s index and the threshold method overestimated the proportion of earlywood, especially in the juvenile wood zone.

Pursuant to the studies by Antony et al. (2012) and Koubaa et al. (2002), polynomial fitting to the juvenile rings representing each of the three southern pine species was done to demonstrate the consequences of different ring profiles (i.e., abrupt vs. gradual earlywood–latewood transitions). Thus, ring number 5 from each loblolly, longleaf, and slash pine wood core was plotted again, but this time normalizing the distance to a percentage of the ring width (Fig. 5). Progression along the ring (left to right) was from earlywood to latewood (pith to bark) to allow polynomial fitting as reported by Koubaa et al. (2002). The first and last point for each plot was that which immediately followed crossing the threshold SG value of 0.48. As to be expected, the best polynomial fit ($R^2 = 0.98$) occurred with the juvenile wood growth ring from loblolly pine, displaying the gradual earlywood–latewood transition. Unlike Antony et al. (2012), a higher earlywood proportion (lower percent latewood) was obtained for loblolly pine juvenile wood with the inflection point method compared to the threshold method (Table 2); the SG at the inflection point along the fitted curve was 0.75, a value essentially equivalent to the whole-core value for latewood SG (0.77). The results here were consistent with those of Koubaa et al. (2002), working with black spruce [*Picea mariana* (Mill) B.S.P.], where higher earlywood proportions (lower percent latewood) and higher earlywood–latewood transition SG values were obtained with the inflection point method.

As illustrated in Fig. 5, erroneous assignments of latewood to the earlywood zones can occur from the application of the inflection point method to the abrupt density profiles displayed for the slash and longleaf pine juvenile wood; the inflection point (IP) arrows on the figure point to the actual density above the corresponding inflection point along the fitted curve. It could be argued that the inflection point method may still be suitable for the demarcation of the earlywood–



◀ **Fig. 5** X-ray densitometry profiles for ring number 5 from loblolly, longleaf, and slash pine wood cores, after plotting from earlywood to latewood (*left to right*), normalizing to 100 % ring width, and polynomial curve fitting. Earlywood–latewood transitions determined by threshold (*T*) and inflection point (*IP*) methods are shown

Table 2 Proportions of latewood and earlywood for juvenile wood growth rings as determined using threshold and inflection point methods

	Threshold method		Inflection point method		
	Latewood (%)	Earlywood (%)	Latewood (%)	Earlywood (%)	SG at inflection point on curve
Loblolly pine	45.8	54.2	25.0	75.0	0.75
Longleaf pine	54.7	45.3	44.6	55.4	0.61
Slash pine	40.5	59.5	33.9	66.1	0.61

latewood transition in loblolly pine juvenile wood; however, in doing so, poor polynomial fitting along the vast majority of growth rings in the rest of the wood core, particularly in the mature wood toward the bark, would result in obviously erroneous assignments of latewood to earlywood. Thus, application of the inflection point method to the southern pines, herein applicable to loblolly pine juvenile wood zone alone, would serve little but to eliminate potential comparisons to wood quality data previously reported in the literature. While there continues to be discourse on which demarcation methods for the earlywood–latewood transition are improvements over established demarcation methods, the present study demonstrates that for at least three pines in the southeastern USA, the threshold method provides an objective and reproducible means to generate wood quality data that can be readily compared.

Conclusion

Solvent extraction of the wood cores before X-ray densitometry had minimal impact on both the shapes of individual ring profiles and the whole-core wood quality data comparisons. An assessment of the inflection point method for determining the earlywood–latewood transition point showed that most growth ring profiles were not amenable to polynomial fitting. Indeed, for the southern pines, the earlywood–latewood transitions are usually as abrupt as the latewood–earlywood transitions. Accordingly, a threshold density deemed appropriate to define the onset of a growth ring would be equally appropriate to define the onset of latewood formation.

Acknowledgments Wood cores were processed by Edward Andrews. Michael Thompson performed X-ray densitometry, and Charles Grier processed the resultant data in consultation with Ray Souter. Karen Reed assisted with wood core extractions and manuscript review. The authors wish to thank Kurt Johnsen for help in coordinating core collection at the Harrison Experimental Forest.

References

- Adamopoulos S, Milios E, Doganos D, Bistinas I (2009) Ring width, latewood proportion and dry density in stems of *Pinus brutia* Ten. Eur J Wood Prod 67:471–477
- Antony F, Schimleck LR, Daniels RF (2012) A comparison of the earlywood-latewood demarcation methods—a case study in loblolly pine. IAWA J 33(2):187–195
- ASTM (1993) D2395, standard test methods for specific gravity of wood and wood-based materials. American Society of Testing and Materials, West Conshohocken
- Bergsten U, Lindeberg J, Rindby A, Evans R (2001) Batch measurements of wood density on intact or prepared drill cores using X-ray microdensitometry. Wood Sci Technol 35:435–452
- Biblis EJ, Carino H, Teeter L (1998) Comparative economic analysis of two management options for loblolly pine timber plantations. Forest Prod J 48(4):29–32
- Bouffier L, Rozenberg P, Raffin A, Kremer A (2008) Wood density variability in successive breeding populations of maritime pine. Can J Forest Res 38:2148–2158
- Chaffey N (1999) Cambium: old challenges—new opportunities. Trees-Struct Funct 13:138–151
- Clark A, Saucier JR (1989) Influence of initial planting density, geographic location, and species on juvenile wood formation in southern pine. Forest Prod J 39(7/8):42–48
- Clark A, Daniels RF, Jordan L (2006) Juvenile/mature wood transition in loblolly pine as defined by annual ring specific gravity, proportion of latewood, and microfibril angle. Wood Fiber Sci 38(2):292–299
- Cole DE, Zobel BJ, Roberds JH (1966) Slash, loblolly, and longleaf pine in a mixed natural stand; a comparison of their wood properties, pulp yields, and paper properties. Tappi J 49(4):161–166
- Eberhardt TL, Sheridan PM, Mahfouz JM, So C-L (2007) Old resinous turpentine stumps as an indicator of the range of longleaf pine in southeastern Virginia. In: Estes BL, Kush JS (eds) Proceedings of the sixth longleaf alliance regional conference, Tifton, GA. Longleaf Alliance Report No. 10, pp 79–82
- Eberhardt TL, Sheridan PM, Bhuta AAR (2011) Revivification of a method for identifying longleaf pine timber and its application to southern pine relicts in southeastern Virginia. Can J Forest Res 41:2440–2447
- Forest Products Laboratory (2010) Wood handbook: wood as an engineering material. General technical report FPL-GTR-190, USDA Forest Service, Forest Products Laboratory, Madison, WI
- Franceschini T, Bontemps J-D, Leban J-M (2012) Transient historical decrease in earlywood and latewood density and unstable sensitivity to summer temperature for Norway spruce in northeastern France. Can J Forest Res 42:219–226
- Franceschini T, Longuetaud F, Bontemps J-D, Bouriaud O, Caritey B-D, Leban J-M (2013) Effect of ring width, cambial age, and climatic variables on the within-ring wood density profile of Norway spruce *Picea abies* (L.) Karst. Trees-Struct Funct 27:913–925
- Fujimoto T, Koga S (2010) An application of mixed-effects model to evaluate the effects of initial spacing on radial variation in wood density in Japanese larch (*Larix kaempferi*). J Wood Sci 56:7–14
- Gapare WJ, Wu HX, Abarquez A (2006) Genetic control of the time of transition from juvenile to mature wood in *Pinus radiata* D. Don. Ann Forest Sci 63:871–878
- Gonzalez-Benecke CA, Riveros-Walker AJ, Martin TA, Peter GF (2015) Automated quantification of intra-annual density fluctuations using microdensity profiles of mature *Pinus taeda* in a replicated irrigation experiment. Trees-Struct Funct 29:185–197
- Grabner M, Wimmer R, Gierlinger N, Evans R, Downes G (2005) Heartwood extractives in larch and effects on X-ray densitometry. Can J Forest Res 35:2781–2786
- Guller B, Isik K, Cetinay S (2012) Variations in the radial growth and wood density components in relation to cambial age in 30-year-old *Pinus brutia* Ten. at two test sites. Trees-Struct Funct 26:975–986
- Harms WR, Whitesell CD, DeBell DS (2000) Growth and development of loblolly pine in a spacing trial planted in Hawaii. Forest Ecol Manag 126:13–24
- Helama S, Vartiainen M, Kolström T, Meriläinen J (2010) Dendrochronological investigation of wood extractives. Wood Sci Technol 44:335–351
- Hodge GR, Purnell RC (1993) Genetic parameter estimates for wood density, transition age, and radial growth in slash pine. Can J Forest Res 23:1881–1891
- Ifju G, Labosky P Jr (1972) A study of loblolly pine growth increments: part 1. wood and tracheid characteristics. Tappi J 55(4):524–529

- Ivković M, Rozenberg P (2004) A method for describing and modelling of within-ring wood density distribution in clones of three coniferous species. *Ann For Sci* 61:759–769
- Jagels R, Telewski FW (1990) Computer-aided image analysis of tree rings. In: Cook ER, Kairiukstis LA (eds) *Methods of dendrochronology: applications in the environmental sciences*. Kluwer Academic Publishers, Boston, pp 76–93
- Jordan L, Clark A, Schimleck LR, Hall DB, Daniels RF (2008) Regional variation in wood specific gravity of planted loblolly pine in the United States. *Can J Forest Res* 38:698–710
- Kantavichai R, Briggs D, Turnblom E (2010) Modeling effects of soil, climate, and silviculture on growth ring specific gravity of Douglas-fir on a drought-prone site in Western Washington. *Forest Ecol Manag* 259:1085–1092
- Koubaa A, Zhang SYT, Makni S (2002) Defining the transition from earlywood to latewood in black spruce based on intra-ring wood density profiles from X-ray densitometry. *Ann Forest Sci* 59:511–518
- Koubaa A, Isabel N, Zhang SY, Beaulieu J, Bousquet J (2005) Transition from juvenile to mature wood in black spruce (*Picea mariana* (Mill.) B.S.P.). *Wood Fib Sci* 37(3):445–455
- Kubler H (1980) Wood as building and hobby material. John Wiley and Sons, New York
- Kumar S (2002) Earlywood-latewood demarcation criteria and their effect on genetic parameters of growth ring density components and efficiency of selection for end-of-rotation density of radiata pine. *Silvae Genet* 51:5–6
- Larson PR (1969) Wood formation and the concept of wood quality. Yale University, School of Forestry, Bulletin No. 74, Yale University, New Haven, CT
- Love-Myers KR, Clark A, Schimleck LR, Jokela EJ, Daniels RF (2009) Specific gravity responses of slash and loblolly pine following mid-rotation fertilization. *Forest Ecol Manag* 257:2342–2349
- Mora CR, Allen HL, Daniels RF, Clark A (2007) Modeling corewood-outerwood transition in loblolly pine using wood specific gravity. *Can J Forest Res* 37:999–1011
- Mork E (1928) The quality of spruce wood with special regard to pulpwood. *Der Papier-Fabrikant* 48:741–747
- Mothe F, Duchanois G, Zannier B, Leban J-M (1998) Microdensitometric analysis of wood samples: data computation method used at Inra-ERQB (CERD program). *Ann Sci Forest* 55:301–313
- Panshin AJ, de Zeeuw C (1980) *Textbook of wood technology*, 4th edn. McGraw-Hill, New York
- Park Y-I, Dallaire G, Morin H (2006) A method for multiple intra-ring demarcation of coniferous trees. *Ann Forest Sci* 63:9–14
- Perneštal K, Jonsson B, Larsson B (1995) A simple model for density of annual rings. *Wood Sci Technol* 29:441–449
- Petterson RC (1984) The chemical composition of wood. In: Rowell R (ed) *The chemistry of solid wood*. American Chemical Society, Washington, D.C., pp 2–126
- Rozenberg P, Schüte G, Ivkovich M, Bastien C, Bastien J-C (2004) Clonal variation of indirect cambium reaction to within-growing season temperature changes in Douglas-fir. *Forestry* 77(4):257–268
- Samuelson LJ, Eberhardt TL, Butnor JR, Stokes TA, Johnsen KH (2010) Maximum growth potential in loblolly pine: results from a 47-year-old spacing study in Hawaii. *Can J Forest Res* 40:1914–1929
- Samuelson LJ, Stokes TA, Johnsen KH (2012) Ecophysiological comparison of 50-year-old longleaf pine, slash pine and loblolly pine. *Forest Ecol Manag* 274:108–115
- Samuelson LJ, Eberhardt TL, Barkowski SM, Johnsen KH (2013) Relationships between climate, radial growth and wood properties of mature loblolly pine in Hawaii and a northern and southern site in the southeastern United States. *Forest Ecol Manag* 310:786–795
- Schmidting RC (1973) Intensive culture increases growth without affecting wood quality of young southern pines. *Can J Forest Res* 3:565–573
- Spurr SH, Hsiung W-Y (1954) Growth rate and specific gravity in confers. *J Forest* 52(3):191–200
- Tasissa G, Burkhart HE (1998) Modeling thinning effects on ring specific gravity of loblolly pine (*Pinus taeda* L.). *Forest Sci* 44(2):212–223
- Williamson GB, Wiemann MC (2010) Measuring wood specific gravity...correctly. *Am J Bot* 97(3):519–524