

VARIATION IN BARK ALLOCATION AND RUGOSITY ACROSS SEVEN CO-OCCURRING SOUTHEASTERN U.S. TREE SPECIES

Timothy M. Shearman and J. Morgan Varner

EXTENDED ABSTRACT

Bark is a complex multifunctional structure of woody plants that varies widely among species. Tree species that occur in frequently burned ecosystems generally develop thicker bark than those found in less flammable environments (Pausas 2015). Outer bark on species that allocate resources to thick bark also tends to be rugose, with bark being thickest at the ridges and thinnest in the furrows. Diameter is often used as a predictor for bark thickness, but little attention has been given to other factors that might affect bark development and allocation.

Our study site was located within the Tallahatchie Experimental Forest, Mississippi. We sampled saplings of *Carya tomentosa* (n = 10), *Nyssa sylvatica* (n = 10), *Pinus echinata* (n = 11), *Pinus taeda*, *Prunus serotina* (n = 10), *Quercus marilandica* (n = 10), and *Quercus falcata* (n = 11), ranging from 1.0–9.4 cm ground-line diameter. Cross-sections along the stem every 10 cm from the base (0 cm) to 100 cm and every 20 cm from 100 cm to 200 cm were measured for cross-section area, outer and inner bark area, and wood area.

Bark rugosity (B_r) was calculated as the ratio of the actual cross-sectional area at each measured height, A_{mht} , to the area of the convex hull at that measured height, $A_{conv(mht)}$. We then take the complement to scale the ratio so that increasing value corresponds to increasing rugosity (fig. 1):

$$B_r = 1 - \frac{A_{mht}}{A_{conv(mht)}}$$

Mixed effect models were fit using bark rugosity, outer and inner bark cross-sectional area as a response variable, and tree individual as a random effect. Fixed effects included species, wood diameter, outer- and inner-bark thickness, wood cross-sectional area, measure height of the cross-section, and height growth rate.

Mean basal diameters were not significantly different between species ($P = 0.83$). Sapling ages ranged from 2 to 24 years across all species but did not significantly differ between species ($P = 0.64$). Outer-bark thickness ranged from 0.01 to 0.77 cm with the thickest maximum outer bark occurring in *P. taeda* (0.77 cm) and the thinnest maximum outer bark occurring in *P. serotina* (0.17 cm). Basal outer-bark thickness was significantly different between species ($P < 0.001$). Multiple comparisons showed that *C. tomentosa* had significantly thinner bark than *P. echinata* ($P = 0.014$), *P. taeda* ($P < 0.001$), and *Q. marilandica* ($P = 0.003$). *Prunus serotina* had significantly thinner bark than *P. echinata* ($P = 0.011$), *P. taeda* ($P < 0.001$), *Q. falcata* ($P = 0.042$), and *Q. marilandica* ($P = 0.002$). Bark rugosity varied among species from 0.00 (very

Author Information: Timothy M. Shearman, Post-Doctoral Scientist, Tall Timbers Research Station, Tallahassee, FL 32312; and J. Morgan Varner, Director of Research and Senior Scientist, Tall Timbers Research Station, Tallahassee, FL 32312.

Citation for proceedings: Willis, John L.; Self, Andrew B.; Siegert, Courtney M., eds. 2022. Proceedings of the 21st Biennial Southern Silvicultural Research Conference. Gen. Tech. Rep. SRS-268. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station. 262 p. <https://doi.org/10.2737/SRS-GTR-268>.

smooth) 0.17 (very rugose) with significant differences between species ($P < 0.001$). *Quercus marilandica* was significantly more rugose than *C. tomentosa* ($P < 0.001$) and *P. serotina* ($P < 0.001$). *Quercus falcata* was also significantly more rugose than *P. serotina* ($P = 0.023$). Height growth varied from 23.7 to 167.5 cm yr⁻¹ with *P. serotina* having the fastest vertical growth and *P. echinata* having the slowest growth among species.

Wood cross-sectional area was a positive significant effect for all outer bark investment models. Height growth rate was a negative effect (i.e., faster height growth had lower bark allocation) for *C. tomentosa*, *N. sylvatica*, *P. taeda*, and *P. serotina*, but not for *P. echinata* or either oak. Measure height also had a negative effect for all species except for *C. tomentosa* and *N. sylvatica*. Fixed effects explained 83–96 percent of the variance of outer bark investment (table 1).

Wood cross-sectional area was a significant fixed effect for all inner-bark models. The measure height had a negative effect on *C. tomentosa*, *Q. falcata*, and *Q. marilandica*, but was not significant for the other species. Fixed effects explained a slightly higher amount of the variance in the inner-bark models than the outer-bark models, explaining 93–98 percent of the variance (table 1).

Outer-bark thickness was the only significant fixed effect in the bark rugosity models. The models suggest a higher slope for *Q. marilandica* (0.28), *N. sylvatica* (0.23), and *Q. falcata* (0.20), than the other species. *Quercus marilandica* had significantly higher slopes than *C. tomentosa*, *P. echinata*, *P. taeda*, and *P. serotina*, but not *N. sylvatica* or *Q. falcata*. *Nyssa sylvatica* and *Q. falcata* also had significantly higher slopes than *P. taeda*, but not with any other species. Species and outer-bark thickness as fixed effects in the full model explained 77 percent of the variance.

Our results suggest that height growth may be a compromise to bark allocation for some species. We found an effect of measure height on outer-bark thickness in the oaks and pines, which indicates that outer bark tapers more than wood in these species. This result is consistent with the findings of others that suggest that pyrophytic species develop thicker bark at the base of the bole as a fire protection strategy (Graves and others 2014, Hammond and others 2015, Kidd and Varner 2019, Shearman and others 2018). However, we also found the effect of measure height in *P. serotina*, which is not consistent with this hypothesis.

The survival benefit of rugose bark is unclear because of its correlation with outer-bark thickness in the species we studied. Barlow and others (2003) found that bark texture (measured categorically as “rough”, “medium”, or “smooth”) was an important determination of tree mortality with surviving trees in burnt forests having significantly rougher bark in the smaller (0.2–0.6 cm) bark thickness classes. Rugosity might therefore benefit smaller diameter trees while larger trees can withstand fire due to having thick bark alone. Therefore, future heat transfer models might benefit from including a rugosity term as proposed in our study. Aside from providing data for several important yet understudied species, our rugosity measures offer promise for incorporating into fluid dynamics fire behavior models.

LITERATURE CITED

- Barlow, J.; Lagan, B.O.; Peres, C.A. 2003. Morphological correlates of fire-induced tree mortality in a central Amazonian forest. *Journal of Tropical Ecology*. 19: 291–299.
- Graves, S.J.; Rifai, S.W.; Putz, F.E. 2014. Outer bark thickness decreases more with height on stems of fire-resistant than fire-sensitive Floridian oaks (*Quercus* spp.; Fagaceae). *American Journal of Botany*. 101: 2183–2188.
- Hammond, D.H.; Varner, J.M.; Kush, J.S.; Fan, Z. 2015. Contrasting sapling bark allocation of five Southeastern USA hardwood tree species in a fire prone ecosystem. *Ecosphere*. 6: 1–13.
- Kidd, K.R.; Varner, J.M. 2019. Differential relative bark thickness and aboveground growth discriminates fire resistance among hardwood sprouts in the southern Cascades, California. *Trees*. 33: 267–277.
- Pausas, J.G. 2015. Bark thickness and fire regime. *Functional Ecology*. 29: 315–327.
- Shearman, T.M.; Wang, G.G.; Ma, P.T.; Guan, S. 2018. Patterns of bark growth for juvenile trees of six common hardwood species in the Eastern United States and the implications to fire-tolerance. *Trees*. 32: 519–524.

Table 1—Outer (ob) and inner (ib) bark area models for saplings of seven native tree species

Species codes	Best model	Coefficients					
		Intercept	Log(wood)	Llog(HTGR)	MHT	r ² _m	r ² _c
CATO	Log(ob)~log(wood) + log(HTGR) + (1 Treenum)	-1.01	1.37	-0.60	—	0.93	0.94
NYSY	Log(ob)~log(wood) + log(HTGR) + (1 Treenum)	0.27	1.36	-0.80	—	0.93	0.95
PIEC	Log(ob)~log(wood) + MHT + (1 Treenum)	-1.36	1.23		-0.53	0.83	0.96
PITA	Log(ob)~log(wood) + log(HTGR) + MHT + (1 Treenum)	-0.25	1.17	-0.29	-0.46	0.96	0.96
PRSE	Log(ob)~log(wood) + log(HTGR) + MHT + (1 Treenum)	0.39	0.86	-0.71	-0.71	0.88	0.89
QUFA	Log(ob)~log(wood) + MHT + (1 Treenum)	-1.47	1.42	—	-0.98	0.87	0.9
QUMA	Log(ob)~log(wood) + MHT + (1 Treenum)	-1.02	1.39	—	-0.37	0.86	0.97
CATO	Log(ib)~log(wood) + MHT + (1 Treenum)	-0.88	1.02	—	-0.22	0.96	0.99
NYSY	Log(ib)~log(wood) + (1 Treenum)	-1.70	0.97	—	—	0.98	0.99
PIEC	Log(ib)~log(wood) + (1 Treenum)	-2.01	0.62	—	—	0.94	0.97
PITA	Log(ib)~log(wood) + (1 Treenum)	-2.33	0.76	—	—	0.93	0.97
PRSE	Log(ib)~log(wood) + (1 Treenum)	-1.97	0.97	—	—	0.97	0.98
QUFA	Log(ib)~log(wood) + MHT + (1 Treenum)	-0.90	0.95	—	-0.23	0.96	0.97
QUMA	Log(ib)~log(wood) + MHT + (1 Treenum)	-0.75	0.95	—	-0.15	0.97	0.99

— = Non-applicable.

CATO = *Carya tomentosa*; NYSY = *Nyssa sylvatica*; PIEC = *Pinus echinata*; PITA = *Pinus taeda*; PRSE = *Prunus serotina*; QUFA = *Quercus falcata*; QUMA = *Quercus marilandica*. All models include a unique tree number (Treenum) as a random effect term. Fixed effects include wood cross-sectional area (wood), average height growth (HTGR), and measure height (MHT). Pseudo-r² values measure the amount of variance explained by the fixed effects (r²_m) and combined fixed and random effects (r²_c). Models were fit using maximum likelihood. Comparisons between nested model structures were made using AICc. All fixed effects were significant at P < 0.05.



Figure 1—Bark rugosity of a cross-section, in this case a sample of *Q. marilandica* at 10 cm height can be measured as the compliment of the ratio of the cross-section area (area of the actual sample) to the area of its convex hull (red line).