

RESEARCH ARTICLE

RELATIVE BARK THICKNESS IS CORRELATED WITH TREE SPECIES DISTRIBUTIONS ALONG A FIRE FREQUENCY GRADIENT

Jennifer L. Schafer^{1*}, Bradley P. Breslow¹, Matthew G. Hohmann²,
and William A. Hoffmann¹

¹Department of Plant and Microbial Biology, North Carolina State University,
2115 Gardner Hall, Box 7612, Raleigh, North Carolina 27695, USA

²US Army Corps of Engineers, Engineer Research and Development Center,
2902 Newmark Drive, Champaign, Illinois 61826, USA

* Corresponding author current address: Department of Biology, William Jewell College,
500 College Hill, Liberty, Missouri 64068, USA
Tel.: +1-816-415-7616; e-mail: schaferj@william.jewell.edu

ABSTRACT

The probability of stem survival after fire is strongly influenced by energy allocation to bark because bark thickness affects heat transfer during fire. Greater relative investment in inner bark versus outer bark should also enhance survival because of greater moisture content of inner bark. We measured stem diameter, bark thickness, and habitat preference of five species typical of long-leaf pine savannas, and six species characteristic of adjacent wetlands (*pocosins*), and calculated relative bark thickness, the inner bark proportion, radial growth, and bark accumulation of each species. We hypothesized that savanna species have thicker bark and greater relative investment in inner bark than *pocosin* species, because fires occur more frequently in savannas than *pocosins*. As hypothesized, savanna species have relatively thicker bark than *pocosin* species. Relative bark thickness and the rate of bark accumulation were correlated with the mean

RESUMEN

La probabilidad de sobrevivencia del tronco después de un incendio está fuertemente influenciada por la energía que recibe la corteza, dado que el espesor de la misma afecta la transferencia de calor durante el fuego. Una mayor inversión relativa en las estructuras internas de la corteza por sobre las externas aumenta la sobrevivencia, debido al mayor contenido de humedad que poseen las estructuras internas. Nosotros medimos el diámetro del tronco, la proporción de estructuras internas de la corteza y las preferencias de hábitat de cinco especies típicas de sabanas de pino de hoja larga (o pino palustre) y de seis especies características de humedales adyacentes (*pocosins*), y calculamos el espesor relativo de la corteza, la proporción de estructuras internas de la corteza, el crecimiento radial, y la acumulación de corteza de cada especie. Hipotetizamos que las especies de sabana tienen una corteza más gruesa e invierten más recursos en la creación de estructuras de la corteza interna, dado que los incendios ocurren más frecuentemente en sabanas que en *pocosins*. Como fuera hipotetizado, las especies de sabana tienen efectivamente la corteza más gruesa que las especies de *pocosins*. El ancho relativo de la corteza y su tasa relativa de acumulación fueron correlacio-

location of a species along the pocosin-to-savanna gradient. However, the inner bark proportion did not differ between savanna and pocosin species. Our results indicate that relative bark thickness is likely the primary bark trait affecting fire-induced topkill and influencing the distribution of species along the pocosin-to-savanna gradient.

nadas con la ubicación media de las especies a lo largo del gradiente desde los *pocosin* hasta la sabana. Por supuesto, la proporción de la corteza interna no difirió entre las especies de sabana y de *pocosins*. Nuestros resultados indican que el espesor relativo de la corteza es prácticamente el atributo más importante que afecta la muerte apical inducida por fuego, e influencia la distribución de especies a lo largo del gradiente entre la sabana y los *pocosins*.

Keywords: bark accumulation, inner bark proportion, longleaf pine savanna, *Pinus*, *Quercus*, stream-head pocosin

Citation: Schafer, J.L., B.P. Breslow, M.G. Hohmann, and W.A. Hoffmann. 2015. Relative bark thickness is correlated with tree species distributions along a fire frequency gradient. *Fire Ecology* 11(1): 74–87. doi: 10.4996/fireecology.1101074

INTRODUCTION

In pyrogenic ecosystems, thick bark allows trees to minimize or escape fire damage by protecting the vascular cambium (Gignoux *et al.* 1997, Hoffmann *et al.* 2009, Midgley *et al.* 2010, Lawes *et al.* 2011a) and xylem (Michaletz *et al.* 2012). Thick bark reduces heat transfer to the cambium during fire and reduces the likelihood that a lethal cambium temperature is reached (Vines 1968, Uhl and Kauffman 1990, Gashaw *et al.* 2002, van Mantgem and Schwartz 2003, Lawes *et al.* 2011a, VanderWeide and Hartnett 2011). Thus, the probability of survival after fire is greater for individuals and species with thicker bark (Harmon 1984, Lawes *et al.* 2011b, Catry *et al.* 2012, Hoffmann *et al.* 2012).

Fire frequency and intensity can select for higher investment in bark thickness (Pausas 2014) due to the importance of thick bark for post-fire survival. In both Brazil and Australia, savannas burn more frequently than adjacent forests, and savanna tree species have relatively thicker bark than forest tree species (Hoffmann *et al.* 2003, Hoffmann *et al.* 2009, Lawes *et al.* 2011a). In North America, oak (*Quercus* spp.) and pine (*Pinus* spp.) saplings

have thicker outer bark (i.e., rhytidome) in ecosystems that experience frequent, low-intensity fire than in ecosystems that experience less frequent, more intense fire (Jackson *et al.* 1999). Furthermore, anthropogenic alteration of fire regimes can change selection pressures for energy allocation to bark and species composition. Frequent anthropogenic fires may favor trees with thicker bark (Stephens and Libby 2006), while fire suppression may allow for increased survival of species with thinner bark that are less resistant to fire (VanderWeide and Hartnett 2011).

Although thick bark can protect adult trees from surface fires, saplings generally lack sufficient bark to escape topkill (Hoffmann and Solbrig 2003, Lawes *et al.* 2011b, Hoffmann *et al.* 2012, Lawes *et al.* 2013). Consequently, the ability to accumulate bark quickly should be particularly beneficial in frequently burned environments. Since bark thickness increases as a function of stem diameter as a stem grows, the rate of bark accumulation will depend not only on the relative investment in bark, but also on the rate of stem growth (Midgley *et al.* 2010, VanderWeide and Hartnett 2011, Hoffmann *et al.* 2012). Allocation of resources to bark, however, may occur at the expense of

growth (Jackson *et al.* 1999), so it is important to consider both stem growth and relative bark thickness when considering plant strategies for survival in frequently burned environments.

In fire-prone ecosystems, bark thickness is likely the best predictor of species differences in topkill after fire (Lawes *et al.* 2011b), but bark characteristics such as moisture content also influence heat transfer (Harmon 1984). In fact, bark moisture has been shown to increase fire resistance (Higgins *et al.* 2012, but see Lawes *et al.* 2011a). If frequent fire selects for increased bark moisture, it could be manifested as an increase in the ratio of inner bark to total bark thickness. Inner bark, which is living tissue, is moister than outer bark (Vines 1968, van Mantgem and Schwartz 2003, Jones *et al.* 2004), and several studies have suggested that inner bark provides greater insulation than outer bark (van Mantgem and Schwartz 2003, Scholz *et al.* 2007).

In this study, we tested the hypotheses that tree species in longleaf pine (*Pinus palustris* Mill.) savannas have relatively thicker bark and a greater proportion of inner bark than tree species in stream-head pocosins (i.e., wetlands). Specifically, we measured relative bark thickness and the proportion of inner bark of tree species in savanna and pocosin habitats in North Carolina, USA. Upland longleaf pine savannas historically had an average fire return interval of approximately two years (Stambaugh *et al.* 2011). Lowland stream-head pocosins, which support tree species characteristic of eastern deciduous forests (e.g., *Acer rubrum* L. and *Liriodendron tulipifera* L.) and occur within the savanna matrix (Schafale and Weakley 1990, Sorrie *et al.* 2006), burn every 7 to 50 years (Frost 1995). The pocosin-to-savanna hydrological gradient therefore also represents a fire frequency gradient. Thus, in addition to hypothesizing that savanna species have relatively thicker bark than pocosin species overall, we hypothesized that relative bark thickness and bark accumulation are correlated with the location of species along the poci-

sin-to-savanna gradient. As fire frequency increases, relatively thicker bark and a greater rate of bark accumulation should be beneficial for protecting the vascular cambium during fire (Gignoux *et al.* 1997, Hoffmann *et al.* 2009, Midgley *et al.* 2010, Lawes *et al.* 2011a). Because inner bark is moister than outer bark (Vines 1968, van Mantgem and Schwartz 2003, Jones *et al.* 2004), and higher moisture content may inhibit temperature change during fire, we hypothesized that savanna species have a greater proportion of inner bark than pocosin species.

METHODS

This study was conducted at Fort Bragg (in Cumberland and Hoke counties) in the Sandhills region of North Carolina. Mean annual precipitation at Fort Bragg is 1275 mm (Sorrie *et al.* 2006), and soils range from well drained ultisols to poorly drained entisols (USDA NRCS 2007). The most abundant vegetation type is upland pine-scrub oak sandhill (i.e., savanna), which is dominated by longleaf pine and *Quercus* spp. (Sorrie *et al.* 2006). Within the savanna matrix, lowland stream-head pocosin wetlands are abundant. Common pocosin tree species include red maple (*Acer rubrum*), tulip poplar (*Liriodendron tulipifera*), and pond pine (*Pinus serotina* Michx.), and the diversity and density of tree species depends on fire frequency (Sorrie *et al.* 2006). Similarly, the width of the ecotone between longleaf pine savanna and stream-head pocosin communities is influenced by fire frequency and intensity, which are determined in part by fuel moisture content (Weakley and Schafale 1991). Longleaf and pond pines are often the only tree species in the ecotone, but other pocosin species may be present (Sorrie *et al.* 2006), particularly in fire-suppressed sites.

Fort Bragg is divided into over 1000 discrete landscape units, which are currently managed with prescribed fire. Each unit is burned approximately every three years. The

longleaf pine savannas are highly flammable, but fire spread into the stream-head pocosins is often limited, likely due to high moisture content of fuels (Weakley and Schafale 1991), the fuel packing ratio, and microclimate (Rothermel 1972). Thus, within a burn unit, savanna species are exposed to fire more frequently than pocosin species.

We selected five savanna species (*Pinus palustris*, *Quercus incana* W. Bartram, *Q. laevis* Walter, *Q. margarettae* [Ashe] Small, and *Q. marilandica* Münchh.) and six pocosin species (*Acer rubrum*, *Liquidambar styraciflua* L., *Liriodendron tulipifera*, *Nyssa biflora* Walter, *Pinus serotina*, and *Quercus nigra* L.) that are relatively common at Fort Bragg (Table 1). *Pinus palustris* is best classified as fire resistant; in the grass stage, it is capable of resprouting from the root collar (Boyer 1990), but after bolting, it is capable of resprouting only from apical buds. All other study species are able to

resprout basally from the root collar or from belowground after fire. Among oak (i.e., *Quercus*) species, savanna oaks generally have greater rhizome resprouting potential than forest oaks (Cavender-Bares et al. 2004a). All study species except *P. palustris* are also likely capable of epicormic resprouting; this occurs most often in *A. rubrum*, *Liquidambar styraciflua*, *Liriodendron tulipifera*, and *P. serotina* (J. Schafer, North Carolina State University, Raleigh, USA, personal observation).

We measured bark thickness and diameter at breast height (DBH; 1.4 m) of 20 to 34 individuals of each species. Individuals were haphazardly selected to cover the range of stem diameters present at Fort Bragg and were located in 34 different sites (i.e., burn units). We used a chisel and mallet to remove three sections of bark (1 cm² to 4 cm²) per stem and measured total bark thickness (at the thickest point) and outer bark (i.e., rhytidome) thickness (with cal-

Table 1. Sample sizes, range of stem diameters, and best fit equations for the relationships between stem diameter (in cm) and bark thickness (in mm) and stem diameter and the proportion of inner bark; n.s. indicates a non-significant relationship. Equations were not forced through the origin. Statistics (i.e., R², F, and P) for the best fit equations are given in Figures 1 and 4. Species are in order of their location along the pocosin-to-savanna gradient.

Habitat	Species	N	Diameter (X) vs. bark thickness (Y)		Diameter (X) vs. inner bark proportion (Y)		
			Diameter range (cm)	Best fit equation	N	Diameter range (cm)	Best fit equation
Pocosin	<i>Acer rubrum</i>	32	0.78 to 20.26	$Y = 0.569 * X^{0.752}$	20	3.30 to 20.26	$Y = -0.083 * \ln(X) + 0.955$
	<i>Nyssa biflora</i>	32	2.07 to 40.59	$Y = 0.693 * X^{0.934}$	29	2.75 to 40.59	n.s.
	<i>Liriodendron tulipifera</i>	32	0.77 to 37.33	$Y = 0.596 * X + 0.120$	27	3.29 to 37.33	$Y = 1.079 * X^{-0.264}$
	<i>Quercus nigra</i>	20	0.95 to 29.72	$Y = 0.835 * X^{0.797}$	17	2.01 to 29.72	n.s.
	<i>Pinus serotina</i>	34	1.87 to 45.22	$Y = 2.038 * X^{0.649}$	34	1.87 to 45.22	$Y = -0.091 * \ln(X) + 0.404$
	<i>Liquidambar styraciflua</i>	30	1.05 to 35.60	$Y = 1.105 * X^{0.840}$	27	2.35 to 35.60	n.s.
Savanna	<i>Pinus palustris</i>	34	1.79 to 40.62	$Y = 3.005 * X^{0.471}$	33	2.23 to 40.62	$Y = -0.100 * \ln(X) + 0.448$
	<i>Quercus marilandica</i>	32	0.85 to 30.47	$Y = 1.964 * X^{0.682}$	31	1.98 to 30.47	n.s.
	<i>Quercus laevis</i>	32	1.18 to 37.63	$Y = 0.686 * X + 2.658$	30	2.55 to 37.63	$Y = 0.737 * X^{-0.216}$
	<i>Quercus margarettae</i>	30	1.18 to 18.00	$Y = 1.449 * X^{0.786}$	25	2.42 to 18.00	$Y = 0.635 * X^{-0.214}$
	<i>Quercus incana</i>	26	0.74 to 22.19	$Y = 1.721 * X^{0.741}$	23	2.34 to 22.19	$Y = 0.575 * X^{-0.136}$

ipers) where the bark was removed. Inner bark thickness was determined as the difference in thickness between total and outer bark. It was not possible to differentiate between outer and inner bark for small individuals (e.g., DBH approximately <3 cm, depending on the species), so only total bark thickness was recorded in these cases. We calculated the mean total bark thickness and the mean proportion of total bark thickness that is inner bark (i.e., the ratio of inner bark thickness to total bark thickness; hereafter referred to as the proportion of inner bark) for each individual.

For each species, we used the regression curve estimation function in SPSS version 19.0 (IBM Corporation, Armonk, New York, USA) to analyze the relationships between stem diameter and bark thickness and between stem diameter and the proportion of inner bark. We calculated relative bark thickness of each individual as the ratio of bark thickness to stem radius (multiplied by 100%; Hoffmann *et al.* 2012). Lawes *et al.* (2013) suggested that relative bark thickness is a reliable measure of fire regime and that relative bark thickness should be determined for trees with smaller diameters because fire is likely to have a greater effect on the survival of these individuals. Thus, we analyzed relative bark thickness and the proportion of inner bark for three sets of individuals: <10 cm diameter, ≥ 10 cm diameter, and all individuals. Overall differences between savanna and pocosin species in relative bark thickness and the proportion of inner bark were analyzed with independent samples *t*-tests. Differences among species in relative bark thickness and the proportion of inner bark were analyzed with one-way ANOVAs with species as a fixed factor. Relative bark thickness was Log_{10} -transformed to meet the assumption of normality. Pairwise differences were determined with *post-hoc* Gabriel tests (Field 2009). Because stem resistance to fire scales as the square of bark thickness (Peterson and Ryan 1986, Lawes *et al.* 2011a), we also calculated bark thickness squared for a

standardized stem size (5 cm diameter) of each species. The overall difference between savanna and pocosin species in bark thickness squared was analyzed with an independent samples *t*-test.

In 2011, we established 29 10 m wide belt transects that spanned the pocosin-to-savanna gradient. All trees >3 cm DBH in each transect were marked and identified to species. Due to differences in the steepness of the hydrological gradient, transect lengths varied from 24 m to 62 m across sites. To permit a relative measure of position along the gradient, each transect was divided into five equally sized plots and each plot was assigned a value based on location along the pocosin-to-savanna gradient: 0 (pocosin), 0.2, 0.4, 0.6, and 0.8 (savanna). Each individual tree was assigned the value of the plot in which it occurred, allowing us to calculate the mean location of each species along the gradient. *Quercus incana* did not occur in any transect because it tends to occur farther upland than the uppermost extent of the transects, so it was assigned a value of 1. We used the regression curve estimation function to test for a significant relationship across species between gradient location and mean relative bark thickness (of all individuals; different trees were used in the determination of gradient location and relative bark thickness). The DBH of each marked individual was measured yearly from 2011 to 2013. For the small individuals (<10 cm DBH) that are most susceptible to topkill during fire (Lawes *et al.* 2011b, VanderWeide and Hartnett 2011, Hoffmann *et al.* 2012, Lawes *et al.* 2013), we calculated the bark increment (i.e., increase in bark thickness per year) for each species by multiplying the mean ratio of bark thickness to stem radius (of individuals <10 cm DBH) by the mean increment in stem radius (mm yr^{-1}) of each species. We used the regression curve estimation function to test for a significant relationship across species between gradient location and mean bark increment. Growth data were not available for *Q. incana* and were available for only

one individual of *Q. margarettae*, so these species were excluded from the analysis of bark increment.

RESULTS

Bark thickness of all species increased with stem diameter (Figure 1). The relationship was curvilinear for most species (Table 1), indicating that relative bark thickness does

not remain constant as trees grow. This had little influence on species comparisons, however, because at the species level, the rank order of relative bark thickness was nearly consistent between small (<10 cm DBH) and large (≥ 10 cm DBH) size classes (Spearman's rho = 0.927, $P < 0.001$; Figure 2A and 2B).

Overall, savanna species had higher relative bark thickness than pocosin species (individuals <10 cm: $t_9 = 4.36$, $P = 0.002$; individ-

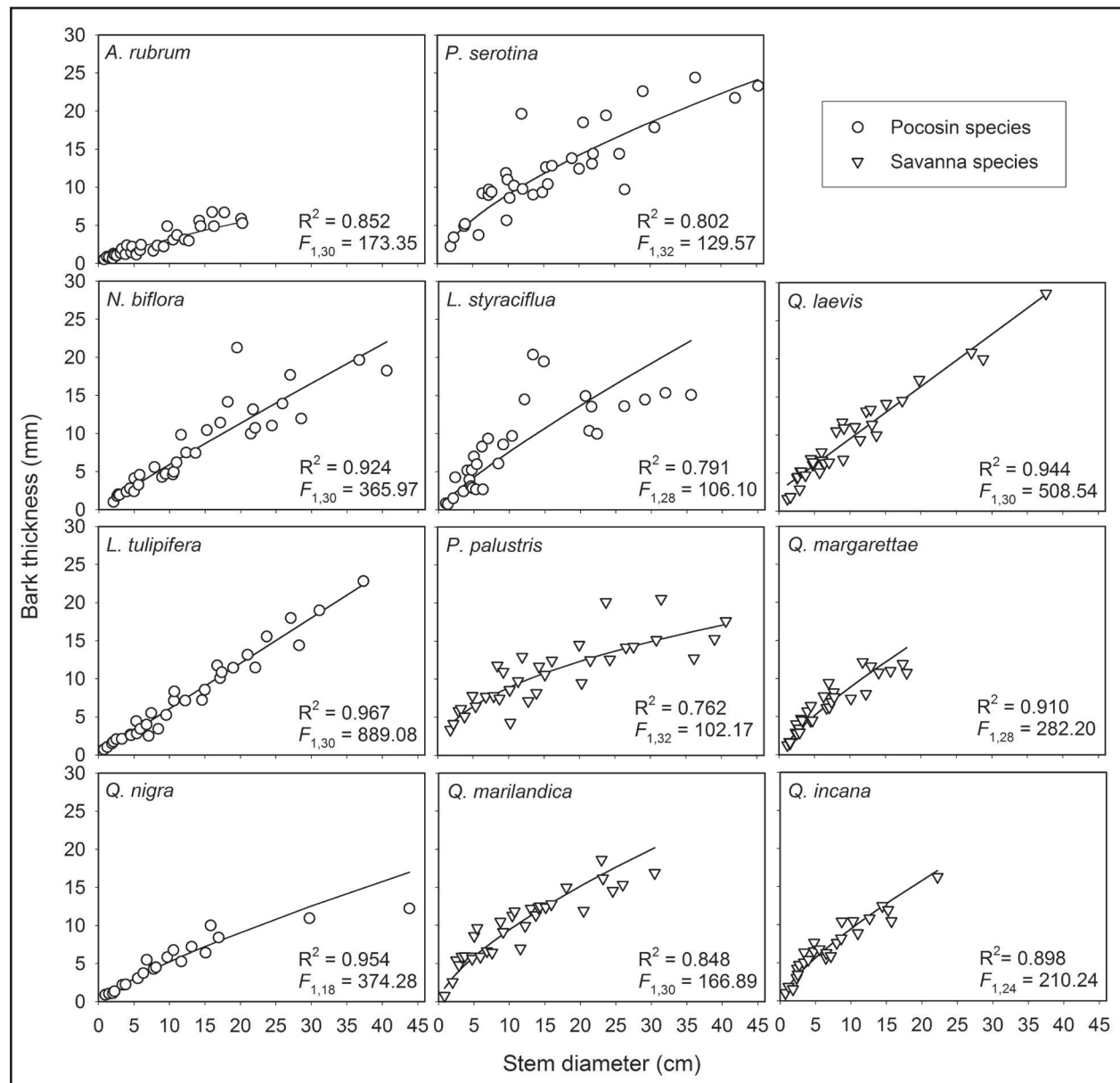


Figure 1. Relationship between stem diameter (in cm) and bark thickness (in mm) for all savanna and pocosin species. Best fit regression lines (Table 1) are shown for each species. $P < 0.001$ for all species.

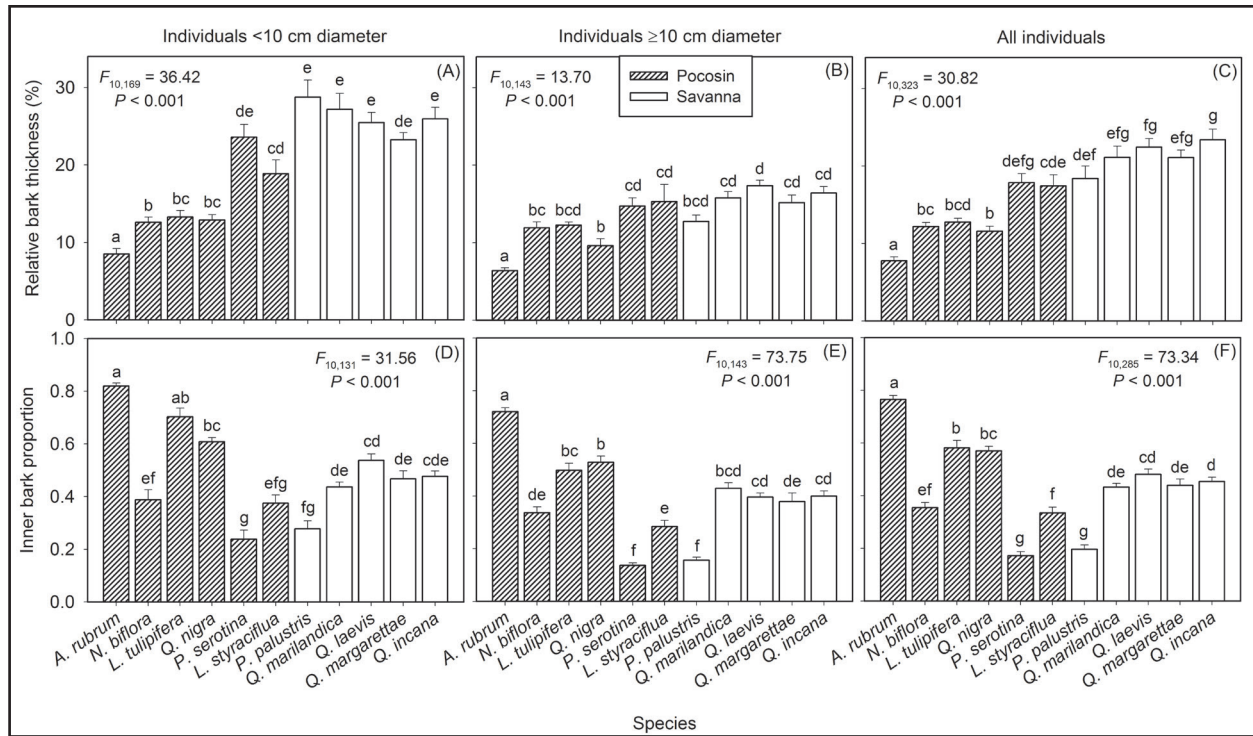


Figure 2. Mean (+SE) relative bark thickness of individuals <10 cm diameter (A), individuals ≥ 10 cm diameter (B), and all individuals (C), and the inner bark proportion of individuals <10 cm diameter (D), individuals ≥ 10 cm diameter (E), and all individuals (F) of each species. Different letters represent significant differences among species at $\alpha = 0.05$. Species are ordered from left to right according to their location along the pocosin-to-savanna gradient.

uals ≥ 10 cm: $t_9 = 2.29$, $P = 0.048$; all individuals: $t_9 = 4.26$, $P = 0.002$). Within genera, savanna oaks had higher relative bark thickness than the pocosin-dwelling *Q. nigra*, while *P. palustris* and *P. serotina* had similar relative bark thicknesses despite different habitat preferences (Figure 2). For a standardized stem size (5 cm diameter), savanna species had greater insulation (bark thickness squared) than pocosin species ($t_9 = 4.81$, $P = 0.001$); the mean square of bark thickness was approximately 2.75 times higher for savanna than pocosin species (42.85 mm² vs. 15.49 mm² for savanna and pocosin species, respectively; Table 2).

Across all species, there was a positive logarithmic relationship between relative bark thickness (of all individuals) and mean position along the pocosin-to-savanna gradient (Figure 3A). Species that occur in the ecotone

had intermediate relative bark thickness. The bark increment for individuals <10 cm DBH increased logarithmically with gradient location (Figure 3B); savanna species accumulated more bark per year than pocosin species. Across species, there was no relationship between growth rate and relative bark thickness (data not shown; $R^2 = 0.015$, $F_{1,7} = 0.108$, $P = 0.752$) or between mean position along the pocosin-to-savanna gradient and growth rate (data not shown; $R^2 = 0.033$, $F_{1,7} = 0.240$, $P = 0.639$).

The proportion of inner bark decreased with stem diameter for four savanna species and three pocosin species (Figure 4; Table 1). Savanna and pocosin species had similar proportions of inner bark (individuals <10 cm: $t_{7.08} = -0.82$, $P = 0.440$; individuals ≥ 10 cm: $t_9 = -0.63$, $P = 0.544$; all individuals: $t_9 = -0.58$, $P = 0.575$). At the species level, the rank order

Habitat	Species	N	Diameter range (cm)	Mean diameter (cm)	Mean relative BT (%)	For 5 cm DBH stem	
						BT (mm)	BT ² (mm ²)
Pocosin	<i>Acer rubrum</i>	21	0.78 to 9.69	4.44	8.51	2.13	4.53
	<i>Nyssa biflora</i>	13	2.07 to 9.41	5.09	12.61	3.15	9.94
	<i>Liriodendron tulipifera</i>	16	0.77 to 9.53	4.79	13.29	3.32	11.04
	<i>Quercus nigra</i>	12	0.95 to 9.68	4.84	12.88	3.22	10.34
	<i>Pinus serotina</i>	12	1.87 to 9.89	6.29	23.60	5.90	34.81
	<i>Liquidambar styraciflua</i>	18	1.05 to 9.11	4.74	18.88	4.72	22.28
Savanna	<i>Pinus palustris</i>	12	1.79 to 9.25	5.45	28.76	7.19	51.70
	<i>Quercus marilandica</i>	15	0.85 to 9.11	4.88	27.18	6.80	46.17
	<i>Quercus laevis</i>	20	1.18 to 9.15	5.07	25.47	6.37	40.55
	<i>Quercus margarettae</i>	22	1.18 to 7.78	4.22	23.24	5.81	33.76
	<i>Quercus incana</i>	19	0.74 to 8.70	4.48	25.94	6.49	42.06

Table 2. Sample sizes, range of stem diameters, mean diameter, and mean relative bark thickness (BT) for individuals <10 cm diameter at breast height (DBH). Because fire resistance scales as the square of bark thickness (BT²), we calculated the bark thickness and the square of bark thickness for a 5 cm DBH individual of each species. Species are in order of their location along the pocosin-to-savanna gradient.

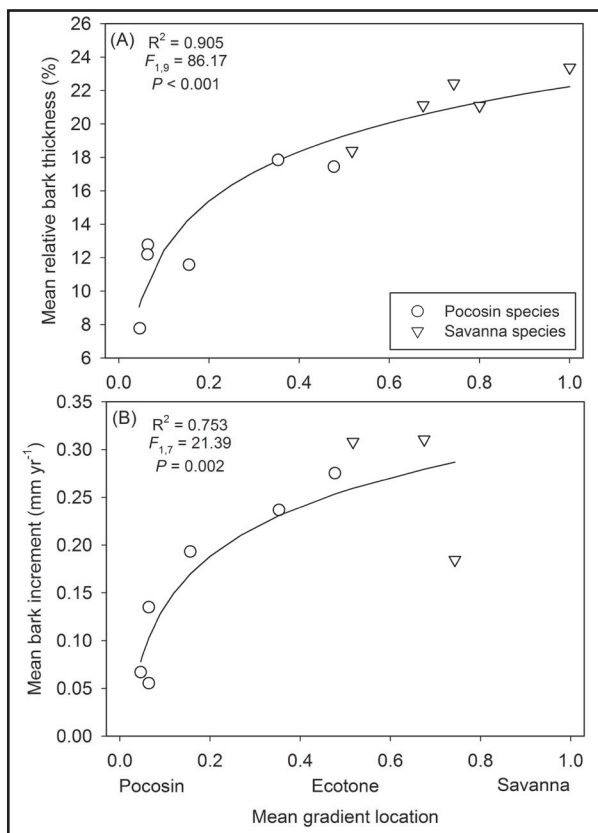


Figure 3. Relationship between mean location along the pocosin-to-savanna gradient and mean relative bark thickness (A; for all individuals) and bark increment (B; for individuals <10 cm DBH). Each point represents one species. *Q. margarettae* and *Q. incana* are not included in panel B.

of inner bark proportion was similar between small and large size classes (Spearman's rho = 0.927, $P < 0.001$; Figure 2D and 2E). The proportion of inner bark in *P. palustris* and *P. serotina* was, on average, approximately half that of other species.

DISCUSSION

Overall, savanna species had higher relative bark thickness than pocosin species, as hypothesized. Bark thickness is correlated with the time required for the cambium to reach lethal temperatures (Gashaw *et al.* 2002, van Mantgem and Schwartz 2003) and, thus, is a strong predictor of stem resistance to fire (Harmon 1984, Lawes *et al.* 2011a, Lawes *et al.* 2011b, VanderWeide and Hartnett 2011). Longleaf pine savannas burn more frequently than adjacent stream-head pocosins (Weakley and Schafale 1991, Frost 1995, Stambaugh *et al.* 2011), so higher relative bark thickness should be beneficial for surviving more frequent fire. In fact, the difference in relative bark thickness between savanna and pocosin species was larger—26% vs. 15%—when considering only the smallest individuals (i.e., <10 cm diameter), which are most susceptible

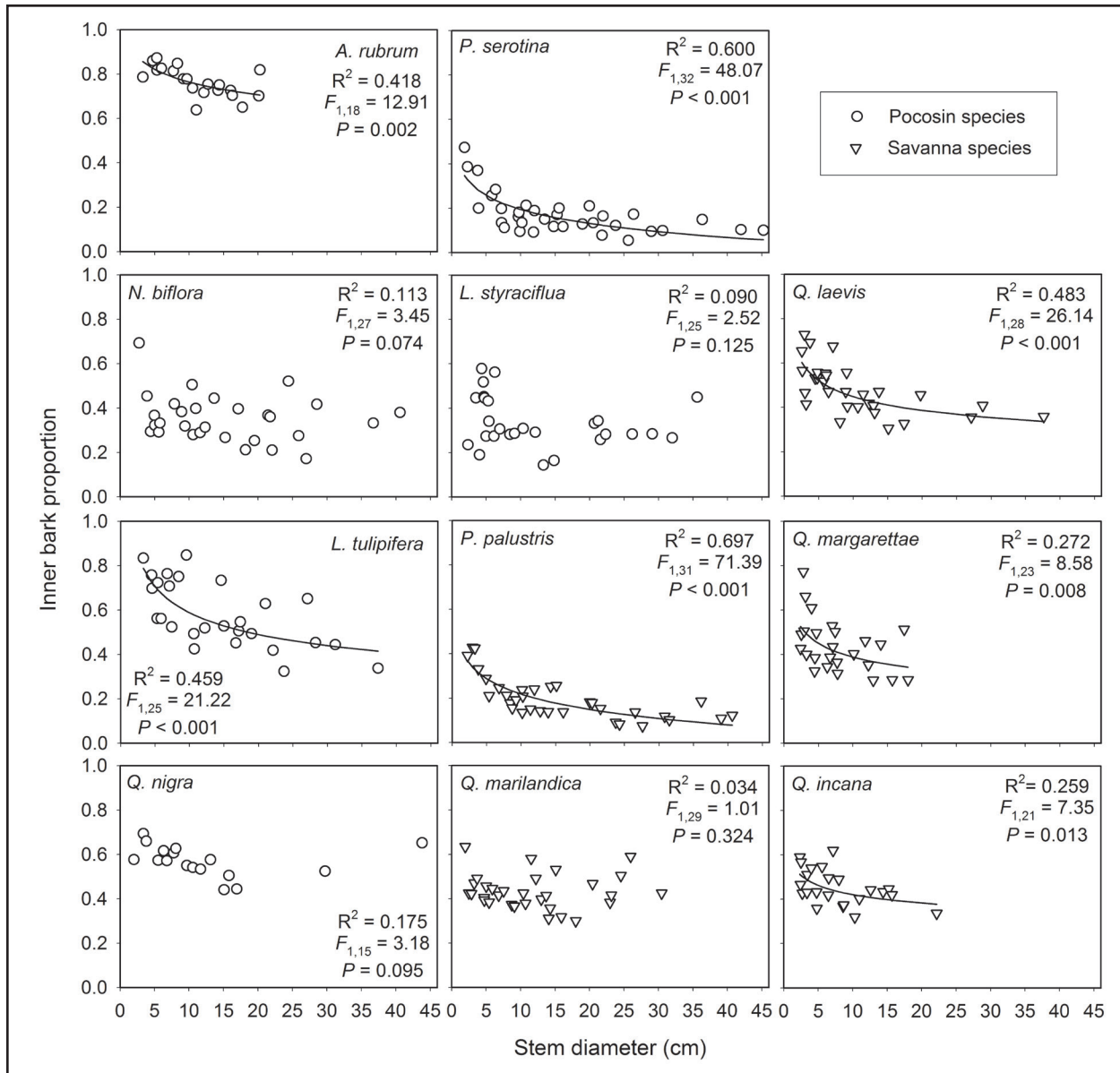


Figure 4. Relationship between stem diameter and the proportion of inner bark for all savanna and pocosin species. Best fit regression lines (Table 1) are shown for significant relationships.

to topkill during fire (Lawes *et al.* 2011b, VanderWeide and Hartnett 2011, Hoffmann *et al.* 2012, Lawes *et al.* 2013), rather than all individuals. Given this difference, and the fact that stem resistance to fire scales as the square of bark thickness (Peterson and Ryan 1986, Lawes *et al.* 2011a), individuals of pocosin species must be approximately 1.6 times larger, on average, than individuals of savanna species to accumulate enough bark to reach

the same level of fire resistance. Our results support other studies that have reported higher relative bark thickness in savanna trees compared to forest trees (Hoffmann *et al.* 2003, Hoffmann *et al.* 2009, Lawes *et al.* 2011a).

Using a more continuous characterization of species habitat, we found that relative bark thickness was related to the mean location of species along the pocosin-to-savanna gradient, as hypothesized. The direction of

causation, however, is not clear because the distribution of our study species may be strongly influenced by water and nutrient availability (Donovan *et al.* 2000), as well as by the direct effects of fire. The decline in soil moisture along the pocosin-to-savanna gradient (J. Schafer, unpublished data) selects for drought tolerance, while the increase in fire frequency selects for thick bark. Thus, due to past environmental filtering, there is a correlation between habitat preference and bark thickness. The higher fire frequency in savannas could select for thicker bark in drought-tolerant species, while drought-tolerant species with inherently thicker bark could be more likely to survive frequent fires due to the protective effects of thick bark (Harmon 1984, Lawes *et al.* 2011b, Catry *et al.* 2012, Hoffmann *et al.* 2012). In addition, among small individuals of oak species, those that prefer dry habitats have greater investment in bark thickness than those that prefer wet habitats (Schwilk *et al.* 2013). Regardless of the mechanisms that control species distributions, greater bark accumulation by ecotone and savanna species indicates that individuals of these species should become fire resistant more quickly than pocosin species.

Contrary to our hypothesis, we found no difference in the proportion of inner bark between savanna and pocosin species overall. We expected savanna species to have a greater relative investment in inner bark because heat is transferred through outer bark faster than through inner bark (van Mantgem and Schwartz 2003) and a higher proportion of inner bark may reduce the susceptibility of topkill. This expectation, however, overlooks tradeoffs and associations between bark traits and functions (Rosell *et al.* 2013, Poorter *et al.* 2014) as well as potential differences in the cost of producing and maintaining these two bark components. Specifically, inner bark is a living tissue that is likely to incur substantial maintenance costs, so ultimately there may be little or no net benefit of greater relative in-

vestment in inner bark. Furthermore, relative allocation to inner versus outer bark may be limited by phylogenetic constraints because outer bark thickness is a somewhat conserved trait in oaks (Cavender-Bares *et al.* 2004b). This is supported in our study: the oak species all had high inner bark proportions, while the pines had low inner bark proportions, regardless of habitat.

Despite the lack of a difference in the proportion of inner bark between savanna and pocosin species, the greater insulation provided by inner bark (van Mantgem and Schwartz 2003, Scholz *et al.* 2007) may be important when considering small individuals, which are more susceptible to topkill (Hoffmann *et al.* 2012). Within species, there was a widespread trend for small stems to have a higher proportion of inner bark than larger stems. Regardless of whether this trend is the result of size-specific differences in natural selection or simply allometry, the greater relative investment in inner bark should benefit stems when they are most vulnerable to fire.

Stream-head pocosin species tended to have relatively thin bark, which suggests that, for stems of a given diameter, pocosin species will suffer greater topkill during fire than savanna species (Lawes *et al.* 2011a, Hoffmann *et al.* 2012). Differences in the proportion of inner bark among species, however, may mediate the influence of bark thickness on stem survival. Nonetheless, our results suggest that species' distributions along the pocosin-to-savanna gradient may be influenced by relative bark thickness. Pocosin species accumulate bark more slowly than savanna species, but a fire return interval of 7 to 50 years (Frost 1995) may allow individuals of pocosin species to grow large enough, increasing in both height and diameter (Lawes *et al.* 2011b), to accumulate thick enough bark to survive fire. A longer fire-free interval, however, may lead to higher fuel loads and more intense fires, which can cause greater stem damage (Bova and Dickinson 2005) and mortality (Glitzen-

stein *et al.* 1995, Adie *et al.* 2011) regardless of stem diameter and bark thickness. On the other hand, changes in species composition over a long fire-free interval (Gilliam and Platt 1999) may reduce fire intensity due to changes in vegetation structure and fuel flammability (van Wilgen *et al.* 1990, Behm *et al.* 2004).

Regardless, fire suppression may contribute to hardwood establishment in savannas (Waldrop *et al.* 1992, Gilliam and Platt 1999, Van Lear *et al.* 2005) by allowing pocosin species to reach a diameter (Chatziefstratiou *et al.* 2013) or accumulate bark thickness sufficient for surviving future fires.

ACKNOWLEDGEMENTS

The authors thank A. Bova for helpful discussions, S. Smith for statistical advice, and J. Gray and S. Pulsipher for logistical support. This manuscript was improved by comments from two anonymous reviewers and an associate editor. This research was supported by a cooperative agreement between the US Army Engineer Research and Development Center and North Carolina State University (W9132T-11-2-0007 to W. Hoffmann).

LITERATURE CITED

- Adie, H., S. Richert, K.P. Kirkman, and M.J. Lawes. 2011. The heat is on: frequent high intensity fire in bracken (*Pteridium aquilinum*) drives mortality of the sprouting tree *Protea caffra* in temperate grasslands. *Plant Ecology* 212: 2013–2022. doi: [10.1007/s11258-011-9945-8](https://doi.org/10.1007/s11258-011-9945-8)
- Behm, A.L., M.L. Duryea, A.J. Long, and W.C. Zipperer. 2004. Flammability of native understory species in pine flatwood and hardwood hammock ecosystems and implications for the wildland-urban interface. *International Journal of Wildland Fire* 13: 355–365. doi: [10.1071/WF03075](https://doi.org/10.1071/WF03075)
- Bova, A.S., and M.B. Dickinson. 2005. Linking surface-fire behavior, stem heating, and tissue necrosis. *Canadian Journal of Forest Research* 35: 814–822. doi: [10.1139/x05-004](https://doi.org/10.1139/x05-004)
- Boyer, W.D. 1990. *Pinus palustris* Mill. longleaf pine. Pages 405–412 in: R.M. Burns and B.H. Honkala, technical coordinators. *Silvics of North America. Volume 1. Conifers*. US Department of Agriculture, Forest Service Agriculture Handbook 654, Washington, D.C., USA.
- Catry, F.X., F. Moreira, J.G. Pausas, P.M. Fernandes, F. Rego, E. Cardillo, and T. Curt. 2012. Cork oak vulnerability to fire: the role of bark harvesting, tree characteristics and abiotic factors. *PLoS ONE* 7(6): e39810. doi: [10.1371/journal.pone.0039810](https://doi.org/10.1371/journal.pone.0039810)
- Cavender-Bares, J., D.D. Ackerly, D.A. Baum, and F.A. Bazzaz. 2004b. Phylogenetic overdispersion in Floridian oak communities. *American Naturalist* 163: 823–843. doi: [10.1086/386375](https://doi.org/10.1086/386375)
- Cavender-Bares, J., K. Kitajima, and F.A. Bazzaz. 2004a. Multiple trait associations in relation to habitat differentiation among 17 Floridian oak species. *Ecological Monographs* 74: 635–662. doi: [10.1890/03-4007](https://doi.org/10.1890/03-4007)
- Chatziefstratiou E.K., G. Bohrer, A.S. Bova, R. Subramanian, R.P.M. Frasson, A. Scherzer, B.W. Butler, and M.B. Dickinson. 2013. FireStem2D—a two-dimensional heat transfer model for simulating tree stem injury in fires. *PLoS ONE* 8(7): e70110. doi: [10.1371/journal.pone.0070110](https://doi.org/10.1371/journal.pone.0070110)
- Donovan, L.A., J.B. West, and K.W. McLeod. 2000. *Quercus* species differ in water and nutrient characteristics in a resource-limited fall-line sandhill habitat. *Tree Physiology* 20: 929–936. doi: [10.1093/treephys/20.14.929](https://doi.org/10.1093/treephys/20.14.929)

- Field, A. 2009. Discovering statistics using SPSS. Third edition. SAGE Publications, London, England, United Kingdom.
- Frost, C.C. 1995. Presettlement fire regimes in southeastern marshes, peatlands, and swamps. *Proceedings of the Tall Timbers Fire Ecology Conference* 19: 39–60.
- Gashaw, M., A. Michelsel, I. Friis, M. Jensen, S. Demissew, and Z. Woldu. 2002. Post-fire regeneration strategies and tree bark resistance to heating in frequently burning tropical savanna woodlands and grasslands in Ethiopia. *Nordic Journal of Botany* 22: 19–33. doi: [10.1111/j.1756-1051.2002.tb01615.x](https://doi.org/10.1111/j.1756-1051.2002.tb01615.x)
- Gignoux, J., J. Clobert, and J.C. Menaut. 1997. Alternative fire resistance strategies in savanna trees. *Oecologia* 110: 576–583. doi: [10.1007/s004420050198](https://doi.org/10.1007/s004420050198)
- Gilliam, F.S., and W.J. Platt. 1999. Effects of long-term fire exclusion on tree species composition and stand structure in an old-growth *Pinus palustris* (longleaf pine) forest. *Plant Ecology* 140: 15–26. doi: [10.1023/A:1009776020438](https://doi.org/10.1023/A:1009776020438)
- Glitzenstein, J.S., W.J. Platt, and D.R. Strong. 1995. Effects of fire regime and habitat on tree dynamics in north Florida longleaf pine savannas. *Ecological Monographs* 65: 441–476. doi: [10.2307/2963498](https://doi.org/10.2307/2963498)
- Harmon, M.E. 1984. Survival of trees after low-intensity surface fires in Great Smoky Mountains National Park. *Ecology* 65: 796–802. doi: [10.2307/1938052](https://doi.org/10.2307/1938052)
- Higgins, S.I., W.J. Bond, H. Combrink, J.M. Craine, E.C. February, N. Govender, K. Lannas, G. Moncreiff, and W.S.W. Trollope. 2012. Which traits determine shifts in the abundance of tree species in a fire-prone savanna? *Journal of Ecology* 100: 1400–1410. doi: [10.1111/j.1365-2745.2012.02026.x](https://doi.org/10.1111/j.1365-2745.2012.02026.x)
- Hoffmann, W.A., R. Adasme, M. Haridasan, M.T. de Carvalho, E.L. Geiger, M.A.B. Pereira, S.G. Gotsch, and A.C. Franco. 2009. Tree topkill, not mortality, governs the dynamics of savanna-forest boundaries under frequent fire in central Brazil. *Ecology* 90: 1326–1337. doi: [10.1890/08-0741.1](https://doi.org/10.1890/08-0741.1)
- Hoffmann, W.A., E.L. Geiger, S.G. Gotsch, D.R. Rossatto, L.C.R. Silva, O.L. Lau, M. Haridasan, and A.C. Franco. 2012. Ecological thresholds at the savanna-forest boundary: how plant traits, resources and fire govern the distribution of tropical biomes. *Ecology Letters* 15: 759–768. doi: [10.1111/j.1461-0248.2012.01789.x](https://doi.org/10.1111/j.1461-0248.2012.01789.x)
- Hoffmann, W.A., B. Orthen, and P.K.V. do Nascimento. 2003. Comparative fire ecology of tropical savanna and forest trees. *Functional Ecology* 17: 720–726. doi: [10.1111/j.1365-2435.2003.00796.x](https://doi.org/10.1111/j.1365-2435.2003.00796.x)
- Hoffmann, W.A., and O.T. Solbrig. 2003. The role of topkill in the differential response of savanna woody species to fire. *Forest Ecology and Management* 180: 273–286. doi: [10.1016/S0378-1127\(02\)00566-2](https://doi.org/10.1016/S0378-1127(02)00566-2)
- Jackson, J.F., D.C. Adams, and U.B. Jackson. 1999. Allometry of constitutive defense: a model and a comparative test with tree bark and fire regime. *American Naturalist* 153: 614–632. doi: [10.1086/303201](https://doi.org/10.1086/303201)
- Jones, J.L., B.W. Webb, D. Jimenez, J. Reardon, and B. Butler. 2004. Development of an advanced one-dimensional stem heating model for application in surface fires. *Canadian Journal of Forest Research* 34: 20–30. doi: [10.1139/x03-187](https://doi.org/10.1139/x03-187)
- Lawes, M.J., H. Adie, J. Russell-Smith, B. Murphy, and J.J. Midgley. 2011b. How do small savanna trees avoid stem mortality by fire? The roles of stem diameter, height and bark thickness. *Ecosphere*. 2(4): art42. doi: [10.1890/ES10-00204.1](https://doi.org/10.1890/ES10-00204.1)

- Lawes, M.J., A. Richards, J. Dathe, and J.J. Midgley. 2011a. Bark thickness determines fire resistance of selected tree species from fire-prone tropical savanna in north Australia. *Plant Ecology* 212: 2057–2069. doi: [10.1007/s11258-011-9954-7](https://doi.org/10.1007/s11258-011-9954-7)
- Lawes, M.J., J.J. Midgley, and P.J. Clarke. 2013. Costs and benefits of relative bark thickness in relations to fire damage: a savanna/forest contrast. *Journal of Ecology* 101: 517–524. doi: [10.1111/1365-2745.12035](https://doi.org/10.1111/1365-2745.12035)
- Michaletz, S.T., E.A. Johnson, and M.T. Tyree. 2012. Moving beyond the cambium necrosis hypothesis of post-fire tree mortality: cavitation and deformation of xylem in forest fires. *New Phytologist* 194: 257–263. doi: [10.1111/j.1469-8137.2011.04021.x](https://doi.org/10.1111/j.1469-8137.2011.04021.x)
- Midgley, J.J., M.J. Lawes, and S. Chamaille-Jammes. 2010. Savanna woody plant dynamics: the role of fire and herbivory, separately and synergistically. *Australian Journal of Botany* 58: 1–11. doi: [10.1071/BT09034](https://doi.org/10.1071/BT09034)
- Pausas, J.G. 2014. Bark thickness and fire regime. *Functional Ecology*. <<http://onlinelibrary.wiley.com/doi/10.1111/1365-2435.12372/abstract;jsessionid=33CE4D51D5A11BD7ADC5565A308325D3.f02t02>>. Accessed 27 Nov 2014. doi: [10.1111/1365-2435.12372](https://doi.org/10.1111/1365-2435.12372)
- Peterson, D.L., and K.C. Ryan. 1986. Modeling of post-fire conifer mortality for long-range planning. *Environmental Management* 10: 797–808. doi: [10.1007/BF01867732](https://doi.org/10.1007/BF01867732)
- Poorter, L., A. McNeil, V.-H. Hurtado, H.H.T. Prins, and F.E. Putz. 2014. Bark traits and life-history strategies of tropical dry- and moist forest trees. *Functional Ecology* 28: 232–242. doi: [10.1111/1365-2435.12158](https://doi.org/10.1111/1365-2435.12158)
- Rosell, J.A., S. Gleason, R. Méndez-Alonzo, Y. Chang, and M. Westoby. 2013. Bark functional ecology: evidence for tradeoffs, functional coordination, and environment producing bark diversity. *New Phytologist* 201: 486–497. doi: [10.1111/nph.12541](https://doi.org/10.1111/nph.12541)
- Rothermel, R.C. 1972. A mathematical model for predicting fire spread in wildland fuels. USDA Forest Service Research Paper INT-115, Intermountain Research Station, Ogden, Utah, USA.
- Schafale, M.P., and A.S. Weakley. 1990. Classification of the natural communities of North Carolina: third approximation. North Carolina Natural Heritage Program, Division of Parks and Recreation, Department of Environment, Health, and Natural Resources, Raleigh, North Carolina, USA.
- Scholz, F.G., S.J. Bucci, G. Goldstein, F.C. Meinzer, A.C. Franco, and F. Miralles-Wilhelm. 2007. Biophysical properties and functional significance of stem water storage tissues in Neotropical savanna trees. *Plant Cell and Environment* 30: 236–248. doi: [10.1111/j.1365-3040.2006.01623.x](https://doi.org/10.1111/j.1365-3040.2006.01623.x)
- Schwilk D.W., M.S. Gaetani, and H.M. Poulos. 2013. Oak bark allometry and fire survival strategies in the Chihuahuan Desert sky islands, Texas, USA. *PLoS ONE* 8(11): e79285. doi: [10.1371/journal.pone.0079285](https://doi.org/10.1371/journal.pone.0079285)
- Sorrie, B.A., J. Bracey Gray, and P.J. Crutchfield. 2006. The vascular flora of the longleaf pine ecosystem of Fort Bragg and Weymouth Woods, North Carolina. *Castanea* 71: 129–161. doi: [10.2179/05-02.1](https://doi.org/10.2179/05-02.1)
- Stambaugh, M.C., R.P. Guyette, and J.M. Marschall. 2011. Longleaf pine (*Pinus palustris* Mill.) fire scars reveal new details of a frequent fire regime. *Journal of Vegetation Science* 22: 1094–1104. doi: [10.1111/j.1654-1103.2011.01322.x](https://doi.org/10.1111/j.1654-1103.2011.01322.x)
- Stephens, S.L., and W.J. Libby. 2006. Anthropogenic fire and bark thickness in coastal and island pine populations from Alta and Baja California. *Journal of Biogeography* 33: 648–652. doi: [10.1111/j.1365-2699.2005.01387.x](https://doi.org/10.1111/j.1365-2699.2005.01387.x)
- Uhl, C., and J.B. Kauffman. 1990. Deforestation, fire susceptibility, and potential tree responses to fire in the eastern Amazon. *Ecology* 71: 437–449. doi: [10.2307/1940299](https://doi.org/10.2307/1940299)

- USDA NRCS [US Department of Agriculture, National Resources Conservation Service]. 2007. Soil survey geographic (SSURGO) database for Fort Bragg, North Carolina, Cumberland and Hoke Counties. <<http://websoilsurvey.nrcs.usda.gov/>>. Accessed 10 Sep 2011.
- Van Lear, D.H., W.D. Carroll, P.R. Kapeluck, and R. Johnson. 2005. History and restoration of the longleaf pine-grassland ecosystem: implications for species at risk. *Forest Ecology and Management* 211: 150–165. doi: [10.1016/j.foreco.2005.02.014](https://doi.org/10.1016/j.foreco.2005.02.014)
- van Mantgem, P., and M. Schwartz. 2003. Bark heat resistance of small trees in Californian mixed conifer forests: testing some model assumptions. *Forest Ecology and Management* 178: 341–352. doi: [10.1016/S0378-1127\(02\)00554-6](https://doi.org/10.1016/S0378-1127(02)00554-6)
- van Wilgen, B.W., K.B. Higgins, and D.U. Bellstedt. 1990. The role of vegetation and fuel chemistry in excluding fire from forest patches in the fire-prone fynbos shrublands of South Africa. *Journal of Ecology* 78: 210–222. doi: [10.2307/2261046](https://doi.org/10.2307/2261046)
- VanderWeide, B.L., and D.C. Hartnett. 2011. Fire resistance of tree species explains historical gallery forest community composition. *Forest Ecology and Management* 261: 1530–1538. doi: [10.1016/j.foreco.2011.01.044](https://doi.org/10.1016/j.foreco.2011.01.044)
- Vines, R.G. 1968. Heat transfer through bark, and the resistance of trees to fire. *Australian Journal of Botany* 16: 499–514. doi: [10.1071/BT9680499](https://doi.org/10.1071/BT9680499)
- Waldrop, T.A., D.L. White, and S.M. Jones. 1992. Fire regimes for pine-grassland communities in the southeastern United States. *Forest Ecology and Management* 47: 195–210. doi: [10.1016/0378-1127\(92\)90274-D](https://doi.org/10.1016/0378-1127(92)90274-D)
- Weakley, A.S., and M.P. Schafale. 1991. Classification of pocosins of the Carolina coastal plain. *Wetlands* 11: 355–375. doi: [10.1007/BF03160756](https://doi.org/10.1007/BF03160756)