

Why does longleaf pine have low susceptibility to southern pine beetle?

Sharon Martinson, Richard W. Hofstetter, and Matthew P. Ayres

Abstract: Pine forests throughout the world are subject to disturbance from tree-killing bark beetles, but pine species differ in their susceptibilities. In the southeastern United States, *Pinus palustris* Mill. suffers far less mortality from the southern pine beetle, *Dendroctonus frontalis* Zimmermann, than do its sympatric congeners. We tested the commonly invoked hypothesis that *P. palustris* has relatively low susceptibility because it has higher oleoresin flow than other pines, especially *Pinus taeda* L. However, seven studies in three states over 6 years refuted the hypothesis that *P. palustris* and *P. taeda* differ in their constitutive resin flow or in their capacity to replace resin depleted by either experimental wounding or natural beetle attacks. Additionally, surveys of natural beetle attacks revealed that *P. taeda* and *P. palustris* were equally likely to be attacked and killed when they cooccurred in front of growing infestations. Thus, the relative susceptibility of these two species changes with the spatial scale at which they are mixed, and the strong landscape-scale pattern of low mortality in *P. palustris* is not because individual trees are physiologically less susceptible. Ultimately, the conspicuous differential impact of *D. frontalis* on *P. taeda* and *P. palustris* may be the product of coevolution between tree defenses and beetle behavior.

Résumé : Partout à travers le monde, les forêts de pin sont sujettes aux perturbations causées par les scolytes qui tuent l'écorce des arbres mais les espèces de pin diffèrent en susceptibilité. Dans le sud-est des États-Unis, *Pinus palustris* Mill. subit beaucoup moins de mortalité due au dendroctone du pin, *Dendroctonus frontalis* Zimmermann, que ses congénères sympatriques. Nous avons testé l'hypothèse généralement invoquée voulant que la susceptibilité de *P. palustris* soit relativement faible à cause de ses écoulements d'oléorésine qui sont plus importants que ceux des autres pins, particulièrement *Pinus taeda* L. Cependant, sept études réalisées dans trois États sur une période de 6 ans ont réfuté l'hypothèse selon laquelle *P. palustris* diffère de *P. taeda* à propos de son écoulement naturel de résine ou de sa capacité à remplacer la résine qui a été épuisée soit par des blessures expérimentales, soit par des attaques naturelles de scolytes. De plus, les relevés d'attaques naturelles de dendroctone ont révélé que *P. taeda* et *P. palustris* avaient la même chance d'être attaqués et tués lorsqu'ils sont présents ensemble à l'avant d'un front d'infection en progression. Par conséquent, la susceptibilité relative de ces deux espèces change selon l'échelle spatiale à laquelle elles sont mélangées et la forte tendance, à l'échelle du paysage, à une faible mortalité chez *P. palustris* n'est pas due au fait que les arbres soient physiologiquement moins susceptibles. Ultimement, la différence évidente d'impact de *D. frontalis* chez *P. taeda* et *P. palustris* pourrait être le résultat de la coévolution entre les mécanismes de défense des arbres et le comportement des scolytes.

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Introduction

It has long been thought that plants and herbivores are engaged in a coevolutionary arms race involving the reciprocal evolution of plant defenses and herbivore counteradaptations (Thompson 1982). With respect to the evolution of plant defenses, Ehrlich and Raven (1964) emphasized the importance of stepwise decreases in plant susceptibility associated with speciation events. An alternative model is that related species share a common defense mechanism with graded variation within and among species in the quantitative expression of the defense trait (e.g., Palo 1984; Ikonen et al. 2001). Distinguishing between these possibilities would aid in understanding the ultimate causes of interspecific differences in patterns of herbivory and may be of additional practical value to understanding the mechanisms of plant de-

fense when the plants are integral to managed ecosystems with value to humans (Schultz 1988; Gould 1991).

In forests of southeastern North America, there have been strong interactions for millennia between native *Pinus* species and the southern pine beetle, *Dendroctonus frontalis* Zimmermann (Coleoptera: Curculionidae: Scolytinae; Farrell et al. 1992; Kelley and Farrell 1998). The strength of these evolutionary interactions is potentially very strong because reproduction of the herbivore requires death of the host plant (Raffa and Berryman 1983; Thompson 1986), and large-scale mortality of pines from *D. frontalis* is common, at least in contemporary forests (Price et al. 1997). *Dendroctonus frontalis* can attack and kill all pine species in its range, yet pine species differ in the degree of mortality caused by beetle attacks (St. George and Beal 1929; Wood 1982). Most *D. frontalis* populations occur in the forested coastal

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plains and uplands of the southeastern United States, which were historically dominated by longleaf pine, *Pinus palustris* Mill. ($\approx 37 \times 10^6$ ha, >85% of these pine forests; Frost 1993). The southeast was largely deforested ca. 1850–1930, and *P. palustris* now occupies <3% of its original area primarily because loblolly pine, *Pinus taeda* L., was favored for regeneration (Frost 1993). *Pinus taeda* constitutes over one-half of the current forests and suffers the greatest mortality from *D. frontalis* (Baker and Langdon 1990). For example, during recent epidemics in Louisiana and Alabama, areas of forest with *P. taeda* sustained 3–18 times more local infestations and 3–116 times more tree mortality than equivalent areas of forest with *P. palustris* (Friedenberg et al. 2007).

The most common explanation for low mortality of *P. palustris* from *D. frontalis* has been that it exudes copious resin in response to beetle attacks (Wakeley 1954; Blanche et al. 1983). Resin, a mixture of carbon-based monoterpenes and resin acids, is the main defense of Pinaceae against myriad pests and pathogens (Berryman 1972; Langenheim 2003). In particular, resin is the primary, efficacious defense against bark beetles, where it has been shown to physically impede beetle entry into trees (Steele et al. 1995; Klepzig et al. 2005). In trees with high resin flow, per capita reproduction of *D. frontalis* is low because resin also interferes with oviposition behavior and sometimes kills attacking adults (Cook and Hain 1987; Reeve et al. 1995). Resin flow varies widely within and among pine species because of both high genetic variance and high phenotypic plasticity (Mason 1971; Roberds et al. 2003).

The premise that *P. palustris* has higher resin flow than *P. taeda* has been based mainly upon three lines of evidence. Throughout the 19th and early 20th centuries, *P. palustris* were favored by the naval stores industry as a source of resin for making turpentine, pitch, rosin, and numerous other products (Wahlenberg 1946; Clements 1974). Presumably, the volume of resin that could be harvested from *P. palustris* exceeded that of many other local pine species (Butler 1998; Earley 2004). A second, empirical line of evidence comes from Hodges et al. (1977, 1979) who reported one study showing that resin flow from standardized wounds was 50%–100% higher for *P. palustris* than for *P. taeda*, *Pinus echinata* Mill. (shortleaf pine), or *Pinus elliotii* Engelm. (slash pine) (mean total volume of resin over 72 h of 18, 12, 9, and 11 mL, respectively). A third, less-direct line of evidence comes from host tree choice of red-cockaded woodpeckers (*Picoides borealis* Vieillot); they choose resinous trees for building nests, because the resin protects nests against intruders (Ross et al. 1997). These birds tend to nest in *P. palustris*, and the nest trees have higher resin flow than the surrounding trees (Conner et al. 1998).

The objectives of our study were to confirm that resin flow is generally higher in *P. palustris* than in other pines, especially *P. taeda*, and then to evaluate if the differences in resin flow were sufficient to explain observed differences in mortality from *D. frontalis*. We compared resin flow of *P. taeda* and *P. palustris* across multiple years, seasons, and locations; when possible, we also included measures of *P. echinata* and *P. elliotii*. Collectively, these species comprise the majority of pines within contemporary forests of the southeastern United States (Hansen et al. 1992; Smith et al. 2003) and, currently, tend to be favored for silviculture and

forest restoration (Alavalapati et al. 2002). We compared pine species with respect to both constitutive levels of resin flow and to their capacity to refill the resin duct system following depletion of the system from wounding (as happens during a bark beetle attack). We were also able to compare the dynamics of resin depletion in *P. taeda* versus *P. palustris* during natural attacks by *D. frontalis*.

To control for effects of site, we made comparisons of resin flow from sites where *P. taeda* and *P. palustris* were growing interspersed (mixed-species sites). Because initial studies within mixed-species sites failed to show higher resin flow in *P. palustris* than *P. taeda*, we went on to test the following scenario, which could explain reduced susceptibility of *P. palustris* as a result of silvicultural practices.

The majority of pines within contemporary forests of the southeastern United States occur in single species stands that are distributed nonrandomly across the landscape. Most forests are managed to match pine species with the sites where they grow relatively quickly (high site index), and (or) where they historically occurred (Baker 1950). When a tree is planted on a site that is considered by silviculturalists and soil scientists to be suitable for that species, it is referred to as “on-site” (Wakeley 1954; Schumacher and Coile 1960). Conversely, “off-site” refers to a situation where the tree species occurs on a site that is regarded as a poor match, perhaps because of expected problems with pests or other sources of premature mortality, because that site historically was dominated by a different species, or because other candidate tree species tend to provide better yield on those sites.

Trees that are planted on-site are generally expected to be more vigorous, grow faster, live longer, and be less susceptible to pests and diseases than trees growing off-site (Boyer 1990; Dale 1996). Alternatively, the growth–differentiation balance hypothesis (GDBH; Loomis 1932; Herms and Mattson 1992) predicts that secondary metabolism (e.g., resin production) will tend to be lowest on sites where trees grow most rapidly. In this case, pine species that are propagated on sites that permit the highest growth would also tend to be most susceptible to pests, not because of genetic differences but because of environmental effects on tree growth and physiology (Lorio 1986). To distinguish between these hypotheses, we compared resin flow of *P. taeda* and *P. palustris* with a nested sampling design that subsampled trees within replicated, age-matched, monotypic stands of each species that were randomly drawn from the population of such stands within a managed forest (USDA Forest Service ranger district of $\approx 79\,000$ ha). Additionally, we compared stands of *P. taeda* and *P. palustris* that were specifically drawn from sites regarded as on-site and off-site for each species.

Methods

Research involved nine different studies that were conducted within US national forests in Alabama (Oakmulgee ranger district of Talladega National Forest), Louisiana (Calcasieu ranger district of Kisatchie National Forest), and Mississippi (common garden planting of South-wide Seed Source Study near Saucier, Miss.). With the exception of the Mississippi samples, study sites were located with respect to “stands,” which are USDA Forest Service management units

that tend to be internally homogenous with respect to age of canopy trees, landform, soil, and land-use history. Within pine stands in these forests, the canopy trees are typically dominated by a single tree species, but occasionally two or more codominant species are interspersed within a stand.

Overview of resin sampling

The basic objective was to quantify the flow of preformed (constitutive) resin from the vertical resin duct system to wounds of the inner bark (Lorio 1988). Methods followed previous studies of resin defenses in conifers (Lorio et al. 1990; Nebeker et al. 1992; Dunn and Lorio 1993; Conner et al. 1998; Lombardero et al. 2000) with some variations that are described within the details of individual studies. A 0.5 in. diameter punch (1 in. = 2.54 cm; 127 mm²) was used to remove the outer bark and phloem without scoring the xylem, creating a measurement wound. The resin that flowed from these measurement wounds during the next 24 h was collected and weighed. On each sampling occasion, we collected one to four samples from each tree (depending on the study) at 1.5–2 m height, with maximal separation to obviate interference between samples (Roberds and Strom 2006).

To measure the capacity for induced resin production, we first quantified the baseline resin flow for each study tree with the above techniques then depleted the local preformed resin on one side of the tree by exposing two horizontal swaths of xylem (5 cm × 20 cm at 1.5 m height, with one wound 30 cm above the other; after Ruel et al. 1998; Lombardero et al. 2000) from which the resin flowed freely. On subsequent days, we remeasured the resin flow from two measurement wounds on each side of each study tree (depleted and control side). We also included measures of resin flow from trees that were not subjected to the depletion treatments (as true controls). Present and previous studies indicated that resin flow on the control side of trees was generally unaffected by the wounding treatment (by comparing them with true control trees), justifying analyses that quantified resin refilling capacity as the difference between treatment and control sides of each tree. This is expected because the resin is synthesized within, and distributed from, resin ducts that run vertically within the sapwood.

The following applies to studies that involved multiple sites within the same study. On each day of sampling, establishment of measurement wounds commenced 2 h postdawn and was completed within 9 h. We randomly determined which pine species to wound first and then alternated between stands of *P. taeda* and *P. palustris* to preclude confounding effects from time of day (Nebeker et al. 1992). The following day, we collected resin in the same order so that the sampling duration was constant across sites. For larger studies that required 2 days to establish measurement wounds in all the study stands, we sampled one-half of the stands for each species on two subsequent days and the other half of the stands on the following 2 days. In these cases, we sampled some trees on both days to test for effects of day on resin flow (and standardize for these effects if necessary).

Resin flow measurements tend to follow a gamma distribution (Roberds et al. 2003), so data were square-root transformed prior to statistical analyses to satisfy assumptions of

normality and homoscedasticity; we present means and SEs from untransformed data in figures and in the text, unless otherwise noted. Within the ANOVA models, tree was always treated as a random effect, and stand was treated as a random effect when study stands had been randomly drawn from the population of such stands in the landscape (Neter et al. 1996). All ANOVA models included all possible interactions. A priori and post hoc multiple comparisons and linear contrasts were tested with Tukey–Kramer honestly significant difference (HSD) with a Bonferroni correction to $\alpha = 0.05$ (Quinn and Keough 2002).

For most studies, we measured the diameter at breast height (DBH), height, percent live crown, and local basal area (English BAF 10× prism) of each study tree. For landscape study 1, we tested for relationships between resin flow and these tree attributes by evaluating all possible simple and multiple linear regressions.

Resin flow in mixed-species plots

Mixed-species study 1

In October 1996, within a common garden planting near Saucier, Mississippi, we compared resin flow from *P. taeda*, *P. palustris*, *P. elliottii*, and *P. echinata* ($n = 38, 24, 22,$ and 22 trees, respectively; one sample per tree). Trees were about 50 years of age. We do not have other descriptive metrics (e.g., DBH, height, and basal area) for these trees.

Mixed-species study 2

In June 2001, in the northwestern region of the Oakmulgee ranger district (USDA Forest Service compartment 17), we measured constitutive and induced resin flow from *P. taeda*, *P. palustris*, and *P. echinata* at six sites where they were growing intermixed; two trees per species per site (two samples per tree for constitutive resin flow). We collected resin on days -1, 1, 3, and 7 (relative to the day of depletion wounding). Site and tree nested within site and species were treated as random effects. Trees were 62–68 years of age and about 40–50 cm DBH.

Mixed-species study 3

In May 1999 in the north-central region of the Oakmulgee ranger district (USDA Forest Service compartment 10), we measured constitutive and induced resin flow from *P. taeda*, *P. palustris*, and *P. echinata* from one stand where they were growing intermixed (15 trees per species; two samples per tree for constitutive resin flow). To quantify inducible production of resin, we collected resin on days 1 and 7 after the day of depletion wounding. Additionally, we measured constitutive resin flow on day 7 from 15 *P. taeda* (two samples per tree) that were not subject to depletion wounding (to serve as true controls). Trees were 40 years of age and 30 ± 5 cm DBH (mean \pm SD). The constitutive measures of resin are the same as those reported in Hofstetter et al. (2005), but in that paper, the means reported for *P. taeda* and *P. palustris* were inadvertently switched.

Mixed-species study 4

In July 2001, in the east-central region of the Oakmulgee ranger district (USDA Forest Service compartments 115 and 130), we compared constitutive and induced resin flow from *P. palustris* and *P. echinata* in one mixed-species site ($n = 8$

and 7 trees, respectively) and from *P. palustris* and *P. taeda* in another mixed-species site ($n = 6$ trees per species). We measured constitutive resin (two samples per tree) on day -1 and sampled induced resin production on days 1, 3, 7, and 10 (relative to the day of wounding). Additionally, we took two samples of constitutive resin on each sample day from four *P. taeda* that were not subject to depletion wounding (to serve as true controls). Because not all sites included all species, we constructed a priori linear contrasts to test for effects due to species, stand, and species \times stand. Study trees were 35 ± 9 cm DBH and 24 ± 3.6 m tall with $55 \pm 8\%$ live crown; stand basal area was 27 ± 7 m²·ha⁻¹.

Mixed species study 5

During 17 July to 10 August 2001, within three mixed-species stands in the east central region of the Oakmulgee ranger district (compartments 115 and 130), we compared resin flow from *P. taeda* and *P. palustris* ($n =$ a total of 20 and 10 trees, respectively) before and during natural attacks by *D. frontalis*. Following Veysey et al. (2003), we quantified the relationship between beetle landing rate and the depletion of tree resin by monitoring beetle landing rates (with two 22 cm \times 28 cm sticky traps at 5 m height, on opposite sides of each tree; every 3 days, numbers of beetles caught on traps were quantified and traps were replaced) from initiation of attacks (as evidenced by pitch tubes and boring dust) until attacks ceased (<5 beetle landings·m⁻²·day⁻¹) or the study was terminated. We calculated the mean number of landing beetles per square metre from two to six trap counts during the attack phase. On the same trees, we measured resin flow just before attacks were initiated (3 samples·tree⁻¹, 1–7 days before attack) and again every 3 days during the attack until resin flow ceased or the study was terminated. We measured and monitored a total of 65 trees to obtain 30 study trees for which we had at least one resin measurement prior to attack and two resin measurements postattack. We regressed the repeated measures of resin flow against days since attack initiation to estimate the daily rate of change in resin flow during attack (regressions included preattack resin flow coded as day 0). These slopes were normally negative, indicating depletion of resin during the attack but were occasionally positive when attack rates were relatively low, indicating inducible increases in resin flow during the attack. Study trees were 28 ± 10 cm DBH and 20 ± 5 m tall with $46 \pm 11\%$ live crown; stand basal area was 29 ± 7 m²·ha⁻¹.

Resin flow at the landscape scale

Landscape study 1

Using the USDA Forest Service geographic information system (GIS) stand layer, we randomly selected a sample of 20 stands each of *P. palustris* and *P. taeda* from the total pool of 102 *P. palustris* and 234 *P. taeda* stands that were 30–60 years old within the Calcasieu ranger district (Evangeline work unit: USDA Forest Service compartments 41, 45, 51, 52, 55–57, 70, 81, and 82), Kisatchie National Forest, Louisiana. This corresponds to the age range of trees most frequently attacked by *D. frontalis* (Lorio and Hodges 1974; Ylioja et al. 2005). The historical patterns of *D. frontalis* activity in this forest are typical of forests across the

region (Friedenberg et al. 2007). Four initially selected stands were inaccessible or incorrectly classified in the GIS database and were replaced with the next randomly selected stand. Age for selected stands was 47 ± 5 (range 37–51) versus 47 ± 6 (range 39–57) years, respectively. Within each stand, five trees (>8 cm DBH) were randomly selected by choosing the tree closest to a predetermined GPS coordinate within the stand and then choosing four additional trees using a random number generator to determine a compass direction and distance (0–100 m) from the first tree. Three resin samples were taken from each tree on each of three sampling dates: 8–10 September 2002, 24–26 June 2003, and 19–21 July 2003. One-half of the stands (10 per species) were used in 2002, and the other half were sampled on both dates in 2003. On the last occasion, we measured the additional resin that flowed 24–48 h and 48–72 h after wounding. One site of each species was removed from the study in 2003 due to fires.

To compare mean resin flow between pine species, we used mean resin flow for each tree as the response variable (Hurlbert 1984) in a general linear model that included year, species, and site nested within species. To compare pine species with respect to variation within and among trees, we separately analyzed the measurements of each species in 2003 (with each resin measurement as an observation) in a general linear model that included month, site, tree nested within site, month \times tree nested within site, and month \times site; in this case, we used the untransformed data so that variance estimates (Neter et al. 1996) would reflect the actual frequency distributions of resin flow.

Because this study included relatively large numbers of stands and trees, we used regression analyses to compare pine species with respect to relationships between resin flow and other attributes of trees and stands. Measurements collected for every tree were height, DBH, basal area, percent live crown, and tree age (tree age was based on USDA Forest Service stand layer information and validated by taking one or more tree cores from each site). To avoid complications from multicollinearity, we performed a principal components analysis (PCA) of these variables and used the resulting PC scores for subsequent regression analyses. The PCA used the correlation matrix from all 190 trees (2 species \times 19 stands \times 5 trees). Stands were characterized by stand-specific means of the PC scores, plus one additional independent variable, site index (expected height of codominant pine trees at age 50 years); the dependent variable was mean (square-root transformed) resin flow for each site, expressed as residuals of tree-specific resin flow relative to the mean for that year (to remove effects of year from the variance among sites). For both pine species ($n = 19$ stands·species⁻¹), we evaluated all possible linear regressions using PC loading scores to predict stand-specific resin flow. In a separate analysis, we explored all possible linear regressions using each tree as an observation. We identified the best model from each regression analysis (PC scores and original tree attributes) by choosing the model that reduced the Akaike information criteria (AIC) by >2 compared with the next best model and (or) that increased the percent variance explained by $>5\%$ (Quinn and Keough 2002). Then, we tested if the best models differed between pine species (using the null hypothesis that slope and intercept was the same for

both species; Neter et al. 1996). We similarly evaluated regressions of tree-specific resin flow (mean for each tree of square-root transformed measurements) as a function of tree-specific PC scores, as well as separately testing tree attributes; to make these analyses mathematically independent of analyses of stand means, the dependent and independent variables were evaluated as residuals from stand-specific means.

Landscape study 2

In the Vernon work unit of the Calcasieu ranger district, Kisatchie National Forest, we compared resin flow of *P. palustris* and *P. taeda* from replicated stands judged to be on-site and off-site plantings of both species based on soil type, drainage, landforms, and historical growth patterns of trees (Wakeley 1954; Baker and Langdon 1990; Boyer 1990; site selection confirmed by J. Barnett and C. Meier, USDA Forest Service, Southern Research Station, Pineville, La., personal communication 2003). Using the USDA Forest Service GIS layers, we randomly selected three on-site and three off-site stands for each species (with reference to data fields for species, soil, landform, preferred species, and drainage with the restriction that eligible stands had trees that were 30–60 years of age). On site for *P. palustris* was defined by having sandy-loamy soils (Betis, Boykin, and Briley) that were well drained (USDA Forest Service drainage values D4 and D5), by being on ridge or slope areas, and by having *P. palustris* listed in the GIS database as the preferred species; we used the following USDA Forest Service compartments and stands: 102-13, 102-20, and 102-24 (Baker and Langdon 1990). On site for *P. taeda* was defined by poorly to moderately drained (D1 to D3) soils (Caddo, Mayhew, and Metcalf) (following Coile and Schumacher 1964) and where it was designated as the preferred species within the USDA Forest Service stand database; compartments and stands used were 108-24, 104-6, and 104-28. Off-site trees of each species were those on sites that matched the on-site criteria for the other species; compartments and stands for *P. palustris* were 132-19, 104-5, and 112-15 and, for *P. taeda*, were 102-20, 102-31, and 105-31. Within each selected stand, four trees were randomly chosen as in landscape study 1, and two resin samples were collected from each tree. Resin sampling occurred 23–25 August 2003. The general linear model included species, on- or off-site, species \times on- or off-site, stand nested within species \times on- or off-site, and tree nested within stand \times species \times on- or off-site. For each study site, we verified tree age from tree cores, measured tree heights of codominant study trees, and used these data to calculate the site index of the stand (expected height at age 50) using species-specific models from Farrar (1973). Study trees were 40 ± 6 cm DBH, 27 ± 5 m tall with $38 \pm 13\%$ live crown; stand basal area was 22 ± 8 m²·ha⁻¹.

Natural patterns of attack and mortality

Differences between pines in their susceptibility to bark beetles might be attributable to different probabilities of being attacked by beetles and (or) different probabilities of surviving attacks. To evaluate these possibilities, we censused patterns of beetle attack and tree mortality within mixed-species stands of *P. taeda* and *P. palustris* that experienced infestations of *D. frontalis*. In July 2002 and 2005,

we surveyed patterns of beetle attack and tree mortality within local infestations (“spots”) of *D. frontalis* that were initiated in spring of the previous year (first detected in aerial surveys in June) and had not been subjected to suppression. We censused trees within 12 such spots in 2002 and 15 additional spots in 2005, all within the Oakmulgee Ranger District of the Talladega National Forest, Alabama, USA. All spots had become naturally inactive by spring of the year after being detected. At each site, we defined a polygon that minimally enclosed all the beetle-killed trees (and defined the spot). To keep the polygons simple and objective, we required that each segment be at least 8 m long and that all internal angles between adjacent segments be $>80^\circ$. Within each polygon, we identified each pine tree (>8 cm DBH) and scored it as attacked or not attacked and killed or not killed. Attacks were defined by the presence of pitch tubes. The occasional trees that had died prior to the beetle infestation were excluded. Surviving trees within the polygons approximated what have been referred to as “escape trees” (Strom et al. 2002).

Comparison of resin sampling techniques

Because our results did not match previously published comparisons of resin flow in *P. palustris* versus *P. taeda*, we tested whether the difference between studies could have been an artifact of different methods. Hodges et al. (1977, 1979) measured flow from a larger area of xylem, using a 2.5 in. equilateral triangle punch (1746 mm²), whereas most studies since then, including our own, have used a 0.5 in. (127 mm²) circular punch. Some studies have used a 1 in. punch (507 mm²), so we also compared that punch with the 0.5 in. punch. Additionally, because previous studies had collected resin for a longer period of time (up to 72 h), we collected resin after 24, 48, and 72 h during both tests. For both studies, we collected four samples per tree, two with each technique.

Technique study 1

On 19–21 July 2003, we compared resin flow from wounds made with the 0.5 in. punch versus the 1 in. punch on four trees in 16 of the 20 stands (8 stands per species) that were selected for landscape study 1.

Technique study 2

On 23–25 August 2003, we compared resin flow from the standard 0.5 in. punch versus 2.5 in. triangular punch on four trees from each of the 12 stands that were selected for landscape study 2.

Results

Resin flow in mixed-species plots

Mixed-species study 1

Resin flow from *P. echinata* was significantly lower than flow from *P. palustris* and *P. taeda*, which were similarly high; *P. elliotii* was indistinguishable from any of the other species (Tukey–Kramer comparisons). Resin flows for *P. palustris*, *P. taeda*, *P. elliotii*, and *P. echinata* were 2.77 ± 0.49 (mean \pm SE), 2.43 ± 0.38 , 1.87 ± 0.29 , and 1.02 ± 0.20 g·day⁻¹, respectively ($F_{[3,104]} = 5.12$, $P = 0.002$).

Mixed-species study 2

Constitutive resin flow was similar for *P. taeda* and *P. palustris*, which was 49%–72% higher than for *P. echinata*: 6.40 ± 0.59 , 5.33 ± 0.53 , and 3.44 ± 0.55 g·day⁻¹, respectively ($F_{[2,18]} = 5.39$, $P = 0.03$). *Pinus palustris* and *P. taeda* also had similar responses to the resin depletion treatment (Fig. 1). On day 1 following depletion wounding, resin flow was reduced by 19%–47%; the level of decreased resin flow (treatment side – control side) was indistinguishable among *P. taeda*, *P. palustris*, and *P. echinata*: -2.04 ± 0.61 , -1.61 ± 0.58 , and -0.51 ± 0.57 g·day⁻¹, respectively ($F_{[2,10]} = 2.43$, $P = 0.14$). From day 1 to day 3, resin flow from the depleted side nearly doubled, and the species did not differ in the amount of change ($F_{[2,10]} = 0.34$, $P = 0.72$; Fig. 1). On days 3 and 7, resin flow from the depleted sides was 40%–81% greater than from the control sides, indicating again that (i) trees responded to depletion by refilling resin ducts beyond constitutive levels, and (ii) species did not differ in the degree to which they refill the system ($F_{[2,10]} < 0.79$, $P > 0.49$ for tests of species differences in treatment side – control side).

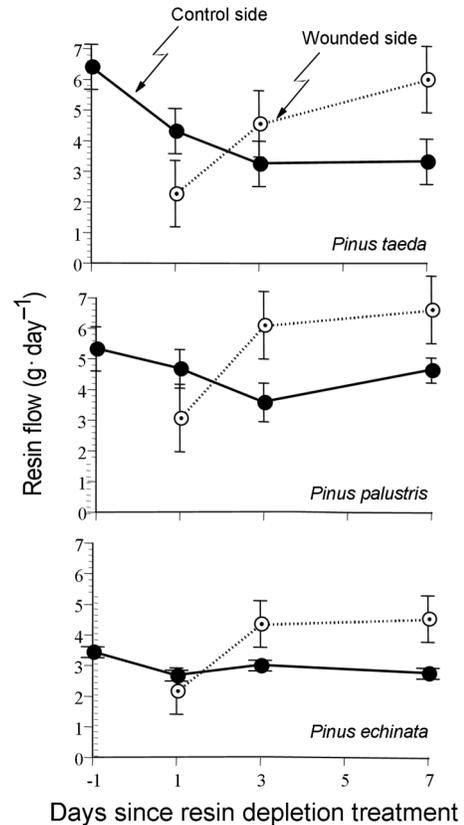
Mixed-species study 3

Again, *P. palustris* did not have higher constitutive resin flow than *P. taeda*, and in this case, it was lower than *P. taeda* and more similar to *P. echinata* (1.42 ± 0.26 versus 2.05 ± 0.33 versus 1.28 ± 0.11 g·day⁻¹, respectively; $F_{[2,42]} = 1.24$, $P = 0.30$). Like mixed-species study 2, these results also failed to indicate greater capacity of *P. palustris* to compensate for depletion of resin. Following depletion wounding, the amount of decrease in resin flow on day 1 (treatment side – control side) did not differ between *P. palustris*, *P. taeda*, and *P. echinata*: -0.19 ± 0.20 , -0.96 ± 0.31 , and -0.61 ± 0.19 g·day⁻¹, respectively ($F_{[2,42]} = 2.52$, $P = 0.09$). Resin flow increased in all species between day 1 and day 7 (day 7 treatment side – day 1 treatment side) but more so in *P. taeda* than in *P. palustris* or *P. echinata*: 2.49 ± 0.33 , 1.01 ± 0.23 , and 1.22 ± 0.13 g·day⁻¹, respectively ($F_{[2,42]} = 10.52$, $P = 0.0002$). The amount of increase in resin flow on day 7 (treatment side – control side) was similar among species: 1.29 ± 0.19 , 0.91 ± 0.20 , and 0.97 ± 0.11 g·day⁻¹ for *P. taeda*, *P. palustris*, and *P. echinata*, respectively ($F_{[2,42]} = 1.38$, $P = 0.26$), and that amount was significantly greater than zero, indicating a rapid induction of resin production (reject null hypothesis that resin flow from treatment side – control side = 0, $t > 4.49$, $P < 0.0005$ for each species). As in previous studies (Ruel et al. 1998, Lombardero et al. 2000), resin flow from true control trees did not differ from the control side of experimental trees ($F_{[1,28]} = 0.04$, $P = 0.89$).

Mixed-species study 4

Again, constitutive resin flow from *P. taeda* was as high or higher than resin flow from *P. palustris* (where grown together, 5.89 ± 0.96 versus 3.99 ± 0.63 g·day⁻¹ (mean ± SE), respectively; $F_{[1,24]} = 1.70$, $P = 0.21$), and this time resin flow from *P. echinata* was very similar to *P. palustris* (compared at site where grown together 2.41 ± 0.44 versus 3.33 ± 0.49 g·day⁻¹, respectively; $F_{[1,24]} = 1.16$, $P = 0.29$). In this study unlike others, resin depletion treatments had no effect on resin flow. As in the other studies, there were no differ-

Fig. 1. Comparison of mean resin flow from *P. taeda*, *P. palustris*, and *P. echinata* before and after a wounding treatment designed to deplete the resin duct system on one side of each tree (mixed species study 2). Error bars are SEs.



ences between *P. palustris* and *P. taeda* in their response to resin depletion. For both species, resin flow from treatment side did not differ from the control side on days 1, 3, 7, or 10 ($t < 1.72$, $P > 0.14$, $df = 13$). Resin flow from true control trees did not differ from the control side of experimental trees ($F_{[1,33]} < 2.57$, $P > 0.12$ for all days).

Mixed-species study 5

When *P. taeda* and *P. palustris* were intermixed at the advancing front of *D. frontalis* attacks, there was no difference between pine species in beetle landing rates during attack (570 ± 90 versus 360 ± 128 landing beetles·m⁻²·day⁻¹ (mean ± SE), respectively; $F_{[1,28]} = 1.79$, $P = 0.19$), nor in the rate of decline in resin flow during attacks (slope of resin flow versus day of attack = -0.37 ± 0.09 versus -0.14 ± 0.10 g·day⁻¹ (mean ± SE); $F_{[1,28]} = 2.20$, $P = 0.15$). Resin flow tended to decline most rapidly in trees that experienced the highest landing rates of beetles (Fig. 2), but there was no difference between species in the relationship between rate of resin decline and beetle landing rate ($F_{[2,26]} = 1.07$, $P = 0.36$ for null hypothesis that slopes and intercepts were equal; $t_{28} = 1.18$, $P = 0.25$ for null hypothesis that slopes were equal).

Resin flow at the landscape scale

Landscape study 1

As with all the studies within mixed-species stands, re-

Fig. 2. The resin flow from *P. palustris* and *P. taeda* declined similarly during 6–15 days of attack by *D. frontalis*: $y = -0.017 - 0.000\ 552\ x$ ($r^2 = 0.33$, $F_{[1,28]} = 13.74$, $P = 0.0009$; regressions did not differ between species). Each point represents one tree within a mixed species pine stand that had become naturally infested with beetles. All of the study trees died as a result of the beetle attacks.

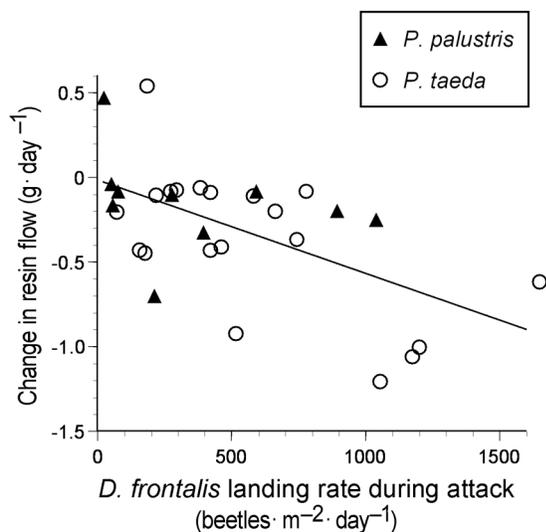
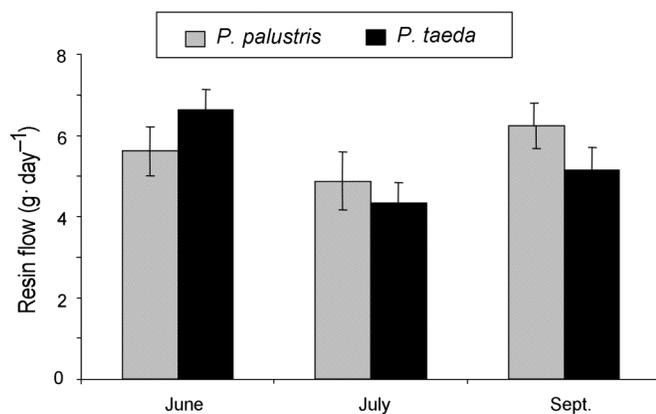
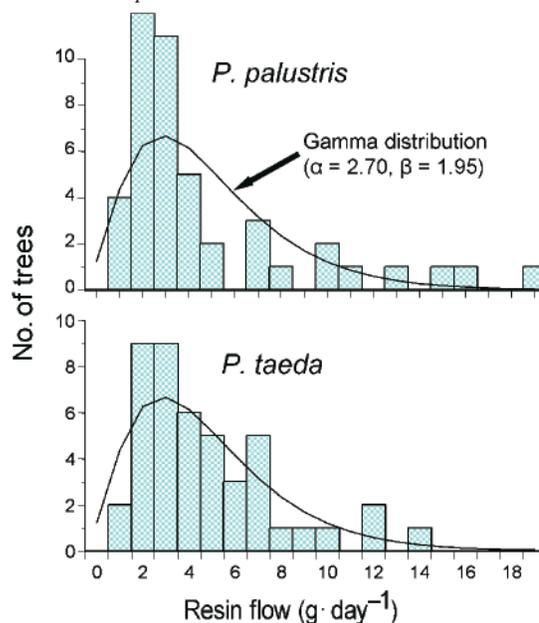


Fig. 3. Mean constitutive resin flow from *P. palustris* versus *P. taeda* in Evangeline Ranger District, Kisatchie National Forest, Louisiana (landscape study 1; $n = 10$ stands-species⁻¹). Error bars are SEs.



sults refuted the hypothesis that constitutive resin flow is generally higher in *P. palustris* versus *P. taeda* (Fig. 3; $F_{[1,36]} = 0.06$, $P = 0.81$ for species effect). Variance in resin flow among stands was quantitatively modest but statistically significant for both species ($F_{[8,36]} > 2.73$, $P < 0.02$). Variance in resin flow among trees within stands was similarly high for both species ($F_{[36,36]} > 8.53$, $P < 0.0001$), and accounted for 42%–58% of the total random variance (compared with 22%–45% for variance within trees, and 17%–21% for the sum of variance attributable to stands, stand \times date interaction, and tree \times date interaction). The variance in resin flow among stands was similar for the two species ($F_{[8,8]} = 1.90$, $P = 0.19$). The variance attributable to trees was somewhat more for *P. palustris* versus *P. taeda* ($F_{[36,36]} = 2.09$, $P = 0.02$), but both species fit the same γ distribution (Fig. 4; test goodness-of-fit of pooled distribution parameters versus species specific parameters; $\chi^2 < 0.41$ $P > 0.93$).

Fig. 4. Comparison of the frequency distributions of tree-specific resin flow from *P. palustris* versus *P. taeda*.



The sampled stands of *P. taeda* and *P. palustris* were statistically indistinguishable with respect to age, basal area, DBH, site index, and percent live crown ($F_{[1,38]} < 2.83$, $P > 0.10$); trees in stands of *P. palustris* were somewhat taller than trees in stands of *P. taeda* (22 ± 1 versus 20 ± 1 m, respectively; $F_{[1,38]} = 5.87$, $P = 0.02$). For both species, the best regression model to predict mean stand-specific resin flow included only DBH: resin flow = $0.03(\pm 0.009; SE)DBH - 1.17(\pm 0.32)$ ($r^2 = 0.27$, $F_{[1,37]} = 13.98$, $P = 0.0006$; regressions did not differ between species: $F_{[2,35]} = 1.14$, $P = 0.33$). The best regression model to predict resin flow among trees within stands also included only DBH: resin flow = $0.02(\pm 0.006)DBH - 0.85(\pm 0.21)$ ($r^2 = 0.08$, $F_{[1,193]} = 17.92$, $P < 0.0001$; regressions did not differ between species: $F_{[2,191]} = 1.36$, $P = 0.26$). The first three axes of the PCA explained 82% of the variation in tree attributes and were readily interpretable (Table 1). However, there were no regression models using any combination of PC1–PC3 that explained more variation in resin flow than the model based on DBH alone. Both *P. palustris* and *P. taeda* produced most of their resin within the first 24 h postwounding (94 ± 1 versus $98 \pm 1\%$ total resin, respectively). Neither species produced more than 0.1% of the total resin after 48 h.

Landscape study 2

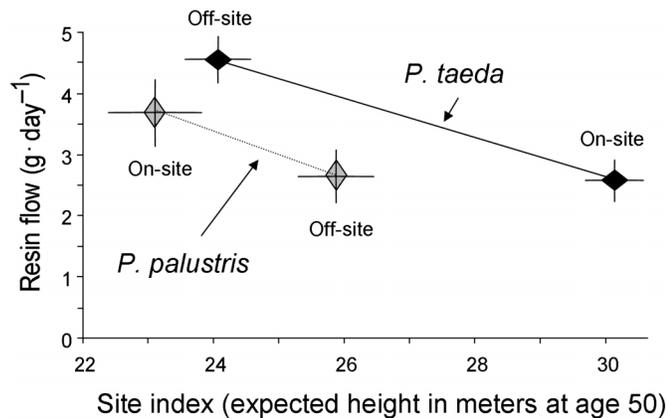
As expected given the study design, site index varied among treatment groups. Mean site index was higher for *P. taeda* that were classified a priori as on-site versus off-site: 30 ± 1 versus 24 ± 1 m, respectively. However, mean site index was lower for *P. palustris* that were classified a priori as on-site versus off-site: 23 ± 0.5 versus 26 ± 1 m, respectively (Fig. 5). There was no main effect of on- or off-site on resin flow ($F_{[1,62]} = 1.30$, $P = 0.26$), nor was the mean resin flow from each species different ($F_{[1,36]} = 0.55$, $P = 0.46$). Resin flow from on-site *P. palustris* was marginally higher than from on-site *P. taeda* (3.83 ± 0.69

Table 1. Results of a principal components analysis of five tree attributes that were hypothesized to influence resin flow.

Tree attribute	Factor loading			Mean ± SD (<i>n</i> = 95 trees-species ⁻¹)	
	PC1	PC2	PC3	<i>P. palustris</i>	<i>P. taeda</i>
Height (m)	0.36	0.69	-0.29	22.1±2.4	20.3±3.4
Live crown (%)	0.44	-0.59	0.08	40±14	39±15
DBH (cm)	0.61	0.20	0.01	37±9	34±9
Basal area (m ² ·ha ⁻¹)	-0.53	0.27	0.12	18.7±8.6	21.3±8.8
Age (years)	0.14	0.23	0.94	47±5	47±6
Variance (%)	40	62	82		

Note: Positive values of PC1 indicated large-diameter trees with relatively low crowding (low basal area). Positive values of PC2 indicated tall trees with relatively small crowns. Positive values of PC3 indicated old trees.

Fig. 5. Comparison of constitutive resin flow from *P. palustris* and *P. taeda* that were growing on soils judged to be on-site and off-site for each species. Classifications of on-site and off-site were related to tree growth (site index), but the relationship was opposite for the two species.



versus 2.70 ± 0.44 g resin-day⁻¹, respectively; $F_{[1,92]} = 2.01$, $P = 0.16$, a priori linear contrast), but the amount of resin produced by off-site *P. taeda* was significantly greater than resin from off-site *P. palustris* (4.62 ± 0.48 versus 2.81 ± 0.56 g resin-day⁻¹, respectively; $F_{[1,92]} = 7.25$, $P = 0.008$, a priori linear contrast). This juxtaposed pattern caused the interaction term in the main model to be highly significant (on- or off-site × species, $F_{[1,62]} = 8.33$, $P = 0.005$). As predicted by the GDBH, resin flow was lower when site index was higher (Fig. 5).

Natural patterns of attack and mortality

Minimal polygons around 27 local infestations of *D. frontalis* contained a total of 4208 pine trees: 3877 *P. taeda*, 240 *P. palustris*, and 91 *P. echinata* (Table 2). Across sites, the mean diameter of pine trees ranged from 13 to 52 cm DBH (overall DBH of 23 ± 10 cm; mean ± SD), and the mean height ranged from 12 to 23 m (17 ± 3 m) (based on random samples of 8–16 pine trees per spot). Only 304 trees (7%) had survived, and the rest (93%) were killed by beetles. We only observed two trees ($\approx 1/2000$) that had pitch tubes from beetle attacks and survived. *Pinus palustris* were no more likely than *P. taeda* to survive when they were within beetle infestations. Within 13 infestations that contained

both species, 19 of 240 *P. palustris* survived versus 180 of 2670 *P. taeda* (7.9 versus 6.7%; $\chi^2 = 0.48$, $P = 0.49$). Thus, when local aggregations of *D. frontalis* encountered a mix of *P. taeda* and *P. palustris*, both species were equally likely to be attacked and equally certain to die if attacked.

Comparison of resin sampling techniques

More resin flowed from larger wounds, and resin flowed longer from larger wounds; however, changes in sampling techniques did not alter comparisons of resin flow between *P. taeda* and *P. palustris*.

Technique study 1

The 1 in. punch produced about 50% more total resin than the 0.5 in. punch (7.7 ± 0.42 versus 5.1 ± 0.37 g·2 days⁻¹ (mean ± SE); $F_{[1,168]} = 51.63$, $P < 0.0001$), but there was no technique × species interaction ($F_{[1,168]} = 1.62$, $P = 0.21$). Both *P. palustris* and *P. taeda* produced the majority of their resin within 24 h: 94 ± 0.4 and $98 \pm 0.3\%$, respectively. Only three *P. palustris* and five *P. taeda* trees (of 32 of each species) produced any resin between 24 and 48 h and always <0.25 g. Nine 1 in. wounds, and one 0.5 in. wound (of 92 wounds of each size) produced resin between 24 and 48 h. No wounds produced resin after 48 h. The small amount of additional resin collected after 24 h did not differ between species ($T_{[1,9]} = 0.35$, $P = 0.73$).

Technique study 2

Triangle wounds produced approximately three times more total resin than 0.5 in. wounds (14.01 ± 0.28 versus 3.49 ± 0.57 g·3 days⁻¹, respectively; $F_{[1,142]} = 517.89$, $P < 0.0001$). Again, there was no technique × species interaction ($F_{[1,142]} = 0.02$, $P = 0.89$). No resin flowed from any 0.5 in. punch wounds after 24 h. Although 43 of the 48 trees produced resin from the triangle wounds for more than 24 h ($F_{[1,142]} = 226.71$, $P < 0.0001$ for comparison of wounding methods), it was a negligible amount and, if anything, was slightly greater in *P. taeda* versus *P. palustris*: 5.07 ± 1.05 versus $2.66 \pm 0.43\%$ of the total resin, respectively ($F_{[1,36]} = 2.31$, $P = 0.14$). No trees produced resin after 48 h.

Discussion

We reject the hypothesis that the relatively low mortality of *P. palustris* from *D. frontalis* in contemporary forests is a

Table 2. Natural patterns of attack and mortality of three sympatric pine species within 27 local infestations (“spots”) of *D. frontalis* in the Oakmulgee Ranger District, Alabama, USA.

	<i>P. taeda</i>		<i>P. palustris</i>		<i>P. echinata</i>	
	Killed	Alive	Killed	Alive	Killed	Alive
No. attacked	3607	2	221	0	76	0
No. not attacked	0	268	0	19	0	15
Survival (%)		7.0		7.9		16.5

result of high constitutive resin flow in *P. palustris*. In none of our seven comparisons was the mean resin flow of *P. palustris* significantly higher than that of the sympatric species (*P. taeda*) that experiences greater mortality from *D. frontalis*. The frequency distributions of tree resin were similar between species (Fig. 4), but the variance was somewhat higher in *P. palustris* than in *P. taeda* (CV = 70% versus 48%). Variance in plant defenses can sometimes be detrimental to herbivores (Karban et al. 1997) but not in this case. Because the relationship between resin flow and beetle reproductive success is an accelerating function (negative exponential; Reeve et al. 1995), greater variance among trees actually tends to increase mean beetle reproduction (Ruel and Ayres 1999).

Constitutive resin flow has high heritability (Roberds et al. 2003), so we assume that much of the variation among trees within species is genetically determined. However, landscape study 1 showed that there is also significant variation among sites chosen at random from the landscape (CV = 23%–41%), which implies environmental effects on resin flow. More specifically, the on- or off-site study (landscape study 2) indicated that resin flow tends to decrease as site quality for tree growth increases (Fig. 5). This pattern is consistent with the GDBH (Lorio 1986; Herms and Mattson 1992) and with studies showing that enhancement of pine tree growth via supplementation of soil moisture or mineral nutrients tends to reduce antiherbivore defenses (Wilkens et al. 1997; Reeve et al. 1995; Warren et al. 1999; Zas et al. 2006). Our results (for *P. taeda*) oppose the hypothesis that on-site trees will be better defended than those grown off-site. High resin flow from on-site *P. palustris* was probably a result of on-site areas for this species having low nutrient and moisture levels, causing trees to grow slowly (on-site *P. palustris* stands had the lowest site index in this study). If forests were propagated such that *P. palustris* tend to be on-site, this could lead to a landscape where *P. palustris*, on average, has marginally higher resin flow than *P. taeda*. However, our random sampling across a large landscape (landscape study 1) failed to indicate the differences in resin flow between *P. palustris* and *P. taeda* that would be expected if the effect of on- or off-site planting was strong.

Even with no differences between pine species in constitutive resin flow, *P. palustris* could be better defended than *P. taeda* against *D. frontalis* if the capacity for rapidly induced resin production were greater in *P. palustris*. However, there was little evidence of such a difference in the three studies in which trees were challenged with experimental depletion of resin (mixed-species studies 2–4). In one comparison in one study (mixed-species study 3), *P. palustris* did appear to have a slightly more rapid induction of

the resin system following the depletion treatment. However, we doubt that this modest difference explains the lower beetle-induced mortality of *P. palustris*, because there were no differences between species in resin dynamics during the course of a natural beetle attack (mixed-species study 5; Fig. 2).

Our results were surprising in that they differed from the previously published comparison of constitutive resin flow in southern pines (Hodges et al. 1977, 1979), which indicated that resin flow from *P. palustris* was about 50% greater than that from *P. taeda*. We rejected the possibility that this difference was due to methodological differences (technique studies), leaving us to conclude that the previous result was less generalizable; we sampled almost 500 trees from three states in various seasons over 6 years, whereas Hodges et al. measured ≈ 50 trees-species⁻¹ (1 sample-tree⁻¹) in one locale. Cook and Hain (1986) compared resin flow from *P. taeda* and *P. echinata* and found no difference. Roberds and Strom (2006) measured resin flow from *P. taeda*, *P. palustris* and *P. elliotii* but did not make comparisons between species.

Our results are also contrary to anecdotal evidence from both the naval stores industry (Wahlenberg 1946; McReynolds et al. 1989) and studies of red-cockaded woodpeckers (Conner et al. 1998), which both suggest that *P. palustris* has higher resin flow than *P. taeda*. However, these examples may not accurately describe tree resin in a way that is meaningful to bark beetles. Techniques of the naval stores industry included repeated wounding of the trees and applications of acid to the wounds (Wahlenberg 1946; Clements 1974; McReynolds et al. 1989). Similarly, red-cockaded woodpeckers protect their nests by persistently pecking at the trees, causing resin to ooze onto the bark, which creates a slick barrier against intruders (Conner et al. 1998). In both cases, the trees are in a sustained state of induced resin synthesis for months or years, which is too long of a time scale to be relevant for bark beetle attacks, which are generally over within 1–2 weeks.

The susceptibility to *D. frontalis* of *P. palustris* versus *P. taeda* appears to depend on the spatial scale at which the species are mixed (see also Ylloja et al. 2005). Local infestations (“spots”) seldom form in stands of *P. palustris* but are common in stands of *P. taeda* (Friedenberg et al. 2007). However, when infestations formed where the pine species were mixed, there was no difference in probability of attack nor in probability of death given attack (Table 2). Therefore, *P. palustris* does not have genetic immunity to *D. frontalis* in the sense of classical models of host–parasite dynamics (Anderson and May 1979; McCallum et al. 2001). Apparently, for *P. palustris*, the low level of beetle-induced mortality that we observe in the landscape is not a function of the susceptibility of individual trees; instead, it appears

to be an emergent property of monospecific stands. Stands of these two species may differ because they are managed differently. For example, stands of *P. palustris* are more frequently burned and thinned, resulting in fewer larger trees, greater spacing among trees, and a relatively open canopy. This can reduce the stability of pheromone plumes that coordinate successful mass attacks of trees by *D. frontalis* (Thistle et al. 2004). *Dendroctonus frontalis* appeared to disperse in similar numbers through stands of both species, even though infestations rarely occur in stands of *P. palustris* (Friedenberg et al. 2007). This indicates that the point of differential susceptibility is the stage where there might or might not be enough beetle attacks on the first tree to start a self-propagating local infestation. We do not dismiss the idea that there may be differences in the chemical or physical properties of resin of *P. taeda* and *P. palustris* that influence defense efficacy and that these traits could be influenced by landscape scale environment–tree interactions, but rather extensive comparisons of resins have generally failed to reveal qualitative differences (Hodges et al. 1977, 1979; Blanche et al. 1983; Hofstetter et al. 2005).

The conspicuous difference between *P. taeda* and *P. palustris* in their mortality rates from *D. frontalis* may reflect the evolutionary history of interactions between *D. frontalis* and the species of *Pinus* that are native to the southeastern United States (Kelley and Farrell 1998; Theis and Lerda 2003). The low mortality rate of *P. palustris* from bark beetles could be the result of a recent autapomorphy in *P. palustris* that enhanced the efficacy of antiherbivore defenses (suggestive of the evolution of a stepwise, qualitative defense in *P. palustris*). Beetle infestations only rarely form in stands of *P. palustris* (Friedenberg et al. 2007), even though *D. frontalis* can attack, kill, and reproduce within *P. palustris* (Table 2, personal observations). This suggests that beetle behavioural avoidance, a counter-offense strategy (Karban and Agrawal 2002), is part of the explanation for low mortality in *P. palustris*. This coevolutionary model posits that *P. palustris* evolved a novel defense that reduced *D. frontalis* fitness, leading to the evolution of adaptive behavioural avoidance in *D. frontalis*. Alternatively, *P. palustris* may be an equally suitable host but is avoided by beetles by chance (e.g., pleiotropy or genetic linkages) rather than adaptation. This nonoptimal host selection model is plausible because *D. frontalis* preferentially attacks *Pinus virginiana* Mill. over *P. taeda*, even though beetle fitness in *P. virginiana* is markedly lower (Veysey et al. 2003; Ylioja et al. 2005). A third model is that *P. palustris* has evolved a novel effective defense, but *D. frontalis* has not evolved behavioral avoidance of *P. palustris*. These alternatives could be distinguished with (i) comparisons of beetle fitness in the two host species and (ii) tests for preattack or oviposition host discrimination by beetles. If there has been coevolution between *Pinus* and *D. frontalis* and if innovations in plant defense have been associated with speciation events as hypothesized by Ehrlich and Raven (1964), there is the further prediction that *P. palustris* is a more recently derived species than *P. taeda*. Recent genetic studies verify that both species are recent and closely related, but their relative ages have not been determined (Price et al. 1998; Germandt et al. 2005).

Although questions remain about the mechanisms and evo-

lutionary history of low beetle-induced mortality in *P. palustris*, the empirical pattern of low mortality is incontrovertible (Friedenberg et al. 2007) and is relevant to contemporary forest management. Because beetle infestations are less frequent in stands of *P. palustris*, such stands are more likely to survive to become mature forests that can produce saleable timber, protect watershed integrity, create recreational opportunities, and promote conservation of the striking biodiversity unique to longleaf pine ecosystems (Noss 1989; Dodd 1992; Kirkman et al. 2001). The reduced susceptibility of *P. palustris* forests to biotic disturbance from *D. frontalis* adds to the case for restoration of this once extensive forest type (Barnett 2000; Alavalapati et al. 2002).

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