Review

A review of southern pine decline in North America

David R. Coyle [a],[*], Kier D. Klepzig [b], Frank H. Koch [c], Lawrence A. Morris [a], John T. Nowak [d], Steven W. Oak [d],[1], William J. Otrosina [e],[1], William D. Smith [c],[1], Kamal J.K. Gandhi [a]

[a] University of Georgia, D.B. Warnell School of Forestry and Natural Resources, Athens, GA, USA
[b] USDA Forest Service, Southern Research Station, Asheville, NC, USA
[c] USDA Forest Service, Southern Research Station, Research Triangle Park, NC, USA
[d] USDA Forest Service, Forest Health Protection, Asheville, NC, USA
[e] USDA Forest Service, Southern Research Station, Athens, GA, USA

ABSTRACT

The southeastern United States is among the most productive forested areas in the world. Four endemic southern pine species – loblolly, longleaf, shortleaf, and slash – contribute significantly to the economic and ecological values in the region. A recently described phenomenon known as Southern Pine Decline (SPD) has been reported as having widespread impact in the southern pine region, particularly on loblolly pine. Root-feeding weevils and their associated fungi have been suggested as causal agents, even though literature and empirical research suggests that they are secondary insects colonizing weakened trees. Further, no published information exists about whether their associated fungi can cause mortality of mature trees in the southeastern U.S. Since there are significant management implications for pine health, we reviewed and critically examined the SPD phenomena on the southern landscape. Our regional analyses of USDA Forest Inventory and Analysis data show no discernable patterns related to pine growth or mortality, especially as related to topographic factors. There are no large-scale patterns related to pine mortality suggesting multiple interacting factors impacting tree health at stand-level. As such, the hypothesis that SPD is a regionally important decline syndrome and labeling declining southern pine stands as SPD is not supported. Instead, we discuss many abiotic (soil types, climate) and biotic (insects, pathogens, genetics) factors that may be interacting with each other and affecting southern pine health. Finally, we suggest management recommendations for landowners with pine health issues.

© 2015 Elsevier B.V. All rights reserved.

Contents

* Corresponding author at: University of Georgia, Warnell School of Forestry and Natural Resources, Building 4-434, 180 E. Green Street, Athens, GA 30602, USA. Tel.: +1 706 542 2152; fax: +1 706 542 8356.
    E-mail address: drcoyle@uga.edu (D.R. Coyle).
  [1] Retired.

1. Factors affecting tree health

Tree diseases are the result of complex interactions among multiple abiotic and biotic factors, and appear when the three components of the disease triangle occur together: (1) a pathogen; (2) a susceptible, present host; and (3) the appropriate environment for the pathogen (Stevens, 1960). As diseases do not appear instantly, Tainter and Baker (1996) added a fourth component – time. Disease etiology can be simple or complex, and the relative importance of the different components is not always apparent (Manion, 1981). In a simple disease model, the pathogen is the primary causal agent. For instance, oak wilt (*Ceratocystis fagacaerum* [Bretz] Hunt) may be considered a simple disease model – the pathogen is the primary tree-killing factor, provided it has access to a host (which generally occurs via being transmitted by nitidulid beetles into natural or human-caused wounds on the tree) and is in an environment conducive to infection (Sinclair and Lyon, 2005). Declines, on the other hand, often have complex etiologies (Manion, 1981) and can be considered complex disease models. Declines feature multiple, interchangeable abiotic and biotic components that interact with each other and have varying levels of importance to the overall health of the host (Houston, 1987). In these cases, the mere presence of the pathogen and access to a host in an appropriate environment does not always cause disease. Often, multiple additional stressors to the host are required prior to disease development (Schoeneweiss, 1975).

Sinclair (1966) defined three categories of factors affecting tree health: (1) predisposing factors such as soil type, climate, and tree genetics that influence trees over the long-term; (2) inciting factors such as defoliation and drought which have short-term influence on tree health; and (3) contributing factors such as opportunistic wood-boring beetles and fungi which further weaken and eventually kill the tree. These lead to a "decline and death spiral" – a progressive process of deterioration in tree health and vigor (primarily in mature trees) followed by decreased growth and increased twig and branch dieback, caused by both abiotic and biotic factors (Manion, 1981).

During the last century, there have been many reports of unexpected levels of landscape-scale tree mortality and deterioration in tree health across various North American ecosystems (Sinclair, 1965; Manion, 1981; Houston, 1987; Miller et al., 1989; Ciesla and Donaubauer, 1994). Often, causes for such phenomena are undetermined, so they are characterized using terminology such as dieback, die-off, and most commonly, decline. Specific examples of tree declines include yellow-cedar decline, aspen decline, oak decline, and more recently southern pine decline (SPD). While other declines have been studied in-depth, summarized, and critiqued (e.g., Jurskis, 2005), similar information is lacking for SPD. Due to the importance of forestry in the southern pine-dominated region, a closer examination of SPD is warranted.

Currently, there is little published information that supports the notion of SPD as a regional threat to southern pine health, and most cases of pine symptomology resembling SPD are likely a manifestation of natural tree mortality and local factors that stress trees. In this paper we examine the recently described SPD phenomenon. We begin by reviewing the history of SPD and pine decline etiology. We then evaluate the current extent and threat posed by SPD in the southern pine landscape using data collected by USDA Forest Service's Forest Inventory and Analysis (FIA) Program. On the basis of results from our FIA analyses, we place SPD in the context of common forest disturbances and, using examples from well-accepted forest declines elsewhere, outline abiotic and biotic factors that can affect pine (*Pinus* spp.) health in the southeastern U.S. Finally, we discuss research limitations related to SPD and suggest management strategies for southern pine forests that can contribute to sustained southern pine health and productivity.

2. The southern pine ecosystem

Forests in the southeastern United States are an integral component of the local, regional, and global economies, and are a diverse mosaic of hardwood and conifer tree species. Endemic pine species including loblolly (*Pinus taeda* L.), longleaf (*Pinus palustris* Mill.), shortleaf (*Pinus echinata* Mill.), and slash (*Pinus elliottii* Engelm.) pine cover ~45% of the total forested area of the southeastern U.S., of which about 42% of this area is planted and commercially managed (Wear and Gries, 2012). Loblolly pine is the dominant species across most of this region, especially in intensively managed commercial plantations. Loblolly pine is present on >12 million ha across 14 states, and this area is projected to increase to >17 million ha by 2020 (Wear and Gries, 2002).

Southeastern forests have a history of disturbance by various abiotic (e.g., wildfires, drought, flooding, and windstorms) and biotic (insect and disease outbreaks, and herbivore browsing) natural disturbances (Hanson et al., 2010). These disturbances create a complex habitat mosaic on the landscape (Turner and Ruscher, 1988), and also interact with each other to produce further landscape heterogeneity. However, anthropogenic disturbances during the last two centuries have arguably had an increasingly greater impact than natural disturbances. Fire suppression programs and subsequent changes in natural fire regimes have modified forest composition and structure across the region (Van Lear et al., 2005). Much of the area now in forest was cleared for agriculture during European settlement and the severe erosion that occurred (Trimble, 2008) profoundly changed the fertility and productivity of the land. Reforestation occurred in the 1920s (MacCleery, 1992), but in many instances the original forest cover-type and associated native species were lost. Due to changes in forest structure and composition, especially in commercial pine plantations, native pest species may have a greater impact and higher populations (e.g., increased attack rates of southern pine coneworm, *Dioryctria amatella* [Hulst], as management intensity increased; Nowak and Berisford, 2000) than in natural settings, along with an increased potential for invasion by non-native species (Sharitz et al., 1990). Southeastern forests are poised for additional alterations, as global climatic changes create new and unique combinations of plants, pests, pathogens, and abiotic conditions (Williams and Jackson, 2007; Klepzig et al., 2012).

3. Southern pine decline – A case study

In the 1950s, declining and dying mature loblolly pine stands were observed on the Oakmulgee District on the Talladega National Forest in Alabama, and a multi-year study was initiated

to investigate the causal factors (Brown and McDowell, 1968). Since that time, this syndrome has been variously termed "loblolly pine die-off", "pine decline", "loblolly pine decline", and more recently, "southern pine decline" (Brown and McDowell, 1968; Brown et al., 1969; Roth and Peacher, 1971; Hess et al., 1999, 2002; Eckhardt and Menard, 2008; Zeng et al., 2014). Stands with apparent health problems have been observed, in particular, along the fall line (i.e. the transitional zone between a landscape covered in rolling hills and one that is more flat; the fall line is also associated with a decrease in elevation from ∼600–900 to ∼200–400 feet above sea level) between the Piedmont and the Atlantic and Gulf Coastal Plain regions. Generally, symptoms were reported for relatively localized areas, and early observations noted decline symptoms common on trees >50 years old. These trees had stress cones for a year prior to death, there was root deterioration and mortality of feeder roots, and also a lack of clear insect and pathogen (especially root pathogen) activity (Brown and McDowell, 1968). One year later the overall condition of the study trees had improved (Brown et al., 1969), and by the end of the initial 5-yr study the syndrome and associated mortality had largely disappeared (Roth and Peacher, 1971). In fact, from 1966–1971 these study plots had <1% mortality per year – a level considered typical in stands >50 years old. Most mortality was attributed to known causes such as bark beetles, lightning, or *Heterobasidion* root rot (Roth and Peacher, 1971). Root pathogens such as *Heterobasidion irregulare* Garbelotto & Otrosina (formerly *Heterobasidion annosum* Fr. [Bref.]) (Otrosina and Garbelotto, 2010), *Phytophthora cinnamomi* Rands, and *Pythium* spp. were present in the stands, and it was hypothesized that most of the pine health issues were related to loblolly pine being planted on sites where hardwood or longleaf pine trees would have been more appropriate. At this time, Roth and Peacher (1971) considered the issue concluded, as all symptoms had disappeared.

Hess et al. (1999) reevaluated these sites in 1996 in an effort to identify the cause of the loblolly pine issues, and found *P. cinnamomi* and *Pythium* spp. to be the primary pathogens responsible for root deterioration; *Leptographium* spp. were present in moderate abundance, and *H. irregulare* was not present. Root pathogens and soil conditions were again assessed in plots showing a range of pine decline in Alabama in 2000 (Hess et al., 2002; Eckhardt et al., 2003). *Heterobasidion irregulare* was not found in the root samples, while *P. cinnamomi* was found in moderate amounts. *Leptographium* and *Grosmannia* spp.[2] that are transmitted by root-feeding weevils such as *Hylastes*, *Hylurgops*, and *Pachylobius* species were recovered from 86–94% of primary and fine roots and 33–50% of soil samples. It was concluded that this particular loblolly pine decline was likely due to interactions between abiotic and biotic factors, although the importance of individual factors was not evaluated (Eckhardt et al., 2003; Hess et al., 2005). Based on the occurrence of root-feeding weevils and their association with the *Leptographium* complex in symptomatic stands, it was proposed that SPD resulted from root infection by the *Leptographium* complex coupled with poor site conditions (Eckhardt et al., 2007). Predisposing factors, including site history, soils, and host condition, were suggested as playing a role in tree decline and insect prevalence.

Recently, it has been suggested that SPD is more common on steep slopes and south/southwest aspects (Eckhardt and Menard, 2008; Menard et al., 2010) – areas that presumably stress the trees. Originally identified as a localized issue in loblolly pine (Eckhardt et al., 2010), SPD has more recently been proposed as a threat to longleaf and slash pine (based on their susceptibility to artificial inoculations with SPD-associated fungi) (Matusick et al., 2008,

2010; Matusick and Eckhardt, 2010a, 2010b). Recent risk mapping efforts suggest widespread risk and occurrence of SPD across the pine-growing region in the southeastern U.S. (Meyerpeter, 2012). This is in direct contrast to previous studies that examined the possibility of a region-wide pine decline, but found that any apparent decline was an artifact of inappropriate analyses (Zeide, 1992; Gadbury et al., 2004).

4. Landscape level evaluation of southern pine decline

One approach to addressing whether or not SPD is present on a regional scale is through use of the USDA Forest Service's Forest Inventory and Analysis (FIA) Program, which is tasked with performing a complete, landscape-scale census of the nation's forest resources. Using a nationally consistent plot design (one sample location for every 2428 ha) and a systematic national sampling design for all lands, key measurements are taken on each plot (Bechtold and Scott, 2005; McRoberts, 2005). In addition, characteristics of both live and dead trees (e.g., height, diameter at breast height, mortality agent when applicable), topography of the plot, as well as whether the plot has been subjected to harvest activity or other noteworthy disturbance are recorded. Each plot is also assigned geographic coordinates.

A key aspect of the FIA inventory protocol is that it is annualized, such that some proportion (generally 20%) of the established plots in a given state are surveyed each year. In turn, all plots in that state are inventoried over a specified number of years, or "cycle", such that some proportion of the plots in all southeastern U.S. states have been re-measured at least once (i.e., surveyed during at least two consecutive 5-yr inventory cycles) since installation of the annualized inventory (i.e., not all plots in a state are measured each year, but all plots are measured on a 5-yr cycle).

To address the question of SPD occurrence in the South, we acquired data for re-measured plots from all states in the southern U.S. Across the region, a total of 6533 re-measured plots occurred in the loblolly pine and loblolly pine-hardwood forest types. We limited our analysis to the subset ($N = 5396$) of these plots that had not been harvested since initiation of the inventory. For each plot in this subset, we calculated the annual rate (m^2/ha/year) of pine mortality, net pine growth (current volume + harvested volume – initial volume), and gross pine growth (current volume + harvested volume + mortality volume – initial volume) based on differences in tree measurements between inventory cycles. We calculated the rates by regressing volume over time using generalized least squares (Smith and Conkling, 2005) to adjust for correlation between the initial and current measurements.

We performed a set of analyses using the calculated growth and mortality rates. First, we identified the re-measured plots in the study region that displayed negative net pine growth (i.e., where pine mortality exceeded growth). We then determined whether any FIA field crews documented any of these plots as disturbed. According to standard protocols outlined in the FIA national field guide (USDA Forest Service, 2014), crews are expected to identify the causal agent in a broad sense (e.g., "insect", "disease", and other categories in Table 1) for any plot disturbance of sufficient extent ($\geqslant 0.4$ ha) and severity ($\geqslant 25\%$ of all trees affected, or $\geqslant 50\%$ of a particular species). In addition, based on the plots' geographic coordinates, we performed two average nearest (geographic) neighbor distance analyses, one for the set of negative net growth plots and the other for the set of all (i.e., non-harvested) re-measured plots. This analysis yields an index calculated as the ratio between the observed average distance and the distance expected given a hypothetical random distribution with the same number of observations over the same total area. If the index value

---

[2] The taxonomy of this group is still being determined, hence, we will refer to the complex of *Leptographium* and *Grosmannia* species as "the *Leptographium* complex".

Table 1
Disturbance activity recorded for the re-measured plots (N = 181) that exhibited negative net pine growth (i.e., where mortality exceeded growth).

Disturbance agent	Frequency	Percent
No disturbance	1	0.55
Insect (e.g., southern pine beetle, *Ips* species)	71	39.23
Disease (e.g., fusiform rust, *Heterobasidion* root disease)	16	8.84
Fire	7	3.87
Domestic animal	1	0.55
Weather (unspecified, but possibly drought)	29	16.02
Ice	1	0.55
Wind (including hurricanes and tornadoes)	21	11.60
Flooding (weather-induced)	1	0.55
Vegetation (e.g., kudzu or other invasive plant)	8	4.42
Human	25	13.81

is <1, this indicates a clustered spatial pattern (e.g., if all plots having negative growth occur adjacent to each other). If the index value is >1, this indicates a dispersed spatial pattern (e.g., if all plots with negative growth were equally dispersed across the landscape). Our objective was to determine whether the set of negative net growth plots had a similar pattern to that observed for all plots.

Our results indicate a total of 181 plots with negative net pine growth, representing 3.4% of the plots in the full data subset (Fig. 1). FIA field crews identified all but one of these plots as substantially disturbed; the plot with no disturbance was in eastern Texas and had a recorded age of 82 years, indicating an old loblolly pine stand. The most common agents were insects and weather (including, ice, wind, and flooding; Table 1, Fig. 2). While we acknowledge the limitations of identifications of disturbance agents in the field, the disturbance agent categories that are most susceptible to misidentification – disease and weather (i.e., unspecified weather) – represented only 25% of the disturbed plots and <1% of the entire sample.

The average nearest neighbor distance analyses produced nearly identical index values for the set of negative net growth plots (ratio = 0.673, $P < 0.001$) and the set of all plots (ratio = 0.683, $P < 0.001$). This indicates that both sets of plots exhibit a clustered spatial pattern, which is expected for most tree species, as their regional distributions are largely shaped by physiographic and climatic constraints. More importantly, the nearly identical index values suggest that there is no distinctive regional pattern of abnormally high pine mortality.
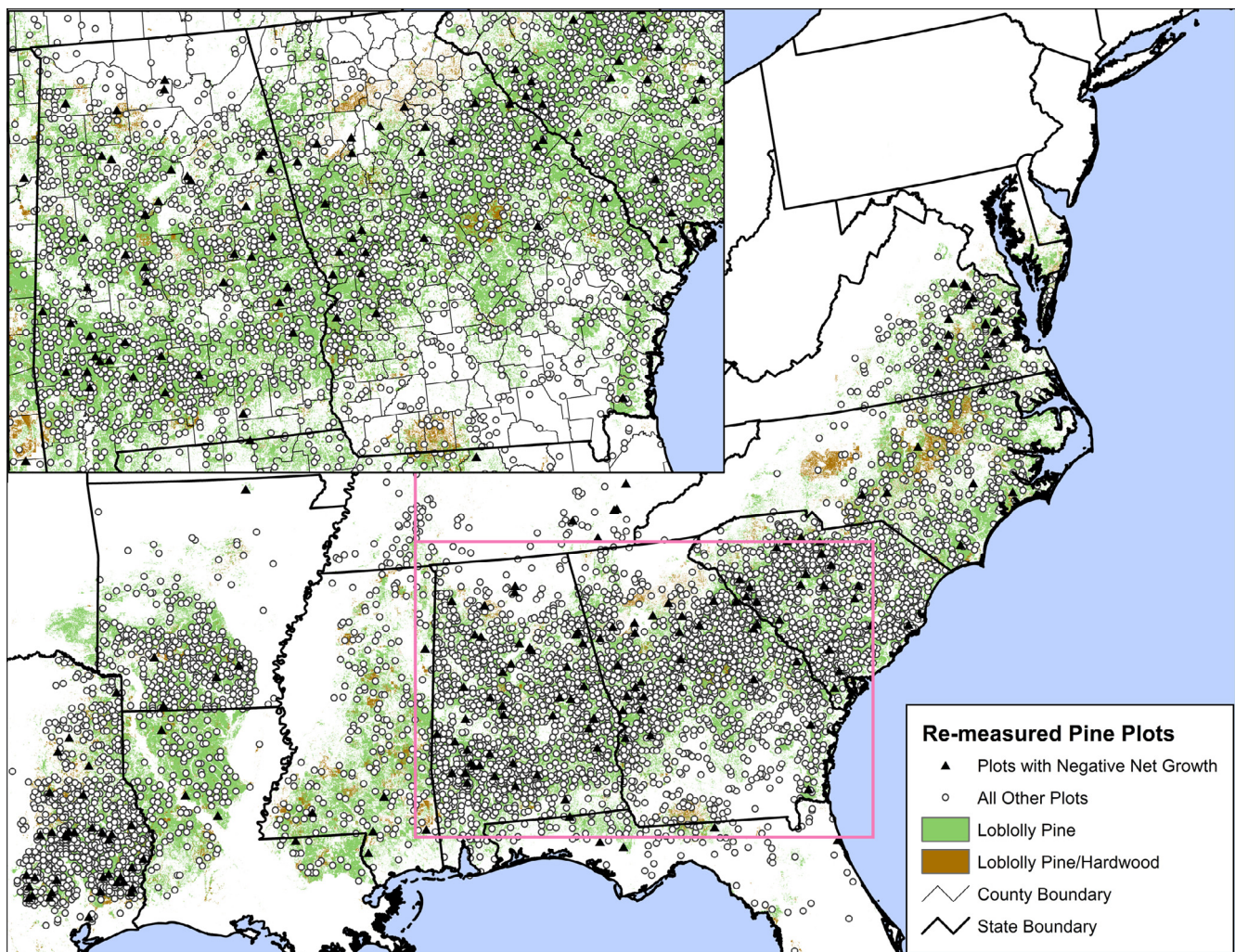

Fig. 1. Locations of re-measured Forest Inventory and Analysis (FIA) plots found in the loblolly pine and loblolly pine-hardwood forest types. The FIA is a comprehensive inventory system, with permanent plots established across all ownership types, that measures forest growth and health. Only plots that were not harvested since installation of annualized inventory are shown. Plots with negative net pine growth are flagged separately (black triangles). Inset map focuses on Alabama and Georgia, the two states where southern pine decline is reportedly most prevalent.
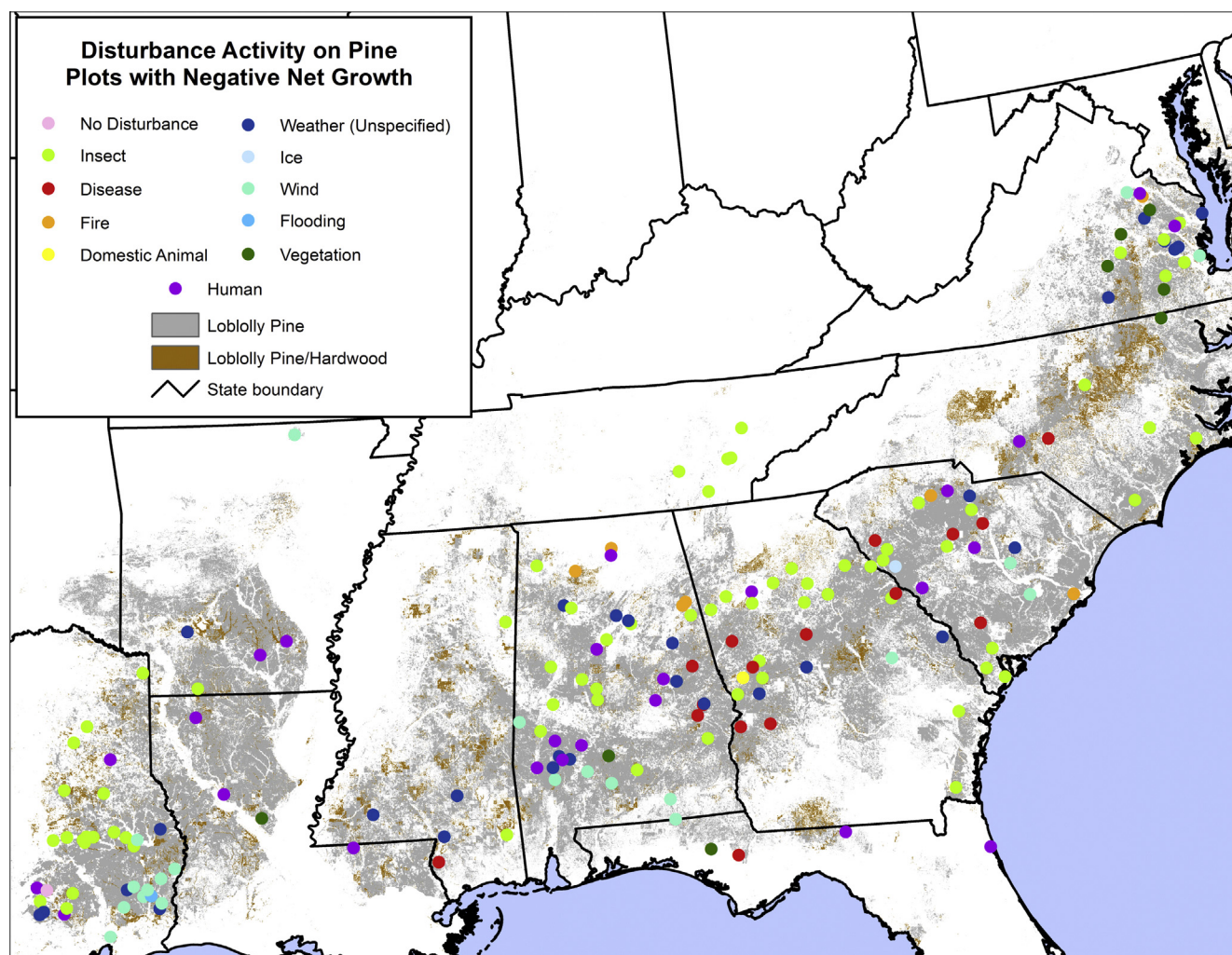
Fig. 2. Locations of re-measured Forest Inventory and Analysis (FIA) plots exhibiting negative net pine growth, labeled according to disturbance agent.

Table 2
Results of pairwise comparisons ($N = 5396$) between slope and aspect risk levels for net pine growth. Comparisons are for plots in the loblolly pine forest type. Significant differences between risk levels are indicated in bold.

Comparison	Entire region			Georgia			Alabama		
	Diff. estimate	SE	P	Diff. estimate	Std. Err.	P	Diff. estimate	SE	P
Slope									
10–15% vs. 5–10%	7.51	4.14	0.27	2.14	7.27	0.99	10.30	7.20	0.48
10–15% vs. <5%	−0.60	3.73	1.00	−7.54	6.83	0.69	4.59	6.86	0.91
10–15% vs. >15%	2.90	5.07	0.94	−2.81	8.09	0.99	18.07	8.94	0.18
5–10% vs. < 5%	−8.12	2.69	**0.01**	−9.68	5.92	0.36	−5.70	4.53	0.59
5–10% vs. >15%	−4.61	4.39	0.72	−4.95	7.43	0.91	7.77	7.45	0.72
<5% vs. >15%	3.50	4.00	0.82	4.74	6.99	0.91	13.47	7.13	0.23
Aspect									
N/NE vs. E, NW	6.92	3.44	0.18	3.64	6.62	0.95	5.22	5.61	0.79
N/NE vs. SE/S/SW	4.52	2.91	0.41	0.20	5.78	1.00	5.76	5.06	0.67
N/NE vs. W	0.66	4.39	1.00	8.50	8.74	0.77	1.66	7.47	1.00
E, NW vs. SE/S/SW	−2.41	4.07	0.93	−3.44	7.27	0.96	0.54	6.62	1.00
E, NW vs. W	−6.27	5.24	0.63	4.86	9.82	0.96	−3.56	8.63	0.98
SE/S/SW vs. W	−3.86	4.91	0.86	8.30	9.28	0.81	−4.10	8.26	0.96

In a separate analysis, we tested the hypothesis, suggested by Eckhardt and Menard (2008), that SPD is associated with particular topographic features: steep slopes and southern-southwestern aspects. In subsequent work, this hypothesis was translated into a geographic risk model for SPD that determined risk ratings based on a site's slope and aspect values (Meyerpeter, 2012). The risk

model included only these two factors, both of which were treated as categorical variables by assigning their values to corresponding risk levels: slopes of <5% were assigned to the lowest risk level of 1; slopes between 5% and 10%, risk level 2; slopes between 10% and 15%, risk level 3; and slopes >15%, risk level 4. With respect to aspect, north/northeastern (N/NE) aspects were assigned to risk

level 1; eastern (E) and northwestern (NW) aspects, risk level 2; western (W) aspects, risk level 3; and southeastern/southern/southwestern (SE/S/SW) aspects, risk level 4.

We analyzed slope and aspect separately, assigning each of the re-measured FIA plots to one of the four risk levels according to the plot's value for the topographic characteristic in question. For both net growth and mortality, we tested for statistically significant differences between risk levels using mixed models (PROC MIXED, SAS v. 9.3, SAS Institute Inc., Cary, NC, U.S.) that accounted for plot stand age, site index, and pine percentage (i.e., included these three factors as model covariates). We used least squares means (LSMEANS) to perform multiple pairwise comparisons. We performed these tests for the entire southeastern U.S. region as well as separately for Georgia and Alabama, the two states where

Table 3

Results of pairwise comparisons (*N* = 5396) between slope and aspect risk levels for net pine growth. Comparisons are for plots in the loblolly pine-hardwood forest type. Significant differences between risk levels are indicated in bold.

Comparison	Entire region			Georgia			Alabama		
	Diff. estimate	SE	*P*	Diff. estimate	SE	*P*	Diff. estimate	SE	*P*
Slope									
10–15% vs. 5–10%	3.03	5.00	0.93	−5.99	8.32	0.89	17.51	7.64	0.10
10–15% vs. <5%	−2.73	4.36	0.92	−5.02	7.59	0.91	7.74	6.94	0.68
10–15% vs. >15%	8.87	5.54	0.38	5.97	7.99	0.88	15.07	9.47	0.39
5–10% vs. <5%	−5.76	3.47	0.34	0.97	6.99	1.00	−9.77	5.60	0.30
5–10% vs. >15%	5.84	4.93	0.64	11.96	7.74	0.41	−2.44	8.71	0.99
<5% vs. >15%	11.60	4.29	**0.03**	10.99	6.94	0.39	7.33	8.17	0.81
Aspect									
N/NE vs. E, NW	9.76	4.30	0.11	11.09	7.81	0.49	0.85	6.61	1.00
N/NE vs. SE/S/SW	7.83	3.50	0.11	15.70	5.91	**0.04**	−0.84	6.24	1.00
N/NE vs. W	1.81	5.01	0.98	7.43	9.60	0.87	−1.03	8.08	1.00
E, NW vs. SE/S/SW	−1.93	5.01	0.98	4.61	8.17	0.94	−1.69	7.86	1.00
E, NW vs. W	−7.94	6.16	0.57	−3.66	11.22	0.99	−1.87	9.41	1.00
SE/S/SW vs. W	−6.02	5.63	0.71	−8.27	9.97	0.84	−0.18	9.15	1.00

Table 4

Results of pairwise comparisons (*N* = 5396) between slope and aspect risk levels for pine mortality. Comparisons are for plots in the loblolly pine forest type.

Comparison	Entire region			Georgia			Alabama		
	Diff. estimate	SE	*P*	Diff. estimate	SE	*P*	Diff. estimate	SE	*P*
Slope									
10–15% vs. 5–10%	0.18	2.15	1.00	0.94	3.20	0.99	−1.56	2.77	0.94
10–15% vs. <5%	−1.57	1.94	0.85	−3.69	3.00	0.61	1.31	2.64	0.96
10–15% vs. >15%	−0.98	2.63	0.98	1.86	3.56	0.95	−5.22	3.44	0.43
5–10% vs. <5%	−1.75	1.40	0.59	−4.63	2.60	0.28	2.88	1.74	0.35
5–10% vs. >15%	−1.16	2.28	0.96	0.92	3.27	0.99	−3.65	2.87	0.58
<5% vs. >15%	0.59	2.08	0.99	5.55	3.07	0.27	−6.53	2.74	0.08
Aspect									
N/NE vs. E, NW	−0.16	1.79	1.00	0.67	2.91	1.00	−2.90	2.15	0.53
N/NE vs. SE/S/SW	−0.05	1.51	1.00	4.04	2.54	0.39	−4.29	1.94	0.12
N/NE vs. W	2.48	2.28	0.70	1.51	3.84	0.98	0.71	2.87	0.99
E, NW vs. SE/S/SW	0.11	2.11	1.00	3.37	3.20	0.72	−1.39	2.54	0.95
E, NW vs. W	2.64	2.72	0.77	0.84	4.32	1.00	3.62	3.31	0.69
SE/S/SW vs. W	2.53	2.55	0.75	−2.53	4.08	0.93	5.01	3.17	0.39

Table 5

Results of pairwise comparisons (*N* = 5396) between slope and aspect risk levels for pine mortality. Comparisons are for plots in the loblolly pine-hardwood forest type.

Comparison	Entire region			Georgia			Alabama		
	Diff. estimate	SE	*P*	Diff. estimate	SE	*P*	Diff. estimate	SE	*P*
Slope									
10–15% vs. 5–10%	1.88	4.89	0.98	0.44	9.57	1.00	−6.90	5.68	0.62
10–15% vs. <5%	1.55	4.27	0.98	−4.30	8.73	0.96	0.42	5.16	1.00
10–15% vs. >15%	−2.91	5.42	0.95	2.88	9.19	0.99	5.26	7.04	0.88
5–10% vs. <5%	−0.34	3.40	1.00	−4.74	8.04	0.94	7.33	4.16	0.30
5–10% vs. >15%	−4.80	4.82	0.75	2.44	8.89	0.99	12.16	6.47	0.24
<5% vs. >15%	−4.46	4.20	0.71	7.18	7.98	0.81	4.83	6.07	0.86
Aspect									
N/NE vs. E, NW	−3.96	4.21	0.78	1.90	9.06	1.00	4.85	4.85	0.75
N/NE vs. SE/S/SW	−3.72	3.42	0.70	−4.92	6.86	0.89	−1.81	4.57	0.98
N/NE vs. W	2.25	4.90	0.97	4.65	11.14	0.98	8.26	5.92	0.50
E, NW vs. SE/S/SW	0.24	4.90	1.00	−6.81	9.48	0.89	−6.66	5.76	0.66
E, NW vs. W	6.21	6.03	0.73	2.76	13.02	1.00	3.42	6.90	0.96
SE/S/SW vs. W	5.97	5.51	0.70	9.57	11.56	0.84	10.08	6.71	0.44

SPD is reportedly most prevalent (Eckhardt et al., 2007; Menard, 2007; Eckhardt and Menard, 2008).

Out of the 36 comparisons for net pine growth in the loblolly pine forest type (Table 2), we found one instance where net pine growth was significantly and negatively related to increasing slope across the entire southeastern U.S. region. Similarly, out of the 36 comparisons for net pine growth in the loblolly pine-hardwood forest type (Table 3), we found one instance where net pine growth was significantly and negatively related to increasing slope across the entire southeastern U.S. region and one instance where net pine growth was significantly and negatively related to increasing aspect in Georgia. With respect to pine mortality, we found no significant differences related to slope in the loblolly pine (Table 4) or loblolly pine-hardwood forest types (Table 5). Overall, the number of significant differences was less than one would expect by random chance (at $\alpha = 0.05$). In contrast to current literature (Eckhardt and Menard, 2008; Meyerpeter, 2012), our results suggest that slope and aspect are not significant factors in pine growth and mortality in the FIA data, after accounting for variation in stand age, site index, and stand composition.

In summary, the hypothesis that SPD is a regionally important decline syndrome is not supported by the FIA data. Only a small percentage of non-harvested pine plots across the southeastern U.S. exhibited negative net growth (i.e., abnormally high mortality), and virtually all of these plots were identified by FIA field crews as having been disturbed by common agents including insects, fire, weather, and invasive vegetation. The lack of a distinctive spatial pattern in these negative net growth plots suggests that there are no obvious hotspots of high mortality that can be linked to even a more localized, smaller-scale phenomenon impacting pine health. Our results related to topographic drivers of SPD risk are similar to those that found no relationship between slope and/or aspect with loblolly pine health in stands at Ft. Benning, Georgia (Ryu et al., 2013). After accounting for expected variation due to stand age, site index, and plot pine proportion, there were minimal differences in pine growth and mortality between steep and gentler slopes, and between south-southwest aspects and all other aspects in the FIA data.

5. Potential factors affecting tree health

The lack of consistent patterns in pine growth or mortality related to individual disturbance factors in region-wide FIA data suggests that SPD may be a stand-specific issue. To further explore this hypothesis, we need to consider major factors (as described in subsequent sections) that typically interact to influence pine health and growth on a particular site.

5.1. Site conditions and soil

Forest growth, productivity, and tree health are a function of site productivity and soil conditions (e.g., McLaughlin et al., 2011) (Table 6). Tree health is impacted by factors that affect soil fertility and the availability of essential plant nutrients, especially in southern pines (Fox et al., 2007). Many soils in the southern U.S.

Table 6
Soil attributes associated with SPD and other tree maladies.

Tree species	Decline/disease	Soil attributes	Incidence, severity, impacts	Reference
	Other regions			
Eastern white pine	Decline	Texture, drainage, pH	Incidence increases in fine-textured soils and poorly drained soils	Halambek (1976)
Western pines	Pole blight	Water retention and soil depth, but details unavailable	Available water-holding capacity in top 32″ of soil inversely related to % BA[a] infected	Copeland and Leaphart (1955)
Red and jack pines	Decline	Texture, pH, OM[b] and nutrients to 60 cm	Higher pH w/lower OM on symptomatic stands	Klepzig et al. (1991)
	Southern region			
Loblolly and slash pines	Heterobasidion root disease	Texture, pH, OM to 15 cm	Damage worse on deep, dry sand pockets with little or no OM and soils w/higher pH and higher % sand or clay	Froelich et al. (1966)
Loblolly and slash pines	Fusifom rust	Texture to 15 cm, SI[c], drainage, site prep	More rust on better-drained soils and sandy loams; less rust on poorly drained and sandy soils	Schmidt et al. (1988)
Loblolly and shortleaf pines	LLD[d]	Drainage and aeration; CO_2 and O_2 in various soils in the greenhouse; *P. cinnamomi*. Develops best in loam-silt soils, poorly in heavy clays and intermediately in sandy soils due to aeration	Root injury by *P. cinnamomi* worst in clayey, wet soils aggravated by poor aeration and fertility	Campbell and Copeland (1954) and Zak (1961)
Shortleaf pine	Decline on LLD sites	Erosion and drainage classes; subsoil characteristics	SPD and LLD observed on eroded soils and those with restrictive layers; None directly measured.	Oak and Tainter (1988)
Shortleaf pine	LLD	Erosivity, permeability, texture and depth	LLD more severe on eroded soils and soils with restrictive layers	Campbell and Copeland (1954)
Shortleaf pine	LLD	Series, texture, aspect, drainage, topographic position	No correlation between silt + clay content in surface horizon and SI or LLD incidence	Copeland and McAlpine (1955)
Longleaf pine	"decline syndrome"	No soils data specified	Decline associated with stressed sites	Matusick et al. (2010)
Sand pines	Sand pine-root disease complex w/*P. cinnamomi*	Drainage and texture; Soil cores at 0–20 cm, but for fungal counts only	Disease worse on poorly drained sandy or heavier clay soils	Barnard et al. (1985)
Southern yellow pines	Pine decline	No soils data specified	Worst incidence on low quality sites	Eckhardt et al. (2010)

[a] BA = basal area.
[b] OM = organic matter.
[c] SI = site index.
[d] LLD = littleleaf disease, *Phytophthora cinnamomi* Rands.

have low inherent soil fertility, in part due to historical land usage patterns (e.g., land clearing, erosion, intense agricultural use). In general, loblolly pine is more nutrient demanding than other southern pines (Jokela et al., 2010). The decision to plant loblolly pine and specific genotypes of loblolly pine on a particular site depends, in part, on the expected silvicultural regime planned during the rotation (McKeand et al., 2006). Loblolly pine genotypes selected for rapid growth are more likely than other species to require fertilization to maintain stand vigor. The vast majority of loblolly pine plantations respond positively to N or N plus P fertilization, and fertilization of loblolly pine plantations at establishment and during the rotation is the norm (Fox et al., 2007). Of particular concern is the potential for significant stress to occur when thinning and fertilization treatments originally scheduled for intensively managed pine stands are skipped due to ownership changes or economic conditions.

Soil fertility is likely a contributing factor in declines. For example, littleleaf disease, *Phytophthora cinnamomi* Rands, of loblolly and shortleaf pine is associated with eroded, low fertility sites with poor internal drainage (Campbell and Copeland, 1954; Zak, 1961). Although soil conditions have been linked to health issues in southern pines (especially regarding *H. irregulare*), these relationships are less consistently observed than for species such as white pine (*Pinus strobus* L.), sugar maple (*Acer saccharum* Marsh.), or yellow cedar (*Cupressus nootkatensis* [D. Don.]).

Tree health is also affected by physical characteristics of soil. In contrast to many areas where forests are restricted to a relatively small range of soils that are too infertile, rocky, thin or wet for other uses, southern pine forests occur across a range of soil types and conditions encompassing productive agricultural lands, former pastures, and severely eroded heavy clay soils. To that end, commercially valuable tree species are often planted outside their natural range (Mead, 2013; Moya et al., 2013; Urban et al., 2013) or on sites that would otherwise be dominated by other species (Nemeth, 1973; Lenhart et al., 1985; Lohrey and Kossuth, 1990). For example, although the natural ranges of southern pines (especially loblolly and longleaf) overlap (Little, 1971), each species tends to dominate different habitats within their overlapping ranges. In the Coastal Plain, loblolly pine grows well on soil with poor surface drainage and a subsoil clay layer; in the Piedmont, uneroded soils are preferred (Londo and Ezell, 2011). Longleaf pine is suited to, and most competitive on, well- to moderately well-drained, often sandy, soils in the Coastal Plain with regularly-occurring fire (Londo and Ezell, 2011). On these sandy sites, loblolly pine requires much greater silvicultural inputs to achieve acceptable growth than longleaf pine (Samuelson et al., 2004; Williams and Gresham, 2006), and many times these inputs are not economically viable.

5.2. Drought and climate change

The southeastern U.S. has undergone several droughts in the past century (Seager et al., 2009; Gilbert et al., 2012; Maxwell et al., 2012). Such drought events can be very severe locally (Morehart et al., 1999), and can be either longer in duration (several years, e.g., 1998–2002 in North Carolina [Weaver, 2005]) or very short, extremely dry spells that persist for less than a year (Manuel, 2008; Seager et al., 2009). In the southeastern U.S., this variability in precipitation has intensified recently (Wang et al., 2010; Li et al., 2011), and weather models predict this trend will continue under future climate change scenarios (Li et al., 2011, 2013). Regardless of the duration, drought events have a profound negative effect on plant growth (Peters et al., 2003), and can result in up to 40% decrease in net primary production (Chen et al., 2012). While the perennial life history of trees may confer several advantages over annual plants, trees are not immune to the effects of drought. Lack of precipitation (or increased variability in rainfall and drought events) and increases in temperature could be major factors responsible for reduced tree growth as well as increased mortality and susceptibility to insects and diseases (Hanson and Weltzin, 2000; Allen et al., 2010; Adams et al., 2012; Williams et al., 2012). Pines are particularly susceptible to the negative effects of drought globally (Bigler et al., 2006; Klos et al., 2009; Kharuk et al., 2013; Granda et al., 2014) and especially in the southeastern U.S. (Vose and Swank, 1994; Bhuta et al., 2009; Bracho et al., 2012; Graham et al., 2012).

Landscape-level repercussions of drought can affect multiple biogeochemical processes and biotic interactions among trophic levels. Smaller trees are more susceptible to drought than larger trees. Loss of leaf cover can result in elevated ground temperatures and increased evapotranspiration, leading to drier conditions for remaining trees (Adams et al., 2012) and further stress on those individuals. Allen et al. (2010) outlined several key knowledge gaps regarding forests and drought, of which three are particularly relevant to this review: (1) "Mechanistic understanding of climate-induced tree mortality requires improved knowledge of belowground processes and soil moisture conditions", (2) "The direct effects of climate on the population dynamics of almost all forest insect pests and other biotic disturbance agents remain poorly understood but are important to modeling climate-induced forest mortality", and (3) "Feedbacks between physiological stress (and tree mortality) driven by climate and other forest disturbance processes (e.g., insect outbreaks, fire) are poorly understood". These crucial knowledge gaps may be particularly relevant to the concept of SPD, as they indicate that we do not yet know enough to accurately and confidently determine whether or not loblolly pines are dying at non-naturally occurring rates, and if so, from what causes. It generally takes multiple years of persistent drought to see high tree mortality (Guarín and Taylor, 2005; Millar et al., 2007), although even short drought periods likely have an impact on tree health and growth. In fact, most evidence of drought-induced tree mortality in conifer forests comes from the western U.S. (e.g., in the Southwest and Sierra Nevada Mountains), which has seen persistent drought conditions over the last two decades. In the southeastern U.S., especially in pine-dominated regions – the North Carolina example of Weaver (2005) notwithstanding – the region generally experiences a pattern of frequent late-summer droughts (Hanson and Weltzin, 2000). This emphasizes our lack of knowledge regarding whether frequent (but not necessarily persistent) seasonal droughts result in enough cumulative tree stress that they likely contribute to "decline" symptoms in susceptible pine stands.

5.3. Insects

Bark and woodboring insects tend to garner much attention as related to tree mortality. For example, certain bark beetle genera such as *Dendroctonus* (e.g., the southern pine beetle, *D. frontalis* Zimmerman [SPB]) are capable of infesting and killing healthy trees. Yet, especially in the southern U.S., bark and woodboring insects are more commonly a secondary factor in the ultimate demise of a tree, and arrive and establish once the tree is sufficiently stressed by other abiotic or biotic factors (Marchetti et al., 2011; Zegler et al., 2012).

In southern pine ecosystems, *Ips* species (*Ips avulsus* [Eichhoff], *I. grandicollis*, and *I. calligraphus* [Germar]) are often found in weak and/or dying pine trees (Berisford and Franklin, 1971; Flamm et al., 1993). *Ips* beetles can attack individual trees or groups of trees within a stand (Bryant et al., 2006), and in rare cases attack and kill entire stands, usually when stand health has been compromised from prolonged drought or because of damage caused by disturbance such as fire or storms (Clarke et al., 2000). Most literature

supports the notion that North American *Ips* species attack weakened, dying, or dead trees (e.g., Erbilgin and Raffa, 2002; Negron and Wilson, 2003), and that healthy trees can generally withstand *Ips* attacks (Anderson and Anderson, 1968).

Seven species of rhizophagous beetles occur in pine ecosystems of the southeastern U.S.: *Dendroctonus terebrans* (Olivier), *Hylastes opacus* Erichson, *Hylastes porculus* Erichson, *Hylastes salebrosus* Eichhoff, *Hylastes tenuis* Eichhoff, *Hylobius pales* (Herbst), *Pachylobius picivorus* (Germar), and *Pissodes nemorensis* Germar. Of these species, *H. opacus* is non-native to North America. *Hylastes salebrosus* and *H. tenuis* have been observed breeding and reproducing in the roots of trees with dying and dead crowns (Matusick et al., 2013). While mass attacks by *D. terebrans* (e.g., Smith and Kowal, 1968) can occasionally kill healthy mature trees (Drooz, 1985; Staeben et al., 2010), there is no similar evidence with respect to *Hylastes*, *Hylobius*, *Pachylobius*, and *Pissodes* species. These beetles primarily attack the lower bole or roots of weakened, stressed, dying, or dead trees, and most can breed in and are attracted to cut stumps or logs (Ciesla and Franklin, 1965; Warner, 1966; Drooz, 1985; Staeben et al., 2010). Rhizophagous weevils are a critical component of stump and root degradation (Wallace, 1953). While a few species (e.g., *Hylobius*, *Pachylobius*, and *Pissodes* species) can be aggressive and impact healthy trees or seedlings, most rhizophagous weevils are considered secondary pests (Sullivan et al., 2003; Matusick et al., 2013).

Rhizophagous beetles may act as fungal vectors (see "Pathogens" section). For instance, in the Great Lakes region of the U.S., red pine plantations have experienced a syndrome called "Red Pine Pocket Decline". Trees are initially stressed or weakened by factors that are uncertain but likely abiotic in nature (e.g., water stress or heat stress) (Klepzig et al., 1991). Red pine is at the southern edge of its natural range in Wisconsin, so it may be that rising temperatures, drought, or heat stress play roles as predisposing factors in the syndrome. This may reduce defensive abilities, allowing infestation by a suite of root and lower-stem feeding beetles. The rhizophagous weevils *Hylobius radicis* Buchanan, *Hylobius rhizophagus* Millers, Benjamin & Warner, *H. porculus*, and *P. picivorus* attack the root collar and coarse roots, while *Dendroctonus valens* LeConte attacks the lower trunk and root collar. These beetle species are associated with moderately virulent fungi, *Leptographium terebrantis* Barras and Perry and *Leptographium procerum* (Kendrick) Wingfield (Klepzig et al., 1991, 1995), which are inoculated into the roots of attacked trees. A key factor in the red pine system is the high degree of root grafting among pine trees throughout affected stands. In comparison, southern pines are much less likely to root graft than red pines. This, coupled with the circular-shaped pattern of decline and mortality observed in red pine pocket decline, indicates fungal infection from a central source and subsequent radial spread. Even so, rhizophagous beetles and fungi in red pine trees do not kill the tree; rather, their presence further stresses and weakens the tree, increasing its susceptibility to stem-colonizing bark beetles such as *Ips* spp. and red turpentine beetles (*Dendroctonus valens* LeConte) (Erbilgin and Raffa, 2002).

5.4. Pathogens

Root disease pathogens, particularly those affecting woody roots, are regarded as key drivers of forest ecosystems (Otrosina, 2005). They may act as primary disturbance agents or secondary consequences of disturbance (Otrosina and Ferrell, 1995) depending upon several pathological, ecological, and environmental factors. Root disease pathogens are often implicated in forest declines, but are usually considered secondary factors (Hansen et al., 1988; Hennon, 1990; Bal et al., 2013). Because root diseases are often cryptic, and in many cases not identified in the initial stages without considerable effort, they are often overlooked in assessments of stand health.

Several root pathogens are prevalent in forests of the southeastern U.S., but rarely implicated as factors in SPD – even if the pathogens are considered primary mortality factors. For instance, *H. irregulare* is an important primary pathogen of conifer forests across the southeastern U.S. This pathogen is spread by aerial spore dispersal and subsequent infection through freshly cut surfaces such as stumps and/or root wounds (Otrosina and Cobb, 1989; and references therein). The fungus then colonizes healthy roots of adjacent trees, spreading from diseased to healthy tissue via root grafts or contact. Growth losses by *H. irregulare* infection can be significant (Tainter et al., 1989), as the additional stress resulting from root disease often renders trees susceptible to stem-colonizing bark beetles (Cobb et al., 1974; Alexander et al., 1981). *Phytophthora cinnamomi* occurs in the Piedmont region of the southeastern U.S. (Mistretta, 1984) and can cause serious damage and economic losses on southern pines (Campbell and Copeland, 1954). *Phytophthora cinnamomi* spores spread via soil-borne water. Fungal spores can infect roots and cause needle shortening and discoloration, thin crowns, branch dieback, and reduced diameter growth (Campbell and Copeland, 1954; Mistretta, 1984). Fertilization can help alleviate disease symptoms. *Pythium* spp. fungi, implicated as factors in littleleaf disease (Lorio, 1966; Hendrix and Campbell, 1970), are often associated with *P. cinnamomi* (Otrosina and Marx, 1975). *Armillaria mellea* (Vahl) P. Kumm., or Armillaria root rot, is a ubiquitous pathogen affecting many plant species around the world (Wargo and Shaw, 1985; Williams et al., 1986). The pathogen either parasitizes living tissue or functions as a saprophyte on dead woody tissue. Armillaria root rot is spread when fungal rhizomorphs or uninfected roots contact each other underground. Damage can include growth reductions and lower stem decay, or tree mortality. This disease may go unnoticed, or its damage may be attributed to other factors (Williams et al., 1986).

While *H. irregulare*, *P. cinnamomi*, *Pythium* spp., and *A. mellea* are all quite common across southeastern U.S. forests, none have been implicated as contributing factors in SPD. In fact, Eckhardt et al. (2007, 2010) indicate that these fungi are either not present in tree roots or not associated with SPD sites. However, one group of Ophiostomatoid fungi – the *Leptographium* complex – has been implicated as an important pathogen in SPD (Eckhardt et al., 2007, 2010). These fungi are associated with (and transmitted by) native root feeding Curculionidae including *Hylastes* spp., *Hylurgops* spp., *Hylobius* spp., and *Pissodes* spp. (Klepzig et al., 1991; Nevill and Alexander, 1992; Eckhardt et al., 2004a). The beetles acquire fungal spores from the microscopic conidiophores inside the insect galleries. Unlike those of *H. irregulare*, *P. cinnamomi*, or *A. mellea*, spores of the *Leptographium* complex are not suited to aerial or water dispersal, and do not persist in soil for more than a few months, making insects the critical component of overland spread (Lewis et al., 1987).

While most of the *Leptographium* complex (not including *L. wageneri* [W.B. Kendr.] M.J. Wingf.) is comprised of opportunistic pathogens infecting previously-compromised trees (Harrington and Cobb, 1988), there are instances where tree mortality in several *Pinus* spp. was associated with the presence of the *Leptographium* complex (Highley and Tattar, 1985; Klepzig et al., 1991; Otrosina et al., 1997, 1999, 2002; Sullivan et al., 2003; Eckhardt et al., 2007). In these examples, closer scrutiny of stand condition, ecological status, and edaphic conditions revealed that factors such as older tree age, high basal area, degraded and eroded soils, silvicultural treatments (e.g., prescribed fire conditions), and trees growing on edge of their ecological range were strongly associated with recovery of these fungi from tree roots and associated tree mortality.

6. Available SPD information and forest management

6.1. Natural pine mortality rates

The background mortality rate for temperate forests in the eastern U.S. is about 1–2% per year on a tree density basis (Brown and Schroeder, 1999). Major disturbances (e.g., hurricanes) might increase forest mortality at a regional scale to 5–15% (Brown and Schroeder, 1999). For loblolly pine plantations in the southeastern U.S., Zeide and Zhang (2006) reported an annual probability of mortality from all causes of 0.038 (i.e., approximately 4 out of every 100 planted trees die each year). Notably, the authors attributed a fair amount of this mortality to insects, specifically the SPB. Loblolly pine on heavily managed and military-used land experienced 8.2% morality, although these plots contained older stands (aged 38–98 yr; Ryu et al., 2013).

At the stand level, mortality rate (like growth rate) depends on site index, stand age, and species. Older stands exhibit an increase in density-dependent mortality due to greater resource competition between trees. Still, this effect of competition is also seen in relatively young stands. Martin and Jokela (2004) reported cumulative mortality rates ranging between 10.8% and 22.5%, depending on site treatment, in 19-year-old stands in north-central Florida (where length of a single rotation ≈ 18 years). The highest mortality rates were in plots subjected to fertilization, but in all cases, the mortality reflected a process of self-thinning, with most mortality occurring in low to average diameter classes (i.e., larger trees are more competitive for resources and have a higher probability of survival). Better survival of larger trees continues as a stand matures. For example, between 25 and 44 years of age, an even-aged loblolly pine stand lost 62% of trees 10–20 cm in diameter (the smallest size class present at that age range), but only 12% of trees 20–40 cm in diameter (Peet and Christensen, 1987).

It can be difficult to distinguish excessive from normal mortality rates in larger, relatively older pine stands (i.e., >40 years old), especially those that have been suggested to be most susceptible to SPD (Eckhardt et al., 2007). Stands sampled having symptoms of SPD ranged from 29 to 65 years old with a mean age of 47 ± 2 years old, and most were grown on poor sites or soils (Brown and McDowell, 1968; Eckhardt et al., 2007). Roth and Peacher (1971) found <1% annual mortality over a 5-yr monitoring period in initial SPD plots in Alabama. In addition, plots symptomatic for SPD had significantly greater fire damage than asymptomatic sites (48.5% compared to 10.5%; Eckhardt et al., 2007). While increased tree age and reduced radial growth have been associated with the presence of the *Leptographium* complex (Eckhardt et al., 2007), pine growth rates decline in older stands due to hydraulic limitation and declining respiration (Drake et al., 2010, 2011) even when site conditions are good (Samuelson et al., 2013).

In short, a low level of annual mortality is to be expected in pine stands regardless of age, and due to many causes, especially competition between trees. In practical terms, a noteworthy health issue only exists if a stand exhibits excessive mortality of relatively large-diameter trees. This further depends on stand age, since at some point all of its trees become large, and thus only large trees can die (Peet and Christensen, 1987). Separating tree mortality resulting from natural or specific factors with that of the SPD is, at this time, impossible to do because of the plethora confounding factors.

6.2. Contribution of abiotic factors to decline and disease

Fire has been implicated in southern pine decline and mortality, as symptomatic roots were associated with increased fire damage (Eckhardt et al., 2007; Menard et al., 2010). Additionally, greater numbers of rhizophagous weevils were captured and a higher incidence of infection by the *Leptographium* complex was observed in severely burned areas (Hanula et al., 2002), highlighting the importance of fire in southern pine health issues. National Forests in the southeastern U.S. use prescribed burning regularly and damage from fire is a primary factor in tree damage leading to mortality (Hanula et al., 2002).

Site suitability for loblolly pine across the landscape may also be influencing southern pine health. The Conservation Reserve Program (CRP) and other federal acquisition programs which resulted in the planting of loblolly pine across millions of hectares of formerly agricultural land in the southeastern U.S., has been acknowledged as potentially contributing to pine health issues, as many CRP plantings had long-term productivity issues (Stubbs, 2014). The relatively greater nutrient demands of loblolly pine, especially for faster growing plantation selections, may contribute to stress and health issues on such sites. For example, Hess et al. (1999) associated loblolly decline symptoms found in sites in the Oakmulgee Ranger District of the Talladega National Forest with littleleaf disease, but noted that the agricultural history of these sites, because it impacted soil nutrient availability and internal drainage, could explain the disease's presence. They also noted that, in some cases, littleleaf disease symptoms have been delayed and tree conditions improved via soil application of inorganic nitrogen. Other researchers (e.g., Mitchell et al., 1991) have implicated biotic agents as factors contributing to pine mortality on former agricultural sites. Many of the SPD sites identified by Eckhardt et al. (2007) and Eckhardt and Menard (2008) were from the Oakmulgee Ranger District, which was largely assembled from formerly agricultural land reclaimed by the CRP or similar programs (Hess et al., 2002); other plots analyzed in central Alabama probably had a similar history considering their location. As such, careful interpretation of any land use history data related to tree decline syndromes is essential.

Based on Sinclair's (1966) model on factors affecting tree health, managing sites that are declining requires identifying the abiotic conditions that predispose the sites to accumulated stress and eventual attack by biotic agents attracted to damaged trees. Reducing fire and mechanical damage, better site selection, nutrient inputs (especially nitrogen), and better matching of planted species to the specific site are viable management options.

6.3. Biotic agents and causality

The death of a tree is a complex ecological process (Franklin et al., 1987; Stephenson et al., 2011), and many factors work in concert to cause tree mortality (Houston, 1981; Manion, 1981; Mueller-Dombois, 1987; Stephenson et al., 2011). Literature from forest decline syndromes around the world supports the notion that predisposing factors are required to weaken trees prior to insect/fungal infection (Sinclair, 1964; Houston, 1981; Hinrichsen, 1987; Ciesla and Donaubauer, 1994; Jurskis, 2005). In fact, specific causes of tree mortality in forest declines are extremely difficult to identify. Dobbertin et al. (2001) and Lännenpää et al. (2008) recorded factors responsible for tree mortality, and the majority of recently dead trees could be associated with a fungus. However, the authors could not determine if the trees were susceptible to fungal infection due to drought or another abiotic factor.

Artificial inoculations with various ophiostomatoid fungi have elicited only relatively small lesions in either seedlings or mature trees (Raffa and Smalley, 1988; Klepzig et al., 1991, 2005; Långström et al., 2001; Eckhardt et al., 2004b; Matusick and Eckhardt, 2010a, 2010b; Matusick et al., 2012) suggesting that the fungi have limited effects in healthy trees. As such, based on the available evidence and complexity of the death process in trees, it would be premature to label fungal agents as causes of SPD or tree mortality associated with SPD.

6.4. Potential for Leptographium complex-induced mortality in mature southern pine

Previous research (Mitchell et al., 1991; Zwolinski et al., 1998; Eckhardt et al., 2007) has linked soil biota to mortality in pine stands, but lacked evidence that rhizophagous beetles and their associated fungi can kill mature trees in the field. Similarly, inoculation studies have indicated that the causal relationship between the *Leptographium* complex and southern pine root diseases have to be interpreted carefully (Eckhardt et al., 2004a). The available data suggest that the *Leptographium* complex is relatively common in the southeastern U.S. forest landscape (http://www.auburn.edu/~eckhalg/PDF%20files/Loblolly_Pine_Decline_and_Leptographium_Overview.pdf). However, causality between tree death and biotic factors in SPD is not clear. While recent research suggests a link between abundance of rhizophagous weevils and SPD (Eckhardt et al., 2007; Zanzot et al., 2010) or stand thinning (Zeng et al., 2014), other research from the southeastern U.S. indicates that healthy stands are not at risk for attack by rhizophagous or stem-infesting beetles. Hines and Heikkenen (1977) found that over 99% of the seven most common bark and woodboring species (including *H. pales* and *H. porculus*) were captured at girdled compared to control Virginia pine (*Pinus virginiana* Mill.) trees. Prior to girdling, <1 *H. porculus*/tree/month was captured on sample trees, but after those same trees were girdled capture rates rose to >65 *H. porculus*/tree/month (Hines and Heikkenen, 1977). Our own work in the southeastern U.S. also indicates that these rhizophagous beetles are primarily associated with girdled (stressed) versus ungirdled (unstressed) pine trees (Helbig, Coyle, Klepzig, Nowak, Gandhi, unpublished data). As such, the idea that these rhizophagous weevils cause pine tree mortality needs to be fully investigated before making pine management decisions.

6.5. Management implications

The hypothesis that southern pine stands with declining trees be labeled SPD is not currently supported in the literature. The term SPD (Zeng et al., 2014) appears to be used based on the common presence of root-feeding weevils and their association with the *Leptographium* complex in unhealthy stands. Managing for a presumed causal agent (e.g., insect or its transmitted fungal pathogen) rather than for the local events' unique circumstances may lead to counter-productive management practices. For example, a focus on the *Leptographium* complex and their vectors as suggested by Eckhardt et al. (2010) may be managing for indicators rather than causes of a forest health problem. Suggesting management practices that focus on secondary invaders such as rhizophagous weevils after thinning (Zeng et al., 2014) instead of primary factors can potentially exacerbate other pine health problems. For example, thinning has long been established as a beneficial silvicultural practice worldwide. It is well-known that as trees age, productivity declines. In stands managed for production, thinning must occur to prevent overstocked stands, which can lead to stressed trees. Thinning leads to growth increases (Della-Bianca and Dils, 1960; Aussenac and Granier, 1988; Zhang et al., 2006), increased physiological functioning (Ginn et al., 1991), and can reduce susceptibility to insect outbreaks (Mitchell et al., 1983; Fettig et al., 2007, 2014; Wallin et al., 2008). Thinning is one of the primary silvicultural prescriptions recommended to increase resistance of pine stands to SPB (Brown et al., 1987; Belanger et al., 1993; Turchin et al., 1999; Nowak et al., 2008). In fact, a recent study definitively showed that thinning can reduce SPB damage on both local and landscape scales (Nowak et al., in press). The conclusion that thinning results in an increased abundance of pathogen-carrying *Hylastes* spp. beetles (Zeng et al., 2014) is not surprising. Thinning, by definition, creates stumps, which are the preferred oviposition substrate for these weevils. Terpenes associated with recently-cut trees (e.g., ethanol and turpentine) are also known attractants for several species of root weevils (Lindelöw et al., 1993). Thus, one would expect a short-term (i.e. 1–2 yr) increase in rhizophagous weevil abundance. A study that monitored insect populations for one year captured this increase via traps and examining stumps (Zeng et al., 2014). However, it is likely that *Hylastes* spp. numbers would have returned to pre-thinning levels, as shown by Sullivan et al. (2003). In addition, health issues were not noted in thinned stands
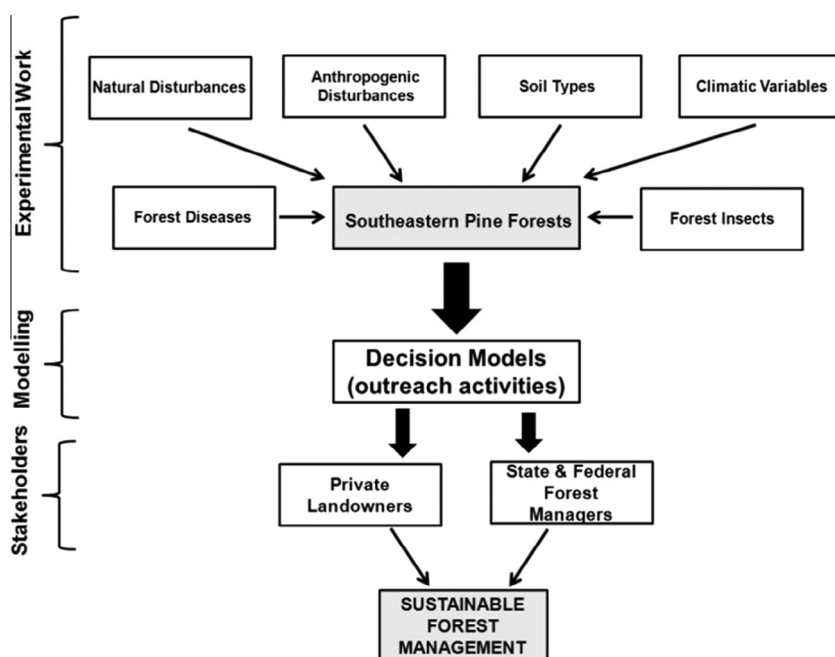

Fig. 3. Conceptual model outlining the complex interactions among factors affecting southern pine health, landowner education, and management decisions needed to ensure sustainable forest management. While this particular model specifies southern pine forests, the model can be adapted to any forest system worldwide.

(Zeng et al., 2014), so the question whether a short-term increase in rhizophagous beetles after thinning leads to tree health issues is still unanswered. A wealth of literature supports thinning as a management strategy to reduce pine stand susceptibility to bark beetle outbreaks. In contrast, there is relatively little literature to support the hypothesis that *Hylastes* spp. colonize healthy trees and contribute to SPD. Therefore, literature and expert opinion continues to strongly support thinning as a silvicultural option to reduce SPB susceptibility, improve tree health, and increase residual tree growth.

Screening for resistance to these secondary individual components of declining trees (e.g., Singh et al., 2014) also seems premature since there is no way to predict how different tree genotypes would perform when subjected to multiple stressors, nor is this a test of their tolerance of insect herbivory. Further, seedlings were used in such trials (Singh et al., 2014) instead of mature trees, which are the host of the fungal vector, *Hylastes* spp. Extrapolating data from seedling inoculation studies to make predictions on mature tree resistance may be premature.

7. Conclusions

Presently, there is little evidence that SPD exists as a region-wide phenomenon or is an emerging forest health issue in the southeastern U.S. Instead, our analyses of FIA data indicate that pine health issues in the southeastern U.S. tend to occur in localized areas (SPB outbreaks notwithstanding), likely resulting from a complex interaction between predisposing and inciting factors. Several factors (predisposing, inciting, and contributing) affect southern pine health and pine mortality. These factors, coupled with the greater nutrient requirements of loblolly pine and reductions in silvicultural treatments during forest rotations, may result in low vigor, reduced growth and increased mortality of pine stands.

There are significant obstacles to sustainable management of southeastern forests, as they represent a patchwork of landscapes having different management histories and current objectives (Butler, 2008). However, effective forest management is possible, especially as related to pine health issues. Depending on stand age, some tree mortality may be expected. Many other factors are likely at play in these situations, including weather, soils, and land use history (Fig. 3). Interplay between those abiotic and biotic factors may assist with building decision models for providing sustainable management guidelines (Fig. 3). Local forest health professionals may continue to consider standard practices that promote forest health, including site preparation, selection of the appropriate tree species, vegetation control, prescribed burning, and thinning at appropriate times. These standard management methods have been honed and tested over time, and in the absence of evidence to the contrary, they are likely the way forward to forest sustainability.

References

Adams, H.D., Luce, C.H., Breshears, D.D., Allen, C.D., Weiler, M., Hale, V.C., Smith, A.M.S., Huxman, T.E., 2012. Ecohydrological consequences of drought- and infestation-triggered tree die-off: insights and hypotheses. Ecohydrology 5, 145–159.

Alexander, S.A., Skelly, J.M., Webb, R.S., 1981. Effects of *Heterobasidion annosum* on radial growth in southern pine beetle-infested loblolly pine. Phytopathology 71, 479–481.

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kizberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.H., Allard, G., Running, S.W., Semerci, A., Cobb, N., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For. Ecol. Manage. 259, 660–684.

Anderson, N.H., Anderson, D.B., 1968. *Ips* bark beetle attacks and brood development on a lightening-struck pine in relation to its physiological decline. Fla. Entomol. 51, 23–31.

Aussenac, G., Granier, A., 1988. Effects of thinning on water stress and growth in Douglas-fir. Can. J. For. Res. 18, 100–105.

Bal, T.L., Richter, D.L., Storer, A.J., Jurgensen, M.F., 2013. The relationship of the sapstreak fungus, *Ceratocystis virescens*, to sugar maple dieback and decay in northern Michigan. Am. J. Plant Sci. 4, 436–443.

Barnard, E.L., Blakeslee, G.M., English, J.T., Oak, S.W., Anderson, R.L., 1985. Pathogenic fungi associated with sand pine root disease in Florida. Plant Dis. 69, 196–199.

Bechtold, W.A., Scott, C.T., 2005. The forest inventory and analysis plot design. In: Bechtold, W.A., Patterson, P.L. (Eds.), The Enhanced Forest Inventory and Analysis Program – National Sampling Design And Estimation Procedures, pp. 37–52. Gen. Tech. Rep. SRS-80. USDA Forest Service, Southern Research Station, Asheville, NC. 85p.

Belanger, R.P., Hedden, R.L., Lorio, P.L., 1993. Management strategies to reduce losses from southern pine beetle. South. J. Appl. For. 17, 150–154.

Berisford, C.W., Franklin, R.T., 1971. Attack patterns of *Ips avulsus* and *I. grandicollis* (Coleoptera: Scolytidae) on four species of southern pines. Ann. Entomol. Soc. Am. 64, 894–897.

Bhuta, A.A.R., Kennedy, L.M., Pederson, N., 2009. Climate-radial growth relationships of northern latitudinal range margin longleaf pine (*Pinus palustris* P. Mill.) in the Atlantic Coastal Plain of southeastern Virginia. Tree-Ring Res. 65, 105–115.

Bigler, C., Bräker, O.U., Bugmann, H., Dobbertin, M., Rigling, A., 2006. Drought as an inciting mortality factor in Scots pine stands of the Valais, Switzerland. Ecosystems 9, 330–343.

Bracho, R., Starr, G., Gholz, H.L., Martin, T.A., Cropper, W.P., Loescher, H.W., 2012. Controls on carbon dynamics by ecosystem structure and climate for southeastern U.S. slash pine plantations. Ecol. Monogr. 82, 101–128.

Brown, H.D., McDowell, W.E., 1968. Status of loblolly pine die-off on the Oakmulgee District, Talladega National Forest, Alabama-1968. Rep. 69–2–28. Pineville, LA: USDA Forest Service, Forest Insect & Disease Management. 22p.

Brown, S.L., Schroeder, P.E., 1999. Spatial patterns of aboveground production and mortality of woody biomass for eastern U.S. forests. Ecol. Appl. 9, 968–980.

Brown, H.D., Peacher, P.H., Wallace, H.N., 1969. Status of Loblolly Pine Die-off on the Oakmulgee District, Talladega National Forest, Alabama. Rep. 70-2-3. Pineville, LA: USDA Forest Service, 9p.

Brown, M.W., Nebeker, T.E., Honea, C.R., 1987. Thinning increases loblolly pine vigor and resistance to bark beetles. South. J. Appl. For. 11, 28–31.

Bryant, C.M., Kulhavy, D.L., Billings, R.F., Clarke, S.R., 2006. Characteristics of bark beetle infestations in East Texas during a period of low southern pine beetle activity. Southwest. Entomol. 31, 187–199.

Butler, B.J., 2008. Family Forest Owners of the United States, 2006. Gen. Tech. Rep. NRS-27. USDA Forest Service, Northern Research Station, Newtown Square, PA.

Campbell, W.A., Copeland, O.L. Jr., 1954. Littleleaf Disease of Shortleaf and Loblolly Pines. Circ. 940. Washington, DC: USDA, 41p.

Chen, G., Tian, H., Zhang, C., Liu, M., Ren, W., Zhu, W., Chappelka, A.H., Prior, S.A., Lockaby, G.B., 2012. Drought in the southern United States over the 20th century: variability and its impacts on terrestrial ecosystem productivity and carbon storage. Climatic Change 114, 379–397.

Ciesla, W.M., Donaubauer, E., 1994. Decline and Dieback of Trees and Forests: a Global Overview. FAO Forestry Paper No. 120. Rome, Italy, 90p.

Ciesla, W.M., Franklin, R.T., 1965. A method of collecting adults of the pales weevil, *Hylobius pales*, and the pitch eating weevil, *Pachylobius picivorus* (Coleoptera: Curculionidae). J. Kansas Entomol. Soc. 38, 205–206.

Clarke, S.R., Evans, R.E., Billings, R.F., 2000. Influence of pine bark beetles on the West Gulf Coastal Plain. Texas J. Sci. 52, 105–126.

Cobb, F.W., Parmeter, J.R. Jr., Wood, D.L., Stark, R.W., 1974. Root pathogens as agents predisposing ponderosa pine and white fir to bark beetles. In: Proceedings of IUFRO Working Party on *Fomes annosus*, 1973 September 17–21, Athens, GA. pp. 1–8.

Copeland Jr., O.L., Leaphart, C.D., 1955. Preliminary Report on Soil-Rootlet Relationships to Pole Blight of Western White Pine. Ogden, UT: USDA For. Serv. Intermt. For. and Range Exp. Stn. Res. Note 22, 6p.

Copeland Jr., O.L., McAlpine, R.G., 1955. Interrelationships of littleleaf, site index, soil, and ground cover in Piedmont shortleaf pine stands. Ecology 36, 635–641.

Della-Bianca, L., Dils, R.E., 1960. Some effects of stand density in a red pine plantation on soil moisture, soil temperature and radial growth. J. For. 58, 373–377.

Dobbertin, M., Baltensweiler, A., Rigling, D., 2001. Tree mortality in an unmanaged mountain pine (*Pinus mugo var. uncinata*) stand in the Swiss National Park impacted by root fungi. For. Ecol. Manage. 145, 79–89.

Drake, J.E., Raetz, L.M., Davis, S.C., DeLucia, E.H., 2010. Hydraulic limitation not declining nitrogen availability causes the age-related photosynthetic decline in loblolly pine (*Pinus taeda* L.). Plant, Cell Environ. 33, 1756–1766.

Drake, J.E., Davis, S.C., Raetz, L.M., DeLucia, E.H., 2011. Mechanisms of age-related changes in forest production: the influence of physiological and successional changes. Global Change Biol. 17, 1522–1535.

Drooz, A.T., 1985. Insects of Eastern Forests. USDA Forest Service, Washington, D.C. Miscellaneous Publication 1426. 608p.

Eckhardt, L.G., Menard, R.D., 2008. Topographic features associated with loblolly pine decline in Central Alabama. For. Ecol. Manage. 255, 1735–1739.

Eckhardt, L.G., Hess, N.J., Menard, R.D., Goddard, A.J., 2003. Assessment of loblolly pine decline on the Oakmulgee Ranger District, Talladega National Forest, Alabama. Rep. 2004-02-01. Pineville, LA: USDA Forest Service, Forest Health Evaluation, Alexandria Field Office. 42p.

Eckhardt, L.G., Goyer, R.A., Klepzig, K.D., Jones, J.P., 2004a. Interactions of *Hylastes* species (Coleoptera: Scolytidae) with *Leptographium* species associated with loblolly pine decline. J. Econ. Entom. 97, 468–474.

Eckhardt, L.G., Jones, J.P., Klepzig, K.D., 2004b. Pathogenicity of *Leptographium* species associated with loblolly pine decline. Plant Dis. 88, 1174–1178.

Eckhardt, L.G., Weber, A.M., Menard, R.D., Jones, J.P., Hess, N.J., 2007. Insect-fungal complex associated with loblolly pine decline in central Alabama. For. Sci. 53, 84–92.

Eckhardt, L.G., Sword Sayer, M.A., Imm, D.W., 2010. State of pine decline in the southeastern United States. South. J. Appl. For. 34, 138–141.

Erbilgin, N., Raffa, K.F., 2002. Association of declining red pine stands with reduced populations of bark beetle predators, seasonal increases in root colonizing insects, and incidence of root pathogens. For. Ecol. Manage. 164, 221–236.

Fettig, C.J., Klepzig, K.D., Billings, R.F., Munson, A.S., Nebeker, T.E., Negrón, J.F., Nowak, J.T., 2007. The effectiveness of vegetation management practices for prevention and control of bark beetle infestations in coniferous forests of the western and southern United States. For. Ecol. Manage. 238, 24–53.

Fettig, C.J., Gibson, K.E., Munson, A.S., Negrón, J.F., 2014. Cultural practices for prevention and control of mountain pine beetle infestations. For. Sci. 60, 450–463.

Flamm, R.O., Pulley, P.E., Coulson, R.N., 1993. Colonization of disturbed trees by the southern pine bark beetle guild (Coleoptera: Scolytidae). Environ. Entomol. 22, 62–70.

Fox, T.R., Allen, H.L., Albaugh, T.J., Rubilar, R., Carlson, C.A., 2007. Tree nutrition and forest fertilization of pine plantations in the southern United States. South. J. Appl. For. 31, 5–11.

Franklin, J.F., Shugart, H.H., Harmon, M.E., 1987. Tree death as an ecological process. BioScience 37, 550–556.

Froelich, R.C., Dell, T.R., Walkinshaw, C.H., 1966. Soil factors associated with *Fomes annosus* in the Gulf States. For. Sci. 12, 356–361.

Gadbury, G.L., William, M.S., Schreuder, H.T., 2004. Revisiting the Southern Pine Growth Decline: Where are We Ten Years Later? Gen. Tech. Rep. RMRS-GTR-124. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 10p.

Gilbert, S., Lackstrom, K., Tufford, D., 2012. The Impact of Drought on Coastal Ecosystems in the Carolinas. Research Report: CISA-2012-01. Columbia, SC: Carolinas Integrated Sciences and Assessments.

Ginn, S.E., Seiler, J.R., Cazell, B.H., Kreh, R.E., 1991. Physiological and growth responses of eight-year-old loblolly pine stands to thinning. For. Sci. 37, 1030–1040.

Graham, J.H., Duda, J.J., Brown, M.L., Kitchen, S., Emlen, J.M., Malol, J., Bankstahl, E., Krzysik, A.J., Freeman, D.C., 2012. The effects of drought and disturbance on the growth and developmental instability of loblolly pine (*Pinus taeda* L.). Ecol. Indic. 20, 143–150.

Granda, E., Rossatto, D.R., Camarero, J.J., Voltas, J., Valladares, F., 2014. Growth and carbon isotopes of Mediterranean trees reveal contrasting responses to increased carbon dioxide and drought. Oecologia 174, 307–317.

Guarín, A., Taylor, A.H., 2005. Drought triggered tree mortality in mixed conifer forests in Yosemite National Park, California, USA. For. Ecol. Manage. 218, 229–244.

Halambek, M., 1976. Dieback of eastern white pine (*Pinus strobus* L.) in cultures. Poljopr. Znan. Smotra 39, 495–498.

Hansen, E.M., Hamm, P.B., Shaw, C.G., Hennon, P.E., 1988. *Phytophthora drechsleri* in remote areas of Southeast Alaska. Trans. Br. Mycol. Soc. 91, 379–384.

Hanson, P.J., Weltzin, J.F., 2000. Drought disturbance from climate change: response of United States forests. Sci. Total Environ. 262, 205–220.

Hanson, C., Yonavjak, L., Clarke, C., Minnemeyer, S., Boisrobert, L., Leach, A., Schleeweis, K., 2010. Southern Forests for the Future. World Resources Institute, Washington, D.C., p. 88.

Hanula, J.L., Meeker, J.R., Miller, D.R., Barnard, E.L., 2002. Association of wildfire with tree health and numbers of pine bark beetles, reproduction weevils and their associates in Florida. For. Ecol. Manage. 170, 233–247.

Harrington, T.C., Cobb Jr., F.W., 1988. *Leptographium* Root Diseases on Conifers. American Phytopathological Society, St. Paul, MN, 149p.

Hendrix, F.F., Campbell, W.A., 1970. Distribution of *Phytophthora* and *Pythium* species in soils in the Continental United States. Can. J. Bot. 48, 377–384.

Hennon, P.E., 1990. Fungi on *Chamaecyparis nootkatensis*. Mycologia 82, 59–66.

Hess, N.J., Otrosina, W.J., Jones, J.P., Goddard, A.J., Walkinshaw, C.H., 1999. Reassessment of Loblolly Pine Decline on the Oakmulgee Ranger District, Talladega National Forest, Alabama. Proceedings of the Tenth Biennial Southern Silvicultural Research Conference, Shreveport, LA. pp. 560–564.

Hess, N.J., Otrosina, W.J., Carter, E.A., Steinman, J.R., Jones, J.P., Eckhardt, L.G., Weber, A.M., Walkinshaw, C.H., 2002. Assessment of loblolly pine decline in central Alabama. In: Outcalt, Kenneth W. (Ed.), Proceedings of the Eleventh Biennial Southern Silvicultural Research Conference, Gen. Tech. Rep. SRS-48. USDA Forest Service, So. Res. Sta. Asheville, NC. pp. 558–564.

Hess, N.J., Eckhardt, L.G., Menard, R.D., Goddard, A.J., 2005. Assessment of Loblolly Pine Decline on the Oakmulgee Ranger District, Talladega National Forest, Alabama. Revised. Rep. 2005-02-04. Pineville, LA: USDA Forest Service, Forest Pest Management. 36p.

Highley, L., Tattar, T.A., 1985. *Leptographium terebrantis* and black turpentine beetles associated with blue stain and mortality of black and Scots pine on Cape Cod, Massachusetts. Plant Dis. 69, 528–530.

Hines, J.W., Heikkenen, H.J., 1977. Beetles attracted to severed Virginia pine (*Pinus virginiana* Mill.). Environ. Entomol. 6, 123–127.

Hinrichsen, D., 1987. The forest decline enigma. BioScience 37, 542–546.

Houston, D.R., 1981. Stress Triggered Tree Diseases – The Diebacks and Declines. NS-INF-41-81, U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, 36p.

Houston, D.R., 1987. Forest tree declines of past and present: current understanding. Can. J. Plant Pathol. 9, 349–360.

Jokela, E.J., Martin, T.A., Vogel, J.G., 2010. Twenty-five years of intensive forest management with southern pines: important lessons learned. J. For. 108, 338–347.

Jurskis, V., 2005. Eucalypt decline in Australia, and a general concept of tree decline and dieback. For. Ecol. Manage. 215, 1–20.

Kharuk, V.I., Im, S.T., Oskorbin, P.A., Petrov, I.A., Ranson, K.J., 2013. Siberian pine decline and mortality in southern Siberian mountains. For. Ecol. Manage. 310, 312–320.

Klepzig, K.D., Raffa, K.F., Smalley, E.B., 1991. Association of an insect-fungal complex with red pine decline in Wisconsin. For. Sci. 37, 1119–1139.

Klepzig, K.D., Smalley, E.B., Raffa, K.F., 1995. *Dendroctonus valens* and *Hylastes porculus*: vectors of pathogenic fungi associated with red pine decline disease. Great Lakes Entomol. 28, 81–87.

Klepzig, K.D., Robison, D.J., Fowler, G., Minchin, P.R., Hain, F.P., Allen, H.L., 2005. Effects of mass inoculation on induced oleoresin response in intensively managed loblolly pine. Tree Physiol. 25, 681–688.

Klepzig, K., Hoyle, Z., Westcott, S., 2012. Southern Research Station Global Change Research Strategy 2011–2019. United States Department of Agriculture, Forest Service, Science Update SRS-046. Asheville, NC, 24p.

Klos, R.J., Wang, G.G., Bauerle, W.L., Rieck, J.R., 2009. Drought impact on forest growth and mortality in the southeast USA: an analysis using Forest Health and Monitoring data. Ecol. Appl. 19, 699–708.

Långström, B., Solheim, H., Hellqvist, C., Krokene, P., 2001. Host resistance in defoliated pine: effects of single and mass inoculations using bark beetle-associated blue-stain fungi. Agric. For. Entomol. 3, 211–216.

Lännenpää, A., Aakala, T., Kauhanen, H., Kuuluvainen, T., 2008. Tree mortality agents in pristine Norway spruce forests in northern Fennoscandia. Silva Fennica 42, 151–163.

Lenhart, J.D., Hunt, E.V. Jr., Blackard, J.A., 1985. Establishment of permanent growth and yield plots in loblolly and slash pine plantations in East Texas. In: Shoulders, E. (Ed.), Proc. Third Biennial South. Silv. Research Conf., pp. 436–437. Gen. Tech. Rep. SO-54.USDA Forest Service, 589p.

Lewis, K.J., Alexander, S.A., Horner, W.E., 1987. Distribution and efficacy of propagules of *Verticicladiella procera* in soil. Phytopathology 77, 552–556.

Li, W., Li, L., Fu, R., Deng, Y., Wang, H., 2011. Changes to the North Atlantic subtropical high and its role in the intensification of summer rainfall variability in the Southeastern United States. J. Climate 24, 1499–1506.

Li, L., Li, W., Deng, Y., 2013. Summer rainfall variability over the southeastern United States and its intensification in the 21st century as assessed by CMIP5 models. J. Geophys. Res. Atmos. 118, 340–354.

Lindelöw, Å., Eidmann, H.H., Nordenhem, H., 1993. Response on the ground of bark beetle and weevil species colonizing conifer stumps and roots to terpenes and ethanol. J. Chem. Ecol. 19, 1393–1403.

Little Jr., E.L., 1971. Atlas of United States Trees, vol. 1, Conifers and Important Hardwoods. USDA Forest Service, Misc. Pub. 1146, Washington, D.C., 9p, 200 maps.

Lohrey, R.E., Kossuth, S.V., 1990. *Pinus elliottii* Englem. slash pine. In: Silvics of North America. Conifers. Agricultural Handb. 654, vol. 1. USDA Forest Service, Washington, D.C., pp. 338–347.

Londo, A., Ezell, A.W., 2011. Planting Southern Pines: A Guide to Species Selection and Planting Techniques. Mississippi State University Extension Service, POD-08-11, 16p.

Lorio, P.L., 1966. *Phytophthora cinnamomi* and *Pythium* species associated with loblolly pine decline in Louisiana. Plant Dis. Rep. 50, 596–597.

MacCleery, D.W., 1992. American Forests, A History of Resiliency and Recovery. USDA Forest Service, Washington, D.C. and Forest History Society, Durham, NC. Publication FS-540, 58p.

Manion, P.D., 1981. Decline diseases of complex biotic and abiotic origin. In: Tree Disease Concepts. Prentice Hall, Englewood Cliffs, NJ, pp. 324–339, 399p.

Manuel, J., 2008. Drought in the Southeast: lessons for water management. Environ. Health Perspect. 116, 168–171.

Marchetti, S.B., Worrall, J.J., Eager, T., 2011. Secondary insects and diseases contribute to sudden aspen death in southwestern Colorado, USA. Can. J. For. Res. 41, 2315–2325.

Martin, T.A., Jokela, E.J., 2004. Stand development and production dynamics of loblolly pine under a range of cultural treatments in north-central Florida USA. For. Ecol. Manage. 192, 39–58.

Matusick, G., Eckhardt, L.G., 2010a. The pathogenicity and virulence of four ophiostomatoid fungi on young longleaf pine trees. Can. J. Plant Pathol. 32, 170–176.

Matusick, G., Eckhardt, L.G., 2010b. Variation in virulence among four root-inhabiting ophiostomatoid fungi on *Pinus taeda* L., *P. palustris* Mill., and *P. elliottii* Englem. seedlings. Can. J. Plant Pathol. 32, 361–367.

Matusick, G., Eckhardt, L.G., Enebak, S.A., 2008. Pathogenicity of *Leptographium serpens* to longleaf pine seedlings under various moisture regimes. Plant Dis. 92, 1574–1576.

Matusick, G., Eckhardt, L.G., Somers, G.L., 2010. Susceptibility of longleaf pine roots to infection and damage by four root-inhabiting ophiostomatoid fungi. For. Ecol. Manage. 260, 2189–2195.

Matusick, G., Somers, G., Eckhardt, L.G., 2012. Root lesions in large loblolly pine (*Pinus taeda* L.) following inoculation with four root-inhabiting ophiostomatoid fungi. For. Pathol. 42, 37–43.

Matusick, G., Menard, R.D., Zeng, Y., Eckhardt, L.G., 2013. Root-inhabiting bark beetles (Coleoptera: Curculionidae) and their fungal associates breeding in dying loblolly pine in Alabama. Fla. Entomol. 96, 238–241.

Maxwell, J.T., Soulé, P.T., Ortegren, J.T., Knapp, P.A., 2012. Drought-busting tropical cyclones in the southeastern Atlantic United States: 1950–2008. Ann. Assoc. Am. Geogr. 102, 259–275.

McKeand, S.E., Jokela, E.J., Huber, D.H., Byram, T.D., Allen, H.L., Li, B., Mullin, T.J., 2006. Performance of improved genotypes of loblolly pine across different soils, climates and silvicultural inputs. For. Ecol. Manage. 227, 178–184.

McLaughlin, J.A., Hsiang, T., Hayden, G.H., Greifenhagen, S., 2011. Abiotic and biotic factors used to assess decline risk in red pine (*Pinus resinosa* Ait.) plantations. For. Chron. 87, 99–115.

McRoberts, R.E., 2005. The enhanced forest inventory and analysis program. In: Bechtold, W.A., Patterson, P.L. (Eds.), The Enhanced Forest Inventory and Analysis Program – National Sampling Design and Estimation Procedures, pp. 11–20. Gen. Tech. Rep. SRS-80. USDA Forest Service, Southern Research Station, Asheville, NC, 85p.

Mead, D.J., 2013. Sustainable Management of *Pinus radiata* Plantations. FAO Forestry Paper No. 170. Rome, FAO.

Menard, R.D., 2007. An assessment of the Risk Mapping System for the Use of Managing Loblolly Pine Decline Sites within Red-Cockaded Woodpecker Habitat. M.S. Thesis. Louisiana State University, Baton Rouge, LA, 50p.

Menard, R.D., Eckhardt, L.G., Hess, N.J., 2010. Assessment of loblolly pine decline and site conditions on Fort Benning Military Reservation, GA. In: Stanturf, J.A. (Ed.), Proc. 14th Biennial South. Silv. Res. Conf., pp. 301–306. Gen. Tech. Rep. SRS-121. USDA Forest Service, Southern Research Station, Asheville, NC, 614p.

Meyerpeter, M.B., 2012. Mapping Loblolly Pine Decline Hazard and Risk Across the Southeastern United States. MS Thesis Auburn University, Auburn, AL, 88p.

Millar, C.I., Westfall, R.D., Delany, D.L., 2007. Response of high-elevation limber pine (*Pinus flexilis*) to multiyear droughts and 20th-century warming, Sierra Nevada, California, USA. Can. J. For. Res. 37, 2508–2520.

Miller, I., Shriner, D.S., Rizzo, D., 1989. History of Hardwood Decline in the Eastern United States. Gen. Tech. Rep. NE-126. USDA Forest Service Northeastern Forest Experiment Station, Bromall, PA, 78p.

Mistretta, P.A., 1984. Littleleaf Disease. Forest Insect and Disease Leaflet 20. U.S. Department of Agriculture, Forest Service, Washington, D.C., 6p. <http://www.na.fs.fed.us/spfo/pubs/fidls/littleleaf/fidl-ll.htm> (accessed 22.12.14).

Mitchell, R.G., Waring, R.H., Pitman, G.B., 1983. Thinning lodgepole pine increases tree vigor and resistance to mountain pine beetle. For. Sci. 29, 204–211.

Mitchell, R.J., Runion, G.B., Kelley, W.D., Gjerstad, D.H., Brewer, C.H., 1991. Factors associated with loblolly pine mortality on former agricultural sites in the conservation reserve program. J. Soil Water Cons. 46, 306–311.

Morehart, M., Gollehon, N., Dismukes, R., Breneman, V., Heimlich, R., 1999. An Economic Assessment of the 1999 Drought: Agricultural Impacts are Severe Locally, but Limited Nationally. USDA Economic Research Service Report, Agriculture Information Bulletin 755, Washington, DC.

Moya, L., Laguarda, M.F., Cagno, M., Cardoso, A., Gatto, F., O'Neill, H., 2013. Physical and mechanical properties of loblolly and slash pine wood from Uruguayan plantations. For. Prod. J. 63, 128–137.

Mueller-Dombois, D., 1987. Natural dieback in forests. BioScience 37, 575–583.

Negron, J.F., Wilson, J.L., 2003. Attributes associated with probability of infestation by the piñon ips, *Ips confusus* (Coleoptera: Scolytidae), in piñon pine, *Pinus edulis*. West. North Amer. Nat. 63, 440–451.

Nemeth, J.C., 1973. Dry matter production in young loblolly (*Pinus taeda* L.) and slash pine (*Pinus elliottii* Engelm.) plantations. Ecol. Monogr. 43, 21–41.

Nevill, R.J., Alexander, S.A., 1992. Transmission of *Leptographium procerum* to eastern white pine by *Hylobius pales* and *Pissodes nemorensis* (Coleoptera: Curculionidae). Plant Dis. 76, 307–310.

Nowak, J.T., Berisford, C.W., 2000. Effects of intensive forest management practices on insect infestation levels and loblolly pine growth. J. Econ. Entomol. 93, 336–341.

Nowak, J., Asaro, C., Klepzig, K., Billings, R., 2008. The southern pine beetle prevention initiative: working for healthier forests. J. For. 106, 261–267.

Nowak, J.T., Meeker, J.R., Coyle, D.R., Steiner, C.A., Brownie, C., 2015. Southern pine beetle infestations in relation to forest stand conditions, previous thinning, and prescribed burning. J. For. 113, in press.

Oak, S.W., Tainter, F.H., 1988. Risk prediction of loblolly pine decline on littleleaf sites in South Carolina. Plant Dis. 72, 289–293.

Otrosina, W.J., 2005. Exotic ecosystems: where root disease is not a beneficial component of temperate conifer forests. In: Lundquist, J.E., Hamelin, R.C. (Eds.), Forest Pathology – From Genetics to Landscapes. APS Press, St. Paul, MN, pp. 121–126, 175p.

Otrosina, W.J., Cobb, F.W. Jr., 1989. Biology, ecology, and epidemiology of *Heterobasidion annosum*, pp. 26–34. In: Proc. Symp. on Research and Management of Annosus Root Disease (*Heterobasidion annosum*) in Western North America. April 18–21, 1989; Monterey, CA. Gen. Tech. Rep. PSW-GTR-116. Berkeley, CA: Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture.

Otrosina, W.J., Ferrell, G.T., 1995. Root diseases: Primary agents and secondary consequences of disturbance, pp. 87–92. In: Forest Health Through Silviculture. Proc. 1995 National Silviculture Workshop, May 8–11, 1995, Mescalero, NM. Gen. Tech. Rept. RM-GTR-267. USDA Forest Service, Fort Collins, CO, 246p.

Otrosina, W.J., Garbelotto, M., 2010. *Heterobasidion occidentale* sp. nov. and *Heterobasidion irregulare* nom. nov.: a disposition of North American *Heterobasidion* biological species. Fungal Biol. 114, 16–25.

Otrosina, W.J., Marx, D.H., 1975. Populations of *Phytophthora cinnamomi* and *Pythium* spp. under shortleaf and loblolly pines in littleleaf disease sites. Phytopathology 65, 1224–1229.

Otrosina, W.J., Hess, N.J., Zarnoch, S.J., Perry, T.J., Jones, J.P., 1997. Blue-stain fungi associated with roots of southern pine trees attacked by the southern pine beetle, *Dendroctonus frontalis*. Plant Dis. 81, 942–945.

Otrosina, W.J., Bannwart, D., Roncadori, R.W., 1999. Root-infecting fungi associated with a decline of longleaf pine in the southeastern United States. Plant Soil 217, 145–150.

Otrosina, W.J., Walkinshaw, C.H., Zarnoch, S.J., Sung, S.-J., Sullivan, B.T., 2002. Root disease, longleaf pine mortality, and prescribed burning. In: Outcault, K.W. (Ed.), Proceedings of the Eleventh Biennial Southern Silvicultural Research Conference. Gen. Tech. Rept. SRS-48. USDA Forest Service, Southern Research Station, Asheville, NC, 622p.

Peet, R.K., Christensen, N.L., 1987. Competition and tree death. BioScience 37, 586–595.

Peters, A.J., Ji, L., Walter-Shea, E., 2003. Southeastern U.S. vegetation response to ENSO events (1989–1999). Climatic Change 60, 175–188.

Raffa, K.F., Smalley, E.B., 1988. Host resistance to invasion by lower stem and root infesting insects of pine: response to controlled inoculations with the fungal associate *Leptographium terebrantis*. Can. J. For. Res. 18, 675–681.

Roth, E.R., Peacher, P.H., 1971. Alabama Loblolly Pine Die-off Evaluation. USDA Forest Service, Southeastern Area, State & Private Forestry, Forest Pest Management Group, Report 72-2-9, Pineville, LA.

Ryu, S.R., Wang, G.G., Walker, J.L., 2013. Factors influencing loblolly pine stand health in Fort Benning, Georgia, USA. For. Sci. Technol. 9, 137–146.

Samuelson, L.J., Johnsen, K., Stokes, T., 2004. Production, allocation, and stemwood growth efficiency of *Pinus taeda* L. stands in response to 6 years of intensive management. For. Ecol. Manage. 192, 59–70.

Samuelson, L.J., Eberhart, T.L., Bartkowiak, S.M., Johnson, K.H., 2013. Relationships between climate, radial growth and wood properties of mature loblolly pine in Hawaii and a northern and southern site in the southeastern United States. For. Ecol. Manage. 310, 786–795.

Schmidt, R.A., Miller, T., Holley, R.C., Belanger, R.P., Allen, J.E., 1988. Relation of site factors to fusiform rust incidence in you slash and loblolly pine plantations in the coastal plain of Florida and Georgia. Plant Dis. 72, 710–714.

Schoeneweiss, D.F., 1975. Predisposition, stress, and plant disease. Annu. Rev. Phytopathol. 13, 193–211.

Seager, R., Tzanova, A., Nakamura, J., 2009. Drought in the southeastern United States: causes, variability over the last millennium, and the potential for future hydroclimate change. J. Climate 22, 5021–5045.

Sharitz, R.R., Schneider, R.L., Lee, L.C., 1990. Composition and regeneration of a disturbed river floodplain forest in South Carolina. In: Gosselink, J.G., Lee, L.C., Muir, T.A. (Eds.), Ecological Processes and Cumulative Impacts: Illustrated by Bottomland Hardwood Wetland Ecosystems. Lewis Publishers, Chelsea, MI, pp. 195–218.

Sinclair, W.A., 1964. Root- and Butt-rot of Conifers Caused by *Fomes annosus*, with Special Reference to Inoculum Dispersal and Control of the Disease in New York. Memoir No. 391, Cornell University Agriculture Experiment Station, New York State College of Agriculture, Ithaca, New York, USA, 54p.

Sinclair, W.A., 1965. Comparisons of recent declines of white ash, oaks, and sugar maple in northeastern woodlands. Cornell Plant. 20, 62–67.

Sinclair, W.A., 1966. Decline of hardwoods: possible causes. Proc. Int. Shade Tree Conf. 42, 17–32.

Sinclair, W.A., Lyon, H.H., 2005. Oak Wilt. In: Diseases of Trees and Shrubs, second ed. Cornell University Press, pp. 238–239.

Singh, A., Anderson, D., Eckhardt, L.G., 2014. Variation in resistance of loblolly pine (*Pinus taeda* L.) families against *Leptographium* and *Grosmannia* root fungi. For. Pathol. 44, 293–298.

Smith, W.D., Conkling, B.L., 2005. Analyzing Forest Health Data. Gen. Tech. Rep. SRS-77. USDA Forest Service, Southern Research Station, Asheville, NC, 33p.

Smith, R.H., Kowal, R.J., 1968. Attack of the black turpentine beetle on roots of slash pine. J. Econ. Entomol. 61, 1430–1432.

Staeben, J., Clarke, S., Gandhi, K.J.K., 2010. The Black Turpentine Beetle. USDA Forest Service, Forest Insect and Disease Leaflet, 12, 8p.

Stephenson, N.L., van Mantgem, P.J., Bunn, A.G., Bruner, H., Harmon, M.E., O'Connell, K.B., Urban, D.L., Franklin, J.F., 2011. Causes and implications of the correlation between forest productivity and tree mortality rates. Ecol. Monogr. 81, 527–555.

Stevens, R.B., 1960. In: Horsfall, J.G., Dimond, A.E. (Eds.), Plant Pathology, an Advanced Treatise, vol. 3. Academic Press, NY, pp. 357–429.

Stubbs, M., 2014. Conservation Reserve Program (CRP): Status and Issues. Congressional Research Service Report R42783, 24p.

Sullivan, B.T., Fettig, C.J., Otrosina, W.J., Dalusky, M.J., Berisford, C.W., 2003. Association between severity of prescribed burns and subsequent activity of conifer-infesting beetles in stands of longleaf pine. For. Ecol. Manage. 185, 327–340.

Tainter, F.H., Baker, F.A., 1996. Principles of Forest Pathology. John Wiley & Sons, Hoboken, NJ, USA, 805p.

Tainter, F.H., Williams, J.G., Hess, N.J., Oak, S.W., Starkey, D.A., 1989. The lack of a long term growth effect of annosus control in southeastern United States. In: Otrosina, W.J., Scharpf, R.F., (Eds.), Proc. Symp. on Research and Management of Annosus Root Disease (*Heterobasidion annosum*) in western North America, April 18–21, 1989. USDA Forest Service, Pacific Southwest Forest and Range Experiment Station, GTR PSW-116. Monterey, CA, 177p.

Trimble, S.W., 2008. Man-Induced Soil Erosion on the Southern Piedmont: 1700–1790, second ed., Soil and Water Conservation Society, Ankeny, Iowa, 80p.

Turchin, P., Davidson, J., Leslie Hayes, J., 1999. Effect of thinning on development of southern pine beetle infestations in old growth stands. South. J. Appl. For. 23, 193–196.

Turner, M.G., Ruscher, C.L., 1988. Changes in landscape patterns in Georgia, USA. Landsc. Ecol. 1, 241–251.

Urban, J., Holušová, K., Menšík, L., Čermák, J., Kantor, P., 2013. Tree allometry of Douglas fir and Norway spruce on a nutrient-poor and nutrient-rich site. Trees 27, 97–110.

USDA Forest Service, 2014. Forest Inventory and Analysis National Core Field Guide. Volume 1: Field Data Collection Procedures for Phase 2 Plots. Version 6.1. USDA Forest Service, Forest Inventory and Analysis Program, 433p.

Van Lear, D.H., Carroll, W.D., Kapeluck, P.R., Johnson, R., 2005. History and restoration of the longleaf pine-grassland ecosystem: implications for species at risk. For. Ecol. Manage. 211, 150–165.

Vose, J.M., Swank, W.T., 1994. Effects of long-term drought on the hydrology and growth of a white pine plantation in the southern Appalachians. For. Ecol. Manage. 64, 25–39.

Wallace, H.R., 1953. The ecology of the insect fauna of pine stumps. J. Anim. Ecol. 22, 154–171.

Wallin, K.F., Kolb, T.E., Skov, K.R., Wagner, M., 2008. Forest management treatments, tree resistance, and bark beetle resource utilization in ponderosa pine forests of northern Arizona. For. Ecol. Manage. 255, 3263–3269.

Wang, H., Fu, R., Kumar, A., Li, W., 2010. Intensification of summer rainfall variability in the southeastern United States during recent decades. J. Hydrometeor. 11, 1007–1018.

Wargo, P.M., Shaw III, C.G., 1985. *Armillaria* root rot: the puzzle is being solved. Plant Dis. 69, 826–832.

Warner, R.E., 1966. A review of the *Hylobius* of North America, with a new species injurious to slash pine (Coleoptera: Curculionidae). Coleop. Bull. 20, 65–81.

Wear, D.N., Gries, J.G., 2002. Southern Forest Resource Assessment – Summary Report. Gen. Tech. Rep. SRS-54. USDA Forest Service, Southern Research Station, Asheville, NC, 103p.

Wear, D.N., Gries, J.G., 2012. The Southern Forest Futures Project: Summary Report. Gen. Tech. Rep SRS-GTR-168. USDA Forest Service, Asheville, NC, 54p.

Weaver, J.C., 2005. The Drought of 1998–2002 in North Carolina – Precipitation and Hydrologic Conditions. U.S. Department of the Interior, U.S. Geological Survey, 88p.

Williams, T.M., Gresham, C.A., 2006. Biomass accumulation in rapidly growing loblolly pine and sweetgum. Biomass Bioenergy 30, 370–377.

Williams, J.W., Jackson, S.T., 2007. Novel climates, no-analog communities, and ecological surprises. Front. Ecol. Environ. 5, 475–482.

Williams, R.E., Shaw, C.G. III, Wargo, P.M., Sites, W.H., 1986. Armillaria Root Disease. Forest Insect and Disease Leaflet 78. U.S. Department of Agriculture, Forest Service, Washington, D.C., 8p. <http://www.na.fs.fed.us/spfo/pubs/fidls/armillaria/armillaria.htm> (accessed 22.12.14).

Williams, A.P., Allen, C.D., Macalady, A.K., Griffin, D., Woodhouse, C.A., Meko, D.M., Swetnam, T.W., Rauscher, S.A., Seager, R., Grissino-Mayer, H.D., Dean, J.S., Cook, E.R., Gangodagamage, C., Cai, M., McDowell, N.G., 2012. Temperature as a potent driver of regional forest drought stress and tree mortality. Nat. Climate Change 3, 292–297.

Zak, B., 1961. Aeration and other soil factors affecting Southern pines as related to Littleleaf Disease. Tech. Bull. No. 1248, SE Forest Exp. Sta., USDA Forest Service. September 1961, pp. 27–29.

Zanzot, J.W., Matusick, G., Eckhardt, L.G., 2010. Ecology of root-feeding beetles and their associated fungi on longleaf pine in Georgia. Environ. Entomol. 39, 415–423.

Zegler, T.J., Moore, M.M., Fairweather, M.L., Ireland, K.B., Fulé, P.Z., 2012. *Populus tremuloides* mortality near the southwestern edge of its range. For. Ecol. Manage. 282, 196–207.

Zeide, B., 1992. Has pine growth declined in the southern United States? Conserv. Biol. 6, 185–195.

Zeide, B., Zhang, Y., 2006. Mortality of trees in loblolly pine plantations. In: Connor, K.F. (Ed.), Proceedings of the 13th Biennial Southern Silvicultural Research Conference. Gen. Tech. Rep. SRS–92. USDA Forest Service, Southern Research Station, Asheville, NC. pp. 305–309.

Zeng, Y., Kidd, K.R., Eckhardt, L.G., 2014. The effect of thinning and clear-cut on changes in the relative abundance of root-feeding beetle (Coleoptera: Curculionidae) in *Pinus taeda* plantations in central Alabama and Georgia. Pest Manage. Sci. 70, 915–921.

Zhang, S.Y., Chaurey, G., Swift, D.E., Duchesne, I., 2006. Effects of precommercial thinning on tree growth and lumber quality in a jack pine stand in New Brunswick, Canada. Can. J. For. Res. 36, 945–952.

Zwolinski, J.B., South, D.B., Droomer, E.A.P., 1998. Pine mortality after planting on post-agricultural lands in South Africa. Silva Fennica 32, 271–280.