

Selected Papers from NAFEW 2009

Guest Editors: Terry L. Sharik and J. P. Hamish Kimmins





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Editorial

Selected Papers from NAFEW 2009

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Our understanding of the ecology and management of North American forests is rapidly evolving as a result of novel approaches to their study, many of which are the results of emerging technologies. The biennial North American Forest Ecology Workshop series attempts to capture these approaches and highlight the ways in which they expand our understanding of forest systems. The ten papers appearing in this issue were drawn from the 7th and most recent workshop, held in June 2009, in which there were over 150 presentations.

The first paper in this special issue attempts to provide an overview of emerging themes in the ecology and management of North American Forests based on all presentations and follow-up discussions at the workshop and concludes with future research needs. The second paper describes the carbon flux of down woody materials in forests of the Northcentral U.S. using recent data from the USDA Forest Service's Forest Inventory and Analysis (FIA) Program and exemplifies the utility of a network of permanent plots for monitoring change over large spatial scales and long time periods. The study described in the third paper is a nice sequel to the second in that it uses FIA data to demonstrate changes in the population levels of an understory tree in eastern North America threatened by an introduced pathogen, among other causes. The authors point out that such data can be used to validate the findings of multiple small-scale studies and to generate hypotheses for testing at smaller scales, thereby reinforcing a workshop-wide call for the study of forest ecosystems at multiple scales.

The fourth paper describes a rapid assessment method for extending the use of Reineke's stand density index (SDI), originally developed for even-aged, monotypic stands, to

mixed species stands in the Northeastern U.S, utilizing point sampling in combination with wood specific gravity to harmonize the density of individual species. The fifth paper applies SDI in combination with tree diameter distributions to characterize complex forest stands in the Florida Keys, which in turn are used as reference sites or standards for restoring forest structure in Everglades tree islands. The sixth paper describes the application of a fairly recently devised environmental variable, Landform Index, in predicting the site index of mesophytic tree species in the Southern Appalachians, in turn reflecting the quality of these sites relative to the production of tree biomass.

The seventh through ninth papers address some dimension of fire as a disturbance agent in North American forests. The first of these and the seventh paper in the special issue is said to represent the first attempt to develop a comprehensive model for predicting fire-induced slash pine mortality in pine forests of the Florida Keys, which in turn may provide insights into the management of these sites through the use of prescribed fire. The situation is complicated by storm surges and associated increases in substrate salinity, which differ in their effect on the structure of slash pine-dominated forests compared to fire, and may be increasingly important with climate-change-mediated increases in the frequency and intensity of tropical storms and in sea level rise. The eighth paper examines the effects of soil temperature during fire on the survival of seeds of herbaceous perennials and woody shrubs in Florida sand pine ecosystems and suggests that small-scale variation in soil surface temperatures is important in the regeneration of these species. The ninth paper reports on the results of laboratory studies aimed at determining the physiological

effects of short-duration smoke exposure on six species of hardwoods and conifers native to the Intermountain West, a phenomenon that has been little studied in the past. Inconclusive with respect to effects on growth or secondary defense compound production in these species, it points to the need for research on the effects of longer-term exposure to smoke.

The tenth and final study examines the potential effects of global increases in the intensity and complexity of radio frequency background on forest decline, using trembling aspen seedlings as a model. Preliminary in nature, the results point to the need for more robust studies of a potentially significant anthropogenically induced impact on forest ecosystems.

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Review Article

Emerging Themes in the Ecology and Management of North American Forests

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The 7th North American Forest Ecology Workshop, consisting of 149 presentations in 16 oral sessions and a poster session, reflected a broad range of topical areas currently under investigation in forest ecology and management. There was an overarching emphasis on the role of disturbance, both natural and anthropogenic, in the dynamics of forest ecosystems, and the recognition that legacies from past disturbances strongly influence future trajectories. Climate was invoked as a major driver of ecosystem change. An emphasis was placed on application of research findings for predicting system responses to changing forest management initiatives. Several “needs” emerged from the discussions regarding approaches to the study of forest ecosystems, including (1) consideration of variable spatial and temporal scales, (2) long-term monitoring, (3) development of universal databases more encompassing of time and space to facilitate meta-analyses, (4) combining field studies and modeling approaches, (5) standardizing methods of measurement and assessment, (6) guarding against oversimplification or overgeneralization from limited site-specific results, (7) greater emphasis on plant-animal interactions, and (8) better alignment of needs and communication of results between researchers and managers.

1. Introduction

Forests are extremely complex systems that respond to an overwhelming number of biological and environmental

factors, which can act singularly and in concert with each other, as exemplified by Puettmann et al. [1]. The complexity of forest systems presents an enormous challenge for forest

researchers who try to deepen their understanding of the structure and function of these systems, and for forest managers who try to deploy practices that emulate natural processes. This paper addresses key issues in forest research and management and is divided into three sections: (1) disturbance, (2) emerging roles of forest detritus, and (3) ecological applications in the management of forest ecosystems. Disturbance emerged as a major theme from the workshop and is, thus, treated at some length and includes a subsection on ecosystem recovery to emphasize the controversy and special challenges of restoration as a management tool. Forest detritus is given a separate section as it is increasingly viewed in a broader context. The ecological applications section highlights the call for alignment between research and management needs and for better communication of results to forest managers. We conclude with future research needs regarding approaches to forest ecosystem studies. (The North American Forest Ecology Workshop biennial series began in 1997 with the objective of providing a forum for ecologists to discuss recent findings and trends in the basic and applied ecology of North American forests [2]. The 2009 workshop, held in Logan, Utah, on June 22–25, <http://www.nafew2009.org/>, was attended by approximately 200 delegates and featured 149 presentations in 16 oral topical sessions and a poster session. There was no specific theme for the workshop; instead, sessions were organized by researchers to explore particular aspects of forest ecology and to reflect current trends in research. A discussion was held at the end of each topical session, led by the organizers and facilitators and open to all session participants, to identify key emerging themes and areas for future research. Poster presentations were included as appropriate. This article represents a synopsis of the emerging themes, with a strong emphasis on implications for management of North American forests. An expanded version of this synopsis, together with abstracts of all workshop presentations and Power Points of a subset of workshop presentations, can be found in the Utah State University Digital Commons at <http://digitalcommons.usu.edu/nafecology/>.)

2. Disturbance

Research is needed to develop an understanding of the mechanisms that regulate how ecosystems change in response to both rapid (e.g., wildfire, wind storms) and more gradual (e.g., climate change) disturbance agents. This will improve our understanding of ecological resilience and assist forest managers in maintaining biological diversity across multiple scales. While we cannot hope to truly emulate natural disturbance in forests, we can take cues from these complex systems to achieve our end goal of ecosystem-based management.

Disturbance interactions are ubiquitous in forest ecosystems and can result in complex dynamics that affect successional trajectories, forest landscape patterns, and ecological processes at multiple spatial and temporal scales [3–5]. Consequently, understanding disturbance interactions, including predicting the magnitude and scale of future interactions, is a challenging area for future forest ecology research.

Interactions may occur among various forest disturbance agents, including insect and disease outbreaks, windthrow, timber harvest, and fire. These complex dynamics have been addressed in past research via field-based research, simulation models, and theoretical models [6]. Core research themes have included (1) investigating the ability of past disturbance events to affect future disturbance intensities and severities (2) determining how spatial legacies created by past disturbance events influence the spatial patterns, frequency, and synchrony of future disturbance events and (3) understanding the potential for synergistic interactions among disturbance agents that can dramatically alter forest composition, structure, and function through time and space. There has been an increasing focus on large landscapes and long-time periods, in part, due to technological and conceptual advances in forest landscape simulation models [7]. Insects, diseases, and fire as disturbance agents emerged as major areas of presentation and discussion, and thus are addressed below in some detail.

2.1. Insects and Diseases. Insects and fungi not only kill trees, but also cause cascading effects in ecosystems. We need a better understanding of host physiology and how it affects host defense and reproductive capabilities. Millions of trees die, but we still do not understand how. In some western forests, white pine blister rust has almost eliminated western white pine (*Pinus monticola*) from the canopy, resulting in conversion to Douglas fir (*Pseudotsuga menziesii*) and true firs (*Abies* spp.) [8]. These replacement species are much more susceptible to bark beetles and root diseases, which have serious impacts on forest structure after about 80 years. Mountain pine beetles not only affect timber volumes and future stand composition, but can also affect water yield in quantity and timing, a key societal demand at least in western Northern American forests. Other insects and fungi are changing species composition with unknown consequences. For example, dogwood anthracnose, a canker caused by the fungus *Discula destructiva*, is reducing the flowering dogwood (*Cornus florida*) population by more than 50% over much of the host range [9], yet we know relatively little about what this means to these ecosystems of which it is a part. Franklin et al. [10] state that “. . . overall the patterns and causes of tree death typically are complex, and we are only beginning to appreciate the complexities.” This statement rings true today as we face ecosystems challenged even further by exotic pathogens and insects, and changing climate.

A prime example of the cascading effects of insects and diseases on forest ecosystems is provided by the whitebark pine- (*Pinus albicaulis*-) dominated forests of western North America. These forests are facing serious decline from the combined effects of an introduced pathogen (white pine blister rust, WPBR, *Cronartium ribicola*) and a native bark beetle (mountain pine beetle, MPB, *Dendroctonus ponderosae*). Since whitebark pine is both a foundation and a keystone species [11], collapse of these forests threatens the integrity of high-elevation ecosystems across the entire distribution of whitebark pine. Both primary threats are exacerbated by climate warming, which in itself poses serious long-term consequences for whitebark pine.

The ecological consequences of whitebark pine loss are already being expressed in altered hydrology and wildlife interactions [12]. The recent magnitude of MPB mortality in whitebark pine is a new phenomenon, and relatively little is currently known regarding the dynamics of MPB populations in these forests. The following research priorities emerged, highlighting significant gaps in our understanding of tree defense chemistry, regeneration ecology, community interactions, monitoring and assessment, host species under consideration, key refugia, and bioclimatic modeling.

(i) Tree chemistry differs between host and nonhost pine species [13]; hence, the apparent reduced effectiveness of tree chemical defenses to MPB may provide a critical key to understanding outbreak dynamics in whitebark pine.

(ii) Information on regeneration is critical for projecting future prospects and effective scenario development for areas where loss of the entire cone-bearing overstory has been observed.

(iii) The loss of cone production has far-reaching impacts on whitebark pine and community associates. Whitebark pine is almost entirely dependent on Clark's nutcracker (*Nucifraga columbiana*) for seed dispersal and planting. The nutcracker, however, is much more of an opportunistic species and will seek other food resources if conedensity drops below a threshold [14]. There is also mounting evidence for preferential selection of WPBR-infected trees by MPB [15, 16]. Such community-level interactions have important implications for the future of whitebark pine.

(iv) Effective monitoring is required to establish the full extent of mortality, which has been hampered by the spatial scale and speed of the MPB outbreaks, and remoteness and ruggedness of the whitebark pine habitat. Effective assessment will require a combination of on-the-ground stand surveys, aerial mapping from fixed-wing aircraft [17, 18], and satellite image interpretation [19]. Monitoring needs to be expanded to all high-elevation 5-needle pines as limber, foxtail, and bristlecone pines (*Pinus flexilis*, *P. balfouriana*, and *P. aristata-longaeva*) are suitable hosts for MPB.

(v) MPB populations have expanded into previously marginal whitebark pine habitat as a result of warming climate conditions [13, 20]. However, some areas are more resistant to climatic disruption than others, and trees <~15.24 cm DBH are not attacked by beetles. Therefore, understory and krumholtz provide a temporal buffer for maintaining whitebark pine in some landscapes. Such potential refugia need to be identified through both on-ground surveys and/or model risk assessment.

(vi) Landscape models for risk assessment have demonstrated predictive value for identifying both at-risk and resilient landscapes. These bioclimatic models can be improved to more fully represent the relationship between weather, host tree, and outbreak potential [21].

2.2. Fire. The study of fire and fire effects primarily describes the myriad of interactions between the prefire environment, fire-severity, and postfire system characteristics and responses. Regardless of ignition, fires are driven by climatic, vegetation, and edaphic factors that may or may not interact

to result in variable fire severity. In turn, fire severity affects a whole host of postfire attributes such as percent mortality, snag dynamics, fuel loading, and wildlife habitat [22]. Definitions of fire severity are usually study specific and driven by the response variable of interest, and even though a fire event affects vertical vegetation strata differently, fire severity is usually defined by its effect on overstory vegetation [23].

Mixed-severity fire regimes are defined as those that kill between 30% and 70% of the overstory [24] and have a wide geographic spread, accounting for as much as 50% of western forest types. The definition of mixed severity is hindered by the concept of severity as it manifests itself in ways that are not part of the current classification (e.g., not just canopy but surface and soil effects). Scientists and managers need to do a more careful job of characterizing fire effects related to the concept of "severity." When used alone, the term "fire severity" has relatively little value; it must be more precisely defined to really understand the effects of fire on biodiversity and ecosystem goods and services and to foster development of more robust scientific models and effective management responses. Comparisons across fires and fire regimes must be made using the same definitions of severity; even then, ecological responses are likely to differ across species, communities, and ecosystems.

The large variety of forest types, fire behaviors, and ecological responses involved also poses a challenge to better understand mixed-severity regimes. New typologies and definitions based on fundamental factors (climate, fuel succession and moisture, topography, vegetation, productivity, and spatiotemporal dynamics) are needed to characterize the major domains of spatial and temporal variability within the mixed-severity regime. Emergent characteristics of fires and fire regimes, such as patch-size distributions, could be used as a means of distinguishing mixed-severity regime types and provide some guidance for fire management. Fire behavior and effects are driven by complex interactions of climate, fuels, topography, and vegetation [25], but little is known about how the relative importance of these factors varies among forest types and among fires within forest types. Topography often plays an important role in structuring the spatial and temporal patterns in fire behavior in many mixed-severity systems and can provide a basis for manipulating fuels to modify fire behavior. Mixed-severity regimes may create spatiotemporal vegetation dynamics that "wander" through ecological space, creating a continual series of unique landscapes. We lack understanding of this process and how landscape-level legacies of past fires and land use practices alter future landscapes. For example, the proportion of late-successional tree species has increased in many forests, increasing the probability that future disturbances will be colonized by seedlings from surviving individuals of these species. Conversely, past removal of pines and other seral dominants from mixed conifer forests has reduced the probability that future disturbance patches will be colonized by these early successional species. Management actions (e.g., thinning, prescribed fire, and planting) may be needed to alter these trajectories to achieve specific or general ecological and social outcomes.

The mixed-severity regime has characteristics of both fuel- and climate-limited fire regimes, thereby bridging the gap between fuel-driven fires of low severity, where management actions can effectively reduce fire hazard, and climate-driven fires of high severity, where management actions to lower the risks of loss of the canopy are typically ineffective. The downside is that a mixed-severity regime does not necessarily indicate whether fuel treatments would affect fire behavior because it straddles the fuel-limited and climate-limited ends of the spectrum. Climate change will affect the spatial and temporal dynamics of fire regimes, possibly increasing the proportion of high-severity patches within forests that were historically characterized by bounded ranges of low, moderate, and high fire severity. Using the historical range of variability (HRV) as a goal for management will not be realistic in many regions given climate change and the cumulative effects of past land use practices. Yet, knowledge of history can provide valuable insights for efforts to achieve desired future conditions. An alternative to HRV as guidance for managers may insure the “resilience” of forests, where resilience is defined as the capacity to sustain biological diversity and produce desired goods and services following disturbances. However, for this concept to become more useful it must be defined and metrics of desired ecological conditions and behaviors must be developed and accepted.

Miyaniishi [26] attributed slow progress in the field of fire ecology to a lack of interaction between environmental biophysics and ecology research disciplines. Wildland fuels should act as a bridge between the two perspectives as understanding the impacts of fuel heterogeneity on wildland fires is critical for both predicting fire behavior and understanding fire effects. Fuel heterogeneity can be defined in many ways and at many scales and can manifest itself clearly through mosaics of burned and unburned patches, and variable fire intensity within burned areas. Heterogeneity in fuels, fire behavior, and fire effects is ubiquitous at all scales but is not well understood and has been largely ignored in the literature. Moreover, the cumulative impacts of small-scale heterogeneity can influence larger-scale spatial dynamics, resulting in unanticipated fire behavior, such as increased fire intensity at the wake of small fuel-free patches. Spatially explicit measurements are critical for deriving mechanistic explanations for spatial heterogeneity-related fire behavior, especially for understanding fuel-fire-atmospheric interactions. Heterogeneity needs to be set in context of relevant scales and dimensions and ideally follows a practical nomenclature that is simple to implement and relevant for guiding management activities. A heterogeneity metric could unify fire research over broad geographic regions and facilitate examination of similarities and differences related to geography and ecosystem variability. Novel technologies, such as LIDAR (LIght Detection And Ranging) and infrared thermography, could address some of the measurement issues. Fire effects on soil are difficult to assess because soil heterogeneity is extensive and often occurs at submeter scales, hampering landscape-scale inferences. It is critical to explore the issue of scalability to determine the level of local detail required to explain landscape-scale patterns.

Fire and fire effect studies are typically focused on the immediate postfire effects rather than the long-term, postfire response to fire activity (e.g., snag dynamics over time). This short-term focus seems to be driven by the immediate postfire reaction of the public and the availability of funding for long-term fire studies. Longer-term information with respect to specific fire events, both pre- and postfire, could provide a more complete picture of what drives the fire and subsequent fire effects and how the ecosystem responds. The long-term study approach should help increase the predictability for future fire events and lead to much-needed, improved models of fire behavior, as indicated below in the discussion of the ecological impacts of mastication fuel reduction treatments. Ultimately, the need for better definitions of fire severity and longer-term studies of fire and fire effects should help to influence funding gaps from sources such as the Joint Fire Science Program.

2.3. Ecosystem Recovery Following Disturbance. The combined influence of climate change and direct human intervention on forest ecosystems has led to a recent focus of research on the recovery of ecosystems following disturbance. The concern is that postdisturbance recovery may be hampered by a lack of species adaptations to novel stresses from disturbances foreign to the ecosystem [27]. Human disturbances in the past have severely hampered ecosystem recovery due to the magnitude, severity, and extent of the disturbance, and poor adaptation of species. A classic example is the poor adaptation of native vegetation to widespread burning by Polynesian settlers in New Zealand [28].

In the context of the systems and attributes examined, the universal conclusion that “ecosystems do recover” depends on how narrowly ecosystem properties are defined. If the definition is based on broadly defined processes, biomass, or even relatively similar stand structure and species composition, then in most cases the ecosystems studied recover to a similar condition. However, if the definition is based on the full suite of species and structure present in the preexisting “natural” condition, then this is not necessarily true. Such a rigidly defined goal for recovery is questionable, especially if the objective is to manage for diversity in forest systems, in light of our evolving understanding of landscape equilibrium in these systems [29, 30]. The exceptions to the general rule that ecosystems do recover may include (1) the impacts of forest harvesting on dead wood and (2) multiple harvest entries that target single tree species. Significant differences in dead wood levels between younger managed stands and all ages of natural stands have been noted in several studies. Moreover, the implications of continued harvest entries, targeting only single or few tree species, for tree species loss and substantial understory changes are also a common theme in recent studies.

Recovery assumes having a target condition in mind. For this approach to be ecologically meaningful, the reference point needs to be carefully considered and elements of the target condition are critical to recovery identified. Often the assumed condition is that of old forest, but in Renard et al.'s [31] recent study of paludified boreal black spruce ecosystems, the management target was an earlier successional

stage with higher timber volumes. It is also unreasonable to expect a young managed stand to have recovered many of the attributes present in an old forest condition; the more appropriate reference is a similar-aged naturally disturbed stand. The question of how important to ecosystem and landscape function a particular ecosystem condition is must be addressed. Human interventions designed to speed up or restore a particular target condition should be treated cautiously. Although well intentioned, these interventions may lead to undesirable consequences as evidenced by our long history of fire exclusion to maintain timber values.

Future direction in recovery research should focus on synthesizing the relatively large pool of data on recovery of multiple components of well-studied ecosystems in order to address the questions stated above. New research should address what valued ecological services the ecosystem provides and at what stage during recovery it provides them, and how ecosystem recovery is linked to maintaining of critical ecosystem processes. In order to maintain ecosystem services and processes it is important that ecosystems be in different stages of recovery across time and space. Future ecosystem recovery studies should also include a wildlife component so that the recovery of stand structure and composition can be linked to habitat recovery and wildlife use. With the rapid advances in new statistical and modeling techniques, collaboration between ecologists and mathematicians will provide some useful insights in this area of ecological research.

2.4. Future Directions for Disturbance Research. Key areas for future research in forest disturbance interactions include (1) incorporating the influence of climatic variability and assessing the likely influence of global climate change on disturbance interactions and their effects (2) assessing the influence of disturbance interactions on key ecosystem processes and components, such as carbon dynamics and forest biodiversity (3) addressing the role of socioeconomic and political influences on disturbance interactions and their effects, such as diverse management histories among different land owners across regional landscapes, (4) addressing disturbance dynamics at appropriate scales, including determination of scale-sensitive detection thresholds for specific disturbance interactions and their effects, (5) considering the degree to which forest management can (or should) emulate more complex disturbance interactions, and (6) using iterative approaches to better coordinate research (e.g., modeling) and forest management such that research informs possible new management directions and the results of management inform and guide future research. Finally, to help accomplish these objectives, better data are often needed to inform both management and research, not only via acquisition of better empirical data from field research and long-term monitoring, but also by developing better access to, or compilations of, existing datasets that encompass large forested landscapes and long-time periods.

3. Emerging Roles of Forest Detritus

The role that dead wood plays in forest ecosystems was first comprehensively detailed nearly three decades ago [32].

Dead wood was initially highlighted as a vital attribute of old growth forests, providing habitat for fauna and niches for plant species regeneration [33]. A slightly divergent track of dead wood research has been that of fire and fuel sciences. Instead of focusing on the role that dead wood plays in forest ecosystem processes, fire research has sought to refine estimates and management of fuel loadings [34]. With the onset of the 21st century, dead wood resources have now been framed as a vital carbon stock [35] in terms of both sequestration and emission (i.e., wildfires)—all within a changing climate [36]. Perhaps due to the diverse array of research directions that have beset dead wood investigations, there has been no focal point for assimilating decades of wide-ranging dead wood study results. To wit, the contribution of standing, down, and buried dead wood to forest ecosystem processes and carbon fluxes is often ignored or underappreciated. Dead wood may be a controlling factor in many forest ecosystem processes such as regeneration establishment, soil carbon efflux, and soil stability. Ultimately, the entire carbon cycle of forest stands may be controlled by dead wood following disturbances (e.g., seedling establishment and disturbance recovery), especially in higher-latitude forests (e.g., boreal). Dead wood carbon stocks may not be as ephemeral as assumed, since buried dead wood in boreal systems can remain for 200–300 years. The contemporary emphasis on utilization of residual dead wood biomass following harvest operations has increased pressure on dead wood resources, possibly altering dead wood ecosystem processes beyond our current understanding. Exacerbating the knowledge gaps of dead wood biomass utilization is that the drivers of dead wood decay processes across the diverse forest ecosystems of North America are vastly unknown. Dead wood simulation models typically do not include climatic variables and are, thus, not sensitive to climate change effects on dead wood accumulation/decay processes [37]. A whole array of forest carbon policy and management decisions that have been predicated on dead wood simulation models may be in error. Even empirical dead wood surveys may not have adequate sample intensities to statistically detect substantial changes in dead wood carbon stocks across large scales. Overall, expanded, systematic/long-term research in the areas of dead wood decay processes is suggested. Furthermore, a joining of forest inventories with dead wood simulation models is suggested to benefit refined forest ecosystem carbon stock estimation. Across North America dead wood resources systematically impact forest ecosystems, and thus are deserving systematic study.

4. Ecological Applications in the Management of Forest Ecosystems

4.1. Alternative Silvicultural Approaches. The use of large-scale alternative silvicultural approaches for achieving multiple objectives of forest management has become increasingly widespread throughout North America [38–40]. Variable retention harvests, fuel reduction treatments, and other

restoration practices have been utilized and studied in systems from the oak-hickory forests of the southern US to the temperate rainforests of the Pacific Northwest and the boreal mixedwoods of Canada. Because forest restoration generally focuses on restoring structure characteristic of older forests, these practices are necessarily long-term endeavors.

There are several critical issues affecting the use of these ecosystem-management approaches. The continuity of research to evaluate the efficacy of treatments over greater spatial and temporal scales is important to determine best practices, but difficult to plan and implement over time. As a result, regeneration responses to these treatments abound [41, 42], but longer-term responses are less well documented. In some cases, this is simply due to the lack of time that has elapsed since initiation of these studies, but often it is due to the difficulty in sustaining long-term funding for such studies. Additionally, there are many tradeoffs involved in these restoration approaches from both a forest resource management perspective and a sociological perspective. Finally, the objectives of these studies are generally very broad (increase structural diversity, restore to historic range of variability) and not precisely defined (how do you measure “greater structural diversity” and will it achieve the ultimate management goals?).

Future solutions to many of these issues may include reviving older studies that have “dropped off the radar” but which may provide the long-term data lacking in more recent studies. Another potentially fruitful approach would be to combine field results with modeling approaches. This would allow longer-term projections to see whether treatments are meeting long-term goals and would also allow continual recalibration of the models with the best available empirical data.

4.2. Long-Term Studies in Experimental Forests. Across North America, a network of experimental forests provides an incredible wealth of records and knowledge of environmental change in natural and managed forest ecosystems. The United States Department of Agriculture Forest Service celebrated the 100th anniversary of its network of 81 experimental forests in 2008. National Research Forests administered by the Canadian Forest Service have similar mandates and legacies. Experimental forests provide places for long-term science and management studies in all the major forest vegetation types in North America. They are living laboratories where discoveries are made and research results are demonstrated for cooperators and stakeholders [43]. Experimental forests provide valuable opportunities to observe changes in forest composition and structure over extended periods, yet many experimental forests are undergoing shifts in research missions as societal demands and needs shift. The following represent some of the key aspects of experimental forests with respect to their establishment, shifting missions, and current emphases.

Many experimental forests were established during or after other dominant land uses had occurred. For example, the Bent Creek (North Carolina), Coweeta (North Carolina), Crossett (Arkansas), Cutfoot Sioux (Minnesota), Fort Valley (Arizona), and Santee (South Carolina) experimental forests

still contain legacies of landscape-scale tree harvesting and railroad logging, fire suppression, livestock grazing, or diversion of water for agriculture. Thus, these sites provide a rich history of past disturbance events and both natural restoration processes and diverse restoration treatments. Because many experimental forests were previously logged during more exploitive periods, a common early research priority was establishment of stands and forests that best represented natural stand structures, demonstrated by early work at Cutfoot Sioux, Santee, Bent Creek, Crossett, and at the Canadian Petawawa Research Forest in Ontario. This work is proven valuable today as federal, state, and provincial forest management strategies have shifted to incorporate a greater emphasis on restoration of structure and processes.

Experimental forests frequently were sites for early research designed to evaluate methods of harvesting and regeneration techniques that aided the timber management industry, including Bent Creek, Crossett, Petawawa, Fort Valley, and Pringle Falls (Oregon). This support, almost universal across the network, now rarely exists. Moreover, experimental forests often provide opportunities to address new questions with existing databases, such as using nearly a century of recorded vegetation dynamics at Coweeta or Fort Valley to evaluate the effects of introduced disease, introduced insects, and climate change or nearly a century of recorded vegetation dynamics under known management regimes at Crossett, Cutfoot Sioux, Petawawa, Fort Valley, and Pringle Falls to evaluate opportunities for biomass conversion and carbon sequestration.

Current long-term research at various experimental forests may provide unique opportunities for linking efforts across similar sites to calibrate and validate landscape- and regional-scale models supporting policy decisions. As a first step, workshop attendees recommend that a catalog of long-term datasets should be developed based on the prototype designed by the Canadian Forest Service in British Columbia.

4.3. Ecological Classification Systems. Ecological classification systems have existed in North America for several decades. However, the importance of these systems in guiding the conservation and management of forest ecosystems has increased substantially within recent years. In particular, policy mandates for the use of ecosystem-based approaches for forest management, driven in large part by forestland certification programs [44], have created a need for the development and verification of systems that classify terrestrial vegetation into ecologically and administratively meaningful units on the landscape. Nationwide efforts, such as the development and refinement of the map of ecological subregions by the US Forest Service, are facilitating efforts to develop forest-wide plans for National Forests and other federal lands. Likewise, regional efforts, such as those in the central Rocky Mountains, Lake States, and British Columbia, are providing locally calibrated classification systems [45, 46] that offer a framework for addressing management and conservation challenges within environmentally complex landscapes.

Collectively, these classification approaches provide an invaluable platform for communicating information about site-level ecological concepts and processes across management and conservation agencies and research institutions. As such, these classification systems are a valuable tool for seeking commonalities across scientific investigations examining issues such as the decline of aspen in the western United States, as well as in evaluating the response of managed ecosystems to novel ecologically based silvicultural treatments. Ultimately, the relevance and utility of these approaches and tools hinge on outreach and education programs that translate the concepts of ecological classification systems to scales relevant to foresters, wildlife biologists, planners, and scientists. Without these efforts, the ability of these tools to facilitate the development of ecosystem management approaches is limited.

4.4. Stand Density Indices. The ideas, applications, and new developments for measuring stand density were examined, using Reineke's [47] original work on Stand Density Index (SDI) as a touchstone. While some practitioners have eschewed SDI, preferring basal area for its simplicity of measurement [48], others have criticized SDI and related approaches for a lack of ecological complexity [49]. Still, Zeide [50] calls SDI the best available stand density metric, and its fascination in silvicultural and ecological research has been enduring.

From boreal mixedwoods in the north to tree hammocks in south Florida and from Oregon in the west to New England in the east, Reineke's ideas continue to provide raw material for a variety of exciting work that attempts to extend the application of his original work in monocultures to mixed-species stands and landscapes. A challenge with SDI is that while it may provide a good measure of stand density within stands of a particular species, between species or in mixed species stands, it may be less appropriate and other measures may perform better. Another recent area of fruitful investigation has been the connection between stand density and dead wood pools at a national scale, focused on interpreting stand density ecologically over a broad range of species composition and dead wood decomposition rates [51].

There is a growing tendency to use density measures related to Reineke's SDI for a range of silvicultural and ecological objectives, far beyond the traditional timber management goals anticipated by Reineke [47] and emphasized in recent reviews (e.g., [50]). Moreover, difficulty of adapting simple density measures to the complexity of mixed species stands continues to challenge researchers with a strong interest in the application of SDI in forest management. Must we capture the full complexity of species interactions to provide a density measure that is informative, or will some simpler approach suffice? And what, given the range of management and scientific objectives, would constitute a sufficient approach? Finally, there is a critical need for testing and comparing different density measures. Evaluating and comparing these measures by treating them as competing hypotheses about ecological behavior remains both valuable and uncommon.

4.5. Mastication Fuel Reduction Treatments. Mastication treatments involve shredding, chopping, or chipping small trees and/or shrubs into small chunks and leaving the material on site as a way to reduce crown-fire risk. Managers and the public are interested in understanding the impacts of the addition of this woody material on forest ecosystems so that they can evaluate the ecological impacts of this novel management technique. Mastication substantially decreases tree density and increases the amount of surface fuel loadings with the majority of deposited fuels <2.54 cm [52–54]. The shifts in the fuelbed composition from a needle-dominated to a woody-dominated fuelbed have been found to impact vegetation recovery and alter soil nutrients and abiotic conditions. Herbaceous plant cover has been observed to increase after mastication treatments in pinyon pine-juniper and ponderosa pine ecosystems, but not in mixed conifer or lodgepole pine ecosystems [55]. Presence of exotic species increases in all masticated areas [55, 56]. The addition of mulch to the forest floor alters soil moisture and temperature by moderating the fluctuation in temperatures, maintaining cooler temperatures in Summer and warmer temperatures in Winter and retaining moisture [57]. Although soil moisture and temperature are altered, impacts to nitrogen availability vary among and within the ecosystems under consideration. Some pinyon-juniper sites show no change in nitrogen mineralization, while others show an increase in ammonium [57, 58]. Nitrogen has been shown to decline with increased mulch depth for the pinyon-juniper and lodgepole pine ecosystems, but not for the ponderosa pine ecosystem [57]. The addition of mulch to the forest floor does not appear to alter the C:N ratio in the pinyon-juniper ecosystem. However, the loss of AMF fungi richness after 2.5 years in the pinyon-juniper ecosystem has been noted [56].

Because of the infancy of this novel management treatment, the ecological impacts are still unclear. While there are some general trends in recent investigations, future research is needed. It is clear that ecosystems differ in their initial and short-term (2 to 4 years post treatment) response to the addition of woody material. However, it is unclear whether changes within a site among years are a result of climatic differences or ecosystem recovery. This highlights the need for continued longer-term studies of these treatments. Chronosequence studies of mulch sites in ecosystems along a latitudinal gradient are needed to examine changes in C:N ratio of the woody material, soil microbial communities, decomposition rates, soil nitrogen, tree regeneration, and tree growth. In addition, studies that assess the long-term impact to herbaceous plant community composition and production are still needed. Longer-term studies are also needed to determine the longevity of these treatments to reduce crown-fire risk. The impact that micro- and macro-vertebrates are having on vegetation recovery and nutrient dynamics in these ecosystems is still unknown. The lack of fire behavior fuel models to describe these new fuel beds hinders our ability to determine the fire behavior and effects on these treatment areas [53, 59]. More research in the development of new fuel models to estimate fuel loads and their physical properties is still needed for each of the ecosystems. Finally, working with managers so that they leave

reference controls within the treatment area is important, so we can assess the impacts of the treatments and provide feedback for adaptive management.

4.6. Aspen Management. Anecdotal evidence from field visits and conversations with land managers suggests that practitioners involved in the management of quaking aspen (*Populus tremuloides*) are operating with assumptions based on 20–30-year-old science. Much of Canadian national and provincial forest management is strongly influenced by commercial timber harvesting, whereas U.S. policy and practice has, in recent years, been dominated by public involvement favoring conservation of species, recreational interests, and aesthetics. Land management geared toward conservation is more prominent in areas where aspen—and forest harvesting generally—is less commercially viable for various reasons (i.e., growth habits, ease of access, and political/economic climates). In the U.S. Lake States and boreal Canada, aspen is considered a prime commercial tree species, whereas in the mountain west of the U.S. this is not the case.

Despite these divergent policy agendas between these two countries, a few prominent themes emerge. It is generally agreed that there is not a single “aspen forest,” but many functional aspen types. Thus, it would benefit managers and researchers to focus on the specifics of how these types differ ecologically and how they might be managed more effectively with that base of knowledge. Recent investigations of the key indicators of aspen health (i.e., sustainability) suggest that pooling findings from various ecosystems for application in monitoring would advance the field. For example, recent Canadian research [60] clearly points to the high value of examining root system status as an indicator of aspen health. In the US, focus on aboveground regeneration “health” has resulted in its emergence as a prominent indicator in stable aspen forests (e.g., [61].) There is also a need to improve monitoring via standardization of methods and terminology. Often researchers show conflicting results in functionally similar aspen communities, and thus send mixed messages to earnest land managers (e.g., contrast [62] with [63]). Upon further scrutiny, differing conclusions are rooted in dissimilar definitions or approaches. Finally, it is worth noting that policy makers throughout aspen’s range either have not understood or are reluctant to act on ecological pleas for the benefits of large-scale disturbance (primarily fire) to aspen systems. One benefit that has been widely discussed is the need to “overwhelm” ungulate herbivory of suckers by affecting much bigger areas of the landscape with prescribed natural fire.

Major research topics in need of further investigation include genetics and phytochemistry, management applications, wildlife habitat, monitoring methods and range of natural variability, connecting ecology to policy, effects of climate warming/drought (i.e., Sudden Aspen Decline in U.S. Southwest and aspen expansion in Canadian Rockies), incorporating social science (e.g., clarify aspen benefits to society), and aspen’s ecological relation to conifer beetle kill. Research has already begun on the first four topics, while the last four topics have seen little or no emphasis to date.

Each of these topics is deserving priority status directed, ultimately, toward answering our respective constituency’s concerns about aspen ecosystem status and health.

5. Future Directions

As a precursor, it should be noted that the voluntary nature of participation in this workshop understandably resulted in the omission of several current topics of keen interest to forest researchers and managers, including climate change, carbon dynamics, biodiversity, invasive species, and biofuels. Hopefully, these and other omissions will encourage others to join the expanding ranks of those who participate in these workshops.

Several “needs” did emerge from the workshop regarding approaches to the study of forest ecosystems, including (1) consideration of variable spatial and temporal scales, (2) long-term monitoring, (3) development of universal databases more encompassing of time and space to facilitate metaanalyses, (4) combining field studies and modeling approaches, (5) standardizing methods of measurement and assessment, (6) guarding against oversimplification or overgeneralization from limited site-specific results, (7) greater emphasis on plant-animal interactions, and (8) better alignment of research with management needs and better translation of results for managers. An elaboration of several of these needs appears above in various sections of this paper.

Of special concern is the fact that conventional studies of limited duration and scale have proven inadequate for examining ecological processes that depend on many complex interactions and function over longer time scales. This observation suggests that a formal discussion concerning the pressing need for coordination among studies should be initiated, with an initial emphasis on a synthesis of current studies of ecosystem processes across geographic regions and ecological circumstances. As a first step, these studies should be gathered together into an international catalog and database, perhaps using the Ecological Society of America (ESA) and U.S. Federal Geographic Data Committee’s (FGDC) National Vegetation Classification (NVC) as a model, together with the Long-Term Ecological (LTER) and National Ecological Observatory (NEON) Networks—sponsored by the U.S. National Science Foundation. A comprehensive metaanalysis of these studies could then be used to identify the most pressing unanswered questions and to set priorities for establishing a more extensive network of long-term studies that encompasses the full range of natural variability and utilizes standardized methods of measurement and assessment based on a combination of field studies and modeling efforts.

An example of research on forest ecosystems that could benefit from better alignment and communication with managers is that on gap dynamics. To date research has often focused on specific conditions within gaps, with little thought for the legacy of dead trees remaining in these gaps and how they affect forest ecosystems. Silvicultural systems that attempt to approximate gap formation typically do so by removing the trees from the system, thereby losing

an important element of natural gap dynamics. This tree-centric focus on the living component is a legacy of past forest management practices for timber-driven values. Dead trees do not disappear rapidly from the system [64]. Snags can impact regeneration by occupying canopy space and reducing ground light levels and can influence the survival of neighboring live trees [65]. These snags also provide habitat for a variety of organisms [66] as do fallen logs [67]. In the current zeitgeist of ecological management, a more holistic approach needs to be taken, not only focusing on altered conditions (composition) created by disturbance, but also placing more emphasis on the role of disturbance (process) in modifying resources. Only then can we achieve our ultimate goal of ecosystem-based management.

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Research Article

Carbon Flux of Down Woody Materials in Forests of the North Central United States

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Across large scales, the carbon (C) flux of down woody material (DWM) detrital pools has largely been simulated based on forest stand attributes (e.g., stand age and forest type). The annual change in forest DWM C stocks and other attributes (e.g., size and decay class changes) was assessed using a forest inventory in the north central United States to provide an empirical assessment of strategic-scale DWM C flux. Using DWM inventory data from the USDA Forest Service's Forest Inventory and Analysis program, DWM C stocks were found to be relatively static across the study region with an annual flux rate not statistically different from zero. Mean C flux rates across the study area were -0.25 , -0.12 , -0.01 , and -0.04 (Mg/ha/yr) for standing live trees, standing dead trees, coarse woody debris, and fine woody debris, respectively. Flux rates varied in their both magnitude and status (emission/sequestration) by forest types, latitude, and DWM component size. Given the complex dynamics of DWM C flux, early implementation of inventory remeasurement, and relatively low sample size, numerous future research directions are suggested.

1. Introduction

For the purposes of this study, down woody materials (DWMs) are defined as detrital components of forest ecosystems comprising fine and coarse woody debris. Coarse woody debris (CWD) are pieces, or portion of pieces, of down dead wood with a minimum small-end diameter of at least 7.62 cm inches at the point of intersection with a sampling transect and a length of at least 0.91 m. CWD pieces must be detached from a bole and/or not be self-supported by a root system with a lean angle more than 45 degrees from vertical [1]. Fine woody debris (FWD) are pieces, or portion of pieces, of down woody with a diameter less than 7.62 cm inches at the point of intersection with a sampling transect excluding dead branches attached to standing trees, dead foliage, bark fragments, or cubicle rot.

It has been estimated that 35 percent of the total forest carbon (C) pool in the U.S. is in live vegetation, 52 percent in the soil, and 14 percent in dead organic material, such as down woody materials (DWMs) [2]. Furthermore, it has been estimated that annual CWD and FWD carbon sequestration offset approximately 1 percent of all CO₂

emissions in the United States [3]. Terrestrial forest C pools, such as FWD and CWD, often represent a balance between the influx of CO₂ fixed in photosynthesis and the efflux of CO₂ through woody decay processes [4]. The decay rates of any individual piece of forest dead wood is determined by substrate quality, microbial activity, air temperature, and available moisture [5]. Similarly, the productive capacity of any given forest is partially governed by climatic variables such as temperature [6]. Some studies have suggested that forest detritus production and decay may be in balance [7], whereas others have suggested that increased detritus decomposition rates due to climate change may ultimately cause forest detritus C pools to become net CO₂ emitters [8, 9]. Recently, Woodall and Liknes [10] have linked FWD and CWD C to climate and indicated that DWM's status as a C sink could be at risk in a world of warming temperatures and concomitant increases in precipitation.

Beyond sensitivity of DWM C stocks to climate change, at smaller spatial and temporal scales there is evidence that DWM C flux is related to stand development and disturbance processes (e.g., fire, density-induced mortality, and branch shedding). In western U.S. forests, fire is often listed as

a control on DWM C stocks [11, 12], while in eastern U.S. forests stand development/management processes may correlate with DWM C flux dynamics [13, 14]. It has been suggested that the dynamics of DWM C flux may be an important determinant as to whether conversion of old-growth to younger managed forests indeed sequester more C [15]. The empirical monitoring of DWM C flux has been achieved using diverse methods at various scales. At small scales, intensive site-specific field methods have been used to estimate the efflux of C from DWM pieces (e.g., see Gough et al. [14]). At larger scales, differences between forest inventories of DWM C at two points in time have been assumed to be the DWM C flux (e.g., see EPA [3]). Despite the higher levels of uncertainty associated with the latter flux monitoring methodology, DWM C flux estimates from forest inventories provide an opportunity to explore DWM C flux from the population perspective. Overall, large-scale empirical assessments of DWM C flux are critical to estimating future U.S. C stock inventories, greenhouse gas offset accounting, and climate change mitigation efforts. The goal of this study is to assess the flux of C in DWM across the north central United States with specific objectives to (1) estimate mean C flux by small FWD, medium FWD, large FWD, and CWD for the entire study area, forest types, and classes of latitude, (2) estimate changes in plot-level CWD diameter and decay distributions as a means to interpret CWD C flux dynamics, (3) examine the relationship between standing live, dead, and down dead woody C stocks, and (4) forward suggestions for additional studies, analytical refinements, and implications of study results on current understanding of C flux dynamics.

2. Methods

2.1. Field Sample Protocols. The field and analytical procedures used to estimate DWM C flux define flux as the change in DWM C from time 1 (2002) to time 2 (2007) using a large-scale forest inventory conducted by the USDA Forest Service's Forest Inventory and Analysis (FIA) program. Although there are numerous methods for estimating annual DWM C flux, this study's methodology allows multistate analyses while unraveling flux dynamics that may be used in development of forest inventory C imputation models. FIA conducts a 3-phase inventory of forest attributes of the United States [16]. The FIA sampling design is based on a tessellation of the United States into hexagons approximately 2,428-ha in size with at least one permanent plot established in each hexagon. In phase 1, the population of interest is stratified and plots are assigned to strata to increase the precision of estimates. In phase 2, tree and site attributes are measured for plots established in the 2,428-ha hexagons. Phase 2 plots consist of four 7.32 m fixed radius subplots on which standing live and dead trees are inventoried (for more information, see [17]).

DWMs are sampled during the third phase of FIA's multiscale inventory sampling design [1, 17]. CWD are sampled on transects radiating from each FIA subplot center (at angles of 30, 150, and 270 degrees, resp.). Each subplot

has three 7.32 m transects, totaling 87.8 m for a fully forested inventory plot. Information collected for every CWD piece intersected by transects is transect diameter, length, small-end diameter, large-end diameter, decay class, and species. Transect diameter is the diameter of a down woody piece at the point of intersection with a sampling transect. Decay class is a subjective determination of the amount of decay present in an individual log. Decay class 1 is the least decayed (freshly fallen log), while decay class 5 is an extremely decayed log (cubicle rot pile). The species of each fallen log is identified through determination of species-specific bark, branching, bud, and wood composition attributes (excluding decay class five). FWD with transect diameters less than 0.61 cm (small FWD) and 0.62 cm to 2.54 cm (medium FWD) are tallied separately on a 1.83 m slope distance transect (4.27 m to 6.09 m on the 150-degree transect). FWD with transect diameters of 2.55 cm to 7.59 cm (large FWD) are tallied on a 3.05 m slope distance transect (4.27 m to 7.32 m on the 150-degree transect).

2.2. Data and Analysis. DWM plots first established in 2002 were remeasured in 2007 for a total of 185 plots in the following states: IA (7), IL (11), IN (9), KS (7), MI (37), MN (30), MO (38), ND (2), NE (4), SD (6), WI (34) (see Figure 1). Individual CWD pieces were matched based on location (± 0.6 m transect length) along the same sample transect in times 1 and 2. The volume and C content of FWD and CWD were determined through application of estimators detailed by Woodall and Monleon [1]. Briefly, for FWD the volume of FWD is estimated per unit area then converted to an estimate of biomass using a bulk density and decay reduction factor based on forest type. An estimate of FWD C is then derived by reducing the biomass estimate by 0.5. For CWD the volume is determined for every CWD piece then used in an estimator to estimate per unit area volume. Volume is converted into biomass and C through the use of decay reduction factors, bulk density, and carbon conversion based on a piece's unique species and decay class [18]. Carbon flux for each DWM component was calculated as the difference in C between times 2 and 1, divided by the number of years between inventories (measurement units = Mg/ha/yr). The juxtaposition of the measurement times allowed calculation of flux using the widely accepted format that increases in C stocks to be negative indicating possible sequestration of C. The means and associated standard errors of C flux by small FWD, medium FWD, large FWD, and CWD were estimated for the entire study area, forest types, and classes of latitude. In order to determine whether stand component flux rates were significantly different from zero, student *t*-tests were conducted ($\alpha = 0.1$).

Finally, the diameter and decay distributions of CWD were estimated at the plot level at times 1 and 2. This methodology differs from other DWM C flux analyses in this study as differences in individual CWD pieces were assessed. Through a CWD piece matching algorithm (for details see Westfall and Woodall [19]), differences in time 1 and time 2 decay class, total volume, large-end diameter, and carbon content estimates were estimated for individual CWD pieces ($n = 380$ pieces).

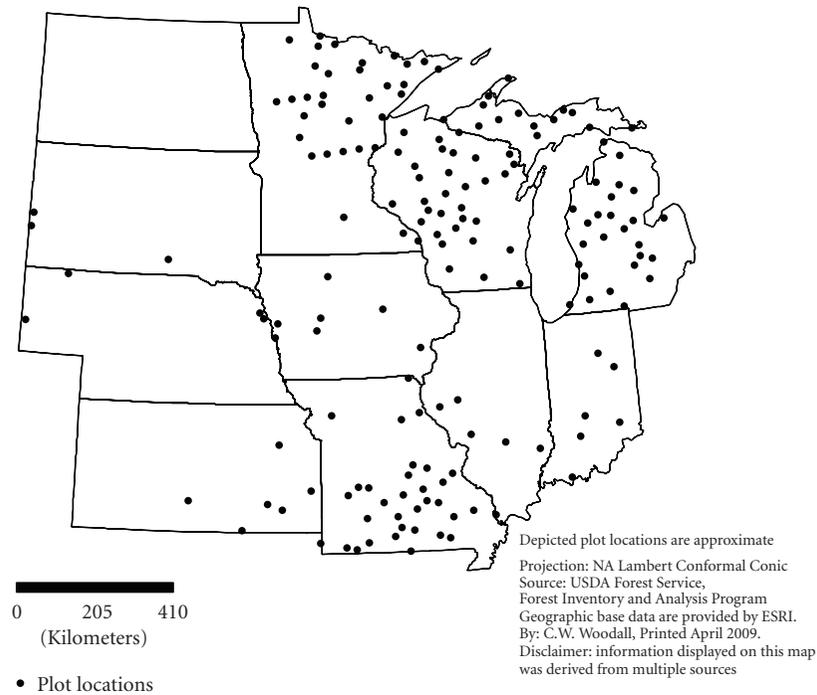


FIGURE 1: Study plot approximate locations across the north central United States, 2002 to 2007.

3. Results

All examined forest stand components (standing live/dead and CWD/FWD) sequestered net C during the 5-year period between measurements (Table 1). Standing live trees sequestered the most C with a mean of -0.25 Mg/ha/yr followed by standing dead trees with a mean of -0.12 Mg/ha/yr. Together, standing live and standing dead trees accounted for nearly 90 percent of the annual sequestration. The minimal sequestration rates of FWD and CWD across the north central states were not statistically different from zero (P values of .55 and .86, resp.). Sequestration rates varied widely by forest type with ranges in C flux rates for standing live, standing dead, FWD, and CWD being -1.85 to 1.48 , -0.53 to 1.21 , -0.95 to 0.71 , and -0.80 to 1.02 Mg/ha/yr, respectively (Table 2). There were no obvious patterns in flux among forest types nor among stand components within forest types.

There were very little discernible trends in C flux in FWD or CWD across latitude classes (Figure 2). The median C flux (Mg/ha/yr) of FWD changed from a net sequestration to a net emission/transfer from latitudes below 38 degrees to the 41–44-degree latitude class. From a net emission/transfer at the 41–44-degree latitude class, FWD C stocks once again sequestered C at latitudes above 47 degrees. It should be noted that the 95th percentile of FWD C sequestration steadily decreased as latitude increased. The median annual flux of CWD hovered steadily around zero across all latitude classes. An interpolation of CWD and FWD flux across the north central states indicated some hotspots of emission/transfer (e.g., southeastern Missouri

and central Indiana) and sequestration (e.g., northeastern Minnesota), possibly reflecting local disturbance events or recovery (i.e., rapid stand growth following stand initiation) (Figure 3).

Between 2002 and 2007, remeasured CWD (through utilization of matching algorithm) indicated an increase in the percentage of recently recruited CWD pieces (≈ 30 percent, CWD decay class 1) along with a decrease in the percentage of highly decayed CWD pieces (≈ 15 percent, decay class 5) (Figure 4(a)). In contrast, there were minimal changes in the distribution of CWD piece size class distribution between times one and two (Figure 4(b)). The exception is the largest transect diameter class (>45.7 cm) where there were less large CWD pieces in time 2 (≈ 30 percent).

Trends in standing live/dead and CWD/FWD annual C flux were examined across classes of stand age (15-year classes) (Figure 5). Standing live trees consistently provided a net sequestration of C across the remeasurement cycle at a regional scale with median values ranging between -0.91 and -0.35 Mg/ha/yr. The median flux rates for standing dead trees, FWD, and CWD were all nearly zero across all age classes, although there was a slight tendency for FWD and CWD to provide net sequestration in younger age classes when compared to a tendency to be net emitters (or transfer to other forest stocks) in older age classes.

Refining comprehension of the relationship between both live and dead trees (standing and down) is important to unraveling of both stand and C flux dynamics. There are four scenarios with regards to these dynamics: (1) live emission/transfer and dead emission/transfer, (2) live sequestration and dead sequestration, (3) live emission/transfer

TABLE 1: Mean stock density (time 1, 2002) and average annual carbon flux for standing live/dead trees and down woody materials (fine and coarse) where a negative estimate indicates a net sequestration north central across the United States, 2002 to 2007 (obs = 182).

Stock	Mean Carbon Stock Time 1 (Mg/ha)	Std. Err. (Mg/ha)	Mean Carbon Flux (Mg/ha/yr)	Std. Err. (Mg/ha/yr)
Standing Live	36.48	1.85	-0.25	0.11
Standing Dead	3.18	0.39	-0.12	0.06
Coarse Woody Debris	3.82	0.42	-0.01	0.07
Fine Woody Debris	2.91	0.21	-0.04	0.06
Small Fine Woody Debris	0.14	0.01	0.00	0.01
Medium Fine Woody Debris	0.83	0.08	-0.01	0.01
Large Fine Woody Debris	1.94	0.16	-0.03	0.06

TABLE 2: Average annual carbon flux by forest type for down woody material components where $n > 3$: live (standing live trees), Sdead (standing dead trees), FWD (fine woody debris), and CWD (coarse woody debris) where a negative estimate indicates a net sequestration north central across the United States, 2002 to 2007.

Forest type	n	Live	Std. Err.	Sdead	Std. Err.	FWD	Std. Err.	CWD	Std. Err.
Red pine	4	-0.87	0.51	-0.03	0.06	-0.13	0.10	-0.14	0.13
Balsam fir	4	-0.17	0.71	-0.36	0.42	-0.18	0.11	-0.34	0.18
Black spruce	4	0.44	0.43	0.10	0.06	-0.09	0.05	-0.80	0.75
Northern white cedar	7	-0.30	0.23	-0.05	0.05	0.13	0.08	0.27	0.15
White/red oak and hickory	31	-0.03	0.32	0.05	0.13	-0.13	0.10	0.23	0.19
White oak	10	-0.91	0.09	0.00	0.02	0.19	0.08	0.17	0.24
Elm/Ash/Black Locust	12	-0.42	0.16	-0.46	0.16	-0.68	0.74	-0.75	0.43
Mixed upland hardwoods	10	0.46	0.76	-0.53	0.68	-0.12	0.19	-0.20	0.24
Black ash/American elm/red maple	8	-0.53	0.32	-0.08	0.21	0.03	0.25	0.30	0.22
Silver maple/American elm	4	-1.85	0.60	-0.12	0.08	-0.20	0.17	-0.28	0.98
Sugar maple/beech/yellow birch	12	0.07	0.40	-0.20	0.14	0.14	0.10	0.34	0.20
Hard maple/basswood	9	-0.31	0.38	-0.33	0.27	-0.20	0.12	0.14	0.39
Aspen	14	-0.36	0.20	-0.02	0.08	0.04	0.13	0.11	0.28
Balsam poplar	4	-0.47	0.20	-0.23	0.20	0.08	0.28	0.04	0.09

and dead sequestration, and (4) live sequestration and dead emission/transfer. An important caveat when viewing these results is that a reduction in any given forest carbon pool C on any given site is not necessarily an emission. Often these C stocks transfer their C to another stock (e.g., live tree C transfer to DWM to soils). Thus, emissions are labeled as emission/transfer. For both standing and down dead trees, the most common occurrence is live sequestration and either emission/transfer or sequestration of dead wood C through decay processes (Figures 6(a) and 6(b)). It appears to be an infrequent event that both live and dead C stocks are both net emitters of C. It is also uncommon that stands have net emission/transfer of live stocks but present net sequestration of dead wood stocks. The scale of flux does vary by scenario, excluding some obvious outliers, with the net live sequestration and net dead wood emission/transfer presenting the largest range in flux.

4. Discussion

This study is an initial assessment of DWM C flux using less than one fifth of the eventual remeasurement dataset for one

region of the U.S. As such, important considerations may be made with respect to how to improve C flux estimation in future analyses. First, sampled forest conditions must be appropriately matched at two points in time. Land conversions, forest type changes, and disturbance events may greatly alter forest conditions, and thus, complicate change analysis techniques. Second, possibly a far larger issue for DWM C flux estimation is the differences in sample designs and lack of tracking individual dead wood pieces through time. Although the DWM sample design did not change between 2002 and 2007, other dead wood monitoring efforts in other regions/nations should focus efforts on utilizing identical sample designs for change estimation, rather than trying to adjust DWM estimators to avoid bias in change estimates. Third, even though the C flux of some DWM components may be fairly substantial, they all need to be couched in the inherent measurement error in these field inventories [20]. A 0.1 cm change in CWD large-end diameter may be negated by the measurement repeatability standard being ± 5.1 cm for field crews [19]. Fourth, the transition in C stocks from standing live to standing dead/CWD is not explicitly tracked. Carbon stocks

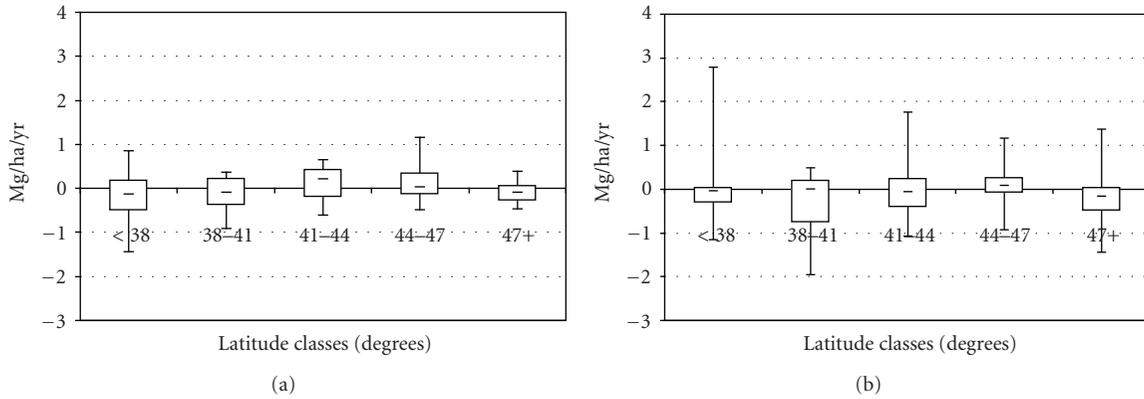


FIGURE 2: Box plots of carbon flux (Mg/ha/yr) by 3 degree latitude classes for (a) fine woody debris and (b) coarse woody debris across the north central United States, 2002 to 2007.

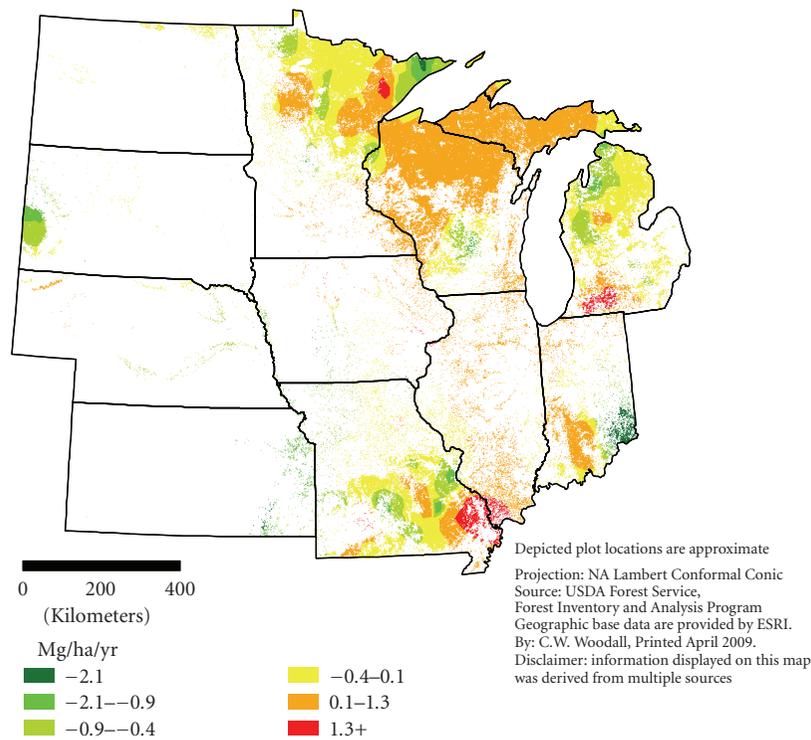


FIGURE 3: Interpolated surface (inverse distance weighting) of annual down dead wood carbon flux across the north central United States, 2002 to 2007.

were calculated at plot levels between time one and time two; therefore, it is entirely possible that a live tree in time one could die and fall outside the plot in time two. In reality, the forest ecosystem did not emit carbon immediately. Hence, there may be errors with tracking stocks of forest ecosystem C (e.g., standing dead or CWD) using forest inventories that may be additional to those commonly calculated (e.g., volume growth) for remeasured standing live trees. Finally, the unique stand disturbance history and live tree mortality attributes of forests may ultimately derive DWM C flux. As

this study was as an initial analysis of large-scale DWM C flux, future examination of DWM C dynamics is suggested based on direction from emerging science [21]. Overall, further evaluation and resolution of these issues should provide a foundation for future work with larger datasets eventually replacing simulations currently used in national greenhouse gas assessments [20, 22].

Despite the use of an initial dataset, preliminary DWM C flux hypotheses may be promulgated. First, how closely do the results of this systematic regional, wide study confirm the

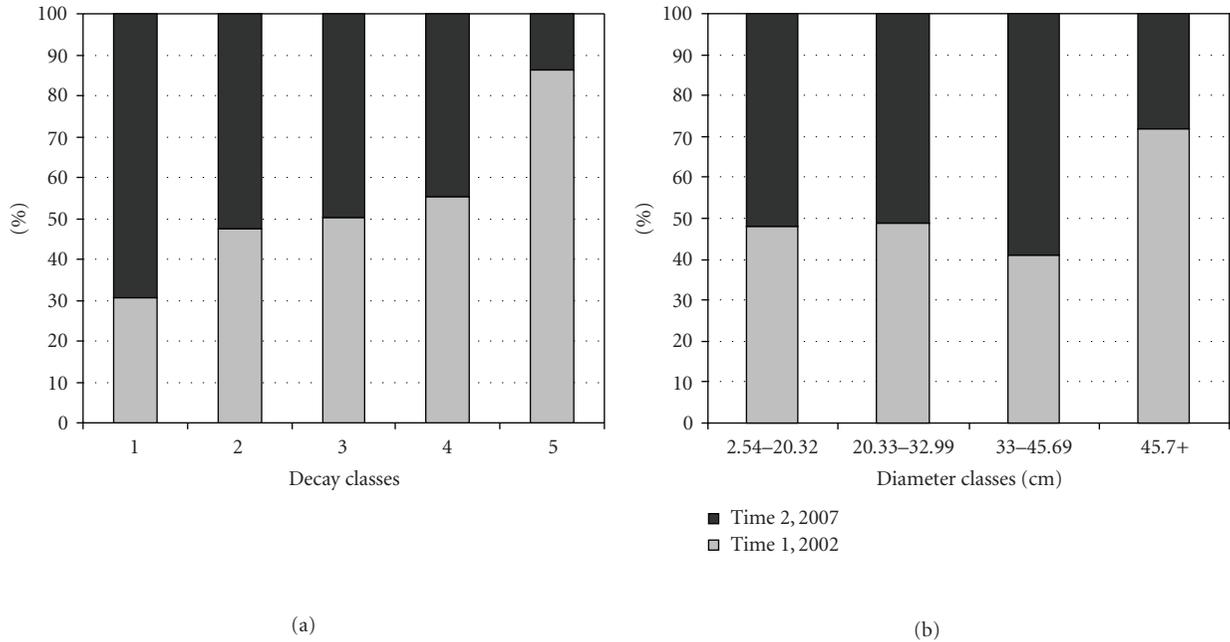


FIGURE 4: Percentage of coarse woody debris pieces in time one (2002) and time two (2007) in (a) decay classes and (b) transect diameter class in the north central United States, 2002 to 2007.

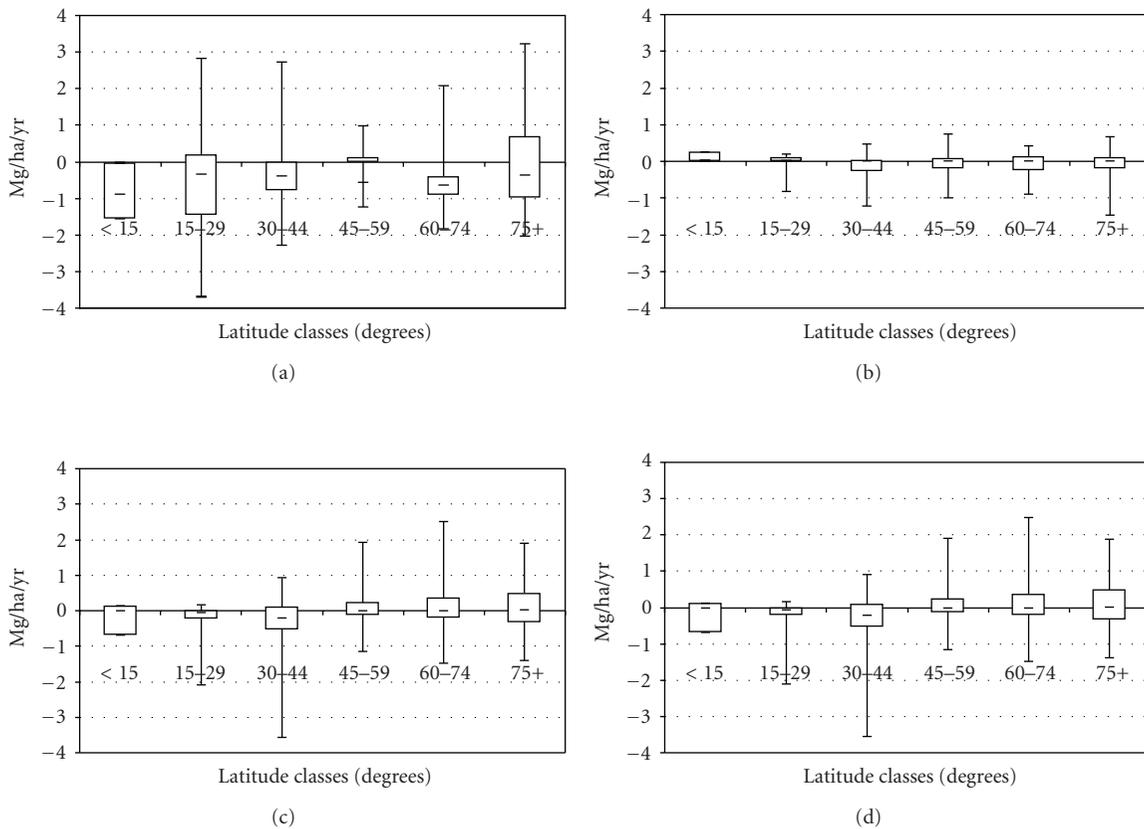


FIGURE 5: Box plots of carbon flux (Mg/ha/yr) by 15-year stand age classes for (a) standing live trees, (b) standing dead trees, (c) coarse woody debris, and (d) fine woody debris across the north central United States, 2002 to 2007.

results of more intensive, yet spatially limited or simulated studies? Gough et al. [14] found an annual CWD flux of -0.21 Mg/ha/yr in a northern hardwood site in Michigan with decay classes four and five CWD pieces comprising a plurality of the sequestration. Most other studies have not explicitly tracked DWM C flux; rather they stated current DWM C stocks and expected residence times which ranged from 5.9 years for CWD in tropical forests [23] to many decades in higher latitude forests [11, 24]. With this study's relative low CWD C flux rate, it may be hypothesized that north central CWD may have a long residence time, therefore affecting the regional forest carbon balance for decades as found in other forest ecosystems [12, 25, 26]. Woodall and Liknes [27] suggested that as the climate warms, increases in decay rates (emission) might more than offset dead wood C sequestration. This study found initial evidence that higher latitudes may be experiencing CWD C emission/transfer on some sites, while FWD C stocks may be remaining static. Standing live tree C stocks can easily increase in a stand with no regeneration simply by relying on individual tree increment. For DWM C stocks, it is a much different situation where the lack of DWM recruitment will always decrease their respective C stocks resulting in an emission/transfer of C.

Refinement of forest stand C dynamics may be gained by viewing C flux by stand component (e.g., standing live and CWD) across classes of stand age. At a regional level, there appear to be no strong trends across classes of stand age for any stand component. The most evident sequestration stand component is that of standing live trees, with the remainder of stand components displaying substantial variation. It does appear that younger stands (15–44 years) had a tendency to have greater fourth quartile sequestration rates in terms of all stand components when compared to older stands. It may be hypothesized that these middle-aged stands are fully stocked with tree biomass undergoing either stem exclusion or understory reinitiation [28]. In addition, the stage of stand development of these stands may have appreciable tree mortality and branch shedding increasing standing dead, CWD, and FWD C stocks. This study does not address the DWM C flux dynamics among stands converted to different stages of stand development and explicitly examined in other studies [15].

Examination of the scatter plots (Figure 6) of dead wood (both CWD and standing dead) versus standing live annual C flux can help indicate dynamics in both the scale (amount) of C flux and the frequency (Figure 7). In the north central U.S., it is a fairly uncommon event that there is both an emission/transfer of dead wood and standing live C. Most assuredly in other forest ecosystems prone to more frequent fire disturbances, this situation may be different (e.g., see [12, 26]). It is also an uncommon occurrence that there is a live tree C emission/transfer with a dead wood sequestration. However, the scale of this flux can be greater than the previous example since there could be a substantial transfer in C from standing live to dead (e.g., widespread stand mortality event or clear cutting) [29]. The most common C dynamics scenario in north central U.S. forests is that of live tree sequestration and either an emission/transfer or

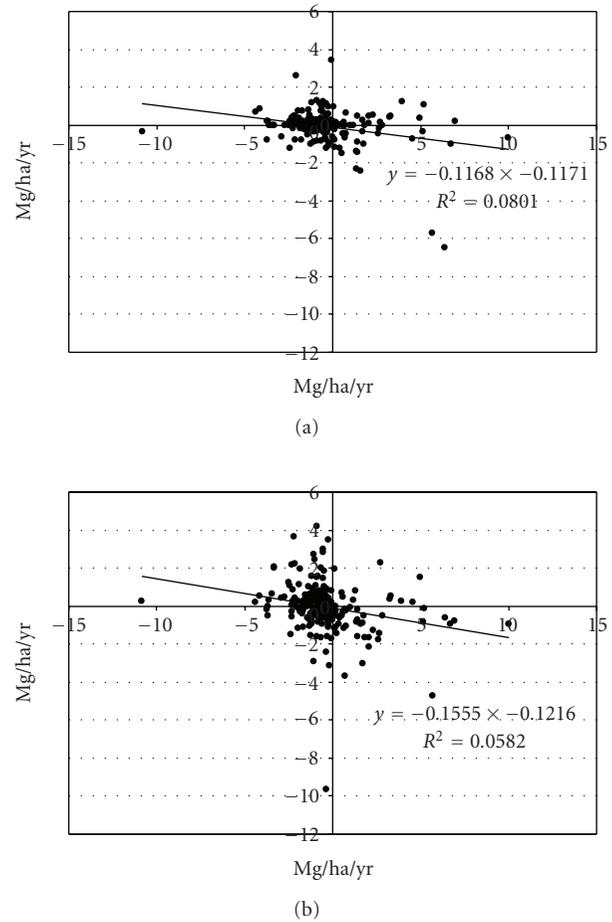


FIGURE 6: Scatter plots of (a) standing dead and (b) down dead woody material C stocks by standing live tree C stocks across the north central United States, 2002 to 2007.

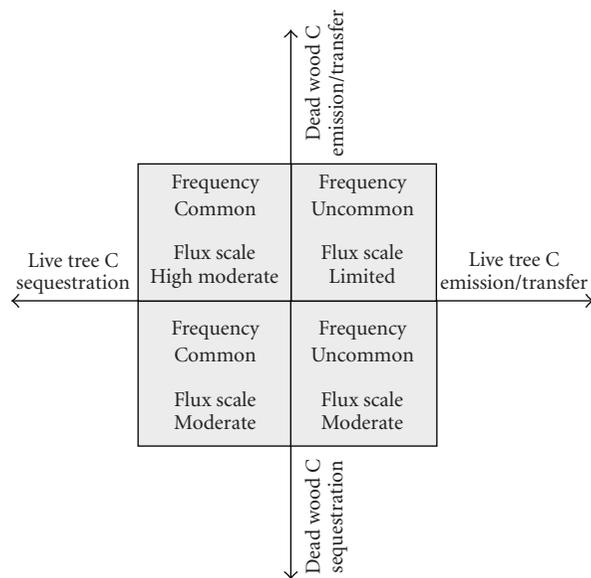


FIGURE 7: Theoretical relationship between standing live tree and dead tree C flux scales and frequencies.

sequestration of dead wood C. If live trees are not dying, it appears that the scale of flux is greater for dead wood emission/transfer as compared to that of sequestration. Since there is no dead wood recruitment, the only direction for dead wood is towards emission/transfer (i.e., atmospheric emission or transfer to soil organic C) as decay rates may be high in moist, lower latitude forests [10].

5. Conclusions

Across the north central United States, forest detritus C pools are relatively static serving neither as a C source nor as a sink. The flux status of DWM C pools should be monitored to determine its sensitivity to disturbance events or climate change. It appears that north central U.S. DWM C pools may greatly increase their sequestration rates through stand disturbance events, while C emission/transfer is often limited by slow decay rates (i.e., dead wood residence times). When considering most above-ground forest stand components and excluding the C balance complexities of stand conversion, the greatest sequestration rates may be found in younger stands in middle stages of stand development (e.g., stem exclusion or understory reinitiation) where branch shedding and shaded understories ensure dead wood retention, while the live trees accrue bole increment at relatively rapid rates. Overall, the DWM C flux dynamics of north central forests inherently depends on transfer from other stand components (e.g., standing live and dead pools) and does not guarantee an overall forest ecosystem sequestration if the residence time of C is decreased (i.e., increased CWD decay rates) or the sequestration capacity of other stand components is reduced (e.g., standing live tree species conversion or regeneration impairment).

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Research Article

Documentation of Significant Losses in *Cornus florida* L. Populations throughout the Appalachian Ecoregion

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Over the last three decades the fungus *Discula destructiva* Redlin has severely impacted *Cornus florida* L. (flowering dogwood—hereafter “dogwood”) populations throughout its range. This study estimates historical and current dogwood populations (number of trees) across the Appalachian ecoregion. Objectives were to (1) quantify current dogwood populations in the Appalachian ecoregion, (2) quantify change over time in dogwood populations, and (3) identify trends in dogwood population shifts. Data from the USDA Forest Service Forest Inventory and Analysis (FIA) database were compiled from 41 FIA units in 13 states for county-level estimates of the total number of all live dogwood trees on timberland within the Appalachian ecoregion. Analysis of covariance, comparing historical and current county-level dogwood population estimates with average change in forest density as the covariate, was used to identify significant changes within FIA units. Losses ranging from 25 to 100 percent of the sample population ($P < .05$) were observed in 33 of the 41 (80 percent) sampled FIA units. These results indicate that an important component of the eastern deciduous forest has experienced serious losses throughout the Appalachians and support localized empirical results and landscape-scale anecdotal evidence.

1. Introduction

Cornus florida L. (flowering dogwood—hereafter referred to as “dogwood”) is widely distributed across the eastern United States (U.S.), including the Appalachian ecoregion. Dogwood is one of the most common understory trees in North America and is an important member of the Eastern deciduous forest that has been and is currently threatened by an imported fungus [1, 2]. Extensive dogwood mortality throughout the east and particularly the Appalachian ecoregion has been attributed to the fungus *Discula destructiva* Redlin (Dogwood anthracnose) [3–5].

Botanical surveys conducted throughout the twentieth century have documented the abundance of dogwood in the eastern U.S. [6]. Measures of high relative density and elevated importance values prior to *Discula destructiva* infestation were reported by Hannah [7] in North Carolina, Quarterman et al. [8] in Tennessee, Muller [9] in Kentucky, Carr and Banas [10] in Virginia, and Sherald et al. [11]

in Maryland. Dogwood is also a common component of second-growth hardwood stands [12, 13], an important understory component of old-growth forests [14, 15], and an important source of calcium, in the form of leaf litter, in the surface horizons of some forest soils [16, 17].

Discula destructiva was identified as the causal agent for dogwood anthracnose in 1991 [4]. This fungus is thought to have originated from Asia and was introduced into the United States through infected *Cornus kousa* L. (kousa dogwood) stock [18]. While symptoms of *D. destructiva* were first observed in 1977 on native *Cornus nuttallii* (Pacific dogwood) in southern Washington, similar symptoms were observed in the eastern U.S. in 1979 throughout southeastern New York and southwestern Connecticut [19]. By 1989 *D. destructiva* had spread through the Appalachian Mountains as far south as Alabama [19]. Although smaller stems appear more susceptible, *D. destructiva* attacks aboveground portions of trees of any size [3]. Mortality results from either repeated defoliation or girdling from cankers [18].

Dogwood mortality is extensive following local colonization by *D. destructiva* [1, 6, 20–22]. While many studies have quantified local losses of dogwood [6, 10, 11, 20–22] specifically attributed to *D. destructiva*, few, if any, studies have quantified large-scale losses across entire ecoregions. These studies have been important for filling knowledge gaps about the impacts of *Discula destructiva* on dogwood populations. However, large-scale assessments are lacking. Both remote-sensing products and field-based large-scale forest inventories, such as implemented by the U.S. Department of Agriculture Forest Service Forest Inventory and Analysis (FIA) program, provide important data for monitoring forest attributes, including tree species population shifts, across large regions. Remote-sensing products are not suited for identifying individual species over large swaths of forests; therefore large-scale inventories must be relied on. Here we estimate natural dogwood populations (number of trees) for the Appalachian ecoregion for two periods, 1984–1993 (time 1) and 2004–2006 (time 2). Estimates are based on state-level forest land inventories conducted by FIA. Changes from time 1 to time 2 are quantified at the county, FIA unit (geopolitical boundaries routinely used by FIA for analysis and reporting), and ecoregion scale, and significant losses or gains are identified. Specific objectives were to (1) quantify current dogwood populations in the Appalachian ecoregion, (2) quantify changes in dogwood populations from the mid 1980's to 2006 and (3) identify trends in dogwood population shifts for the same period. Our hypothesis is that significant losses are widespread throughout the Appalachian ecoregion. While *D. destructiva* is known to reduce dogwood populations, we do not identify the one or most culpable agent of loss. The primary objective is to quantify large-scale changes, through comparisons of large-scale forest inventories, to the population of a tree species known to be experiencing localized losses due to a pathogen with a large geographical distribution.

2. Materials and Methods

The forest inventory conducted by FIA is a year-round effort to collect and disseminate information and statistics on the extent, condition, status, and trends of forest resources across all ownerships [23]. In the late 1990s, FIA began a transition from irregular and asynchronous periodic inventories to annual inventories [24]. Before 2000, most inventories were periodic; after 2000 most states have been inventoried annually. FIA applies a nationally consistent sampling protocol using a quasisystematic design covering all ownerships in the entire nation [24]. For this study, data were collected from 41 FIA units in 13 states (Figure 1). Fixed-area plots were installed in locations that have accessible forest land cover [24]. Field crews collect data on more than 300 variables, including land ownership, forest type, tree species, tree size, tree condition, and other site attributes (e.g., slope, aspect, disturbance, land use) [25, 26]. Plot intensity for field-collected data is approximately one plot for every 2,400 hectares (6,000 acres) of land. Briefly, the plot design for FIA inventory plots consists of four 7.3-meter (24-ft.) fixed-radius subplots spaced 36.6 meters (120 ft.) apart

in a triangular arrangement with one subplot in the center [24]. All trees with a diameter at breast height (dbh) of at least 12.7 cm (5 in.) are inventoried on forested subplots. Within each subplot, a 2.1-meter (6.8 ft.) radius microplot is established wherein all live tree saplings (dbh ≥ 2.54 cm and < 12.7 cm) are tallied according to species.

The public Forest Inventory and Analysis (FIA) database (FIADB) contains both current and historical inventory data [27]. Forest Inventory Mapmaker 3.0 [28] was used to access the FIADB and capture county-level estimates of the total number of all live trees ≥ 2.54 cm for dogwood and total volume and number of all live trees for all species on timberland (forest land not administratively withdrawn from timber production (e.g., wilderness areas or “reserved” forest land)) within a broad definition of the Appalachian ecoregion. We included data from FIA units that intersected any one of the seven level-III EPA Ecoregions [29] that comprise the Appalachian region. The Level III Ecoregions are the Ridge and Valley, Blue Ridge, Central Appalachians, Southwestern Appalachians, North Central Appalachians, Northern Appalachian Plateau and Uplands, and the Western Allegheny Plateau.

County-level estimates of natural dogwood populations and the number and volume of all live trees for all species were generated for two periods in time and labeled time 1 and time 2 (Table 1). Perfect alignment of inventory dates was not possible due to the nature of past periodic inventories and variability in transition times between periodic and annual inventory designs [24]. The data labeled “time 1” ranged from 1984 in Virginia to 1993 in New York (Table 1) and represents a time period early in the spread of the disease. The dates for the data labeled “time 2” ranged from 2003 to 2006. Individual counties were assigned to FIA units that correspond to both political and ecological boundaries. Average county-level absolute change and relative change were calculated for each county. Average annual change was calculated by dividing the difference between times 1 and 2 for each county by the remeasurement period.

Simple linear regression (PROC REG) in SAS [30], relating dogwood population change to changes in all live volume (trees greater than 12.7 cm dbh), was used to determine the amount of change that may be attributed to changes in stand structure. An analysis of covariance (ANCOVA) Type III test of fixed effects (PROC GLM) was used to identify significant changes in dogwood tree populations within FIA units between times 1 and 2. Change in volume of all live trees greater than 12.7 cm dbh (a proxy for changes in forest density) for each county was included in the analysis as a covariate. Average annual change and relative change was then mapped according to FIA unit for visual interpretation.

3. Results

The dogwood population in the Appalachian ecoregion decreased approximately 57 percent between times 1 and 2 and losses occurred in all dogwood diameter classes (Figure 2). The current dogwood population estimate in the Appalachian ecoregion is 2.215 billion individuals, down from an estimated 5.162 billion. Considerable variation

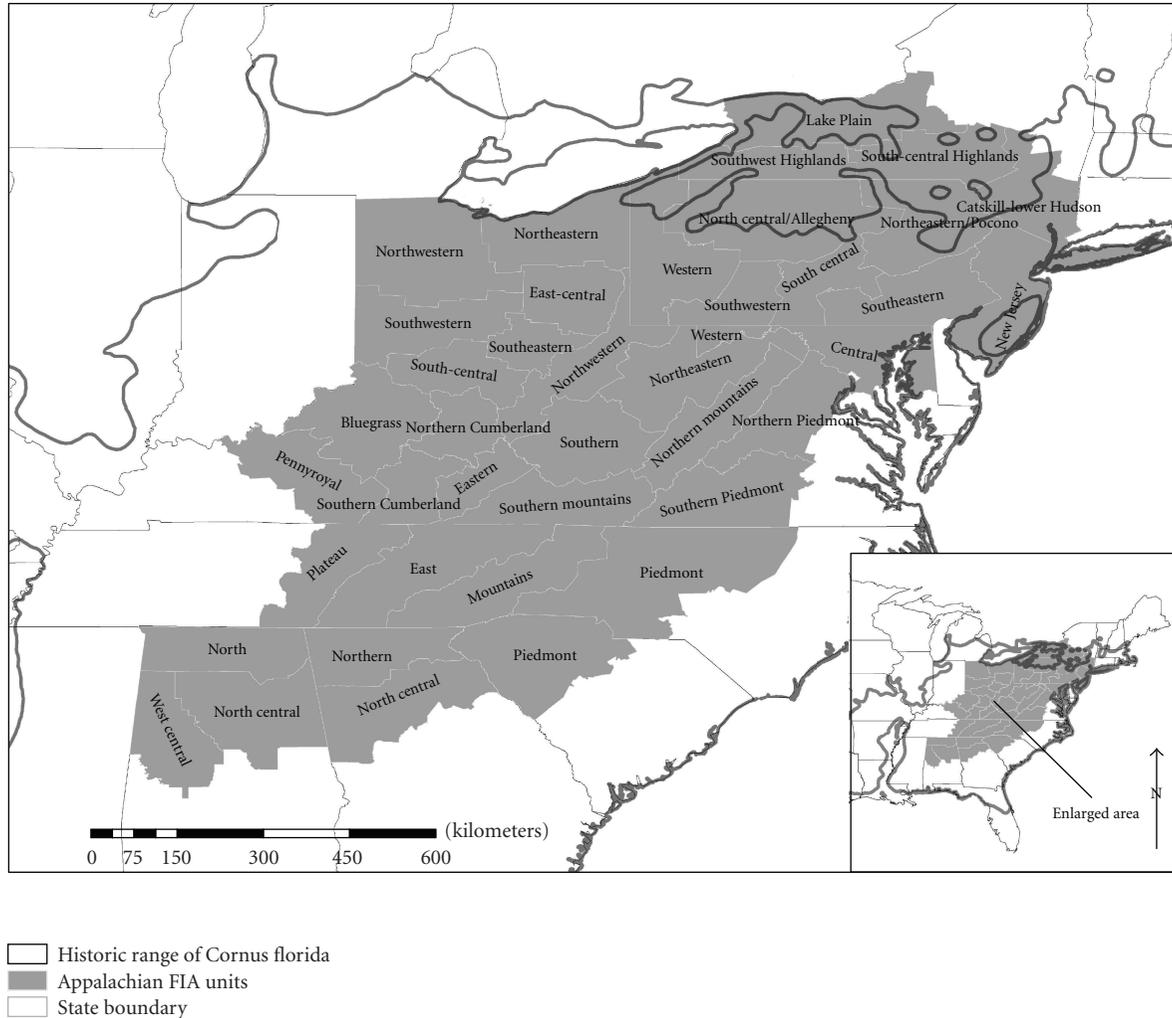


FIGURE 1: The Appalachian ecoregion and associated FIA unit boundaries.

existed among the estimates of county-level populations within each time period. Time 1 averaged 9.15 million (std. dev. = 8.06 million, max. = 42.02 million, min. = 0) individuals per county while time 2 averaged 3.93 million (std. dev. = 4.26 million, max. = 32.94 million, min. = 0) individuals per county.

Areas in West Virginia, Virginia, Tennessee, Ohio, North Carolina, New York, and Maryland showed the largest losses (Table 1). Sixty-three percent (353) of Appalachian counties experienced dogwood population losses greater than 50 percent while thirty-seven percent exhibited losses of greater than 75 percent.

The regression analysis indicated that a significant relationship existed between county-level dogwood population change and all live-tree volume ($P < .0001$) between times 1 and 2, confirming the decision to use change in all live tree volume as a covariate in the regional analysis by FIA unit. The regional analysis (ANCOVA) showed significant ($\alpha = 0.05$) losses in 33 of the 41 (80 percent) sampled FIA units (Figure 3). While the central and southern portions of the Appalachian ecoregion experienced larger

absolute losses (Figure 3(a)) of dogwood, the populations in the northern portions experienced greater proportional losses (Figure 3(b)). FIA units in New York, Ohio, and Pennsylvania experienced severe losses relative to population estimates at time 1. In New York, dogwood populations in FIA units decreased 100, 98, 83, and 56 percent in the South-Central Highlands, Southwest Highlands, Catskill-Lower Hudson, and Lake Plain units, respectively (Table 1). In Ohio, population losses were 85, 82, 77, 77, 72, and 62 percent for the Northwestern, Southwestern, South-Central, Northeastern, Southeastern, and East-Central FIA units, respectively. Populations in Pennsylvania decreased by 76, 75, 75, 67 and 44 percent in the Southwestern, Southeastern, South Central, Western, and Northeast/Pocono units, respectively. While the mean county-level dogwood population increased in the North Central Allegheny unit of Pennsylvania, the increase was not statistically different from 0. The largest absolute mean county-level decrease was a loss of 13.80 million trees per county ($P = .0001$) in the Southern unit of West Virginia. The largest relative loss occurred in the South-Central Highlands unit of New York (100 percent).

TABLE 1: Estimates of mean county level dogwood populations for times 1 and 2, mean difference, relative mean difference, and result of ANCOVA for each FIA regional unit.

State	FIA Unit Name	$n^{(1)}$	Time 1			Time 2			ANCOVA ⁽³⁾					
			Mean ⁽²⁾	SE	trees	Mean	SE	trees	Difference	percent	$F_{(1,m)}$	P-value	Covariate effect	$F_{(1,m)}$
Alabama (1990–2006) ⁽⁴⁾	West Central	9	20,695,764	3,274,020	10,031,008	2,016,787	10,031,008	2,016,787	-10,664,756	-52	12.29	.0032	4.68	.0472
	North Central	15	21,507,327	2,943,946	13,406,251	1,840,435	13,406,251	1,840,435	-8,101,076	-38	9.17	.0054	3.31	.0799
Georgia (1989–2005)	North	10	9,244,358	1,878,898	2,912,652	805,238	2,912,652	805,238	-6,331,706	-68	20.47	.0003	8.89	.0084
	North Central	32	7,313,091	805,778	4,458,056	577,459	4,458,056	577,459	-2,855,035	-39	19.63	<.0001	44.85	<.0001
Kentucky (1988–2005)	Northern	21	13,073,967	1,412,887	7,310,997	944,318	7,310,997	944,318	-5,762,970	-44	24.93	<.0001	29.96	<.0001
	Eastern	8	10,306,397	1,743,985	6,442,801	1,630,781	6,442,801	1,630,781	-3,863,597	-37	7.01	.0201	6.21	.0270
Maryland (1986–2005)	Northern Cumberland	13	9,990,609	1,275,932	4,001,196	800,892	4,001,196	800,892	-5,989,413	-60	18.77	.0002	2.21	.1510
	Southern Cumberland	12	13,763,014	2,296,954	7,067,097	938,907	7,067,097	938,907	-6,695,917	-49	18.32	.0003	10.98	.0033
New Jersey (1987–2005)	Bluegrass	23	1,039,546	424,357	974,558	198,036	974,558	198,036	-64,988	-6	0.40	.5308	1.71	.1981
	Pennyroyal	20	5,654,549	833,179	4,102,760	724,316	4,102,760	724,316	-1,551,789	-27	7.07	.0115	17.84	.0002
New York (1993–2003)	Central	14	3,056,785	868,256	854,696	355,430	854,696	355,430	-2,202,089	-72	6.15	.0202	0.71	.4081
	Western	2	6,446,816	4,483,348	2,721,425	2,721,425	2,721,425	2,721,425	-3,725,392	-58	18.82	.1442	18.74	.1445
North Carolina (1984–2005)	New Jersey	10	1,988,159	832,293	1,056,032	670,973	1,056,032	670,973	-932,127	-47	0.70	.4155	0.02	.8852
	Lake Plain	4	888,319	647,869	391,994	391,994	391,994	391,994	-496,325	-56	0.77	.4216	0.73	.4332
Ohio (1991–2005)	Southwest Highlands	3	979,608	393,482	21,541	21,541	21,541	21,541	-958,067	-98	3.03	.1801	0.81	.4347
	South-Central Highlands	6	845,510	262,091	0	0	0	0	-845,510	-100	8.41	.0176	0.08	.7787
Ohio (1991–2005)	Catskill-Lower Hudson	7	2,637,366	668,206	446,236	218,787	446,236	218,787	-2,191,130	-83	8.52	.0139	0.00	.9883
	Piedmont	35	12,946,425	1,185,717	6,299,325	678,232	6,299,325	678,232	-6,647,100	-51	46.25	<.0001	30.34	<.0001
Ohio (1991–2005)	Mountains	21	15,561,452	2,239,385	3,889,770	1,055,649	3,889,770	1,055,649	-11,671,681	-75	40.21	<.0001	13.74	.0006
	South-Central	10	12,575,259	3,327,952	2,949,358	917,571	2,949,358	917,571	-9,625,901	-77	18.20	.0005	9.59	.0065
Ohio (1991–2005)	Southeastern	7	16,271,863	3,664,634	4,594,509	820,116	4,594,509	820,116	-11,677,355	-72	12.12	.0051	1.88	.1981
	East-Central	11	9,344,192	1,808,647	3,547,333	1,074,389	3,547,333	1,074,389	-5,796,859	-62	9.69	.0057	1.91	.1827
Ohio (1991–2005)	Northeastern	14	2,358,145	635,583	542,080	168,966	542,080	168,966	-1,816,064	-77	7.47	.0114	0.11	.7412
	Southwestern	10	2,640,831	1,469,844	468,895	210,824	468,895	210,824	-2,171,937	-82	6.54	.0204	9.85	.0060
Ohio (1991–2005)	Northwestern	8	1,822,098	797,893	266,995	185,833	266,995	185,833	-1,555,103	-85	6.53	.0240	7.36	.0177

TABLE 1: Continued.

State	FIA Unit Name	$n^{(1)}$	Time 1			Time 2			ANCOVA ⁽³⁾					
			Mean ⁽²⁾	SE	SE	Mean	SE	SE	Difference	percent	$F_{(1,n)}$	P-value	Covariate effect	$F_{(1,n)}$
Pennsylvania (1989–2004)	South Central	9	4,059,553	803,890	321,546	1,012,088	321,546	321,546	-3,047,465	-75	18.65	.0006	4.60	.0489
	Western	11	6,083,886	1,372,618	646,447	2,025,858	646,447	646,447	-4,058,028	-67	9.47	.0062	2.71	.1162
	North Central/Allegheny	12	1,530,963	347,328	649,859	1,543,194	649,859	1,265,416	12,231	1	0.11	.7466	1.49	.2358
SouthCarolina (1986–2006)	Southwestern	5	6,139,095	3,209,492	1,265,416	1,490,563	1,265,416	1,265,416	-4,648,532	-76	2.50	.1579	0.80	.4009
	Northeastern/Pocono	11	1,476,173	435,794	548,256	831,137	548,256	548,256	-645,036	-44	1.84	.1908	5.77	.0267
	Southeastern	11	2,750,142	669,852	269,232	681,959	269,232	269,232	-2,068,183	-75	15.54	.0009	11.55	.0030
Tennessee (1989–2005)	Piedmont	18	14,121,375	1,782,213	937,465	8,456,840	937,465	937,465	-5,664,534	-40	12.76	.0011	4.68	.0379
	Plateau	16	14,451,884	2,345,046	510,643	4,144,037	510,643	510,643	-10,307,847	-71	32.60	<.0001	10.72	.0027
	East	27	9,121,866	1,349,548	480,197	3,603,451	480,197	480,197	-5,518,414	-60	24.19	<.0001	9.10	.0040
Virginia (1984–2006)	Southern Piedmont	17	14,397,395	1,386,403	677,451	8,384,910	677,451	677,451	-6,012,485	-42	32.03	<.0001	15.67	.0004
	Northern Piedmont	17	11,557,137	1,619,409	785,853	4,384,169	785,853	785,853	-7,172,968	-62	45.37	<.0001	25.94	<.0001
	Northern Mountains	14	12,462,577	1,997,602	576,140	2,373,419	576,140	576,140	-10,089,157	-81	41.67	<.0001	13.44	<.0001
WestVirginia (1989–2005)	Southern mountains	17	9,589,499	853,928	508,146	3,115,279	508,146	508,146	-6,474,220	-68	63.99	<.0001	10.33	<.0001
	Northeastern	18	7,646,410	1,342,850	942,141	2,716,840	942,141	942,141	-4,929,570	-64	8.85	.0054	0.07	.7944
	Southern	14	15,904,120	1,773,008	696,818	2,106,411	696,818	696,818	-13,797,709	-87	59.06	<.0001	3.03	.0940
	Northwestern	19	8,519,707	1,562,666	1,043,101	4,188,189	1,043,101	1,043,101	-4,331,518	-51	12.45	.0012	20.05	<.0001

⁽¹⁾Number of counties located within the unit.

⁽²⁾Mean number of dogwood stems greater than 1-inch diameter in counties located within the unit.

⁽³⁾Type III tests comparing time 1 county-level estimates to time 2 county-level estimates with change in stand density as the covariate.

⁽⁴⁾Inventory year associated with each state for both time 1 and time 2.

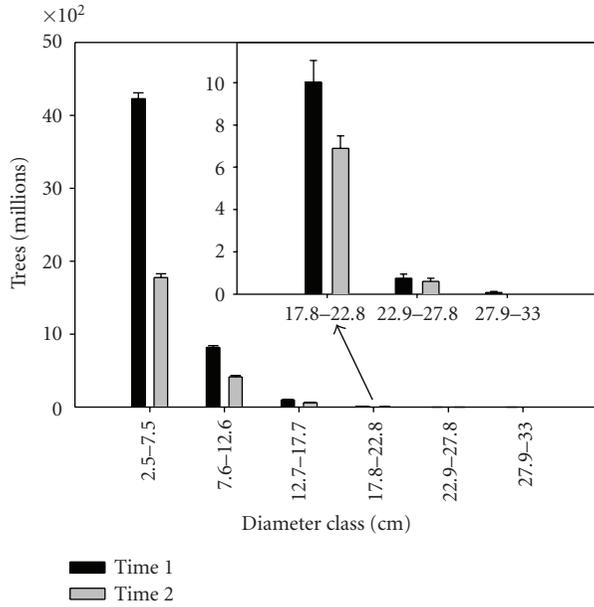


FIGURE 2: Estimated dogwood populations for the Appalachian ecoregion for times 1 and 2 by diameter class.

Average annual losses were the largest in the Southern unit of West Virginia (Figure 3(a)) which lost an average of approximately 0.86 million trees per year (Table 2). The smallest average annual loss of 3,800 trees per year was found in the Bluegrass unit of Kentucky. However, this unit is one of the least forested sections of Kentucky. The only positive mean annual change was in the North Central unit of Pennsylvania.

While all species experienced losses in the smallest diameter classes (likely a result of forest maturation), dogwood appeared to suffer disproportionate losses (Figure 4). With the exception of a complete loss of the largest diameter class of dogwood (27.94–33.01 cm), the relative loss decreased with increasing size class. That is, the largest losses were in the smaller diameter classes. All diameter classes experienced relative losses of at least 20 percent. Conversely, for all tree species relative gains were found in all diameter classes larger than 17.78 cm, and no diameter class experienced a loss of greater than 12 percent (Figure 4).

4. Discussion

Dogwood populations decreased considerably across the Appalachian ecoregion during the period studied. Proportional losses were greater in the north than in the south. Williams and Moriarty [21] indicated that dogwood is a relatively minor component of many forest types near the northern periphery of its range and therefore considerable losses may have been realized in relatively small initial populations. However, symptoms of what was once labeled as “lower branch dieback” [31] and eventually attributed to *D. destructiva* [4] were first recognized in New York in the spring of 1979 [19]. Therefore, many stems could have succumbed to *D. destructiva* prior to sampling in the

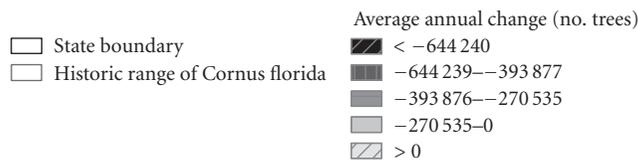
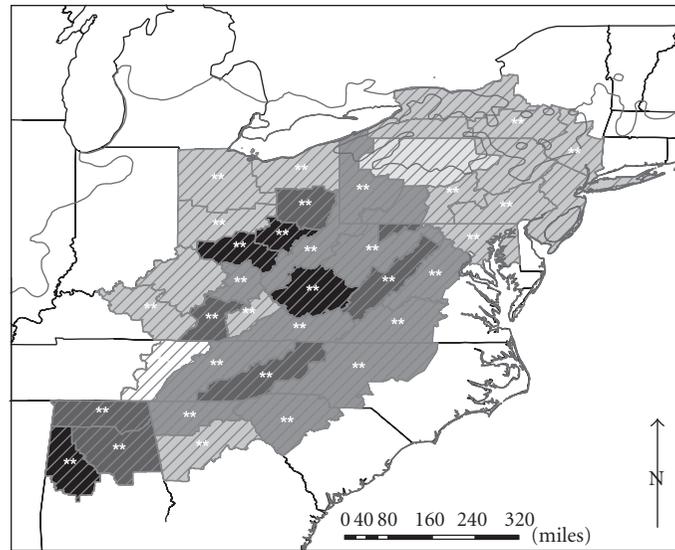
Northern FIA inventories during the late 1980s. While the Southern FIA inventories could have been impacted, the lag time that resulted from the movement of *D. destructiva* southward may have resulted in fewer stems counted because of the shorter period between infestation and inventory dates. In contrast to proportional changes in dogwood populations, absolute losses were greater in the south than in the north.

Despite the detection of significant losses in this study, our estimates of change were generally less than many documented studies at much smaller scales. For example, we found a 60-percent decline in the dogwood population in east Tennessee and 71 percent on the Cumberland Plateau; Hiers and Evans [6] reported dogwood losses of approximately 98 percent compared to population estimates first reported by McGee [32] in Tennessee. Myers et al. [33] also observed a significant decrease in dogwood on the Cumberland Plateau in Tennessee and documented the species complete disappearance from the subcanopy on their study site. Though we found smaller relative changes on the Cumberland Plateau in Tennessee than those noted by Myers et al. [33], losses were still substantial and averaged more than 10 million stems per county (Table 1). Dogwood populations were reduced by approximately 165 million trees, total, on the Cumberland Plateau over the time period studied.

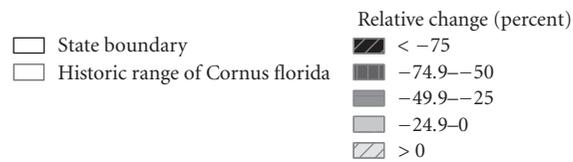
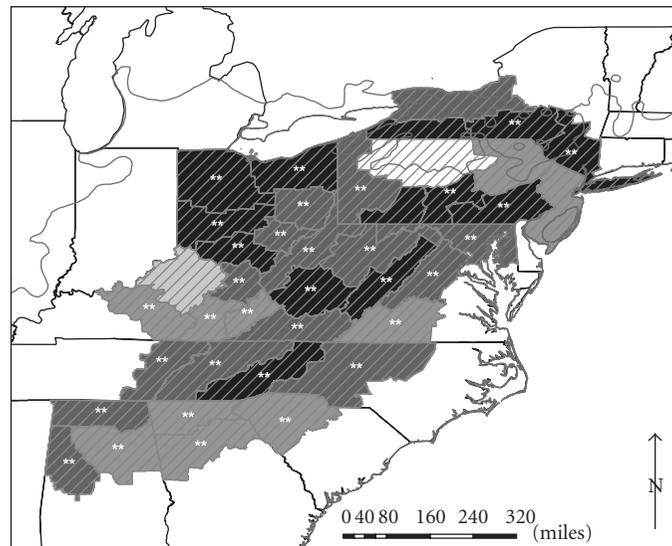
In Maryland, our study noted population declines of 58 and 72 percent in the Central and Western units. Similarly, Sherald et al. [11] documented dogwood mortality at approximately 77 percent between 1976 and 1992. Relative losses of dogwood populations in Pennsylvania FIA units ranged from 44 to 76 percent in this study, with the exception of the North Central Allegheny unit, which experienced no change. Williams and Moriarty [21] reported dogwood mortality between 58 and 68 percent throughout the area corresponding to the North Central Allegheny, Western Allegheny, Southwestern and Southwest Highlands FIA units (Figure 1). The lack of significant change in some units in Pennsylvania could be a result of the lower densities of dogwood [21], or a limited number of counties. For example, the Western unit in Maryland has only 2 counties.

The estimates reported here for time 1 were generated during a time when FIA implemented periodic inventories while time 2 estimates originated from the FIA program’s annual inventory design [24]. As a result, some uncertainty is introduced when comparing estimates across time. However, analyses at broad scales, such as the one here, reduce the probability of the additional uncertainty appreciably influencing the results. Fei and Steiner [34] used similar methods (time 1 data were from periodic inventories and ranged from 1980 to 1995 while time 2 data were from annual inventories with a much smaller range) to identify large-scale increases in *Acer rubrum* L. (red maple) populations in eastern forests.

This analysis does not identify causal agents of dogwood mortality. However, given that we controlled for changes in stand structure through the use of changes in all live volume as a proxy for forest density, coupled with losses that correlate



(a)



(b)

FIGURE 3: Estimates of (a) average annual county-level change and (b) total relative change of dogwood tress for all FIA regional units comprising the Appalachian ecoregion. **Denotes a significant difference between Time 1 and Time 2 (alpha = 0.05). State boundary shapefile is provided by ESRI. FIA Unit boundary shapefile is provided by Joe McCollum, USDA Forest Service, Southern Research Station Forest Inventory & Analysis.

TABLE 2: Average annual county-level change (AAC), associated sampling error in number of trees and relative AAC of dogwood trees for each FIA unit in the Appalachian ecoregion.

State	FIA Unit Name	Average Annual Change (AAC)		
		<i>trees</i>	<i>SE</i>	<i>percent</i>
Alabama	West Central	-666,547	197,863	-3.22
	North Central	-506,317	150,897	-2.35
Georgia	North	-395,732	76,690	-4.28
	North Central	-178,440	34,580	-2.44
Kentucky	Northern	-360,186	68,195	-2.75
	Eastern	-227,270	109,481	-2.21
	Northern Cumberland	-352,318	95,554	-3.53
Maryland	Southern Cumberland	-393,877	112,491	-2.86
	Bluegrass	-3,823	18,666	-0.37
	Pennyroyal	-91,282	38,283	-1.61
	Central	-244,677	88,207	-8.00
New Jersey	Western	-413,932	195,769	-6.42
	New Jersey	-51,785	66,824	-2.60
New York	Lake Plain	-49,633	84,915	-5.59
	Southwest Highlands	-95,807	41,190	-9.78
	South-Central Highlands	-84,551	26,209	-10.00
	Catskill-Lower Hudson	-219,113	79,132	-8.31
North Carolina	Piedmont	-316,529	41,673	-2.44
	Mountains	-555,794	88,388	-3.57
Ohio	South-Central	-687,564	220,690	-5.47
	Southeastern	-834,097	260,894	-5.13
	East-Central	-414,061	130,431	-4.43
	Northeastern	-129,719	41,143	-5.50
	Southwestern	-155,138	99,974	-5.87
	Northwestern	-111,079	48,328	-6.10
Pennsylvania	South Central	-203,164	55,932	-5.00
	Western	-270,535	82,221	-4.45
	North Central/Allegheny	815	47,812	0.05
	Southwestern	-309,902	131,873	-5.05
	Northeastern/Pocono	-43,002	39,767	-2.91
	Southeastern	-137,879	43,230	-5.01
South Carolina	Piedmont	-283,227	77,810	-2.01
Tennessee	Plateau	-644,240	135,510	-4.46
	East	-344,901	70,056	-3.78
Virginia	Southern Piedmont	-273,295	63,397	-1.90
	Northern Piedmont	-326,044	49,764	-2.82
	Northern Mountains	-458,598	80,040	-3.68
	Southern mountains	-294,283	37,583	-3.07
West Virginia	Northeastern	-308,098	57,479	-4.03
	Southern	-862,357	102,240	-5.42
	Northwestern	-270,720	78,845	-3.18

geographically with the known *D. destructiva* distribution, it can be assumed that *D. destructiva* is a major cause. We assume that a considerable amount of the dogwood loss we observed can be attributed to the impacts of the fungus *D. destructiva*; other factors are likely to have played some role. For example, Pierce [35] attributed dogwood

mortality in Indiana to competition with *Acer saccharum* Marsh. (sugar maple) mediated by fire suppression activities. In Kentucky, McEwan et al. [22] reported a 36-percent decrease in dogwood density in an old-growth stand prior to *D. destructiva* infestation. While it is possible that *D. destructiva* was present without having been documented,

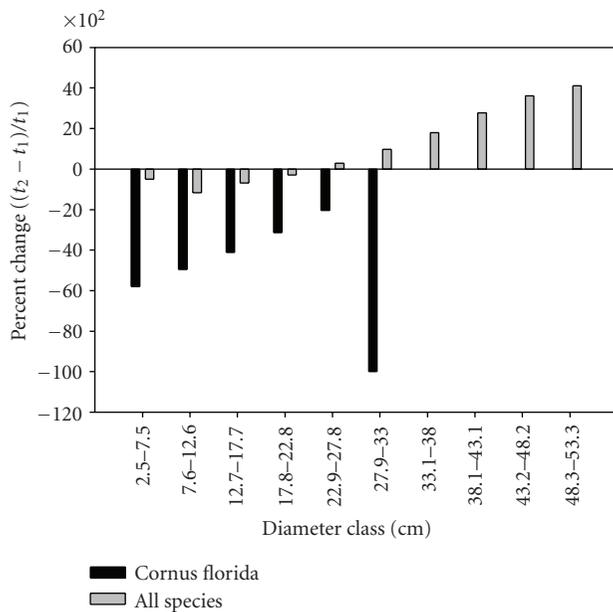


FIGURE 4: Total relative change of dogwood populations and populations of all species by diameter class.

McEwan et al. [22] suggested that factors such as canopy closure, drought, and natural canopy gap-dynamics may have been an important factor. We support this notion, as changes in dogwood populations were significantly related to changes in all live volume. The well-documented deleterious impacts of *D. destructiva*, however, cannot be ignored. According to reports from Anderson [36] and Knighten and Anderson [37, 38], *D. destructiva*-mediated dogwood mortality increased from 0 to 23 percent in the Appalachians between 1988 and 1993. Concomitantly, the area estimated to be infected with *D. destructiva* increased from 0.5 to 17.3 million acres over the same period [19]. Moreover, Windham et al. [39] reported widespread infection and rapid die-off of dogwood throughout the Great Smoky Mountains National Park in the early 1990's.

Slightly smaller losses in this study compared with other studies are likely an artifact of the data. FIA data are collected over a much larger scale. Therefore, the influence of localized events such as complete mortality in a specific area can be lessened. While small-scale studies with a more limited scope are able to provide specificity, FIA data are able to provide a more holistic ecosystem-wide view of forest changes. Used in combination, large-scale FIA and localized studies can be complementary wherein FIA data are used for hypothesis generation as a precursor to more focused small-scale studies of cause and effect. Or, as in this case, FIA data can be used to validate the findings of multiple small-scale studies at much larger scales.

5. Conclusion

This study empirically explored changes in dogwood populations in the Appalachian ecoregion by comparing estimates

from large-scale forest inventories from two different points in time that covered approximately twenty years. Dogwood is an important tree in the Appalachian ecoregion. Its population has declined more than 50 percent in the last 2-3 decades. Decreases were widespread throughout almost all of the FIA units comprising the Appalachian ecoregion. In some areas dogwood populations have decreased to the point where an FIA inventory no longer detects the species. Our results confirm many smaller, localized investigations of dogwood mortality as well as a vast body of anecdotal evidence that has accumulated over time. Such large-scale reductions in dogwood populations, particularly in the midstory of eastern deciduous forests, may result in further expansion of generalist species like red maple as the vacated niche is filled.

Acknowledgments

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Research Article

Rapid Assessment of Relative Density in Mixed-Species Stands of the Northeastern United States

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Basal area has shortcomings as a measure of stand density, but it is often preferred for operational assessments because it is easy to measure. Previous work has demonstrated that an additive version of Reineke's stand density index can be estimated by a simple tree count using a modified horizontal point sampling technique. We show that this technique can be extended further to estimate a mixed-species density measure that has been developed for complex stands in the northeastern United States, using wood specific gravity to harmonize the density contributions of different species. The sampling technique provides design-unbiased estimates of stand density from a weighted tree count, where the weights depend on specific gravity but not on diameter. Rounding the specific gravity values for different species in the calculation of estimates introduces a trivial amount of bias but streamlines the procedure for rapid use in the field.

1. Introduction

The ability to measure forest stand density is fundamental for both description and prescription in applied ecology including silviculture, forest health, and wildlife habitat management [1, 2]. Basal area is the most commonly used density metric in practice, primarily because it is very fast and simple to measure in the field [3–5]. However, the basal area at which key ecological behaviors occur (such as crown closure, the onset of self-thinning, and asymptotic density) depends on the size of the trees in the stand, the species of those trees, and also potentially on the age and site quality of the stand. Other metrics, such as Reineke's [6] Stand Density Index (SDI) and related metrics such as those of Curtis [7] and Long and Daniel [8], offer improvements over basal area for monospecific stands. Reineke's [6] SDI is

$$SDI = N \left(\frac{D_q}{25} \right)^{1.6}, \quad (1)$$

where N is number of trees per hectare, and D_q is stand quadratic mean diameter. SDI has units of trees/ha. Zeide ([2, page 5]) writes that SDI is "still the best [metric] we have" for assessing stand density.

Recent research efforts have attempted to extend Reineke's [6] basic work to more complex stands than the even-aged, monospecific subjects of the original SDI. Long and Daniel [7] developed an additive version of SDI closely related to an index explored by Curtis [8]:

$$ASDI = \sum_i N_i \left(\frac{D_i}{25} \right)^{1.6}, \quad (2)$$

where N_i and D_i are the number of trees per hectare and diameter of size classes of trees, and the summation is taken over an exhaustive, mutually-exclusive set of classes. (For continuous diameter distributions, the summation in (2) can be replaced by an integral and N_i can be replaced by the product of N and an appropriate probability density function; see [9, 10], e.g.) Several authors [1, 7, 11] have suggested using ASDI for multicohort stands. More recently, Woodall et al. [12, 13], building on earlier mechanistic work [14], suggested that the maximum ASDI of mixed species stands could be estimated as a function of the mean specific gravity of the wood of trees on the plots and proposed a

modified density measure. Ducey and Knapp [15], building on [12], suggested a relative density metric of the form

$$RD = \sum_{ij} N_{ij} (b_0 + b_1 SG_j) \left(\frac{D_i}{25} \right)^{1.6}, \quad (3)$$

where N_{ij} is the number of trees per hectare in the i th diameter class of the j th species, b_0 and b_1 are parameters to be estimated from plot data, and SG_j is the specific gravity of wood for the j th species.

A challenge for any stand density metric more complex than basal area is that of obtaining a fast and simple estimate in the field. That challenge seems more and more difficult as stand density metrics such as that in (3) attempt to encompass stands that are more complex in diameter distribution and species mixture. Rapid field estimates are particularly valuable for diagnosis and description of stand conditions when a density metric will be used in situ in conjunction with expert opinion, and for controlling the marking of thinnings, shelterwoods, single-tree selection, and other partial harvests. Basal area would seem to have a distinct advantage in these situations, because a simple count of trees using a prism or other angle gauge, multiplied by the basal area factor of that gauge, provides a direct estimate of basal area per hectare [16, 17]. However, a modified prism technique can provide estimates of ASDI through a simple count as well [18].

The goal of this study is to show how the modified prism technique [18] can be modified to provide direct estimates of the Ducey and Knapp [15] relative density for mixed species stands. We provide tables and instructions for implementing the approach and illustrate its application with data from a mixed-species stand in southeastern New Hampshire.

2. Theory

2.1. Mixed-Species Density Measure. Ducey and Knapp [15] proposed RD as a stand density metric for the mixed-species forests of New England and New York in the USA. They used data from the Forest Inventory and Analysis program of the U.S. Forest Service to estimate $b_0 = 0.00015$ and $b_1 = 0.00218$, using specific gravity at 12% moisture content for each species. RD is a unitless fraction, scaled so that $RD = 0$ represents a completely empty stand, and $RD = 1$ represents a stocking level consistent with “normal” or A-line stocking using conventional stocking guides. For example, if $RD = 0.5$ for a particular stand, that stand has 50% of the stocking level implied by “normal” or A-line stocking.

Now, consider (3). It can be rewritten as

$$\begin{aligned} RD &= \sum_j (b_0 + b_1 SG_j) \left[\sum_i N_{ij} \left(\frac{D_i}{25} \right)^{1.6} \right] \\ &= \sum_j (b_0 + b_1 SG_j) ASDI_j \end{aligned} \quad (4)$$

which makes clear that RD is simply a weighted form of ASDI, where the weights for different species are determined by their specific gravity.

Ducey and Valentine [18] developed a technique analogous to sampling for basal area with a prism, in which tree count times a factor gives ASDI. We will show that it is possible to modify that technique to give RD as a sum of weights for the tallied trees. First, we review the modified prism technique for ASDI.

2.2. Direct Sampling Technique. Recall that in ordinary horizontal point sampling (HPS) with a prism, relascope, or other angle gauge, each tallied tree represents the same amount of basal area per hectare [16]. That quantity is called the basal area factor or BAF, and that quantity is constant for a given gauge because the area of the inclusion zone (the area within which a specific tree will be tallied) is directly proportional to the basal area of the individual tree. This result follows from the geometry of the gauge: the radius of the inclusion zone (also called the limiting distance) equals the gauge constant (or ratio of length to width) times the diameter of the tree. Mathematical proofs are provided by [19], while [20] provides a thorough discussion of HPS in its many applications.

If the inclusion zone radius could be made proportional to $D^{0.8}$, rather than proportional to D , then inclusion zone area would be proportional to $D^{1.6}$ and each tallied tree would represent a constant amount of ASDI [18]. This quantity is called the stand density factor (SDF), by analogy to the BAF of ordinary HPS. Recall that ASDI has units of trees/ha; so SDF also has units of trees/ha. If the method of [18] is used, and if m trees are tallied at n points, then the estimate of ASDI is simply

$$ASDI = \left(\frac{m}{n} \right) SDF. \quad (5)$$

If the SDF is chosen with reasonable care, then the limiting distances for a given SDF are very close to those for the BAF that would ordinarily be used in similar stand conditions [18] (Figure 1). The slight departure, depending only on tree diameter, could easily be adjusted in the field by “pushing the point” or “pulling the point.” Pushing the point [21] consists of holding the prism not directly over the sample point but extended toward the tree of interest. In ordinary HPS pushing the point is a common field error, and it creates biased estimates. Pulling the point consists of holding the prism back and sighting across the sample point to determine whether a tree should be tallied. A simple table of the distance to push or pull the point, in relation to D for individual trees, is adequate to provide a sample with a constant SDF [18]. In practice, it is not usually necessary to know the exact D of an individual tree to determine whether it should be included in the sample. Because the degree of push or pull changes slowly with D , an initial ocular estimate is usually sufficient. D should be measured on borderline trees, and if an estimate of ASDI is desired for different diameter classes, then D can be measured on the tallied trees as well.

Now suppose that we wish to modify the technique to estimate RD, building on (4). Let m_j be the number of trees

of the j th species tallied, using n sample points as before. Then

$$\text{ASDI}_j = \left(\frac{m_j}{n}\right) \text{SDF} \quad (6)$$

provides an estimate of the ASDI of species j , and

$$(b_0 + b_1 \text{SG}_j) \text{ASDI}_j = (b_0 + b_1 \text{SG}_j) \left(\frac{m_j}{n}\right) \text{SDF} \quad (7)$$

provides a natural estimator of the summand in (4). Rearranging slightly, and substituting, we have

$$\text{RD} = \sum_j \left(\frac{m_j}{n}\right) [(b_0 + b_1 \text{SG}_j) \text{SDF}] \quad (8)$$

as a natural estimator for RD. In other words, RD can be estimated as a weighted tree count, in which each tree at a single sample point represents $[(b_0 + b_1 \text{SG}_j) \text{SDF}]$ units of RD. Recall that RD is a unitless fraction; therefore the weight or contribution of an individual tree $[(b_0 + b_1 \text{SG}_j) \text{SDF}]$ is also a unitless fraction. Proofs of unbiasedness of (5), (6), and (8) are given in the appendix.

In practice, if “exact” (or at least, unrounded) values of SG_j are used, the quantity $[(b_0 + b_1 \text{SG}_j) \text{SDF}]$ will likely be a cumbersome fraction. This is not a problem if, for example, field computers are used to provide nearly instantaneous feedback on sample results. However, for the cruiser or timber marker who desires a simple, rapid field procedure, it may be more convenient to group species and use an approximate value so that $[(b_0 + b_1 \text{SG}_j) \text{SDF}]$ is always a nearly round percentage. This requires advance tabulation of species into groups, which we undertake hereinafter. Furthermore, it does introduce a small amount of bias due to rounding error. As we show, this is likely to be negligible for samples taken at typical operational intensities.

3. Application

One of the first steps in direct sampling for ASDI is to choose a BAF and corresponding SDF [18]. In the northeastern United States, a BAF of 2.3 m²/ha is a common choice but can lead to nondetection errors; so a larger BAF is desirable [22, 23]. Prisms with a BAF of 4 m²/ha are widely available and fall within the range recommended for the region [24]. For a given BAF, the SDF should be chosen such that the limiting distances are similar. This allows the push or pull to be done quickly and accurately. A good match to BAF 4 m²/ha is an SDF of 50 trees/ha: the limiting distances differ by less than 2 m over a broad range of DBH, and “pulling the point” is only necessary for rare trees with DBH > 85 cm. The limiting distances and push/pull for an SDF 50 using a BAF 4 are shown in Table 1.

Ducey and Knapp [15] tabulate SG for all the species found in New York and New England in the USFS FIA database. However, for fast application in the field it is useful to tabulate rounded values of $[(b_0 + b_1 \text{SG}_j) \text{SDF}]$ as weights. This is done in Table 2, with weights multiplied by 100 so that they reflect percents rather than fractions.

Armed with Tables 1 and 2, it is straightforward to conduct field sampling and to calculate estimates. For example, suppose that we have used our prism and Table 1 to determine which trees to sample at a single point. We tallied 7 trees: 3 *Betula papyrifera*, 1 *Picea rubens*, 2 *Abies balsamea*, and 1 *Fagus grandifolia*. We can immediately determine that the ASDI at this point is $7 \times 50 = 350$, and RD is $3 \times 7 + 1 \times 5 + 2 \times 5 + 1 \times 8 = 44\%$, or 0.44.

4. Field Demonstration

To illustrate the calculations associated with the method, we conducted sampling in a 4.3 ha mixed-species stand located in Durham, NH. 12 sample points were located systematically on a 60 m by 60 m grid. We used a BAF 4 m²/ha prism, and the push-pull values from Table 1, to obtain a sample of trees with an SDF of 50 trees/ha. Both the exact weights as calculated from the specific gravities tabulated in [15], and rounded weights from Table 2, were used to estimate RD for comparison.

A total of 133 trees were tallied on the 12 plots. Of these, 49 were *Tsuga canadensis*, 33 were *Pinus strobus*, 31 were *Acer rubrum*, 10 were *Quercus rubra*, 5 were *Fagus grandifolia*, 4 were *Betula allegheniensis*, and 1 was *Quercus alba*. RD as calculated using the exact weights was 65.6%, with a standard error of 7.6%; the coefficient of variation of the sample points was 40%. RD as calculated using the rounded weights was 63.3%, with a standard error of 7.7%; the coefficient of variation of the sample points was 42%. In this stand at least, the difference caused by rounding the weights is trivial in comparison with the sampling variability of RD.

5. Discussion and Conclusions

Metrics of stand density can be viewed in two ways: as hypotheses about or models of stand dynamics and as operational aids to silviculture. From the first perspective, stand basal area has long been rejected. Even in single-species, single-cohort stands, the inadequacy of basal area for comparing density in stands of different tree size and species was known long before Reineke’s [6] work and provided much of the impetus for his efforts. Even in those stands, Reineke’s work represents a simplification, obscuring potentially important interspecific differences in allometry and growth [25]. Extension of Reineke’s ideas to multicohort stands and other stands with complex structure has been an important area of recent work [7, 26–28]. While empirical tests of those efforts in comparison to previous measures have been relatively rare [9, 29], some progress has been made at least in understanding how one might approach the design of experiments [10].

A variety of studies have explored adaptations of SDI to mixed-species stands [12, 13, 30–36]. However, the Ducey and Knapp [15] formulation has two properties that are both required for the straightforward use of the sampling method developed here. The first property is additivity [9]. An index is said to be additive if, for two stand components A and B , the density of A and B considered together equals the density

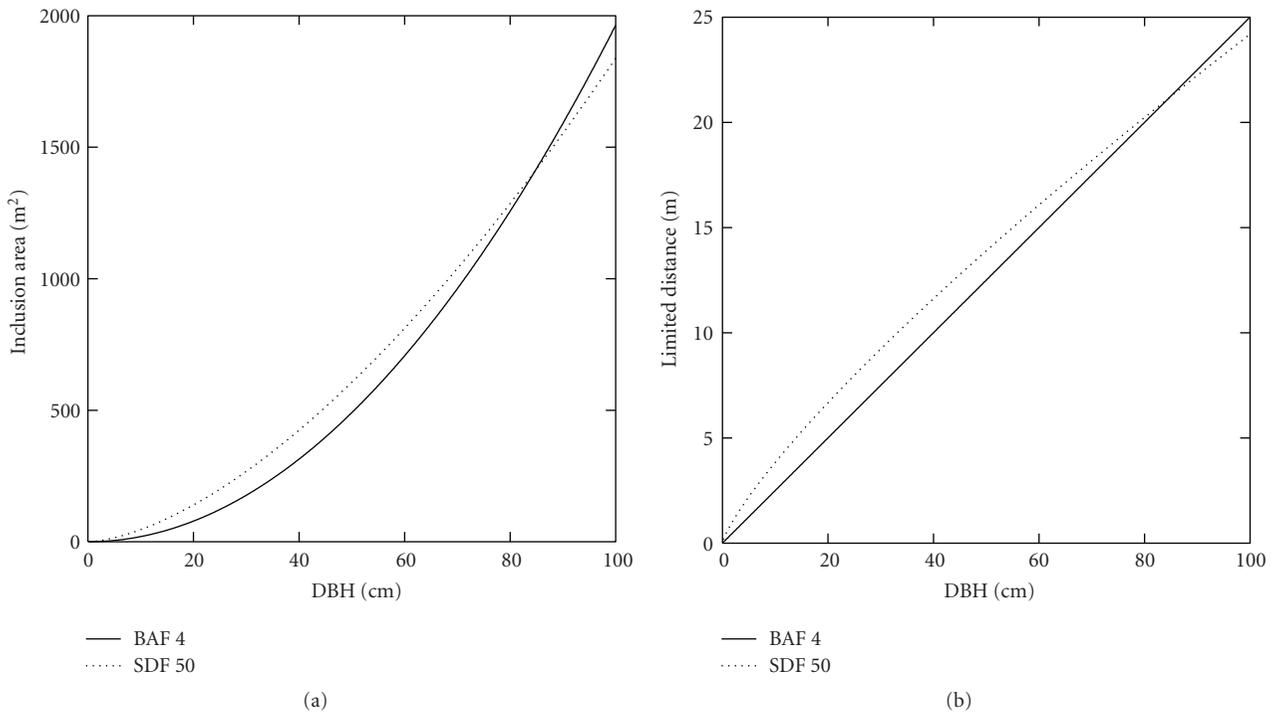


FIGURE 1: Area of the inclusion zone and limiting distance (or inclusion zone radius), for ordinary HPS with a BAF 4 m²/ha gauge and direct sampling for ASDI with a stand density factor of 50.

TABLE 1: Critical distances and required “push” for sampling with a stand density factor (SDF) of 50, using a basal area factor (BAF) 4 m²/ha prism. When the “push” is shown as negative, the prism must be pulled back across the point.

DBH, cm	BAF = 4 Critical Distance, m	SDF = 50 Critical Distance, m	Required Push, m
5	1.25	2.20	0.95
10	2.50	3.83	1.33
15	3.75	5.30	1.55
20	5.00	6.67	1.67
25	6.25	7.98	1.73
30	7.50	9.23	1.73
35	8.75	10.44	1.69
40	10.00	11.62	1.62
45	11.25	12.77	1.52
50	12.50	13.89	1.39
55	13.75	14.99	1.24
60	15.00	16.07	1.07
65	16.25	17.14	0.89
70	17.50	18.18	0.68
75	18.75	19.21	0.46
80	20.00	20.23	0.23
85	21.25	21.24	-0.01
90	22.50	22.23	-0.27
95	23.75	23.21	-0.54
100	25.00	24.19	-0.81

TABLE 2: Rounded weights (values of $100 \times [(b_0 + b_1 SG_j)SDF]$) for common species in New York and New England, using an SDF of 50.

Species	Specific Gravity Range	Weight
<i>Maclura pomifera</i>	0.84	10
<i>Carpinus caroliniana</i> , <i>Carya</i> spp. (except <i>laciniosa</i>), <i>Cornus florida</i> , <i>Ostrya virginiana</i> , <i>Quercus bicolor</i>	0.72–0.78	9
<i>Acer platanooides</i> , <i>Acer saccharum</i> , <i>Betula allegheniensis</i> , <i>Betula lenta</i> , <i>Betula nigra</i> , <i>Carya laciniosa</i> , <i>Crataegus</i> spp., <i>Fagus grandifolia</i> , <i>Gleditsia tricanthos</i> , <i>Malus</i> spp., <i>Quercus alba</i> and the other white oaks (except <i>bicolor</i>), <i>Quercus rubra</i> and the other red oaks (except <i>velutina</i> and <i>ilicifolia</i>), <i>Robinia pseudoacacia</i> , <i>Ulmus thomasi</i>	0.62–0.69	8
<i>Acer rubrum</i> , <i>Amelanchier</i> spp., <i>Betula papyrifera</i> , <i>Celtis occidentalis</i> , <i>Fraxinus</i> spp. (except <i>nigra</i>), <i>Juglans nigra</i> , <i>Larix laricina</i> , <i>Quercus velutina</i> , <i>Quercus ilicifolia</i> , <i>Ulmus rubra</i>	0.53–0.61	7
<i>Acer montanum</i> , <i>Acer negundo</i> , <i>Acer pennsylvanicum</i> , <i>Acer saccharinum</i> , <i>Betula populifolia</i> , <i>Fraxinus nigra</i> , <i>Juniperus virginiana</i> , <i>Nyssa sylvatica</i> , <i>Platanus occidentalis</i> , <i>Picea mariana</i> , <i>Pinus resinosa</i> , <i>Pinus rigida</i> , <i>Pinus sylvestris</i> , <i>Prunus</i> spp. (except <i>pennsylvanica</i> and <i>virginiana</i>), <i>Sassafras albidum</i> , <i>Sorbus americana</i> , <i>Ulmus americana</i>	0.44–0.52	6
<i>Abies balsamea</i> , <i>Castanea dentata</i> , <i>Juglans cinerea</i> , <i>Liriodendron tulipifera</i> , <i>Picea</i> spp. (except <i>mariana</i>), <i>Pinus</i> (except <i>rigida</i> and <i>sylvestris</i>), <i>Populus</i> spp. (except <i>balsamifera</i>), <i>Prunus pennsylvanica</i> , <i>Prunus virginiana</i> , <i>Salix</i> spp., <i>Tilia americana</i> , <i>Tsuga canadensis</i>	0.35–0.43	5
<i>Chamaecyparis thyoides</i> , <i>Populus balsamifera</i> , <i>Thuja occidentalis</i>	0.31–0.34	4

of A considered alone, plus the density of B considered alone. Additivity is required for unbiased estimation of any stand density metric using traditional methods (such as fixed-area plot sampling or HPS, or any method that can be identified as using a Horvitz-Thompson [37] estimator) [38, 39]. Among previous mixed-species indices, only that of Stout and colleagues [31, 32] is additive; that of Woodall et al. [12, 13] meets the criterion of separability but not additivity [9]. By analogy with site index curves, we may also say that a density measure is anamorphic if, for two different species, the density contribution of an individual of species X divided by that of an individual of the same D but of species Y is a constant that does not depend on D . The density measure of Stout and colleagues [12, 13] is not anamorphic. If a density measure is not anamorphic, then a different “push” or “pull” would be required for each species or species group. Thus, the Ducey and Knapp [15] formulation has certain practical advantages from a measurement standpoint.

We caution, however, that simplicity and practicality may be advantageous but do not imply biological correctness [9]. Both additivity and anamorphism are likely incorrect from a strictly biological and mechanistic standpoint [9, 25, 40]. On the other hand, detecting departures from additivity and anamorphism implies the availability of an additive, anamorphic measurement from which to construct a baseline.

At its heart, a stand density index is a model, hypothesis, or conjecture about the relationship between measurable quantities and ecological behaviors. Statistician G.E.P. Box [41, page 2] wrote “Models, of course, are never true, but fortunately it is only necessary that they be useful.” The durability of basal area as a practical measure of stand density points to the importance of rapid, simple measurement as a component of utility. Box [42, page 792] also wrote “Since all models are wrong the scientist must be alert to what is importantly wrong. It is inappropriate to be concerned about

mice when there are tigers abroad.” One tiger abroad in stand density measurement is sampling variability. Fast, repeatable measurement with relatively low sampling variability has been a reality for basal area since the seminal work of Bitterlich [16] on HPS. However, the recent generalization of HPS for ASDI [18], and the approach for RD as explored here, may close the gap somewhat.

In theory, the modified HPS approach [18] and this method could be used as a general sampling approach, if tree diameters are measured. However, the need to push (or pull) the point does open the door to field errors. The results from ordinary HPS should be more precise and less prone to operator error, even when a final variable of interest is RD. Rather, the strength of the approach we present here is for near-instantaneous estimation of stand density in three primary situations.

(1) The first situation is to allow quick assessment and description of stand conditions. Fast calculation of RD would allow more effective coupling between quantitative measurement and subjective, expert opinion [18]. Density indices and related diagrams are best viewed as complementary to qualitative silvicultural expertise [43]; a rapid measurement technique can make quantitative information available to the forester or ecologist on-site.

(2) The second one is to enable control of residual density while marking partial harvests such as thinnings and shelterwoods.

(3) The third one is to provide a simple point density estimate for use in ecological studies that would be available immediately for stratification or subsampling purposes.

Appendix

Equation [7] provides an estimating equation for RD when trees are sampled using the modified point sampling technique. In this appendix, we present a formal proof of design-unbiasedness for this estimating equation.

Suppose that we are interested in the population of trees occurring in a tract of area A . Let the trees be indexed by $k = 1, \dots, K$, where K is the total number of trees. K is fixed but unknown, as are the diameters D_k of the trees at the outset of sampling. Without loss of generality, let us locate a single point at random and with uniform density within the tract. This point will be our sample point, and from it we will include all trees located at a distance no greater than $cD^{0.8}$, where c is a constant chosen in advance. Denote the inclusion area of the k th tree by a_k ; a_k is the area where the sample point may fall and the k th tree will be included. From basic geometry we have

$$a_k = \pi(cD^{0.8})^2 = \pi c^2 D_k^{1.6}, \quad (\text{A.1})$$

and the probability p_k that the k th tree will be included in the sample (ignoring boundary slopover, which can easily be corrected using the walkthrough method [44]) is

$$p_k = \frac{a_k}{A}. \quad (\text{A.2})$$

We can rewrite (2) as

$$\text{ASDI} = \left(\frac{1}{A}\right) \sum_k \left(\frac{D_k}{25}\right)^{1.6}. \quad (\text{A.3})$$

Now let d_k be an indicator variable taking the value 1 if the k th tree is included in the sample, and 0 otherwise; the expectation is $E[d_k] = p_k$. The total number of trees included in the sample is

$$m = \sum_k d_k, \quad (\text{A.4})$$

and its expectation is

$$E[m] = E[\sum_k d_k] = \sum_k p_k = \left(\frac{\pi c^2}{A}\right) \sum_k D_k^{1.6} = [\pi c^2 25^{-1.6}] \text{ASDI} \quad (\text{A.5})$$

from which it follows directly that if $\text{SDF} = 25^{1.6}/(\pi c^2)$, then $m\text{SDF}$ is a design-unbiased estimator of ASDI, since

$$E[m \text{SDF}] = \text{SDF} E[m] = \text{ASDI}, \quad (\text{A.6})$$

and if we collect data at n such sample points, the sample mean ($m/n \text{SDF}$) will also provide a design-unbiased estimate. This proves the unbiasedness of the estimator in (5). Furthermore, if we restrict the population to consist only of trees of species j and replace m with m_j and ASDI with ASDI_j in the above equations, the equations still hold; this proves the unbiasedness of the estimator in (6).

In general, if there is an attribute y_k associated with the k th tree, an estimator of the form

$$Y = \frac{\sum_k d_k y_k}{p_k} \quad (\text{A.7})$$

is a Horvitz-Thompson [37] estimator and provides a design-unbiased estimate of the population total $\sum_k y_k$. Now, consider (4), rewritten as a population total:

$$\text{RD} = \left(\frac{1}{A}\right) (b_0 + b_1 \text{SG}_k) \left(\frac{D_k}{25}\right)^{1.6}, \quad (\text{A.8})$$

where SG_k is the specific gravity of the k th tree, so that

$$y_k = \left(\frac{1}{A}\right) (b_0 + b_1 \text{SG}_k) \left(\frac{D_k}{25}\right)^{1.6}. \quad (\text{A.9})$$

Now, if we substitute this into the basic Horvitz-Thompson estimator, we obtain

$$\begin{aligned} Y &= \frac{\sum_k d_k \left[(1/A)(b_0 + b_1 \text{SG}_k)(D_k/25)^{1.6} \right]}{p_k} \\ &= \sum_k d_k \left[\left(\frac{1}{A}\right) (b_0 + b_1 \text{SG}_k) \left(\frac{D_k}{25}\right)^{1.6} \right] / [\pi c^2 D_k^{1.6}/A] \\ &= \sum_k d_k \left[\frac{(b_0 + b_1 \text{SG}_k) 25^{1.6}}{\pi c^2} \right] \\ &= \text{SDF} \sum_k d_k (b_0 + b_1 \text{SG}_k). \end{aligned} \quad (\text{A.10})$$

Now, recognizing that all trees of the j th species have the same specific gravity for our purposes, and letting SG_j represent the specific gravity of the j th species as before, we see that

$$Y = \sum_j m_j \left[(b_0 + b_1 SG_j) SDF \right] \quad (\text{A.11})$$

is the design-unbiased Horvitz-Thompson estimator associated with a single sample point, and the mean of several sample points is identical to (8), which must also be design-unbiased.

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Research Article

Using Florida Keys Reference Sites As a Standard for Restoration of Forest Structure in Everglades Tree Islands

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In south Florida, tropical hardwood forests (hammocks) occur in Everglades tree islands and as more extensive forests in coastal settings in the nearby Florida Keys. Keys hammocks have been less disturbed by humans, and many qualify as “old-growth,” while Everglades hammocks have received much heavier use. With improvement of tree island condition an important element in Everglades restoration efforts, we examined stand structure in 23 Keys hammocks and 69 Everglades tree islands. Based on Stand Density Index and tree diameter distributions, many Everglades hammocks were characterized by low stocking and underrepresentation in the smaller size classes. In contrast, most Keys forests had the dense canopies and open understories usually associated with old-growth hardwood hammocks. Subject to the same caveats that apply to off-site references elsewhere, structural information from mature Keys hammocks can be helpful in planning and implementing forest restoration in Everglades tree islands. In many of these islands, such restoration might involve supplementing tree stocking by planting native trees to produce more complete site utilization and a more open understory.

1. Introduction

The best developed tree islands in the Florida Everglades play many roles in the landscape: as forest refugia for wide-ranging animals and tropical hardwoods; as raised features that focus surface water flow into deeper channels; as habitat for rare ferns, epiphytes, and other shade-loving plants; as seed sources for the establishment of new islands; as carbon sinks; as attractants and sinks for nutrients, especially phosphorus, whose deficiency characterizes the surrounding marsh ecosystems [1, 2]. Having served for centuries as oases for humans as well as animals that passed through the vast and inhospitable wetland [3], their structure today carries a long legacy of human use. At the same time, natural disturbance agents play a continuing role in shaping stand structure. Their disturbance regime includes infrequent wildfires, which may kill aboveground vegetation and consume organic soils, and more frequent tropical storms and hurricanes, which topple and severely prune the exposed emergent trees in the forest canopy [4]. In

many cases, the complex interaction of human and natural disturbance agents has led to open, slow-to-recover canopies that encourage the encroachment of widely dispersed vines, weedy herbs, and nonnative trees and shrubs, and may interfere with tree island function in the landscape. With tree island condition an important concern of recent efforts to restore full ecological function to the Everglades, embodied in the Comprehensive Everglades Restoration Plan [5], the ability to assess stand structure and its effects on other functions of these poorly understood forests is sorely needed.

Consideration of stand structure in ecological restoration should include both the overall utilization of the site by trees, and how site utilization is distributed among different size classes. Tree density is not a sufficient metric of site utilization, because even when a site remains fully occupied or “stocked” throughout the development of a stand, density declines as trees grow larger and compete with their neighbors [6]. Metrics by which site utilization is represented should therefore account for both tree density and size. Reineke [7] recognized that the density of trees in fully

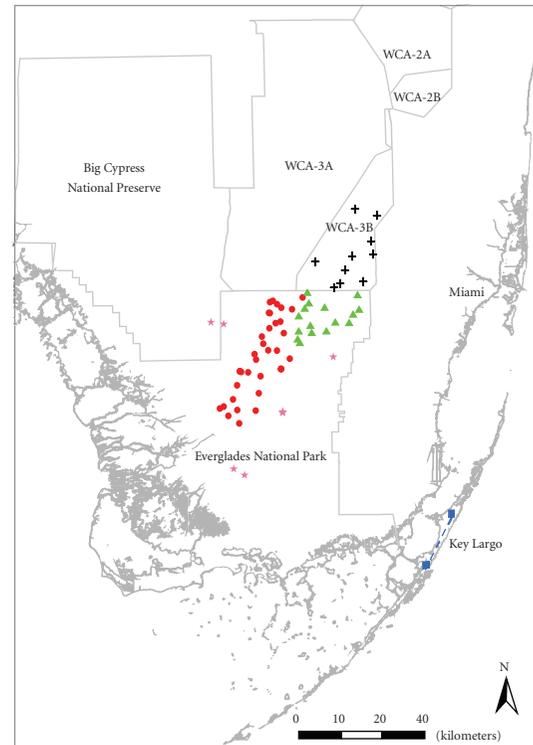
stocked, monospecific, even-aged stands of the same average stand diameter was quite constant, and largely independent of age and site productivity. Based on empirical relationships between average stand diameter and density in fully stocked stands, Reineke's Stand Density Index (SDI) projects a stand's existing size structure to the number of trees that would be present in a similarly stocked stand at an average stand diameter (ASD: diameter at breast height [DBH] of the tree of mean basal area) of 10 inches (25 cm). Long and Daniel [8] showed that Reineke's SDI could be modified to express site utilization in uneven-aged forests, and more recently Woodall et al. [9] explored the influence of species composition on the maximum attainable SDI in mixed-species stands.

Use of the stand density concept in actively managed forests involves the interdependent manipulation of tree density and average stand diameter within a zone judged to represent full stocking [10]. For instance, in his application of stand density principles to Central States hardwoods, Gingrich [11] defined a "full stocking" zone broad enough to encompass a wide range of potential forest products, including timber, wildlife, and other resources. Similarly, ecosystem restoration efforts such as those underway for Everglades tree islands require that a range of states or conditions that represent acceptable forest structure be defined. But how should such standards be determined? One approach is to settle on a limited set of reference communities, for example, old-growth forests, or "pristine" wetlands remote from human impact. In the restoration of Everglades tree islands, forests of the Florida Keys may serve well as references, for several reasons. First, a substantial proportion of Florida Keys forests have undergone little direct human disturbance since at least the 1930s, and were never subjected to the high intensity of human use that has been concentrated on many of the high Everglades tree islands. Second, successional dynamics in Keys hammocks has been thoroughly documented (e.g., [12, 13]), while forest succession in Everglades tree islands has never been directly addressed. Finally, though growing on different substrates and in slightly different climatic regimes, Keys hammocks and Everglades tree islands are dominated by many of the same tree species, suggesting similar environmental controls.

In this paper, we examine the structure of mixed-species and uneven-aged south Florida forests, addressing not only whole-stand SDI, but also the contribution to SDI made by the full range of diameter classes present. We describe the stand structure of several regional variants of Everglades tree islands, as well as Florida Keys forests of similar composition but distinctly different disturbance history. Our primary objective in these analyses is to determine whether mature Florida Keys forests might serve as references for the establishment of structural guidelines for Everglades tree islands.

2. Methods

2.1. Study Area. Our tree island study area included Shark Slough and adjacent prairies in Everglades National Park



Sampled tree islands region
 * Marl Prairie + WCA-3B
 ▲ Northeast Shark Slough ■ Extent of Key Largo transects
 ● Shark Slough

FIGURE 1: Map of 69 sampled tree islands included in this study, with location of reference hammocks in Key Largo.

(ENP) and Big Cypress National Preserve, as well as state-managed wetlands in Water Conservation Area 3B (WCA-3B; Figure 1). Stretching across a latitudinal range of about 1 degree, tree islands of the area vary broadly in hydrologic conditions in the surrounding marsh, as well as in recreational use. Surrounded on all sides by levees, the peatlands in WCA-3B are dependent on local rainfall, and the area's southward-sloping topography creates deeper water in the south than in the north. While ENP marshes drain freely to the southwest, the volume and distribution of water entering the Park from the north deviates from predevelopment conditions. Overall, delivery is greatly reduced and concentrated in the western reaches of Shark Slough, while marshes in Northeast Shark Slough, south of WCA-3B, are largely rainfall dependent. Marl Prairies on the eastern and western peripheries of Shark Slough are slightly higher in elevation, and water levels are shallower than in the Slough proper.

Tree islands throughout the Everglades have a history of human use dating back at least 5000 years [14–16]. Besides providing relative comfort as sites for the hunting camps or more permanent residences of native Americans, tree islands provided seclusion for the activities of moonshiners, plume hunters, and alligator poachers. After the establishment of

ENP in 1947, access to these areas came under regulation within the Park boundaries, which have expanded from an initial 186,000 ha to 611,000 ha today. Designation of most of ENP for Wilderness Use in 1964 curtailed tree island access further. Today, public use of tree islands in ENP is limited, largely directed to a few interpretive sites near Park roads, as well as several sites in Northeast Shark Slough, the latest addition to the Park. In contrast, access to tree islands in WCA-3B is largely unrestricted, and many sites are used regularly by picnickers, campers, and hunters, and for ceremonial and other uses by members of the Miccosukee Tribe of Indians, who enjoy a right of perpetual use of state lands within the area.

Like the rest of the Everglades, tree islands are impacted by a range of natural disturbances, including lightning strikes [17], freeze events [18], fires [19], and hurricanes or tropical storms [20]. The closed canopy of tree islands moderates temperature and desiccation, and thereby provides protection from fire and freeze, especially in the interior of large islands. While the canopy architecture of tree island communities may also offer some degree of shelter from windstorms, crowns of the tallest trees on the high ground at the island center are very exposed, and are frequently pruned, damaged, or uprooted by winds.

Of the eight types of south Florida tree islands recognized by Craighead [1], hardwood hammock is the one whose surface is most elevated above the water table, and the only one to develop on well-drained soils. In contrast to the more hydric tree island types, which are often dominated by temperate species, tree assemblages in hardwood hammocks in the interior of ENP are comprised primarily of tropical species of West Indian origin [4]. With their surface a meter or more above the adjacent marsh, these hammocks are frequently ringed by swamp forests which, in portions of the peatland with strong directional flow, complete a mixed forest of tear-drop shape. Hammocks in the heads of such islands usually occupy less than 1000 m², while the entire tree island may encompass ten hectares or more. Small and isolated as they are, tree species richness in these hammocks does not approach that found in similar areas within the extensive forests of the nearby Florida Keys. Nevertheless, many of the common tropical species in Everglades tree islands (e.g., *Bursera simaruba*, *Ficus aurea*, *Sideroxylon salicifolia*, *Sideroxylon foetidissimum*, *Eugenia axillaris*, *Simarouba glauca*, *Coccoloba diversifolia*) are also abundant in the Keys hammocks. Soils in the large tree islands in the interior Everglades differ dramatically from those in Florida Keys hammocks. The former are deep, phosphorus-rich soils with high mineral content, while the latter are well-drained, thin, and organic-rich [21, 22]. Despite these differences, heights of dominant trees in Everglades tree islands and in hammocks of the upper Florida Keys are similar (10–12 meters at maturity).

2.2. Sampling Design and Analytical Methods. Analysis of stand structure was based on three data sets, each derived from different sampling techniques. The most extensive of these was a one-time vegetation survey of 52 tree islands in Shark Slough, Northeast Shark Slough, and WCA-3B,

conducted in 2005–2007 (“Extensive” survey). A second set of 16 permanent tree island plots in Shark Slough and adjacent marl prairies was established in 2005–2006, and sampled most recently in 2008–2009 (“Permanent Plot” survey). Finally, structural data representing Florida Keys hammocks (“Keys” survey) were derived from 23 sites examined in Key Largo in 1994 (Figure 1).

Prior to initiating both the Extensive and Permanent Plot surveys in 2005, we used 1999 aerial photographs to examine Shark Slough and WCA-3B tree islands for evidence of the relatively high (compared to adjacent swamp forests) canopies associated with hardwood hammock forests. We then completed a reconnaissance flight by helicopter over both study areas, confirming or rejecting that each of the islands identified on the aerial photos contained a patch of hardwood hammock at least 10 × 10 m in size. Ten of the hardwood hammocks in Shark Slough were selected for the establishment of permanent plots based on distribution and logistical factors, while the rest of the islands were sampled using Extensive survey methods. The set of permanent plots was supplemented by six additional hammocks, selected from the many tree islands scattered throughout the marl prairies adjoining Shark Slough on the east and west.

Sampling in the Extensive survey plots employed multiple nested circular subplots for estimation of canopy cover in understory and overstory layers, as well as the community structure of tree species. In most cases, five subplots were sampled at the center of the hammock and midway between the center and the edges of the stand along its major and minor axes, respectively. In each subplot, four concentric circles rooted at the subplot center were delineated for sampling of different forest elements. Tree seedlings <1 m in height were counted by species in the inner, 0.57-m radius circle. Herb cover, and density of shrubs (>1 m height) and saplings (1–5 cm DBH) were determined by species in a 1-m radius circle. The species and diameter (5-cm classes) of trees 5–25 cm in DBH were enumerated in a 2-m radius circle, and trees >25 cm were sampled similarly in a 3-m radius circle. Individual stems of multitrunked trees were measured, and a DBH equivalent was computed based on their composite cross-sectional area. Using a spherical densiometer [23, 24], we estimated overstory canopy cover on the basis of a pair of north- and south-facing readings from the subplot center.

Permanent plot size was fit to the dimensions of each hammock; all were square or rectangular and 225–625 m² in area. Each plot was gridded into 5 × 5 m cells, and herbs, seedlings, and shrub stems were sampled as in the extensive plots, that is, in 0.57-m and 1-m radius circular plots surrounding a stake at the center of each cell. Saplings were counted by size class throughout the plot, while the diameter of each tree (>5 cm DBH) throughout the plot was measured. Multitemmed trees were treated as in the Extensive survey plots.

Florida Keys sampling represented a chronosequence of known time since abandonment from agriculture or other human activities in Key Largo. Examination of sequential aerial photos indicated that the youngest stands sampled had been cleared 14 years prior to our 1994 survey, while five stands showed no evidence of human disturbance since at

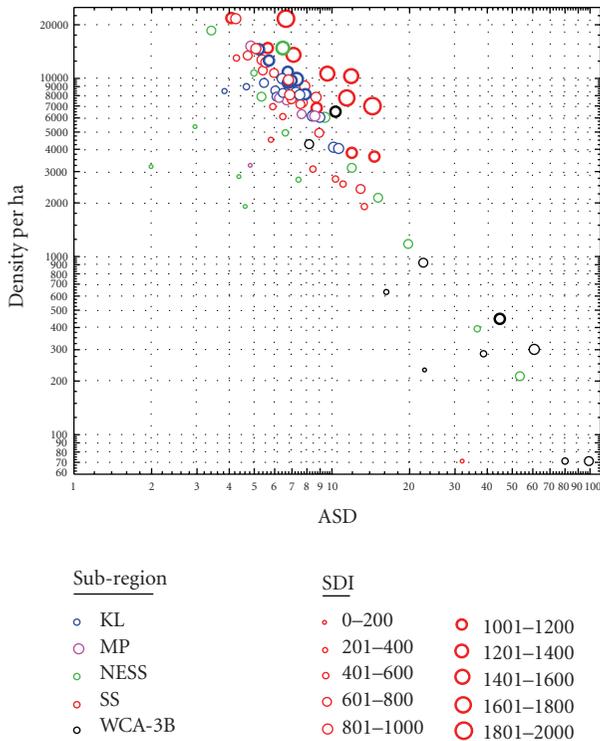


FIGURE 2: Tree density, Average Stand Diameter (ASD), and SDI in 92 south Florida tropical hardwood hammocks. Subregions include: Key Largo (KL), Marl Prairie (MP), Shark Slough (SS), Northeast Shark Slough (NESS), and WCA-3B.

least 1926. Since the northern portions of Key Largo had been dealt a glancing blow from Hurricane Andrew (August 1992) only two years prior to our survey, we recorded species and DBH of both live and hurricane-killed trees along belt transects 60–100 m long. We measured all stems 1–10 cm DBH within 1 meter of the transect, all trees 10.1–25.0 cm in diameter within 2 meters of the line, and all trees >25 cm DBH within 5 meters of the transect. Successional relationships suggested by the composition of these stands have previously been described [12].

To assess structural variation in Everglades tree islands and Keys hammocks, we calculated tree density, basal area, Average Stand Diameter (ASD), and Stand Density Index (SDI) based on all trees >1 cm DBH. We chose a low diameter limit because of the ubiquity and importance of small trees in the species-rich south Florida hammocks, where a number of common taxa rarely exceed 10 cm. SDI was calculated as

$$SDI = \sum \text{tph}_i \left(\frac{DBH_i}{25} \right)^{1.6}, \quad (1)$$

where tph_i is tree density in the i th diameter class, and DBH_i is the DBH of the class midpoint [25]. We also calculated the proportion of SDI attributable to each 5-cm diameter class through 50 cm diameter, and to trees that exceeded 50 cm.

Principal Component Analysis (PCA) was applied to the combined data set consisting of 92 sites from the three study

areas. Six variables were used: SDI and the proportional contribution to SDI from five tree-size categories at each site. Of the 23 Keys stands, 21 were defined as reference sites within the PCA site ordination; two 14 year-old forests were deemed inappropriate to serve as structural references due to their immature developmental condition. Using the standard distance tool in ArcMap 9.3, a 2-s.d. circle was created around the geometric mean center of the PCA distribution of the 21 reference hammocks [26]. Islands were divided into groups based on this analysis; Everglades tree islands falling within this circle were identified as “Keys-like,” while those islands falling outside this circle were considered “Not Keys-like.” Mean overstory canopy cover, understory cover, and seedling density of the two groups were compared through T -tests, once assumptions of homogeneity of variance were met.

3. Results

Based on the 92 hardwood hammocks sampled across the region, south Florida sites supported forests of mean tree (≥ 1 cm DBH) density of ~ 7300 stems \cdot ha $^{-1}$, comprising a basal area of ~ 34 m 2 \cdot ha $^{-1}$, with means for ASD of 12.2 cm and SDI of 803. Around these means, considerable intraregional variation in SDI and associated stand-level metrics was also observed (Table 1). Mean SDI was the highest in Key Largo and Shark Slough forests, but the former were relatively homogeneous in this and other parameters, while the latter were far more variable. This is illustrated in Figure 2, where Key Largo stands are restricted to a small range in tree density, ASD, and SDI, Shark Slough hammocks are more broadly distributed. For instance, the six densest stands sampled, with SDI’s exceeding 1400, were all located in Shark Slough, but many stands with SDI < 600 were also present within the subregion. SDI never exceeded 1200 in WCA-3B; mean ASD in this subregion was much greater than elsewhere, but tree densities were consistently low (Table 1; Figure 2). Mean SDI was significantly lower in Northeast Shark Slough than in either Key Largo or Shark Slough (Table 1), but Northeast Shark Slough tree islands displayed the broadest range in tree density and ASD of the five subregions (Figure 2). The few Marl Prairie islands sampled were characterized by low ASD and basal area, but SDI and tree density were intermediate.

As suggested above, hammocks in the five subregions differed not only in stand-level structural characteristics, but also in how these attributes were distributed among the tree-size classes that comprised each stand. In Figure 3, mean proportional contributions of individual 5-cm DBH classes to SDI are expressed as cumulative curves for each subregion. Three patterns emerge from these curves. Small size classes were very important in Key Largo and Marl Prairie forests, with $\geq 80\%$ of SDI due to trees 20 cm DBH and less, and little or no contribution from trees more than 30 cm DBH. Trees less than 20 cm DBH also played a substantial role in site occupancy in Shark Slough and Northeast Shark Slough stands, but larger trees were also structurally important. In WCA-3B, small size classes were generally absent, and most of SDI was due to large (>40 cm DBH) trees.

TABLE 1: Means (\pm S.E.) for four structural parameters in hardwood hammocks in five south Florida subregions. Site means within a column followed by same superscript do not differ at $\alpha = 0.05$.

Subregion	n	Tree density (ha^{-1})	Basal area ($\text{m}^2 \cdot \text{ha}^{-1}$)	Average stand diameter (cm)	Stand density index
Key Largo	23	8584 (489) ^a	31.6 (1.7) ^a	7.0 (0.3) ^b	925 (41) ^a
Marl prairies	6	7677 (1654) ^{ab}	24.8 (4.1) ^a	6.5 (0.6) ^b	679 (102) ^{ab}
NESS	17	5516 (1238) ^{ab}	25.0 (4.1) ^a	12.0 (3.3) ^b	568 (81) ^b
SS	36	8968 (917) ^a	38.9 (4.1) ^a	8.8 (0.8) ^b	897 (69) ^a
WCA-3B	10	1368 (691) ^b	41.8 (7.8) ^a	40.4 (9.8) ^a	654 (97) ^{ab}

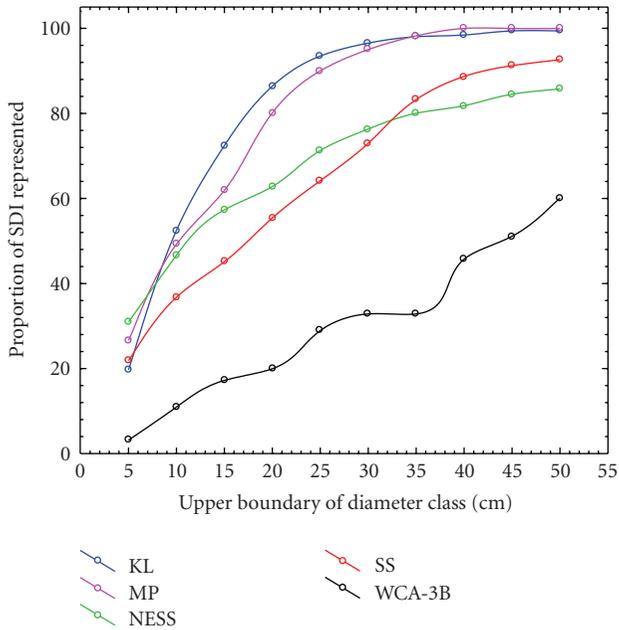


FIGURE 3: Cumulative SDI curves for Key Largo (KL old and mature sites), Marl Prairie (MP), Shark Slough (SS), Northeast Shark Slough (NESS), and WCA-3B hardwood forests.

Factors 1 and 2 of the PCA explained 31% and 24%, respectively, of the total variation in the structural data from all sites (Figure 4). Factor 1 generally distinguished stands in which large trees were major contributors to SDI (high scores) from stands in which small trees were especially important (low scores). SDI was the strongest correlate with Factor 2; high SDI was associated with a large proportional contribution from mid-size (DBH 15–25 cm) trees, and a lower than normal sapling (<5 cm) contribution (Figure 4). The distribution of sites in the PCA ordination space is presented in Figure 5. Mature and old-growth Key Largo forests grouped together in the lower left corner of the graph (high SDI, many small and medium-sized trees, few saplings). Marl Prairie tree islands were mostly clustered nearby, but Shark Slough and Northeast Shark Slough islands were spread throughout the ordination space. WCA-3B islands were mostly confined to the far right of the figure (high Factor 1). Still, at least two representatives of each tree island type were located within 2 s.d. of the centroid of the reference Keys stands, that is, a total of 18 “Keys-like” islands. These islands had significantly higher canopy

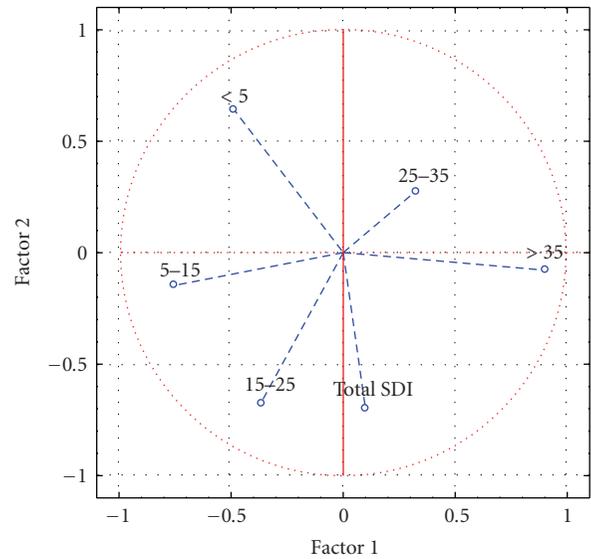


FIGURE 4: Projection of six structural variables on the factor plane formed by PCA Axes 1 and 2. 92 sites from hardwood hammocks in the Keys and Everglades were analyzed, and the first two PCA axes accounted for 55% of the total variation.

cover and lower ground cover than the 51 “Not Keys-like” islands that were distant from the reference group in PCA space (Figures 6(a)-6(b)). While seedling density did not differ significantly between the two groups, there was a tendency for higher densities beneath the more disturbed, open canopies in the “Not Keys-like” stands (Figure 6(c)).

4. Discussion

In this study, we quantified and assessed several aspects of the structure of one type of tree island community, the tropical hardwood hammock, across a swathe of the southern and central Everglades, using for reference similar forests from nearby Key Largo, which in the recent years have received much less human disturbance. Compared to the Key Largo reference group, Everglades tree islands exhibited high variability within and among subregions in stand-level structural characteristics, that is, SDI, basal area, ASD, and tree density. In Northeast Shark Slough and especially WCA-3B, where recent human impact was most extensive, high average tree size, low tree density, and low SDI were the rule. Repeated episodes of clearing and reversion to forest concentrated growth on a few very large trees, and site

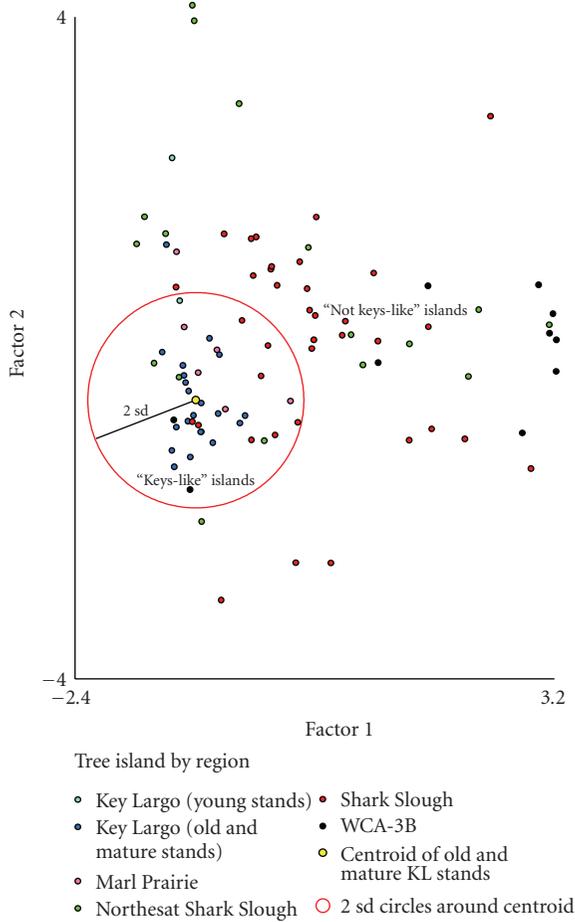
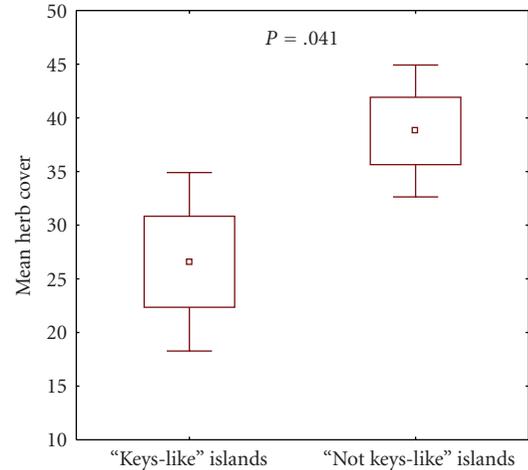


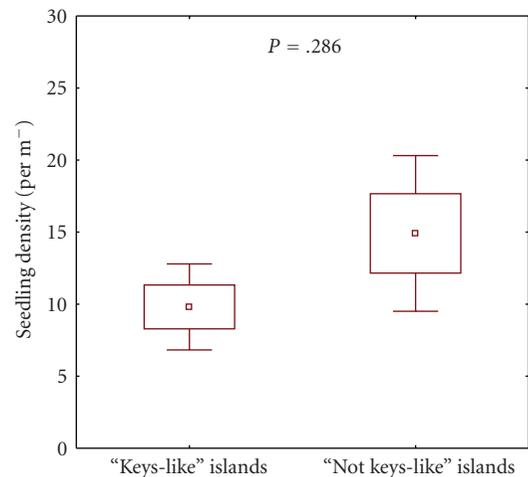
FIGURE 5: Factor coordinates of cases from PCA ordination of 6 structural variables. Factors 1 and 2 are represented on the X and Y axes, respectively. A 2 s.d. circle from the centroid of the Key Largo mature and older stands separates “Keys-like” islands from “Not Keys-like” islands.

occupancy was slow to recover between disturbances. Even in Shark Slough, where the tree islands have been protected within ENP for decades, variation in disturbance history has left many stands with SDI far below the maximum for the type. With their high canopies extending far above the surrounding landscape, residual emergent trees in Shark Slough tree islands are very exposed to the hurricanes that periodically cross the area, and many canopy species are vulnerable to breakage or uprooting even in less severe windstorms. Most of these species resprout reliably, but the success of seedling regeneration in gap-filling is limited by the encroachment of native and nonnative vines, and by the rooting activities of feral hogs that frequent the tree islands. Despite these impediments, tropical hardwood forests with stocking levels above the mean for the reference stands in Key Largo can be found here and there throughout ENP.

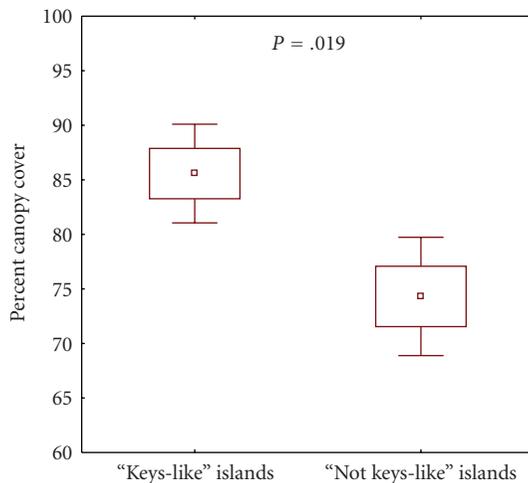
Mature and old Key Largo hammocks are products of an extended successional sequence that features a sharp turnover in species composition within the first century following catastrophic disturbance [12, 13]. Given their



(a)



(b)



□ Mean
 □ Mean ± SE
 I Mean ± 1.96*SE

(c)

FIGURE 6: Box plots comparing three forest characteristics in “Keys-like” islands and “Not Keys-like” islands. (a) Percent herb cover, (b) seedling density, and (c) percent canopy cover.

close compositional affinities with Everglades tree islands, it is likely that, in the absence of human disturbance, the latter would follow a similar trajectory, also taking on an uneven-aged stand structure. While SDI effectively expresses site occupancy in such stands [8], it communicates nothing about their internal, within-stand structure, which is a fundamental concern in the management of uneven-aged forests [6]. In summarizing stand structure for our combined data set, we therefore supplemented SDI with information about tree diameter distribution, expressed as the proportional contribution of each size class to SDI. These analyses highlighted important subregional variation in tree island structure, with small trees the majority contributors to SDI in Key Largo and Marl Prairie tree islands, very large trees the overwhelming contributors in WCA-3B, and relatively even contributions from small and large trees in Shark Slough and Northeast Shark Slough. Disturbances of human or natural origin that affect SDI are also likely to affect the size structure of forests, and certainly have a role in the subregional patterns. Another possible factor is site quality, as self-thinning may be less intense or slower to develop on low-productivity sites, enabling small trees to survive longer in competition with their larger neighbors [27]. The grouping of Key Largo and Marl Prairie stands is notable in this context, as the thin, low P soils on which both of these hammock variants are found may provide less rooting volume and nutrient availability than the richer and deeper sediments of the Shark Slough, Northeast Shark Slough, and WCA-3B islands [21, 22], possibly leading to lower inherent site productivity. Two studies that used similar methods to monitor litterfall in Key Largo and Shark Slough found about 35% higher production in the latter [12, 28].

Information from reference sites can be used to define restoration goals, develop site-specific restoration plans, and assess restoration success [29]. In forest ecosystems, where canopy structure exerts a profound influence on ecosystem processes in subordinate layers, restoration assessments should include effective metrics of stand structure. In this study, we used SDI, which was initially developed as a metric of site utilization in managed, even-aged forests of the western U.S. [7], but has only recently been extended to uneven-aged forests more characteristic of the Eastern U.S., especially the tropical and subtropical hardwood forests of south Florida and the Caribbean basin [8, 9]. Our statistical approach, which incorporated both SDI and the contributions to SDI attributable to different tree size classes, was aimed at summarizing the variability inherent in unmanaged stands. In the ordination of sites based on these structural variables, Key Largo forests grouped together, but were joined by a substantial cohort of similarly-structured Everglades tree islands. Among the few associated variables we measured, “Keys-like” stands had more closed canopies and lower understory cover, both characteristics of old-growth south Florida tropical forests [30], than neighboring, structurally different tree islands. Because stand structure drives many biological functions taking place within the forest [27], the “Keys-like” structure of these islands may translate as well to other desirable forest characteristics,

for example, high species diversity and trophic complexity, moderated microclimate, and closed nutrient cycles [31–33].

The use of reference sites as targets of restoration effort is a staple of the science. However, caution must be applied in each case, because the developmental history and environmental conditions that produced the reference stands are never an exact match for those of the restoration sites. In the south Florida situation we described, variation in site potential and natural disturbance regime experienced at reference and restoration sites are undoubtedly ecologically significant at some level of detail, and their impacts should be studied further. Still, the Key Largo hardwood hammocks are recognized to be among the best examples of old-growth tropical hardwood hammock remaining in the region [30], and can provide guideposts for restoration of tropical forests on the south Florida mainland. In particular, they may serve at least initially as references for activities (e.g., underplanting, exotic species control) needed to augment site occupancy by native trees, and develop a more balanced uneven-aged stand structure on under-stocked Everglades tree islands. In the Everglades, such restoration activities would take place within a large-ecosystem restoration project that is based on the axiom “Get the water right” [5]. Suitable hydrologic conditions are necessary but not sufficient for restoration of ecological function in Everglades tree islands. Achievement of the habitat-specific targets indicated in this study would also require active management to increase site utilization by trees in many poorly stocked stands.

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Research Article

Effects of Landform on Site Index for Two Mesophytic Tree Species in the Appalachian Mountains of North Carolina, USA

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The effects of soil and topographic variables on forest site index were determined for two mesophytic tree species, northern red oak (*Quercus rubra* L.) and yellow-poplar (*Liriodendron tulipifera* L.) in the Southern Appalachian Mountains of North Carolina. Stand variables included soil solum thickness, soil A-horizon thickness, elevation, aspect, slope gradient, and landform index. Landform index is a recently devised environmental variable that has been used to quantify the influence of topography surrounding a stand on productivity. Regression analysis indicated that among the variables only landform index had a significant ($P < .05$) relationship with site index and explained 46 percent of the variation for northern red oak and 56 percent for yellow-poplar. Plot data from this study were also used to validate a previously developed prediction equation for estimating yellow-poplar site index and results indicated that unbiased estimates would be within 2.5 m. Results from this study suggest that landform accounts for variation in site index of mesophytic species in mountainous terrain that is not explained by conventional stand variables associated with soil and topography.

1. Introduction

Forest site quality prediction models have often used environmental variables associated with availability of soil moisture during the growing season, such as aspect, slope gradient, slope position (e.g., upper, lower), and soil texture [1]. Landforms (e.g., cove, ridge) also affect soil moisture [2] and slope position is often used as a surrogate in soil-site models [3]. However, the two-dimensional categories of slope position are a poor substitute for landform because they may not account for environmental factors, such as the effects of wind that are associated with the 3-dimensional shape of land surfaces [4, 5]. Classes of landform have accounted for significant variation in site index for some species [6, 7], but determination of categorical variables in the field is subjective and their use in regression analysis can be problematic [8]. Perhaps the primary reason landform has not been included in studies of forest site quality is lack of a suitable and easily applied method for its quantification, which is available for other topographic-related environmental variables such as elevation and aspect.

An objective measure of landform as a continuous variable has been devised that overcomes many of the problems associated with conventional categories such as slope or ridge [9]. The landform index (LFI) quantifies the environmental influence of topography on a stand and has accounted for significant variation in site quality of a mesophytic tree species (e.g., yellow-poplar) in the Southern Appalachian Mountains [9] and was important in a multivariate analysis of the landscape distribution of species assemblages [10, 11].

LFI has been a useful independent variable in a number of recent multivariate ecological classification studies [12, 13], but little is known about its value in other applications, such as forest soil-site studies. A range of environmental effects are logically associated with landform, particularly soil moisture and soil physical properties. Although LFI in combination with other topographic variables is important for predicting site index of yellow-poplar, it has neither been evaluated in combination with soil variables nor has it been evaluated for prediction of site index for other tree species. In addition, the value of LFI for field application to evaluate site quality could be strengthened by using an independent data

set to test an early model for prediction of yellow-poplar site index [9].

Here, I report results of a study to evaluate the relative value of LFI for prediction of forest site quality. My study had two objectives: (1) determine the effect of landform, in combination with conventional topographic and soil variables, on site index of hardwood tree species and (2) with an independent data set, test the accuracy of a previously developed model based on LFI for predicting site index of yellow-poplar [9]. The results of this study are intended to provide additional insight into environmental factors affecting forest site quality in mesic stands of mountainous landscapes in the Southern Appalachians.

2. Methods

2.1. Study Area. I conducted the study in the Southern Appalachian Mountains of North Carolina (Figure 1). The climatic regime of this area is classified as temperate humid. Elevation ranges from 600 m to more than 2000 m. Mean monthly air temperature ranges from 2.5°C in January to 23.5°C in July. Annual precipitation varies with elevation and ranges from about 950 mm to over 1,500 mm; it is distributed uniformly with no pronounced wet or dry seasons [14]. Geologic formations are primarily Precambrian metaigneous and metasedimentary gneisses and schists with differing amounts of quartz, feldspars, and micas that have weathered to form highly dissected landscapes of low to moderate relief [15]. Soils are generally deep (>100 cm), acidic (pH < 5.5), and infertile except in valleys where fertility is higher likely resulting from greater depth of soil and organic matter associated with colluviums [15]. In general, soils present in the study areas are uniform with productivity differing mainly in water-holding capacity that is probably associated with solum depth and texture.

Forests in the study area are characterized by a canopy of deciduous hardwoods [15]. Ridges and upper to middle portions of slopes are typically dominated by chestnut oak (*Q. prinus* L.), and scarlet oak (*Q. coccinea* Muenchh.). Many lower slopes and coves are dominated by yellow-poplar (*Liriodendron tulipifera* L.) and lesser amounts of northern red oak (*Q. rubra* L.) (hereafter referred to as red oak). White oak (*Q. alba* L.) occurs throughout, along with midstory species such as red maple (*Acer rubrum* L.), sourwood (*Oxydendrum arboreum* (L.) DC), and flowering dogwood (*Cornus florida* L.). Common conifers include shortleaf pine (*Pinus echinata* Mill.) and pitch pine (*P. rigida* Mill.) on ridges and eastern hemlock (*Tsuga canadensis* (L.) Carr.) along streams. Eastern white pine (*Pinus strobus* L.) is a minor component of many upland hardwood stands. American chestnut (*Castanea dentata* (Marsh.) Borkh.) was a major canopy constituent of many stands before being eliminated by an introduced pathogen (*Cryphonectria parasitica*) in the 1920s. About two-thirds of the study area is forested.

2.2. Site Quality. I obtained data from 41 forest stands sampled by the Natural Resources Conservation Service

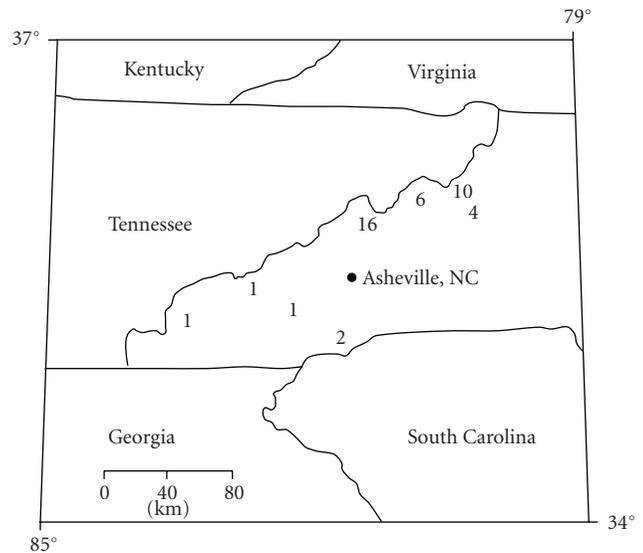


FIGURE 1: Number of plots and approximate location of stands sampled in the Southern Appalachian Mountains of North Carolina, USA.

(NRCS), an agency of the U.S. Department of Agriculture. The stands were selected by NRCS primarily to describe natural variation in characteristics of soil series taxonomic units [16] and also to determine productivity of tree species associated with the soil mapping units. Primary criteria for stand locations were diversity of soil taxonomic units, lack of recent observable disturbance, and an even-aged canopy ranging between 30 and 70 years of age. Each stand was located within a contiguous mapped soil unit where soil characteristics were well within the acceptable range for that series, as determined by examination of the profile in an excavated pit.

Forest site quality was quantified using site index, the average total height of the dominant and codominant stand component at 50 years [17]. Equations to determine site index for any combination of current tree age and height are available for many commercial forest tree species [18]. In order to determine stand age from annual ring counts, increment cores were extracted from three or more suitable trees at a stem height of 1.37 m. Total height was measured to the nearest 0.3 m with a handheld clinometer on three or more dominant or codominant trees for one or more species. Nine tree species occurred on 1 to 17 stands; site index was determined for each species in each stand. Field data were collected from sample trees that met the criteria for site index determination [17]. The data were well suited for this study of site quality because sample stands had been selected primarily for another purpose (soil pedon description), thereby reducing bias and subjectivity in my application of modeling site index in relation to soil and topographic environmental variables.

2.3. Soil and Topographic Variables. Six soil and topographic variables were measured at each stand sampled.

- (i) Thickness (cm) of the soil A-horizon from an excavated pit.
- (ii) Thickness (cm) of the soil solum from an excavated pit.
- (iii) Elevation (m) from a topographic map.
- (iv) Aspect (degrees azimuth) with a hand-held compass.
- (v) Gradient (percent), or slope steepness, with a hand-held clinometer.
- (vi) Landform index (percent expressed as a decimal) with a hand-held clinometer.

An explanation of the development of LFI is presented in detail elsewhere [9]. Briefly, however, LFI is defined as the mean inclination of the horizon (i.e., the apparent intersection of the earth and sky) in relation to a location in the stand being studied. An example illustrates the necessary decisions, methods, and calculations necessary to determine LFI for a location. First, the observer must determine the number of samples of the population of inclinations to the horizon around a stand that are needed to estimate the mean with some desired precision. I have found that eight samples are usually adequate in the subdued mountainous topography of the Southern Appalachians, but the number may range from 1 to more than 360 depending on variability of the landscape surrounding the stand. Generally, the same number of inclination samples should be used for all stands included in the study.

Assume, for example, that the observer decides to sample the inclination to the horizon in five directions of equal azimuth (i.e., the horizontal angular distance from a reference direction) at a location in a stand. A handheld clinometer, graduated in either percent or degrees, is adequate for this purpose. Data for quantifying LFI are obtained using a stratified random sampling method at the selected location in the stand. Beginning in a random azimuth, for example 254°, and continuing in increments of 72° (i.e., 360°/5 directions) the inclination to the horizon at azimuths of 254°, 326°, 38°, 110°, and 182° are measured as +43%, +24%, 0%, -3%, and +38%, respectively. The LFI for the sample stand is calculated by the relationship

$$\overline{\text{LFI}} = \frac{\sum I_i}{n}, \quad (1)$$

where $\sum I_i$ is the algebraic sum of inclinations to the horizon sampled in equal increments of azimuth from a location in the stand n is the number of inclinations sampled. Solving (1) using the example data, with inclination percents expressed as decimals, results in LFI calculated as

$$\text{LFI} = \left(\frac{(0.43 + 0.24 + 0.0 - 0.03 + 0.38)}{5} \right) = \frac{1.02}{5} = 0.204. \quad (2)$$

Similar values of the mean inclination to the horizon can result from many variations of landforms. Horizon inclinations from different stands that result in similar values of LFI, however, are presumed to account for similar proportions of variation of stand response variables. As with

other important variables used to characterize the physical environment of a stand at a location on a landscape, LFI has little utility for use in a prediction equation until its relationship is determined for a response variable, which is one of the objectives of this study.

2.4. Data Analysis. Species present in ≥ 10 of the 41 stands sampled were retained for analysis. Of the six environmental variables included in this study, only aspect required transformation. Because azimuth is a circular measurement of aspect, I transformed it using the cosine relationship described by Beers et al. [19]. LFI is a continuous measure and was used in the analysis as a common topographic variable. I used t -tests to (1) determine significant correlation between pairs of soil and topographic variables for each species and (2) detect differences between environmental variables associated with each species. I used multiple regression analysis to determine the relationship between the dependent variable of site index and the six independent variables for each species. I evaluated coefficients of the independent variables for significance using F -tests under the null hypothesis that the parameters were equal to 0 and thus had no real effect on site index.

Two types of models were developed for each species: overfitted and parsimonious. Overfitted models may include variables that account for little variation in site index and are used primarily for exploratory purposes to determine the relative importance among the variables of interest [8]. A parsimonious model was developed for each species that included only the single most significant environmental variable identified in the overfitted models. Inclusion of additional variables in the parsimonious model was not warranted because of the small size of the data set. Equation coefficients are omitted because model development was not the objective of my study and the available data set was inadequate for that purpose. Tests of significance were made at the 0.05 level of probability.

2.5. Model Validation. I used data from the stands where yellow-poplar was present for an independent validation of a previous model [9] developed for prediction of site index using LFI. The previous model was a prototype that had been developed for a larger region of the Southern Appalachian Mountains, which included the smaller area of this study, and is referred to as the SAM model. Validation was done using scatter plotting and the microcomputer program DOSATEST [20]. The DOSATEST program, which tests mean bias and precision of a prediction equation with an independent data set, implements rationale for accuracy developed by Reynolds [21]. Bias, defined as the average error in predictions made by the model, was calculated as the mean difference between actual and predicted site index. Precision was the tolerance interval that delineated 95 percent confidence intervals for 95 percent of future errors.

3. Results

Nine tree species were present in the 41 sample stands. Two species were present in ≥ 10 stands, red oak ($n = 17$)

TABLE 1: Mean and range of site index, soil, and topographic variables by species for stands sampled in the Southern Appalachian Mountains of North Carolina, USA.

Model variables	<i>Red oak</i> ($n = 17$)		<i>Yellow-poplar</i> ($n = 14$)	
	Mean	Range	Mean	Range
Site index (m)	25.5	18–30	32	25–38
A-horizon thickness (cm)	15.8 ^a	8–36	22.1 ^a	8–41
Solum thickness (cm)	83.2 ^a	36–152	89.6 ^a	43–140
Elevation (m)	966.6 ^a	442–1329	909.4 ^a	646–1165
Aspect (deg)	159.3 ^a	45–330	186.3 ^a	10–355
Gradient (percent)	28.9 ^a	10–60	20.7 ^a	2–38
Landform index	0.133 ^b	0.01–0.27	0.225 ^b	0.08–0.38

^aIndicates no significant difference ($P < .05$) between the two species.

^bIndicates significant difference ($P < .05$) between the two species.

and yellow-poplar ($n = 14$), and were retained for analysis (Table 1). Broad overlap occurred in the ranges of environmental variables measured in stands occupied by the two species. Among the six environmental variables measured in the stands where yellow-poplar occurred, only elevation and LFI were significantly correlated ($r = -0.53$, $P = .05$). For red oak stands, however, thickness of the A-horizon was correlated with elevation ($r = 0.50$, $P = .04$) and particularly with solum thickness ($r = 0.82$, $P = .001$). The low level of correlation between the environmental variables indicated that the effects of multicollinearity would be problematic only if both soil variables were included in the site index model for red oak. Mean LFI was the only variable that differed significantly ($P < .05$) between stands where the two species were present.

3.1. Environmental Relationships with Site Index. Simple correlation coefficients between site index and each of the environmental variables were generally low ($r < 0.2$) and, except for elevation and LFI, were not significant for either species (Table 2). The Pearson correlation coefficients between site index and LFI were $r = 0.75$ ($P = .0005$) and $r = 0.73$ ($P = .003$) for red oak and yellow-poplar, respectively.

The relative importance of variables in the overfitted multiple regression models was generally similar to that for the simple correlations (Table 2). With the six environmental variables present in the model, LFI alone accounted for significant ($P < .02$) variation of site index for both species. Elevation did not account for significant variation of site index when included with LFI for the overfitted prediction model of either species. The relationships for both species were significantly ($P < .05$) associated with predicted site index and accounted for 46 percent of the variation in site index of red oak and 56 percent for yellow-poplar.

Parsimonious site index regression equations were developed for both species that utilized LFI (Figure 2), which was the only environmental variable that accounted for significant variation in the overfitted models. Similarity of regression slopes suggests common response to LFI by both species. Comparison of the two simple linear regression

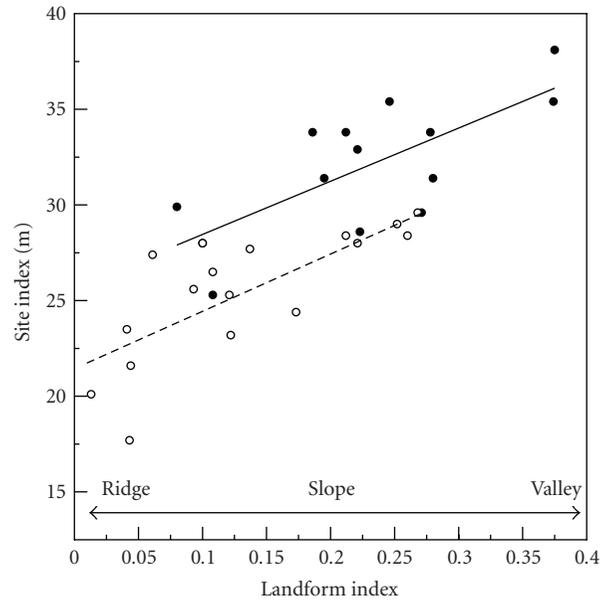


FIGURE 2: Comparison of linear models for predicting site index from landform index for northern red oak (open circles) and yellow-poplar (closed circles) in the Southern Appalachian Mountains of North Carolina, USA. Classes of landform associated with values of the landform index are shown above the x-axis.

equations indicated no significant ($F = 3.65$, $P > .05$, $df = 1, 27$) difference between slopes (beta coefficients), but highly significant ($F = 7.75$, $P < .01$, $df = 1, 29$) differences between intercepts (alpha coefficients). Therefore, a single regression line cannot be used to quantify the relationship between site index and LFI for red oak and yellow-poplar.

3.2. SAM Model Validation. LFI for 11 of the yellow-poplar stands in this study was within the range of data used to develop the SAM model (0.15–0.40), but LFI was lower (< 0.15) for three stands (Figure 3). However, site index observed in the 14 stands in this study was all within the 95% confident interval for future values predicted by the SAM model (Figure 3). Fifty seven percent of the observed values of site index were within 2 m of the value predicted by the SAM model. Observed yellow-poplar site index was significantly correlated ($r = 0.73$, $P = <.01$) with values predicted by the SAM model (Figure 3 inset). Even though correlation between observed and predicted site index was high, the SAM model over-predicted site index by 0.546 m. The DOSATEST analysis indicated that, however, this bias is not significantly different from zero and that future errors will be within a prediction interval of 5.26 m.

4. Discussion

Among the six soil and topographic variables examined for their influence on site quality of forest hardwood tree species, only elevation and LFI were correlated with site index. The significantly smaller value of mean LFI for red oak (0.133) compared to that for yellow-poplar (0.225)

TABLE 2: Pearson correlation coefficients (r) of environmental variables with site index and overfitted regression significance levels ($P > t$) for a site index model with all independent environmental variables by species for stands sampled in the Southern Appalachian Mountains of North Carolina, USA.

Environmental variable	Pearson correlation (r)		Variable significance ($P > t $)	
	Red oak	Yellow-poplar	Red oak	Yellow-poplar
A-horizon thickness	-0.06 ^a	0.23 ^a	0.82	0.89
Solum thickness	0.02 ^a	-0.08 ^a	0.78	0.1
Elevation	-0.50 ^b	-0.58 ^b	0.16	0.85
Aspect	-0.07 ^a	0.03 ^a	0.93	0.61
Gradient	0.10 ^a	-0.14 ^a	0.5	0.1
Landform index	0.75 ^b	0.73 ^b	0.02	0.01
Model significance	-	-	0.05	0.05

^aPearson correlation coefficient was not significant at $P < .05$.

^bPearson correlation coefficient was significant at $P < .05$.

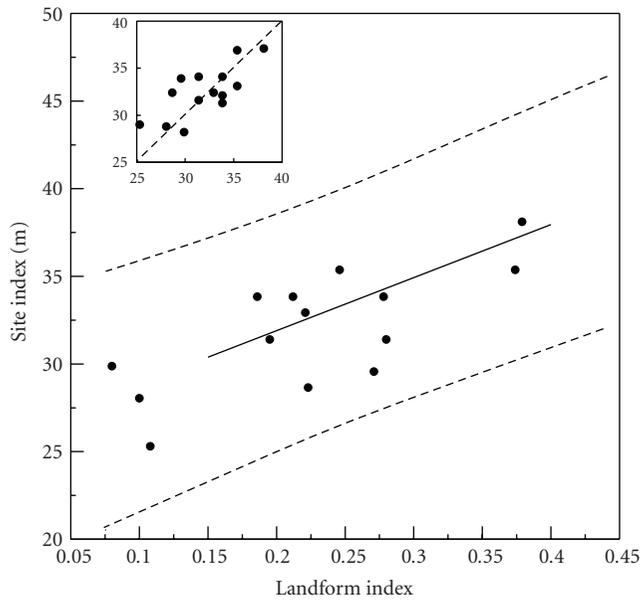


FIGURE 3: Observed site index for yellow-poplar from the 14 stands sampled in this study was within the 95% confidence limits (two dashed lines) for individual predictions from a model (solid line) reported in a previous study [9] conducted throughout the Southern Appalachian Mountains (SAM). The length of the solid line indicates the range of landform index (0.15 to 0.40) used in development of the SAM model. The inset shows the significant relationship ($r = 0.72, P < .01$) between yellow-poplar site index observed in this study (x -axis) and site index predicted by the SAM model (y -axis). The diagonal dashed line in the inset represents perfect correlation between observed site index and site index predicted by the SAM model.

indicates that red oak stands tended to occur on linear to concave landforms (e.g., slopes to valleys), but yellow-poplar was associated with concave landforms (e.g., valleys). Only LFI accounted for significant variation in site index for both red oak and yellow-poplar in the overfitted regression models that included all of the measured environmental variables. Although elevation was significantly correlated with site index for both species (Table 1), its effect was

not important in the regression models likely because it was also slightly correlated with LFI for red oak ($r = -0.33$) and yellow-poplar ($r = -0.39$). Callaway et al. [22] found that productivity of forested sites in the central Great Smoky Mountains was influenced most strongly by an index of landform weighted by aspect; soil variables were also significant, but of minor importance. In the Southern Appalachian Mountains of northeastern Georgia, Ike and Huppuch [6] reported that site index of red oak and yellow-poplar were associated with landform classes (e.g., valley, ridge). My results are in general agreement with theirs [6] and more clearly quantify the effects of landform on site quality for red oak and yellow-poplar.

The lack of significance of the conventional topographic variables with site index was not unexpected. My finding that aspect was not important as a site factor for either species agrees with results from several studies in the Blue Ridge province. Whittaker [23] reported that aspect seemed to have little influence on forest productivity in the Smoky Mountains, perhaps because annual precipitation is ample and well distributed. Helvey et al. [2] found that soil moisture in the Southern Appalachians was not associated with aspect between 600 m and 1500 m elevation. However, Ike and Huppuch [6] reported decreasing site index of red oak from northerly to southerly aspects, but little difference between east and west aspects.

The relative importance of soil characteristics on site quality varies in the Southern Appalachian region. My finding that thickness of the A-horizon and solum thickness did not influence site index agrees with results of Ike and Huppuch [6]. However, in the less mountainous Appalachian Piedmont, the study of site quality by Della-Bianca and Olson [24] suggested an increased importance of soil variables relative to topographic factors. Soil properties were more important than topographic variables for explaining the differential growth of among tree species in some parts of the Southern Appalachians with parent materials that differ from those in my study [22, 25].

An important part of this study was testing accuracy of the SAM model for predicting yellow-poplar site index based on LFI [9]. Although the SAM model had been developed for a much broader area of the Southern Appalachian

Mountains, site index for the 14 yellow-poplar stands in this study was estimated within a confidence interval of about 2.4 m for a new observation, which is probably adequate for many forest management purposes. Even though yellow-poplar in this study was present in three stands where LFI was lower than in the dataset used to develop the SAM model, the relationship was consistent between site index and LFI.

In summary, a measure of topography surrounding the sampled stands, quantified by the landform index, accounted for significant variation in site index of two mesophytic tree species in a mountainous region of the Southern Appalachians. The higher site index of stands with larger values of LFI was likely caused by favorable environmental factors affecting soil moisture and fertility that may be associated with large concave landforms [26]. A definitive explanation for the growth response of trees to complex environmental relationships in forest stands will likely be difficult to obtain for reasons summarized by Jarvis and McNaughton [27]. As Peet [28] suggests, "...no simple measure is available which incorporates all the important components of site moisture."

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Research Article

Tree Mortality following Prescribed Fire and a Storm Surge Event in Slash Pine (*Pinus elliottii* var. *densa*) Forests in the Florida Keys, USA

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In fire-dependent forests, managers are interested in predicting the consequences of prescribed burning on postfire tree mortality. We examined the effects of prescribed fire on tree mortality in Florida Keys pine forests, using a factorial design with understory type, season, and year of burn as factors. We also used logistic regression to model the effects of burn season, fire severity, and tree dimensions on individual tree mortality. Despite limited statistical power due to problems in carrying out the full suite of planned experimental burns, associations with tree and fire variables were observed. Post-fire pine tree mortality was negatively correlated with tree size and positively correlated with char height and percent crown scorch. Unlike post-fire mortality, tree mortality associated with storm surge from Hurricane Wilma was greater in the large size classes. Due to their influence on population structure and fuel dynamics, the size-selective mortality patterns following fire and storm surge have practical importance for using fire as a management tool in Florida Keys pinelands in the future, particularly when the threats to their continued existence from tropical storms and sea level rise are expected to increase.

1. Introduction

In fire-dependent plant communities, such as pine (*Pinus* spp.) forests, prescribed fire is an efficient tool to reduce fuel loads, control the growth of hardwood species, promote pine regeneration, and restore diversity in the ground layer herbaceous community [1–3]. Prescribed fire is commonly practiced in South Florida pine rocklands, which is an imperiled ecosystem, and important for preservation of endemic plants and endangered wildlife, such as Key Deer (*Odocoileus virginianus clavium*). Predicting post-fire pine tree mortality is needed for effective use of prescribed fire in the pine forests, since pine mortality may alter fuel dynamics, destroy the live seed source necessary for pine regeneration, and affect ecosystem processes, altering plant population and community structure [4].

Models that predict post-fire tree mortality have been developed for a number of North American tree species

[5–8]. However, only a few studies have described post-fire mortality of South Florida slash pine [9, 10], and predictive models for post-fire slash pine mortality in the Florida Keys pine forests are not available. Moreover, studies of post-fire tree mortality are generally based on observations made only during the first year after fire, though delayed mortality in subsequent years may also be important [11]. Delayed mortality is a common phenomenon in South Florida pine forests where insect outbreaks and hurricane-related wind damage usually increase the probability of pine mortality after fire [10, 12]. In the Florida Keys, pine forests are found at low-elevation coastal settings where freshwater is present in a shallow groundwater lens, and the forests are occasionally flooded by storm surge that kills salt-sensitive pine trees [13]. Hence, an assessment of the interacting effects of fire and other disturbances on slash pine mortality is important for development and implementation of any fire management plan in Florida Keys pine forests.

Post-fire mortality depends on tree morphology and physiology and fire behavior. Tree species differ in their susceptibility to fire, and even within species, trees at different growth stages vary in response. Likewise, fire intensity also influences tree mortality. Therefore, models that predict post-fire mortality usually include tree attributes and apparent fire damage characteristics as independent variables. The most commonly used tree attributes are diameter at breast height (DBH) and bark thickness, which may be interactive in their effects. Bark thickness protects the cambium by increasing its resistance to injury from fire [5, 14]. At the same time, bark thickness is often positively correlated with DBH [15]. For species in which DBH and tree height are strongly correlated, DBH can also reflect crown susceptibility to scorching, though such relationships depend on fire history, stand structure, and the specific burn [16, 17].

Fire damage measurements in trees include the extent of tissue damage in their various parts, including roots, stems, crown leaves, and buds [7]. Fire damage to fine roots of trees can be crucial for their post-fire survival. Although ground surface burn severity is often used as a proxy of root damage [18], the severity may not always reflect the extent of damage, especially when fire is reintroduced after a long period of fire suppression in systems dependent on frequent fire [19]. Stem damage and crown damage are commonly used as surrogate measures of fire intensity and also as predictors of post-fire tree mortality. Measures of stem damage include bole char height, bole char depth, bark char ratio, and visible cambium injury. Among them, bole char height has been widely used either alone or in combination with crown damage to predict tree mortality after fire [9, 17, 18]. Char height sometimes is preferable to measures of crown scorch because of its permanence, ease of collection, and strong correlation with fire intensity. In several conifer forests, however, and percent crown scorch, expressed in terms of a number of variables, such as crown scorch height, percent crown scorch volume, and so forth, has also been used to predict post-fire tree mortality [7]. While crown scorch height represents fire intensity well, post-fire tree mortality is more directly related to crown scorch volume [20, 21].

In the Florida Keys, both coastal and upland ecosystems, including pine forests, are vulnerable to hurricane-associated winds and storm surge. Slash pine mortality due to wind damage depends on hurricane intensity and stand age. Large trees in old-growth stands are more likely to be killed than small trees or those in second-growth stands [12]. While tree mortality from wind damage is a mechanical phenomenon, storm surge-induced mortality is physiologically based, resulting from flooding and salinity stress. Response of nonhalophytic plants to these stresses depends on species, flooding duration, salinity, and plant growth stage [22].

In this study, we examined the effects of prescribed fire and a storm surge event on tree mortality in Florida Keys pine forests. Our objectives were twofold, (i) to develop a model to predict the probability of post-fire mortality of slash pine in Florida Keys pine forests as a function of burn season, tree size and fire characteristics, and (ii) to examine the effects of storm surge events on pine tree mortality. We expected higher tree mortality following summer, growing

season burns than winter, dormant season fires. We also hypothesized that post-fire slash pine mortality would be negatively correlated with tree size, and positively with fire intensity expressed in terms of stem and crown damage. Slash pine mortality was also expected to be higher in storm-surge impacted burned plots than in unimpacted burned and unburned plots.

2. Materials and Methods

2.1. Study Area. The study area is located in the National Key Deer Refuge (NKDR) in the Lower Florida Keys (Figure 1). Pine forests in the Florida Keys are characterized by a canopy of South Florida slash pine (*Pinus elliottii* var. *densa*), a diverse understory dominated by West Indian tropical hardwoods and several palm species, and a diverse herb layer [23]. In this forest, fire usually improves Key Deer habitat by preventing succession towards a dense hardwood community [24]. Currently, less than 1000 ha of Lower Keys pinelands are scattered over seven islands, where low-elevation pine forests are occasionally flooded by salt waters associated with hurricane-induced storm surge. Our study focused on pine forests on Big Pine Key, which is the largest island in the Lower Florida Keys and contains the vast majority of Keys pine forest [13].

2.2. Experimental Design. The study on pine mortality was a part of an experiment carried out to characterize fuel loads to examine relationships among stand age, fuel load, and fire characteristics and to assess the effects of fire on pine and hardwood trees, understory shrubs and palms, and ground layer flora, including endemic species [25–27]. The experimental design has been described in detail elsewhere [25, 26]. In brief, the study site included 18 1 ha plots, established in six homogeneous blocks, each with three plots. The blocks were in one of two characteristic understory types: (i) a relatively sparse shrub layer (open), and (ii) a dense shrub layer (shrubby). Shrubby and open plots were chosen to represent different understory fuel conditions that would influence fire intensity. Moreover, since burning conditions and growth patterns of slash pine trees differ between rainy (summer) and winter seasons, the experimental design called for burns to be carried at two times of the year. Thus, the three plots in each block were randomly assigned to the three treatments: (1) summer burn, (2) winter burn, and (3) control, to be carried out during three consecutive years (1998, 1999, and 2000). The 18 plots were identified by year of intended treatment, characteristic understory (open, shrubby), and treatment (summer burn, winter burn, control). For instance, the shrubby plot to be burned in the summer of 1998 was designated as 1998-S-S, and winter-burned plot in the same block was 1999-S-W.

Because of weather and logistic constraints, all experimental burns were not carried out as planned and only eleven of the 18 plots were burned under prescription during the study. Eight plots were burned during the early part of the rainy season (summer season), when lightning-caused fires are likely to occur [28, 29], and three plots were burned

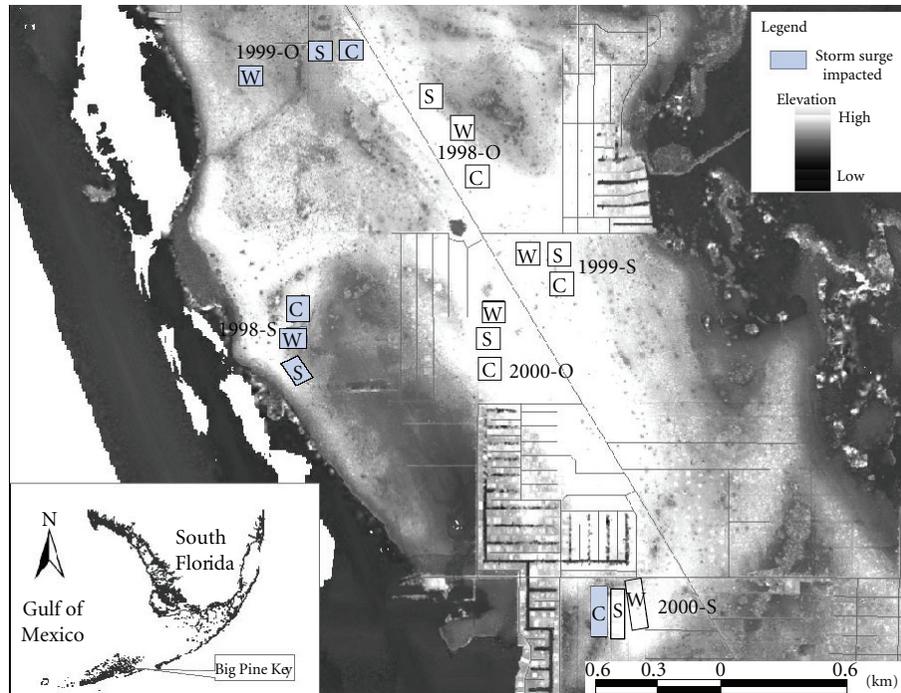


FIGURE 1: Study area map showing the layout of experimental plots. The background is the ground elevation (m)—the lighter the area, the higher the ground elevation—derived from LiDAR data.

during December/January (winter season), when plants were most dormant and burning conditions were relatively mild (Table 1). In 1998, the summer and winter burns in 1998-O and 1998-S blocks burned on schedule. In 1999, only the summer burns were completed in the 1999-O and 1999-S blocks. The winter burn for the 1999-O block was completed a year late, in December 2000, and the 1999-S-W plot was never burned. In the summer of 2001, the summer and winter burn plots in both 2000-O and 2000-S blocks were burned.

In addition to the targeted experimental burns, 6 plots in two blocks, 1998-O and 1998-S, were burned by NKDR staff in 2004. Two plots, 1998-O-S and 1998-O-W, were only partially (50% and 75%, resp.) burned. In 2005, much of Big Pine Key was flooded by storm surge caused by Hurricane Wilma. Five burned and 2 unburned plots located in the low elevation (<1 m) area on the west side of the island were especially affected. The plots located on relatively high ground or in the northeast part of the island were either not flooded or flooded only modestly. Since none of the sites were sampled immediately prior to the hurricane, we could not distinguish between fire- and storm surge-caused tree mortality in plots that experienced both disturbances. Our analysis of only storm surge-caused tree mortality was therefore restricted to effects observed in unburned plots.

2.3. Fire Intensity, Char Height, and Percent Crown Scorch. Fire temperature, which is a direct measure of fire intensity,

was not measured. Instead, we measured char height and percent crown scorch within one month after the fires in all burned plots. Char height, the maximum height of charring on the bole, was measured directly on individual trunks irrespective of direction [30]. Percent crown scorch (CVS, percent crown scorch volume, [7]), a measure of the amount of live needles killed by the fire, was estimated using the following scale: 0%, 10%, 25%, 50%, 75%, 90%, and 100%. There was essentially no needle consumption in any of the fires, mainly because fires were of low to medium intensity and the flames never reached the crowns of the trees.

2.4. Tree Measurements. All pine and hardwood trees (≥ 5 cm dbh) were tagged and their DBH was measured in the year when plots in a block were assigned to be burned. Post-fire pine mortality was investigated annually for three years in both summer and winter burns plots in the 1998-O and 1998-S blocks, for two years in summer burn plots in the 1999-O and 1999-S blocks, and for one year in winter burn plot in the 1999-O Block (Table 1). Pine mortality was recorded also in the control plots of these four blocks. In two blocks, 2000-O and 2000-S, burned plots were only surveyed seven years after the prescribed burn, which took place in 2001. All burned and unburned plots were revisited in 2008, when the DBH of all trees was remeasured.

2.5. Statistical Analysis. We analyzed differences in tree characteristic and post-fire percent pine tree mortality among

TABLE 1: Experimental plots within six blocks with the burn dates, mean ground elevation (m; NAVD-1988), number of live trees, mean DBH (cm), char height (m), percent crown scorch (%), and years when post-fire status (live and dead) of trees was recorded. Each block had one of two characteristic understory types: open (O), and shrubby (S). The three treatments were control (C), summer (S), and winter (W). NB: not burned. In 2008, 3 years after Hurricane Wilma, status of tree was recorded and dbh was measured in all 18 plots.

Block	Burning treatment	Plot ID	Experimental burn date (1)	Secondary burn date (2)	Elevation (m)	No. of trees	DBH (cm) Mean (Range)	Char height (m) Mean (\pm SD)	Crown Scorch (%) Mean (\pm SD)	Post-fire (burn-1) tree survey	Storm-Surge		
			burn date (1)	burn date (2)	(m)	trees	Mean (Range)	Mean (\pm SD)	Mean (\pm SD)	Yr-1	Yr-2	Yr-3	Yr-7
1998-O	C	1998-O-C	NB	2nd Aug, 04	1.327	417	13.2 (5.1-29.4)						
	S	1998-O-S	16 Aug, 98	2nd Aug, 04	0.888	457	12.5 (5.0-30.6)	2.5 \pm 1.6	61 \pm 36	1999	2000	2001	
	W	1998-O-W	15 Dec, 98	2nd Aug, 04	0.762	612	11.5 (5.0-30.7)	1.7 \pm 1.1	46 \pm 44	1999	2000	2001	
1998-S	C	1998-S-C	NB	2nd Aug, 04	0.968	355	13.8 (5.0-38.6)						Impacted
	S	1998-S-S	17 Aug, 98	2nd Aug, 04	0.762	494	13.3 (5.0-38.0)	2.9 \pm 2.0	66 \pm 37	1999	2000	2001	Impacted
	W	1998-S-W	15 Dec, 98	2nd Aug, 04	0.565	336	13.6 (5.0-40.4)	1.3 \pm 0.9	21 \pm 34	1999	2000	2001	Impacted
1999-O	C	1999-O-C	NB		0.822	543	12.4 (5.0-29.7)						Impacted
	S	1999-O-S	18 July, 99		0.559	360	15.1 (5.0-33.0)	2.1 \pm 1.4	55 \pm 38	2000	2001		Impacted
	W	1999-O-W	12 Dec, 00		0.618	662	11.2 (5.0-35.3)	1.3 \pm 1.0	39 \pm 37	2001			Impacted
1999-S	C	1999-S-C	NB		1.296	780	10.1 (5.0-25.2)						
	S	1999-S-S	22 June, 99		1.224	643	10.3 (5.0-26.4)	2.8 \pm 1.7	84 \pm 32	2000	2001		
	W	1999-S-W ^A	NB		1.395	1006	9.2 (5.0-21.7)						
2000-O	C	2000-O-C	NB		1.422	516	12.6 (5.0-33.0)						
	S	2000-O-S	19 July, 01		1.619	444	13.5 (5.0-30.1)	2.0 \pm 1.1	58 \pm 34				2008
	W	2000-O-W ^B	19 July, 01		1.515	474	13.1 (5.1-32.7)	3.4 \pm 1.6	84 \pm 24				2008
2000-S	C	2000-S-C	NB		0.765	527	9.8 (5.0-31.4)						Impacted
	S	2000-S-S	18 July, 01		1.163	642	11.5 (5.0-26.6)	2.6 \pm 1.8	66 \pm 36				2008
	W	2000-S-W ^B	18 July, 01		1.147	693	10.5 (5.0-27.4)	2.7 \pm 1.6	74 \pm 31				2008

^ANever burned. ^BBurned in summer

different levels of understory conditions (U: shrubby and open), burning treatments (T: control, summer burn and winter burn), and year (Y: 1998 and 1999) using three-way analysis of variance (ANOVA). Since the plots were not burned as planned resulting in an unbalanced design with a missing value, we used a General Linear Model (GLM). To stabilize within group variances, we transformed percent pine tree mortality data using an arcsine-square root transformation. In the model, understory conditions (U), burning treatments (T), and their interaction (U*T) were the fixed effects, and year (Y) and its interactions (Y*U, Y*T) were considered as random effects. The three-way interaction was not evaluated. Instead, it was used as the mean square (MS) error to test the first-order interaction effects. Since complete records of post-fire pine tree mortality in all plots burned between 1998 and 2000 were available for the first year after fire only, analysis of variance was restricted to the percent mortality within one year.

In burned plots, DBH, char height and percent crown scorch within the groups compared were not normally distributed (Kolmogorov-Smirnov normality test; $P < .001$). We used Mann-Whitney's nonparametric U test to examine the differences in tree size and fire-induced damage characteristics between two groups of trees, live and dead. In addition, post-fire tree mortality models were developed using a binary logistic regression model of the following form:

$$P(m) = \frac{1}{1 + e^{-(\beta_0 + \beta_1 X_1 + \dots + \beta_k X_k)}}, \quad (1)$$

where $P(m)$ = probability of post-fire mortality, X_1, \dots, X_k are independent variables, and $\beta_0, \beta_1, \dots, \beta_k$ are the regression coefficients.

The models were developed to predict the probability of fire-induced pine tree mortality one year after fire in the plots burned in 1998, 1999, or 2000, and seven years after fire in the plots burned in 2001. We used season of burn (S), tree size (DBH), char height (CH), and percent crown scorch (CVS) as independent variables to predict probability of slash pine mortality. An indicator variable with the values 1 and 0 for the summer and winter seasons, respectively, was created to represent the categorical variable Season of Burn. Since char height generally represents fire intensity well and is significantly related to preburn fuel loads in Florida Keys pine forest [26], a reduced model, including only DBH and char height as independent variables, was also developed. In addition, a reduced model with only percent crown scorch as the predictor variable was developed.

The merits of using the logistic model include the predictions of binary dependent variables, having a value of 0 or 1, from continuous, nominal, or ordinal independent variables, and the data do not need to be normally distributed. Logistic regression models estimate the coefficients for the independent variables using a maximum likelihood process. We computed maximum likelihood estimates of model parameters and used Wald χ^2 test statistic to assess the significance of individual parameters. Model performance was assessed using Receiver Operating Characteristic (ROC) curve analysis [21]. The ROC curve analysis is a method

for assessing the performance of diagnostic decision making process, consisting of a stimulus and a response [31]. In evaluating tree mortality prediction models, the observed status of tree—live or dead—is the stimulus, and probability of mortality, scaled from 0 to 1, is the response. In this method, the probability of a true positive prediction (“hit”, i.e., a dead tree is classified as dead) versus the probability of a false positive prediction (“miss”, e.g., a live tree is classified as dead) is plotted across the continuous probability of mortality cutoff ranges from 0 to 1. In an ROC plot, concordance value, that is, the area under the curve (AUC) statistic (or the C-statistic) is used for evaluating the model performance. AUC varies between 0 and 1, and the greater the AUC, the better the performance [21]. Although criteria for ROC value cut-off vary with types of error, models with ROC values >0.9 are considered outstanding, between 0.8 and 0.9 excellent, and between 0.7 and 0.8 acceptable in discrimination [31].

We developed a simple least square regression model to examine the effects of storm surge on percent tree mortality at the plot level. In the model, we used mean ground elevation as a surrogate measure of storm surge, based on the assumption that the impact of storm surge on standing trees would be inversely correlated with elevation. Plot level mean elevation was obtained from a digital terrain model (DTM) developed from LiDAR data by Robertson and Zhang [32]. The DTM was in the form of high-resolution (1×1 m grid) raster map and had the vertical accuracy of 0.17 m at the 95% confidence interval.

Changes in stand structure in the plots were analyzed by comparing mean stand diameter and basal area measured in the beginning of experimental burns and in 2008. We calculated change in mean diameter and basal area for four groups of plots: (i) no burn and no storm surge (Unburn), (ii) burned but no storm surge (Burned), (iii) no burn but storm surge (Unburn-SS), and (iv) burned and storm surge (Burned-SS), and used one-way analysis of variance (ANOVA) to examine among group differences. Finally, changes in tree size distribution were examined by fitting curves to the mean number of trees in a range of dbh classes in both surveys. Two curves were compared using the following F -statistic:

$$F = \frac{(SS_C - SS_I)/(DF_C - DF_I)}{SS_I/DF_I}, \quad (2)$$

where SS_I and DF_I are total sums-of-squares and degrees of freedom, respectively, from each individual fit, and SS_C and DF_C are sum-of-squares and degrees of freedom from the combined data. We used SPSS version 17.0 (SPSS, Chicago, IL, USA) for logistic regression analysis, and STATISTICA ver. 7.0 (StatSoft) for all other statistical analyses and graphics.

3. Results

Pine tree mortality in Big Pine Key pine forests varied among plots, depending on whether the plots were burned or not, and/or were impacted by Hurricane Wilma. During the

TABLE 2: *F*-statistic and *P*-value from a General Linear Model (GLM) used to test differences in mean percent pine mortality after one year of prescribed burns. The plot-level mean tree mortality data from 12 plots in four blocks (1998-O, 1999-S, 1999-O, and 1999-S) were used. The mortality data in the plot 1999-S-W were missing. In the model, understory conditions (U), burning treatments (T), and their interaction (U*T) were the fixed effects, and year (Y) and its interactions (Y*U, Y*T) were the random effects. The three-way interaction (U*T*Y) was used as the mean square (MS) error for the interaction effects. Error terms for the fixed main effects, U and T, were U*Y and T*Y, respectively, and for the random effect, Y, the error term was $MS(U*Y) + 0.889*MS(T*Y) - 0.889*MS(error)$.

Effects	df (effects, error)	<i>F</i>	<i>P</i> -value
Intercept	1, 1	269.90	.039
Understory (U)	1, 1	1.13	.481
Treatment (T)	2, 2	46.15	.021
Year (Y)	1, 0.08	.023	.907
U*T	2, 1	1.08	.562
U*Y	1, 1	1.18	.473
T*Y	2, 1	0.13	.891

TABLE 3: Mean (± 1 SD) tree size and fire damage characteristics of live and dead slash pine trees. The *P*-value shows results of Mann-Whitney *U*-tests between live and dead trees after one year of prescribed fire in seven plots burned between 1998 and 2000.

	Live (<i>n</i> = 2,870)	Dead (<i>n</i> = 680)	<i>P</i> -value
DBH (cm)	12.5 \pm 5.8	10.6 \pm 5.6	<.001
Char height (m)	1.80 \pm 1.38	3.35 \pm 1.73	<.001
Crown scorch (%)	45.2 \pm 39.7	95.5 \pm 17.0	<.001

period 1998–2008, overall pine mortality ranged between 8.1% in 1999-S-C plot and 97.3% in 1999-O-W plot (Figure 2). In general, burned plots in each block had higher pine mortality than unburned plots in the same block, except in the 2000-S block, where the unburned control plot (2000-S-C) experienced high pine mortality following the 2005 storm surge event. In the other comparable, low elevation blocks (1998-S, 1999-O), plots that were burned and also impacted by storm surge had higher mortality than unburned and unimpacted burned plots.

In a forest that does not experience a catastrophic natural or anthropogenic disturbance, annual background tree mortality rate is assumed to be consistent over a given period. On Big Pine Key, three experimental plots, 1999-S-C, 1999-S-W, and 2000-O-C, which neither burned during the 10-year study period nor were impacted by storm surge in 2005, had a background rate of pine tree mortality of less than 1.5% per year.

3.1. Tree Mortality from Fire. One year after fire, plot level mean pine mortality did not differ between open and shrubby understory conditions ($P = .481$) and between 1998 and 1999 groups ($P = .907$), but there was significant effect ($P = .021$) of burn treatments (Table 2). However, the post hoc test (Unequal N; Tukey's HSD) failed to detect significant differences among three treatments (control, summer, and burn), probably due to low power. A subsequent analysis (One-way ANOVA) on pooled data revealed that mean

percent mortality (0.81%) in control plots ($n = 4$) was significantly lower (Tukey's HSD, $P = .02$) than the mean mortality in summer burn ($n = 4$; 25.3%) but did not differ ($P = .116$) from the mortality in winter burn ($n = 3$; 7.6%). Difference in one-year post-fire mean tree mortality between summer and winter burns was not statistically significant. In the three paired sets of summer and winter burns also, the difference between summer and winter burn plots was not significant (Wilcoxon Pair test; $P > .05$).

Before prescribed burn, plot level mean tree size (dbh) did not significantly differ between shrubby and open plots ($P = .169$), among three burn treatments ($P = .578$), control, summer, and winter burns, or between years ($P = .10$) in which plots were to be burned. After prescribed burn, however, fire-induced mortality of individual trees in burned plots was influenced by both tree size and immediate fire damage to trees. Over all burned plots, in which the trees were resurveyed after one year of fire, DBH, char height, and percent crown scorch differed between dead and live trees (Mann-Whitney *U* test: $P < .001$). Dead trees had smaller DBH and larger char height, and percent crown scorch than the live trees (Table 3). Individual plot-level tests (Mann-Whitney *U*-test) of significance for these three independent variables revealed that dead trees had larger percent crown scorch than live trees in all burned plots. DBH and char height also differed between live and dead trees in five of seven plots. However, in two plots, 1998-S-W and 1999-O-W, there were no significant differences in DBH and Char height between live and dead trees. Moreover, in four unburned plots, background tree mortality was uniform across all tree sizes.

Logistic regression results for tree mortality after one year of fire also revealed that the best predictive model included DBH, char height, and percent crown scorch as predictive variables (Table 4). The Likelihood Ratio (χ^2) statistic was highly significant ($P < .001$) and the area under the ROC curve (*C*) indicated 91.1% concordance between predicted probabilities and observed outcomes. Burn season, entered as a categorical variable in the model for three pairs of plots burned in summer and winter seasons, was not significant

TABLE 4: 1- and 7-year post-fire tree mortality models for slash pine after prescribed burns carried out between 1998 and 2001 in Big Pine Key, Florida.

Models	n	Variables			Coefficients				H-L (χ^2)	P	C
		X ₁	X ₂	X ₃	β_0	β_1	β_2	β_3			
1-year post fire											
1	3523	DBH	CH	CVS	-5.8901 (0.4041)	-0.1166 (0.0133)	0.5379 (0.0407)	0.0546 (0.0041)	292.2	.001	0.911
2	3530	DBH	CH	—	-1.2808 (0.1212)	-0.2105 (0.0129)	0.9168 (0.0396)		157.6	.001	0.845
3	3550	CVS	—	—	-7.2966 (0.4162)	0.0720 (0.0044)			444.8	.001	0.888
7-year post fire											
4	2227	DBH	CH	CVS	-1.1753 (0.1890)	-0.1109 (0.0117)	0.3974 (0.0363)	0.0171 (0.0018)	36.1	.001	0.768

n: number of trees observed.

Standard error of constant and independent variable coefficients are given in the parenthesis with each coefficient value.

DBH: Diameter at breast height (cm); CH: Char height (m); CVS: Percent crown scorch (%).

H-L (χ^2): Hosmer and Lemeshow chi-square statistic for assessing goodness of fit.

P: Statistical significance of Hosmer and Lemeshow (χ^2) test statistic.

C: Concordance value which is equivalent to area under the curve in the receiver operations characteristic (ROC) curve analysis for assessing the performance of the model.

in predicting the probability of tree mortality. Likewise, the contribution of interaction terms between DBH and char height, and DBH and percent crown scorch did not improve the model. Test of model performance with and without these interaction terms was almost identical, as they increased the concordance value only by 0.001. One year after burn, the probability of post-fire pine mortality decreases with increases in tree size and increases with increases in both char height and percent crown scorch (Table 4). Char height was the strongest predictor, as indicated by the highest odd ratio ($Exp\beta$) among all three predictors. A reduced model, including only char height and DBH as predictors of mortality, was also highly significant ($\chi^2 = 157.6; P \leq .001$) and had an acceptable level of concordance ($C = .845$). The response surface for probabilities of post-fire tree mortality as a function of DBH and char height revealed that the probability of tree mortality of similar DBH increased with increasing char height, and at the same fire intensity, the mortality risk decreased with increasing DBH (Figure 3). However, percent crown scorch always entered at the first step of the stepwise procedure, suggesting the importance of crown damage in predicting tree mortality. A simple logistic model with a single independent variable, percent crown scorch, was also significant ($\chi^2 = 444.8; P < .001$) and had an acceptable level of concordance ($C = 0.888$). Probability of tree mortality increased exponentially when trees had >80% of crown scorch (Figure 4).

In the four burned plots in which post-fire tree status was recorded for three consecutive years after fire, tree mortality significantly differed (One-way ANOVA; $F_{2,9} = 23.2; P < .01$) among years. There was over 15% tree mortality in the first year and an additional 1.53% and 0.87% in the second and third years, respectively (Figure 5). The fire-induced tree mortality was not significantly different (Tukey's HSD; $P = .973$) between second and third years after fire. Moreover,

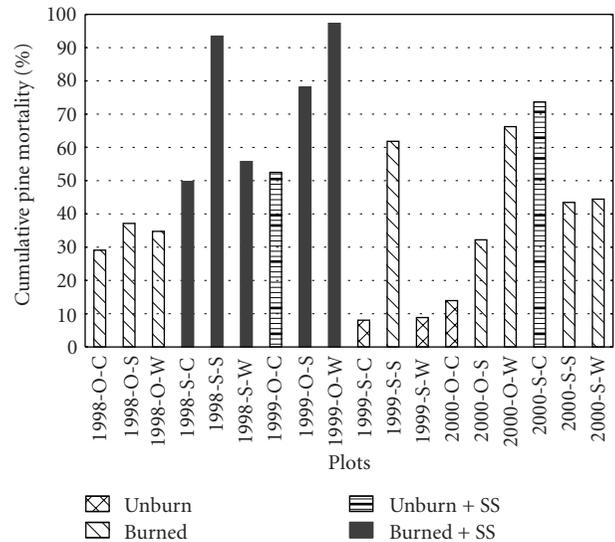


FIGURE 2: Total pine tree mortality in the 18 experimental plots recorded over 8–10 years (8 years in 2000-S and 2000-O blocks, 9 years in 1999-S and 1999-O blocks, and 10 years in 1998-S and 1998-O blocks). Based on fire and storm-surge impacts, plots were in one of four groups: (i) unburned, (ii) burned, (iii) unburned+SS, and (iv) burned+SS. Burned referred to both prescribed burns (1998 and 2001) and nontargeted burns (2004). SS: Impacted by storm-surge caused by Hurricane Wilma in 2005.

there was no significant difference (K-W Test; $n = 343, P = .251$) in mean rank DBH between the trees killed in the 1st year and the trees killed in second or third year, suggesting that most of the large slash pine trees did not suffer mortality from fire. Three years after fire in these plots, the mean (\pm SD) DBH of the dead trees (11.4 ± 6.6 cm) was smaller than live trees (12.8 ± 5.7 cm).

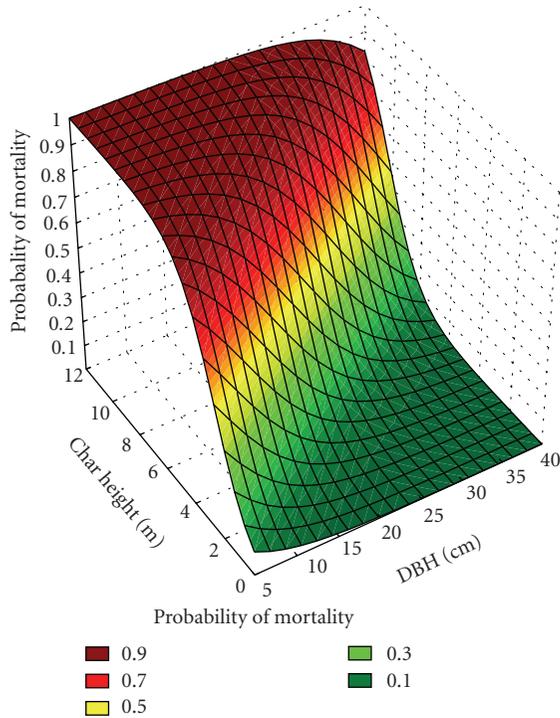


FIGURE 3: Response surface for logistic regression model for probability of 1-year post-fire tree mortality (Model 2) as a function of DBH and char height for slash pine (*Pinus elliottii* var. *densa*) after the experimental prescribed fires (1998–2000) in Big Pine Key, Florida. The number of live and dead trees used to develop the model was 2,849 and 681, respectively.

In the two blocks burned in 2001 (2000-O and 2000-S), the status (live/dead) of trees was recorded only after 7-years. These two blocks differed in understory conditions and time since last fire. However, plot-level mean percent mortality did not differ between 2000-O (49.2%) and 2000-S (44.0%) blocks. The best predictive model ($\chi^2 = 36.1$; $P \leq .001$) for predicting 7 year post-fire tree mortality also included DBH, char height, and percent crown scorch as predictors (Table 4). However, the model had relatively low concordance ($C = 0.768$), suggesting that the predictive ability of tree size and immediate fire damage to the stem and crown declined over time.

3.2. Tree Mortality from Storm Surge. Five burned and two unburned plots located in low elevation (<1 m) areas were severely impacted by storm surge (Table 1). Cumulative pine tree mortality over 8–10 years was higher in storm surge-impacted burned and unburned plots than in unimpacted burned and unburned plots, respectively. A negative exponential model was significant ($n = 13$; $r^2 = 0.29$; $P < .05$), suggesting that tree mortality in storm-surge impacted burned plots was relatively high (Figure 6). In unburned plots, however, a statistically significant negative correlation ($n = 5$; $r^2 = 0.92$; $P < .001$) between elevation and pine tree mortality suggested that the impact of storm surge was influenced by elevation. Mean ground elevation in the

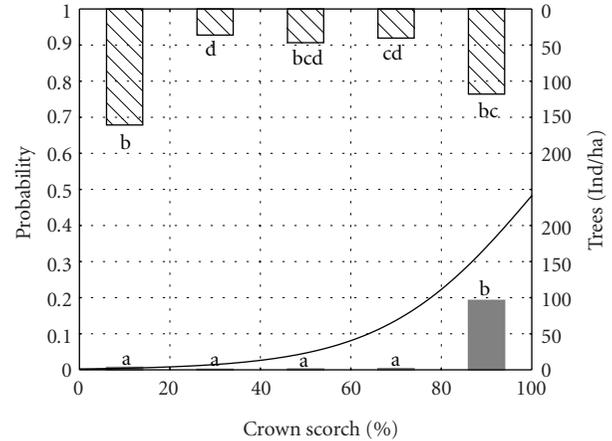


FIGURE 4: 1-year post-fire tree mortality probabilities predicted using logistic regression model as a function of percent crown scorch (Model-3) for slash pine (*Pinus elliottii* var. *densa*) after the experimental prescribed fires (1998–2000) in Big Pine Key, Florida. The number of live and dead trees used to develop the model was 2,870 and 680, respectively. Upright and hanging bars in the figure are the mean number of dead and live trees, respectively, in five crown scorch categories averaged over seven burned plots. The right Y-axis is scaled accordingly to represent the number of both dead and live trees. Different letters above/below the bar indicate significant differences in mean number of trees among percent crown scorch categories in burned plots ($n = 7$) (Kruskal-Wallis H -test) separately for live and dead trees, and between live and dead categories (Mann-Whitney U -test) within each scorch category.

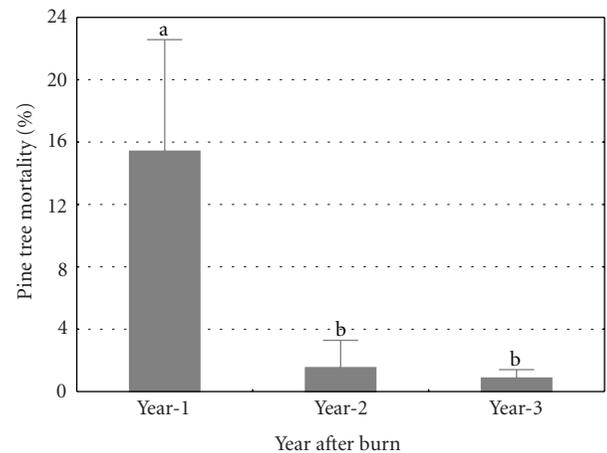


FIGURE 5: Mean (± 1 Std. error) post-fire pine tree mortality percent in three consecutive years in experimental plots ($n = 4$) burned in 1998 in Big Pine Key. The different letters above the bars indicate significant differences in mortality between years.

impacted unburned plots (0.793 m) was significantly (One-way ANOVA; $F_{1,3} = 114$; $P = .002$) lower than in the unimpacted unburned plots (1.371 m).

Storm surge tree mortality was size dependent. In unimpacted burned plots, the likelihood of tree mortality decreased with increasing DBH, whereas in surge-impacted burned plots, no such relationship was observed, suggesting

that more trees in larger sized classes were killed by storm surge. Two unburned plots that were impacted by storm surge showed mixed results. While together they did not show a significant relationship between tree mortality and DBH, one of them, 2000-S-C, which was close to the coast and was severely impacted, had tree mortality positively related with tree size.

3.3. Change in Stand Structure. Over a decade, stand structure was substantially influenced by fire and the storm surge event. Among four groups: (i) no burn and no storm surge (Unburn), (ii) burned but no storm surge (Burned), (iii) no burn but storm surge (Unburn-SS), and (iv) burned and storm surge (Burned-SS), the mean change in both basal area and stand diameter differed significantly (One-way ANOVA; $F_{3,14} = 25.6$; $P < .001$). In a majority of sites (15 of 18 experimental plots), there was a significant reduction in total basal area. Only three plots, 1999-S-C, 1999-S-W, and 2000-O-C plots, which were neither burned nor influenced by storm surge showed an increase in total basal area (Figure 7). The plots that were burned and severely impacted by storm surge had the greatest reduction in basal area. In these plots, mean stand diameter also decreased over the period (Figure 8). In contrast, mean stand diameter increased in the unflooded burned plots, as fire-induced tree mortality in those plots was mostly in small size classes. Size-selective mortality caused by fire and storm surge also affected the overall size distribution of pine trees in Big Pine Key pinelands. At both the beginning and end of the decade-long study, forest structure was characterized by inverse-J diameter distributions (Figure 9). However, the distribution curves differed significantly ($F_{3,11} = 23.7$; $P = .0004$) between the two surveys. The distribution curve for 2008 survey is flatter than the first survey, suggesting a decrease in the number of trees, particularly in smaller size classes. The reduction in number of trees was not uniform in all size classes, resulting in an obvious shift in the proportion of trees among size classes. The proportion of trees in small (5–10) and large (>20 cm) size classes decreased from 46.7% and 9.2% to 40.8% and 7.9%, respectively, but increased from 44.2% to 51.4% in intermediate-sized (10–20 cm) trees.

4. Discussion

South Florida slash pine forest requires fire for its maintenance. Fire influences stand structure by killing vulnerable pine trees, promoting pine regeneration, regulating establishment and growth of hardwoods, and directing herb layer dynamics. In addition to fire, insect infestations and hurricanes are other disturbances that kill trees in southern Florida pine forests. The frequency and strength of these disturbances determine stand composition, particularly when their influences on tree mortality vary across different size classes.

Variation in fire intensity across the landscape depends on microtopography, prevailing weather conditions (e.g., wind speed and humidity), and fuel heterogeneity, and has a direct bearing on post-fire tree mortality. In the present

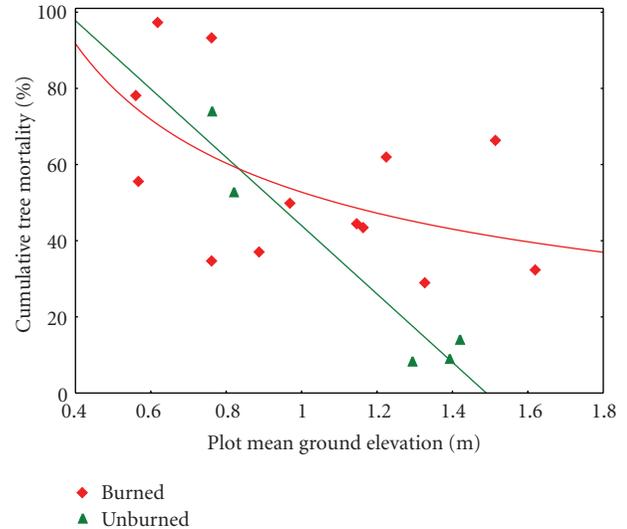


FIGURE 6: Cumulative pine tree mortality in relation to mean ground elevation in 18 stands. Two separate models were fit for burned and unburned plots. (i) Burned plots ($n = 13$): $T_m = 52.7 * Elev^{-0.60}$. (ii) Unburned plots ($n = 5$): $T_m = 133.7 - 89.7 * Elev$. T_m = cumulative tree mortality.

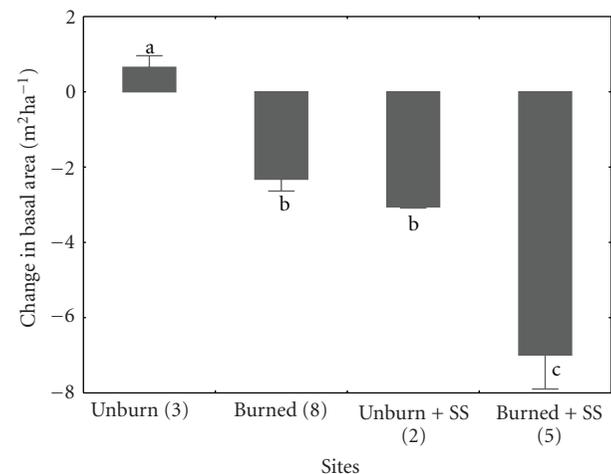


FIGURE 7: Change in mean (± 1 SE) total basal area ($m^2 ha^{-1}$) in 4 groups of sites. Four groups were (i) No burn and no storm surge, (ii) Burned but no storm surge, (iii) No burn but storm surge, and (iv) Burned and storm surge. SS: Storm surge. Number of plots in each group is given in parenthesis. Different letters above/below the bar indicate significant differences (ANOVA; $P < .05$) between groups.

study, variation in fire-induced pine mortality among stands may be attributed to differences in stand age and fuel loads that influenced fire intensity. Previous work in Florida Keys pine forests showed that fuel loads, particularly surface fuels and mid-canopy palms, were positively related to fire intensity, signified by char height [26]. Char height of individual trees was an important predictor of post-fire tree mortality in the present study as well. In contrast, surface fuel consumption, which is also an indicator of fire severity,

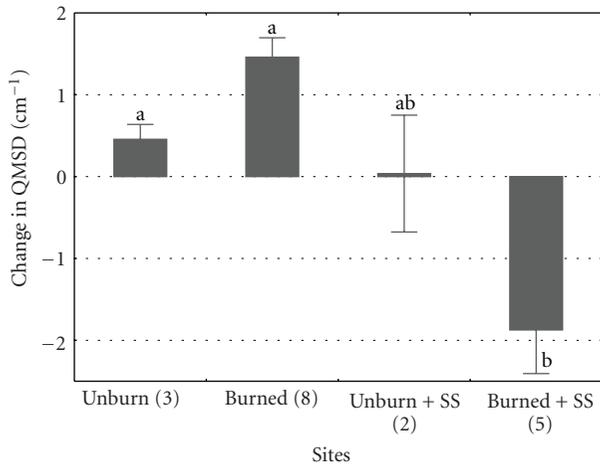


FIGURE 8: Change in mean (± 1 SE) quadratic mean stand diameter (cm) in 4 groups of sites. Four groups were (i) No burn and no storm surge, (ii) Burned but no storm surge, (iii) No burn but storm surge, and (iv) Burned and storm surge. SS: Storm surge. Number of plots in each group is given in parenthesis. Different letters above/below the bar indicate significant differences (ANOVA: $P < .05$) between groups.

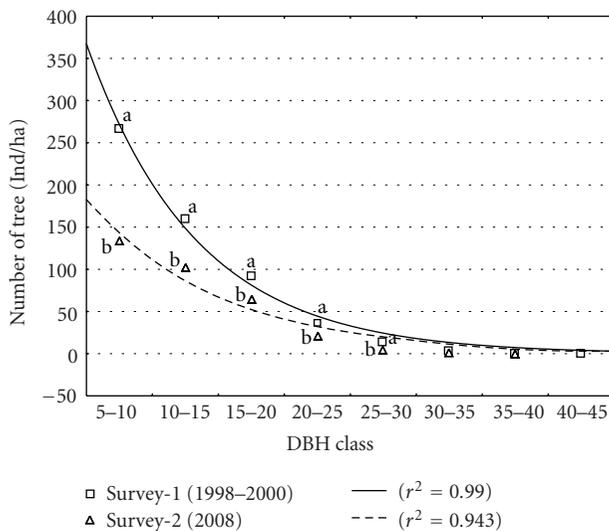


FIGURE 9: Tree size distribution in experimental plots after two surveys, 1998–2000 and 2008. The models were fitted to the mean number of trees in each DBH class averaged over all 18 plots. The fitted models are (i) $T = 116.6 * \exp^{-0.119 * X_1}$, (ii) $T = 92.9 * \exp^{-0.101 * X_1}$. T: Number of trees in a given dbh class. X_1 : mean DBH. Different letters above/below the — indicate significant differences (ANOVA: $df = 1,34$; $P < .05$) in mean number of trees within each DBH class between two surveys.

was not significantly related to plot level mean percent tree mortality.

Even though understory fuel loads are generally higher in shrubby than open plots, we did not find significant effects of understory conditions on pine tree mortality. While it could partly be attributed to the limited power of statistical analysis caused by inadequate replicates, the

results are in concurrence with earlier findings in Florida Keys pinelands. In these plots, fine scale fire intensity was negatively correlated with the quantity of hardwood shrubs mainly because these fuels were associated with moist environments, and therefore resistance to fire [26], which might have protected fine roots from burning. However, contrary to our expectation, season, which earlier had shown strong effects on fine scale fire intensity [26], was not significant in predicting stand level 1-year post-fire pine mortality. Our findings differed from the results of Menges and Deyrup [10], who found higher tree mortality in fall (October-December) burns than in fires in other seasons. In our study, three sites burned in December were considered winter burns, and mortality was not consistently different in these fires than in early summer burns. In other conifer forests, differences in tree mortality between burn seasons have been attributed to differences in fire intensity [33] or to physiological activity and carbohydrate storage [34]. Though South Florida slash pine trees are physiologically active in winter, radial growth slows or ceases early in the fall (Ross unpublished data), indicating differences in physiological activity between the two seasons. Moreover, effect of season may have mediated through char height and/or percent crown scorch, the indicators of fire intensity and severity, respectively. A study on fuel consumption has also shown that the direct effect of season on the consumption was low, and most of its effect was through char height [26]. The small number of fires, three winter and three summer burns, in our study might have also contributed to the lack of a statistically significant seasonal effect. But, the results do suggest that regardless of burn season, trees of similar size and identical stem and crown damage bear the same probability of mortality in the Florida Keys pine forests.

The likelihood that pine trees were killed by fire was strongly influenced by tree size (DBH). The greater fire resistance of trees with increasing diameter is attributed to increased insulation caused by thicker bark in large trees [14, 35]. Our findings again differed from those of Menges and Deyrup [10], who found that DBH was a weak predictor of post-fire tree mortality, and inferred that DBH and bark thickness may be poorly related in their study area. Mean DBHs in Florida Keys were smaller than in the study of Menges and Deyrup, and that holds true even for long-unburned (>30 years) plots. In Lower Florida Keys, since likelihood of fire-induced tree mortality was higher in small dbh classes, the long-unburned plots also experienced as high percent mortality as did the short unburned (≤ 14 years) plots, both burned in the same season in the year. The reason could be that the fires in this study were of relatively low to medium intensity. The inverse relationship that we found between DBH and tree mortality may also be explained by covariation with tree height. As DBH increases, so does tree height, increasing the distance between meristematic tissues in branches and the flame front [36]. This may explain why DBH was also negatively related to percent crown scorch in the present study. Our observation of a decrease in post-fire mortality with increasing DBH in South Florida slash pine was consistent with findings from other pine species [18, 37–41]. In contrast, our results for delayed mortality

differed from studies of wildfires, where delayed mortality often occurs in larger DBH classes, possibly as a result of root damage [11, 42]. In our low intensity prescribed fires, delayed mortality, particularly two and three years after fire, was very low. Approximately 94% of fire-induced slash pine mortality occurred within one year, a pattern also observed by others [9, 10]. Processes that lead to delayed post-fire mortality, for example, pathogenic attacks and increased water stress triggered by root damage, particularly in sites where fire is reintroduced after a long period of fire suppression [43], might not have crossed critical thresholds after the prescribed fires we studied.

Immediate crown and stem injuries and fire resistance mechanisms are important determinants of fire-induced tree mortality. Although researchers have emphasized measures of both foliage and stem damage as important predictors of tree mortality [7, 18], percent crown scorch has frequently been found to be the single best predictor of tree mortality [17]. In the present study, a model with percent crown scorch as the sole independent variable was highly significant (Table 4). Trees that died suffered a large proportion (>80%) of crown scorch. Nevertheless, even trees with >80% crown scorch had >50% chance of survival, suggesting that slash pine trees have the ability to survive severe crown scorch. The fate of trees with high levels of crown scorch depends on how well the buds are protected in tree crowns. In this study, buds might have been killed by severe scorching of foliage. In most individuals, however, buds did not succumb, probably because buds in slash pine are shielded from lethal effects of fire by long needles. In many conifers, the lower portions of crowns are less efficient in photosynthesis [11], and therefore scorching of that portion may not significantly reduce photosynthesis. Instead, scorching of lower crowns may help the trees by reducing the transpiration to cope with increased water stress after fire. Hence, in the present study, trees with even a small portion of the top crown intact or inflicted with light scorch after fire easily recovered from injury.

Stem damage from fire primarily involves injury to the cambium, which is measured indirectly in terms of stem charring. The depth of stem char relates positively with the degree of cambial injury and depends on the residence time of fire. Maximum char height or relative char height (max char height in relation to tree height) is the representation of flame length or fire intensity. In our study, we did not measure tree height, but a model that included both char height and DBH was highly significant (Table 4). Nonetheless, the effects of these two variables were inversely related. The likelihood of tree mortality increased with increasing char height, but at the same char height, smaller trees were more likely to be killed (Figure 3). This suggests that mature slash pines are resistant to intense surface fire. Our finding that char height and DBH together predict post-fire tree mortality well is consistent with results of several other researchers [6, 17, 37, 39]. Nonetheless, a full model that included tree size, and measures of both stem and foliage damages as predictors, was the best (ROC = 0.911) in predicting post-fire tree mortality in Florida Keys pine forests, probably due to added predictive ability of percent crown scorch in small DBH classes.

Insect infestations and hurricane-associated events are known to cause additional pine mortality in post-fire years. In slash pine forests, infestation by *Ips* (pine engraver beetles) has been found to contribute to post-fire tree mortality [9, 10]. We did not study pest infestations after prescribed fire, but elevated post-fire tree mortality was observed in storm-surge impacted sites. Slash pines are considered resistant to wind damage [12], but they are sensitive to salinity stress, and their tolerance to salinity stress may vary with growth stage. In general, salt tolerance of nonhalophytic woody plants increases progressively with increasing age [44]. In our study, however, storm surge-caused pine mortality centered in large DBH classes suggested that large trees were particularly susceptible to salinity. Storm surge is a pulse disturbance [13]. After the surge, storm water gradually receded, but it is likely that ground water in the freshwater lens was affected for a long period thereafter. Driven mainly by long tap roots and the necessity of fulfilling a high transpiration requirement, large trees accessing the deeper ground water might have suffered from both water and salinity stress for an extended period—longer than small-sized trees.

In burned plots, the loss of small trees exclusively would cause a shift in the size structure of trees from a negative exponential (inverted J) distribution towards the unimodal size distribution. In our study, tree distribution pattern also exhibited a gradual shift (Figure 9), but the size distribution still retained the shape originally observed prior to the burns. In plots that experienced both fire and storm surge, however, a drastic change in stand structure occurred, resulting in a decrease in mean stand diameter. In contrast, plots that were burned but not impacted by the storm surge exhibited an increase in mean stand diameter. Such changes in mean stand diameter resulted from a contrast in size-selective mortality initiated by fire and by storm surge. The effects of pulse events like storm surge on post-fire pine tree mortality could be additive, resulting from additional damage to morphological structures and physiological characteristics, or synergistic, particularly when fire modifies the susceptibility of trees to subsequent stresses. A continuous monitoring program designed to assess the interacting effects of prescribed fire and other disturbances would help to decouple their effects on tree mortality and stand structure.

5. Conclusions

Our results indicate that tree size (DBH) and fire characteristics, expressed in terms of stem and crown damage (char height and percent crown scorch), are key determinants of fire-induced slash pine mortality. The study supports other research findings that large pine trees are resistant to damage from surface fire, which may be of practical importance for the use of prescribed fire to reduce the mid-story cover while retaining the large trees. In pine forests, mature large trees are the source of cones necessary for continuing regeneration, and needles, a major component of the surface fuels necessary to conduct prescribed fire. This study did not directly assess secondary influences on slash pine mortality in subsequent years after fire, though

most of the mortality observed a year after fire reveals that the secondary agents, for example, post-fire insect attacks were not important. This study included tree mortality in response to hurricane-associated storm surge. Our study adapted indirect analysis for evaluating the size-selective mortality pattern caused by fire and storm surge. However, their effects might have been confounded in our analysis, as we did not know the immediate prehurricane status of the trees or have real-time measurements of the depth or duration of salt water inundation. Some sites which we considered to be unimpacted by the storm surge might have been affected to some extent but was not noticeable during our study. Moreover, this study did not address synergistic effects of fire and storm surge, that is, whether earlier fires enhanced, inhibited, or did not modify the effects of subsequent storm surge on pine mortality. Nevertheless, this study was the first effort of its kind towards developing comprehensive, predictive models for fire-induced slash pine mortality in the Florida Keys. A cautious approach will need to be taken to generalize these models to other South Florida pine forests, as the topography, microclimate, and stand structure of pine forests in the Keys are different from those on the mainland, and fires in this study were only low to medium intensity. In addition, the statistical power of analysis was limited due to inadequate replicates in the experimental design, and the problems in carrying out the originally intended experimental burns, resulting in missing values for some treatments. Nevertheless, our findings of size-selective mortality caused by fire and storm surge have practical importance for the use of prescribed fire as a management tool in the future, when increased frequency and intensity of tropical storms combined with sea level rise may threaten the continued existence of Florida Keys pine forests.

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Research Article

Effects of Soil Temperature during Fire on Seed Survival in Florida Sand Pine Scrub

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Soil temperatures recorded with thermocouples and temperature-sensitive paints were quantified during Florida sand pine scrub prescribed fires at Ocala National Forest and Archbold Biological Station in May 1993. Thermocouples and glass petri dishes painted with temperature-sensitive paints and containing seeds of *Eriogonum floridanum* were placed at 0 cm and 2 cm depth, and in vegetated and open microsites. Maximum temperatures were higher and peak temperature durations shorter at 0 cm than at 2 cm depth. Temperatures did not differ between microsites during the Ocala fire, but were higher in open microsites during the Archbold fire, probably due to combustion of well-aerated litter. Maximum temperatures of petri dishes were lower than those of adjacent thermocouples due to time required to melt paints. All *Eriogonum* seeds recovered from petri dishes after the Archbold fire failed to germinate. Germination was quantified for *Eriogonum floridanum* and *Garberia heterophylla* seeds heated to 100°C and 60°C under laboratory conditions. Seeds failed to germinate at 100°C, while germination was similar to controls for seeds exposed to 60°C. Results from this study suggest that small-scale spatial variation temperatures at the soil surface during fires is essential for seed survival and subsequent post-fire recruitment.

1. Introduction

Seeds that survive fires in the soil contribute to postfire recruitment to varying degrees among fire-influenced communities [1, 2]. The capacity of species in these communities to establish seedlings after fire from seeds in a soil seed bank should be influenced by several factors including (1) magnitude and duration of high or elevated temperatures during fire at soil depths and in microsites where viable seeds are located, and (2) seed germination responses to elevated temperatures.

A large volume of field research and laboratory research has been conducted on temperatures reached during natural fires [3–24], and on seed germination responses to elevated temperatures [4, 6, 9, 13, 16, 25–35]. These two lines of research usually have been mutually exclusive, and have concentrated largely on Mediterranean-climate ecosystems and their species.

Researchers generally have used either temperature-sensitive paints or thermocouples to quantify soil temperatures reached during fires. Although recorded temperatures

have varied among ecosystems and with differences in burning conditions, several patterns have been consistent across studies. Maximum soil temperatures generally decrease as depth in the soil increases, but durations of elevated temperatures increase [3, 6, 9, 12, 13, 16–19]. Soil temperatures reached during fires also tend to vary with microsites, with temperatures in open microsites lower than temperatures in microsites with higher fuel accumulations [12, 15].

In laboratory germination studies, plant species from several ecosystems have demonstrated positive germination responses after being exposed to temperatures typically reached during fires. Taxa or functional groups with this response include legumes in the southeastern United States, California, and Australia [9, 13, 17, 25, 28, 29, 32]; obligately seeding shrubs in California chaparral and in southern France [25, 27, 30, 34], and annual species in California chaparral [25, 29]. Other species, however, have responded to elevated temperatures with decreased or no germination. Some functional groups that have demonstrated this response are herbaceous perennials [29] and other species that do not establish seedlings after fires [30].

This study documents soil temperatures during fires, and seed germination responses to elevated temperatures in sand pine scrub, a community occurring primarily in Florida on well-drained sandy soils of former Miocene to Pleistocene dunes. Sand pine scrub is dominated by woody shrubs including several oak species (*Quercus* spp.), rusty lyonia (*Lyonia ferruginea*), Florida rosemary (*Ceratiola ericoides*), and occasionally scrub hickory (*Carya floridana*); often an overstory of sand pine (*Pinus clausa*) is present [36]. Small-statured (<2 m tall) perennial species are usually sparse, and annual species are virtually absent.

Natural fires are lightning-initiated, and usually occur during the wet growing season during the months of April through July. Although frequency of lightning strikes is extremely high in Florida [37], sand pine scrub fires occur infrequently, approximately every 10 to 100 years. A combination of fuel characteristics and season of burning influences fire frequency—ground litter and other fine fuels are often sparse, most living vegetation is neither highly flammable nor easily ignited, and fuels are rarely dry during the lightning season. Consequently, fires tend to occur under extreme conditions of high fuel buildup, dry weather, or high winds, and often are intense [36].

As in other fire-influenced communities, plant species in sand pine scrub vary in their responses to fire. Most woody shrub species resprout and do not establish seedlings immediately following fires. In contrast, seedling establishment occurs primarily or exclusively after fire for some plant species that are killed by fire (e.g., *Pinus clausa*, *Ceratiola ericoides*, *Dicerandra frutescens*, *Calamintha ashei* [36, 38–40]), as well as for some small-statured species that resprout following fire (e.g., *Eriogonum floridanum*, *Garberia heterophylla* [41, 42]).

Although heat- and smoke-induced germination have not been documented in sand pine scrub as in some other fire-influenced communities [33, 43], seeds of some sand pine scrub species germinate after surviving fire in a soil seed bank [39, 44]. In a recent study conducted at Archbold Biological Station, viable seeds were present in soil samples collected less than three months after fires, from 0–7 cm depth in the soil (Kohfeldt *personal communication*).

Temperatures reached during fires and germination responses to those temperatures are relatively unknown for sand pine scrub. Only one other study has measured temperatures at the soil surface during a sand pine scrub fire [24], and germination responses to high temperatures of most species have not been studied. Additional information on soil temperatures during fires and germination responses after fires should further elucidate the plant community response to fire in sand pine scrub, and could potentially increase effectiveness of rare species conservation through use of fire.

The first of two objectives of this study was to measure soil temperatures at different depths and in different microsites during fires in sand pine scrub. Lower peak soil temperatures and longer temperature durations were expected with increasing depth in the soil, as documented in other studies. Spatial patterns of combustible fuel in sand pine scrub are defined primarily by a widespread matrix of

woody shrub vegetation underlain by moderate amounts of ground litter, interspersed with canopy openings with little or no litter. In this study, soil temperatures in microsites under vegetation (e.g., shrubs) were expected to be higher than those in openings.

The second objective of this study was to quantify germination responses of two small-statured perennial species after exposing the seeds to temperatures typically reached during sand pine scrub fires. Small-statured perennial species were chosen for study because much of the postfire seedling establishment response in sand pine scrub is attributable to species from this general group [42]. The two study species (hereafter referred to by their generic names), *Eriogonum floridanum* (Polygonaceae; Reveal 1981) and *Garberia heterophylla* (Asteraceae), were chosen because (1) both species establish seedlings primarily after fire; (2) although both species are relatively common locally, they are endemic to Florida, occur primarily in sand pine scrub, and are subjects of conservation concern (*Eriogonum floridanum* is federally listed as threatened).

Eriogonum is an herbaceous perennial and *Garberia* a woody shrub; both species have strong postfire resprouting and flowering responses [42]. As documented for other herbaceous perennials, germination was expected to decrease for *Eriogonum* seeds after exposure to an elevated temperature at any depth in the soil. Seeds of resprouting shrub species have exhibited a variety of responses to high temperatures and to high temperatures in combination with smoke [45, 46], making the *Garberia* germination response in this study potentially less predictable. Consequently, in this study *Garberia* seed germination was expected to decrease, remain unchanged, or possibly increase after exposure to an elevated temperature at any depth in the soil.

2. Materials and Methods

2.1. Field Experiments. Study areas were sand pine scrub sites at Ocala National Forest in Marion County, Florida (29° 08', 81° 45') and Archbold Biological Station in Highlands County, Florida (27° 15', 81° 15'). The Ocala site and Archbold site last burned in 1935 and 1927, respectively. Both sites had a dense shrub layer consisting primarily of several species of oaks (*Quercus* spp.). Overstories differed in the two sites, however; sand pine was the only species in the overstory at Ocala, while at Archbold sand pines were interspersed with south Florida slash pines (*Pinus elliottii* var. *densa*).

Controlled burns were conducted at the Ocala and Archbold sites on May 10, 1993 and May 25, 1993, respectively. Before each fire, a datalogger (21X Micrologger, Campbell Scientific, Inc.) connected to 16 copper-constantan, 0.51 mm diameter thermocouples via insulated leads was buried in the site to be burned. The thermocouple leads were 1.5–4 m long, and were buried approximately 2 cm deep; the datalogger was placed in a fiberglass case and buried approximately 50 cm deep.

Each thermocouple was placed either at the soil surface or at 2 cm depth, and either in an open microsite or under vegetation. The 2 cm depth was chosen because seeds typically are

found at this depth [47, Kohfeldt *personal communication*], yet were expected to be relatively insulated from high surface temperatures reached during a fire. Each depth-microsite combination was replicated four times through placement of individual thermocouples. Adjacent to each thermocouple, a glass petri dish containing 10 *Eriogonum* seeds was placed at the same soil depth and microsite. In each petri dish, *Eriogonum* seeds were placed on top of a layer of sand completely covering the bottom of the petri dish. Six petri dishes with *Eriogonum* seeds also were placed at a nearby control site that did not burn.

At Archbold the sides of each petri dish were painted with 19 temperature-sensitive paints (Tempilaq, Tempil Division, Big Three Industries, Inc.). Manufacturer-specified melting temperatures of paints ranged from 37.8°C to 815.6°C. In addition to petri dishes adjacent to thermocouples, petri dishes also were placed throughout the site so that each depth-microsite combination was replicated eight additional times.

During each fire, the datalogger recorded thermocouple temperatures every five seconds. Temperature recording occurred from 90 minutes before the fire until 90 minutes after the flame front went through at the Ocala site, and from 90 minutes before the fire to 60 minutes after the flame front went through at Archbold.

After each fire, the datalogger and all petri dishes were recovered. Intact seeds were extracted from soil in the petri dishes, and were classified as charred or noncharred. All noncharred seeds were placed on moist filter paper in clean petri dishes, and observed for germination for one month. Viability of non-germinated seeds was assayed with a tetrazolium test [48]. At Archbold, maximum temperature reached during the fire was quantified for each petri dish by determining which temperature-sensitive paints melted.

Data on thermocouple maximum temperatures and temperature durations were analyzed separately for the Archbold and Ocala fires. Analyses of variance were conducted on rank-transformed maximum thermocouple temperatures to detect differences due to depth in the soil and microsite [49]. Temperature duration was defined for each thermocouple as the length of time that 75% of the maximum thermocouple temperature was maintained or exceeded. Kolmogorov-Smirnov tests were used to compare median temperature durations between thermocouples placed at the soil surface and those placed at 2 cm depth [50].

Maximum temperatures during the Archbold fire of petri dishes placed at the soil surface and at 2 cm depth were compared using a chi-square test, and a *t*-test was used to compare maximum temperatures of petri dishes and adjacent thermocouples. Data from both fires on *Eriogonum* seeds recovered from petri dishes were combined to determine the immediate fire effect on the seeds. Numbers of petri dishes with charred *Eriogonum* seeds at the soil surface and at 2 cm depth were compared using a linear model analysis (Proc CATMOD in SAS) [51].

2.2. Laboratory Experiments. Seeds of *Eriogonum* and *Garberia* were observed for germination after being exposed to a

TABLE 1: Weather conditions and fire characteristics for Florida sand pine scrub fires at Ocala National Forest and Archbold Biological Station during May 1993.

	Ocala	Archbold
Date of fire	May 10, 1993	May 25, 1993
Time of measurements	1150–1205	1259–1305
Air temperature	28°C	29°C
Relative humidity	46%	52%
Wind speed	0.89 m/s	0.54 m/s
Wind direction	SE	SE
Flame length	3–5 m	6–15 m
Rate of spread	12 m/min	12 m/min

control temperature (25°C) and elevated temperatures and durations representative of those sustained at the soil surface and at 2 cm depth during the experimental fires. Elevated temperatures used were 100°C (commonly sustained at the soil surface for 4–6 minutes, but usually not reached at 2 cm depth) and 60°C (commonly sustained at 2 cm depth for 4 to >91 minutes).

Experiments were conducted from December 8–17, 1993, and from December 14, 1995 to January 7, 1996 for *Eriogonum* and *Garberia* seeds, respectively. Separate experiments, using 160 seeds in each, were conducted for each species and for each elevated temperature. Half of the seeds were placed in a drying oven and exposed to the elevated temperature for five minutes or 30 minutes in the experiments using 100°C and 60°C, respectively. The remaining seeds in each experiment were kept at room temperature. Then seeds were placed on moist filter paper in petri dishes and observed for germination. Seed germination responses were compared between 25°C and 100°C treatments using Fisher exact tests [48]; *t*-tests were used to compare germination responses between 25°C and 60°C treatments.

To determine times required to melt temperature-sensitive paints on petri dishes, trials were conducted in which a petri dish painted with a temperature-sensitive paint was placed in a muffle furnace (Thermolyne, Sybron Corporation) with the door open, and timed until the paint melted. A minimum of five trials was conducted for each of 13 paints, with manufacturer-specified melting temperatures ranging from 37.8°C to 704.4°C. After five trials, if the coefficient of variation was >0.25, additional trials were conducted. Up to 14 trials were conducted to record times required to melt paints with melting temperatures between 50°C and 125°C, the temperature range likely relevant to seed survival versus mortality during fires.

3. Results

3.1. Field Experiments. Weather conditions and fire characteristics were similar for the two fires, but flame lengths in the Archbold fire were greater than those in the Ocala fire (Table 1). Although soil temperatures quantified with thermocouples and their temporal patterns varied widely

TABLE 2: ANOVA of the effects of soil depth and microsite on maximum temperatures recorded during a controlled burn in sand pine scrub at Ocala National Forest, Florida. Temperatures were recorded with copper-constantan thermocouples placed at the soil surface and at 2 cm depth, and in open and vegetated microsities. Data were rank-transformed prior to the ANOVA.

Source	SS	df	F ratio	P
Depth	182.3	1	19.5	$P < .005$
Microsite	25.0	1	2.7	$P > .10$
Depth \times microsite	20.3	1	2.2	$P > .10$
Error	112.5	12		

TABLE 3: ANOVA of the effects of soil depth and microsite on maximum temperatures recorded during a controlled burn in sand pine scrub at Archbold Biological Station, Florida. Temperatures were recorded with copper-constantan thermocouples placed at the soil surface and at 2 cm depth, and in open and vegetated microsities. Data were rank-transformed prior to the ANOVA.

Source	SS	df	F ratio	P
Depth	121.0	1	11.2	$.005 < P < .01$
Microsite	64.0	1	5.9	$.025 < P < .05$
Depth \times microsite	25.0	1	2.3	$P > .10$
Error	130.0	12		

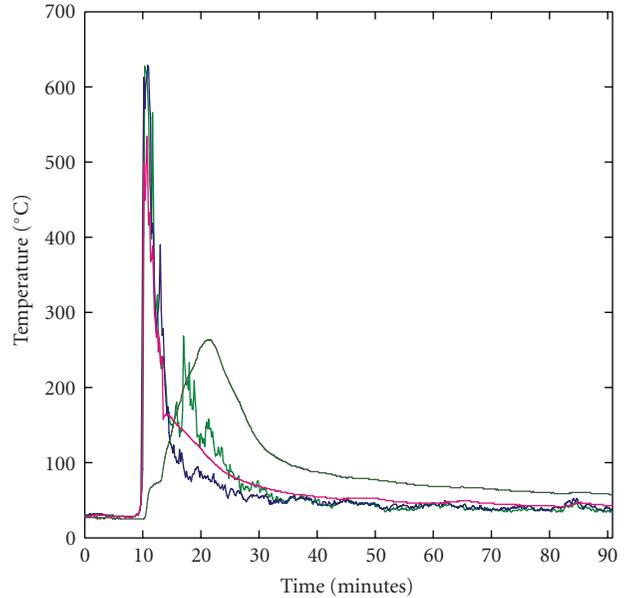
TABLE 4: Temperature durations of copper-constantan thermocouples placed at the soil surface and at 2 cm depth in the soil. Temperatures were quantified during prescribed fires conducted during May 1993 at Ocala National Forest and Archbold Biological Station, Florida. Temperature duration was defined as length of time that ($0.75 \times$ maximum thermocouple temperature) was maintained or exceeded.

Site	Depth in soil (cm) ($n = 4$)	Temperature duration (s) (median (range))
Archbold	0	105 (20–>3260)
	2	2020 (160–>3250) ^(a)
Ocala	0	80 (65–1555)
	2	2918 (675–>4625) ^(a)

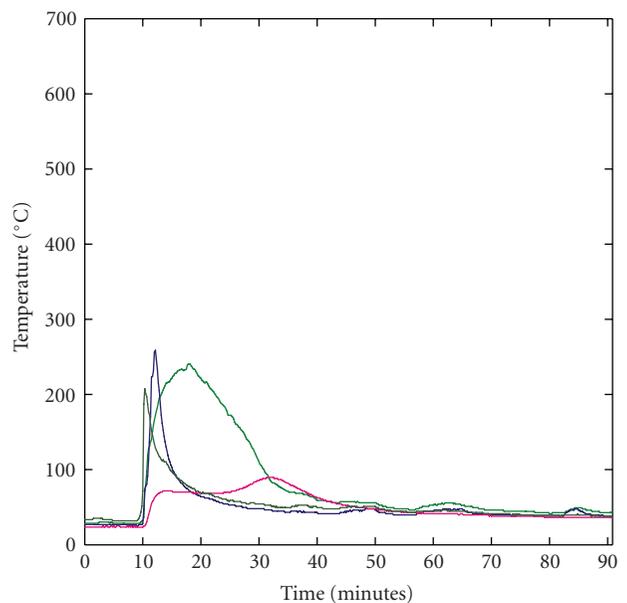
^(a)Separate Kolmogorov-Smirnov tests were conducted for Archbold ($P = .05$) and Ocala ($P < .01$) sites to test for difference in temperature durations with depth in soil.

both within and between microsite treatment combinations during both fires (Figures 1, 2, 3, and 4), temperatures were higher at the soil surface than at 2 cm depth as expected (Ocala: $F_{1,12} = 19.5$, $P < .005$; Archbold: $F_{1,12} = 11.2$, $.005 < P < .01$), (Tables 2 and 3). Temperatures at the soil surface reached maxima of 628.8°C and 621.7°C during the Ocala and Archbold fires, respectively; in contrast, maximum temperatures at 2 cm depth were less than half those at the surface (Figures 1–4). The higher temperatures at the soil surface also had shorter durations than temperatures at 2 cm depth (Kolmogorov-Smirnov test; Ocala: $P < .01$; Archbold: $P = .05$) (Table 4).

Temperatures in vegetated versus open microsities differed from predicted patterns, however. Although temperatures during the Ocala fire tended to be higher in vegetated



(a)

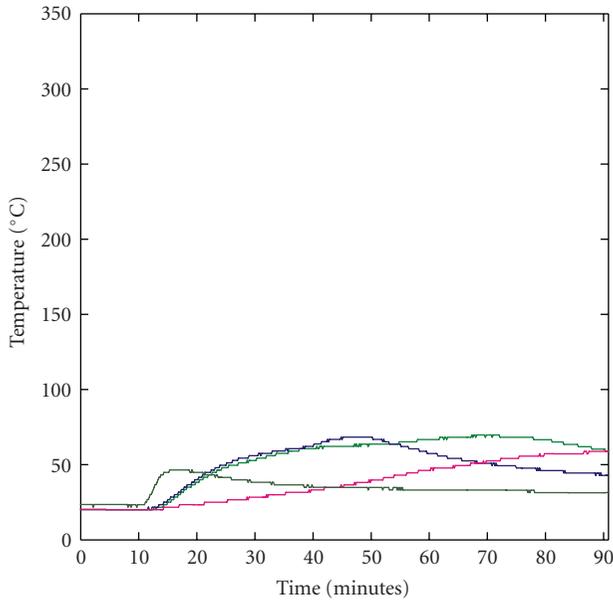


(b)

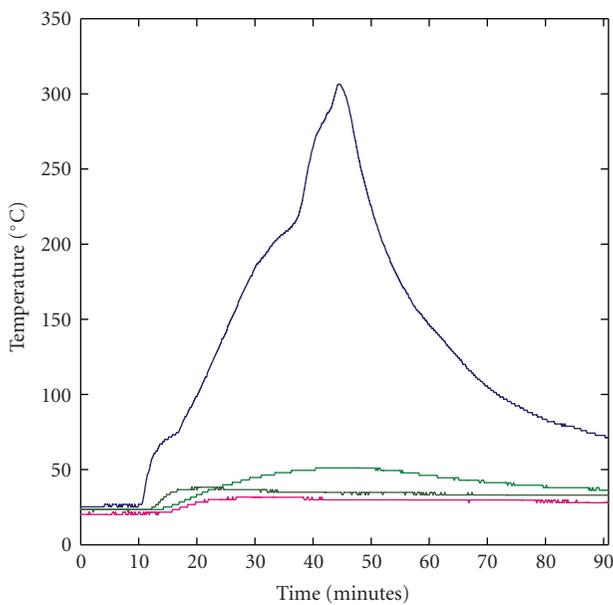
FIGURE 1: Soil temperatures at the soil surface during a prescribed sand pine scrub fire at Ocala National Forest, Florida on May 10, 1993. Temperatures were recorded with copper-constantan thermocouples placed in vegetated (a) and open (b) microsities. Each microsite location was replicated four times.

than in open microsities, a large range of temperatures within microsities resulted in no statistically significant difference in temperatures between microsities (Table 2). Temperatures during the Archbold fire were higher in open microsities than in vegetated microsities ($F_{1,12} = 5.9$, $.025 < P < .05$; Table 3), in contrast to the expected trend.

As with thermocouple-quantified temperatures, patterns of melted paints on petri dishes at the Archbold site showed



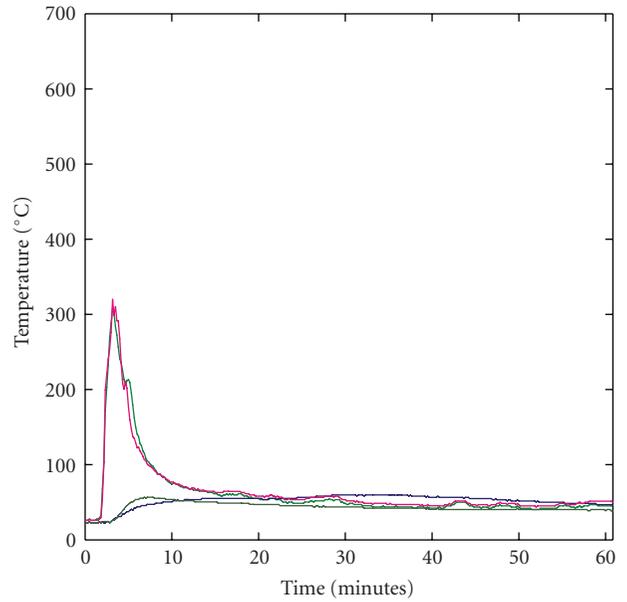
(a)



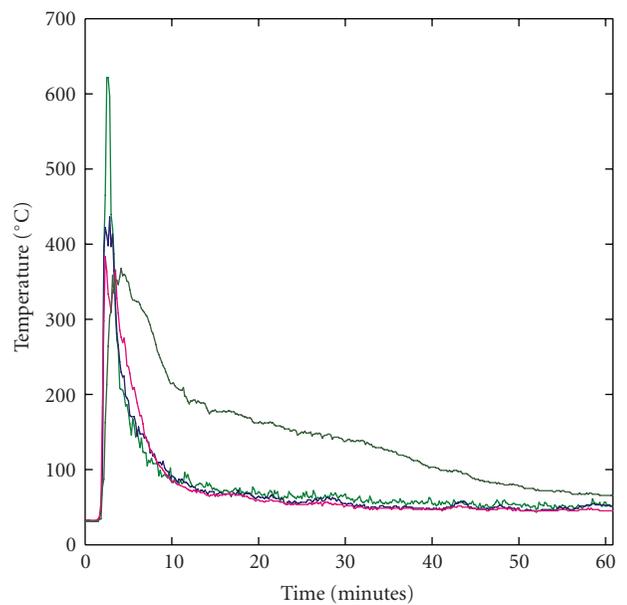
(b)

FIGURE 2: Soil temperatures at 2 cm depth during a prescribed sand pine scrub fire at Ocala National Forest, Florida on May 10, 1993. Temperatures were recorded with copper-constantan thermocouples placed in vegetated (a) and open (b) microsites. Each microsite location was replicated four times.

that maximum soil temperatures were higher at the surface than at 2 cm depth ($\chi^2 = 33.6, P < .001$). Maximum temperatures of petri dishes placed at the soil surface varied widely. Most temperatures ranged from 93°C to 315°C, but 4 of 24 surface petri dishes reached temperatures >343°C, while 2 surface/open petri dish temperatures were <37.8°C (Figure 5). In contrast, maximum temperatures of petri dishes placed at 2 cm depth were more similar; only 1 of 24



(a)



(b)

FIGURE 3: Soil temperatures at the soil surface during a prescribed sand pine scrub fire at Archbold Biological Station, Florida on May 25, 1993. Temperatures were recorded with copper-constantan thermocouples placed in vegetated (a) and open (b) microsites. Each microsite location was replicated four times.

petri dishes placed at 2 cm depth exceeded 100°C (Figure 5). Although differences between temperatures of petri dishes in open versus vegetated microsites were not tested statistically due to small sample sizes, temperatures appeared similar among microsites (Figure 5). Comparison of thermocouple maximum temperatures with maximum temperatures of adjacent petri dishes showed that temperatures quantified via the two methods differed ($t = 25.0, .02 < P < .05$)

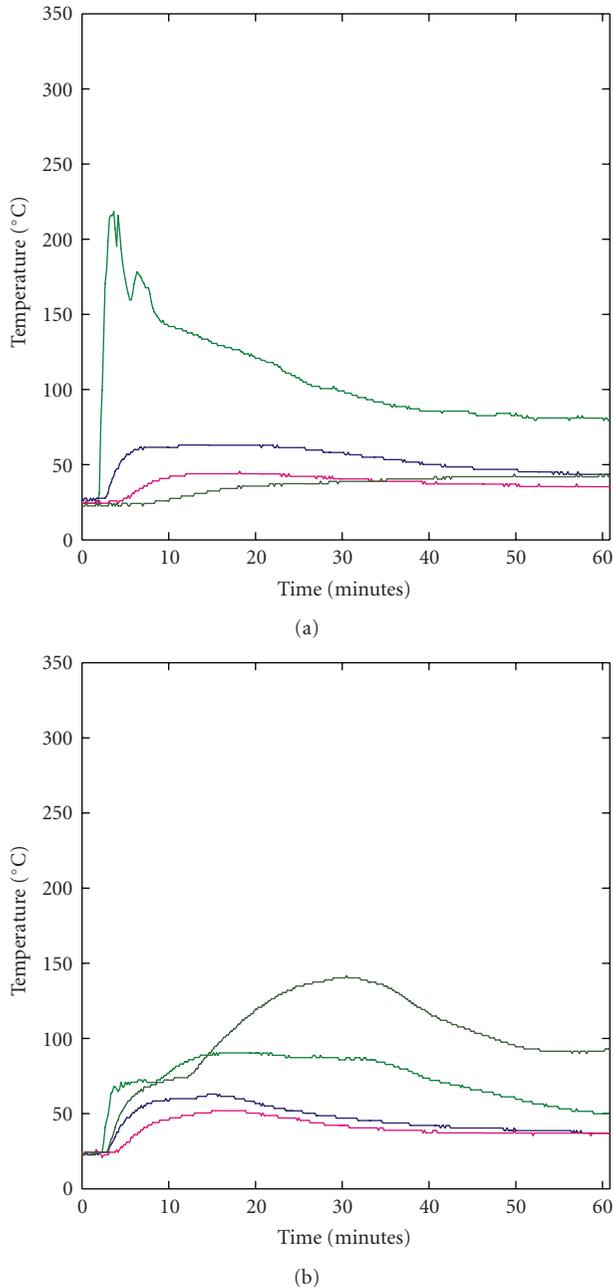


FIGURE 4: Soil temperatures at 2 cm depth during a prescribed sand pine scrub fire at Archbold Biological Station, Florida on May 25, 1993. Temperatures were recorded with copper-constantan thermocouples placed in vegetated (a) and open (b) microsites. Each microsite location was replicated four times.

(Table 5), presumably due to time required to melt paints on petri dishes (Figure 6).

Most non-charred *Eriogonum* seeds recovered after both fires were from petri dishes placed at 2 cm depth ($\chi = 43.95$, $P < .001$). Of a total of 34 petri dishes recovered from the soil surface after the fires, only one dish contained non-charred seeds. Numbers of petri dishes with charred seeds did not appear to differ between open and vegetated microsites,

TABLE 5: Maximum temperatures at 0 cm and 2 cm soil depth, and in open and vegetated microsites, during a prescribed fire in sand pine scrub at Archbold Biological Station, Florida. Temperatures were quantified with copper-constantan thermocouples and with temperature-sensitive paints placed on adjacent glass petri dishes.

Depth	Microsite	Maximum Temperature	
		Thermocouple	Paint ^(a)
0 cm	open	621.7	163.7
0 cm	open	436.2	107.2
0 cm	open	383.5	289.8
0 cm	open	367.8	<37.8
0 cm	vegetated	308.1	260.0
0 cm	vegetated	59.8	287.8
0 cm	vegetated	319.8	232.2
0 cm	vegetated	56.9	162.8
2 cm	open	63.0	<37.8
2 cm	open	90.4	<37.8
2 cm	open	52.0	<37.8
2 cm	open	141.7	<37.8
2 cm	vegetated	218.3	<37.8
2 cm	vegetated	63.0	<37.8
2 cm	vegetated	45.6	<37.8
2 cm	vegetated	43.6	<37.8

^(a)Temperatures represent the manufacturer-specified melting temperatures of the paints that melted.

TABLE 6: Number of petri dishes from which charred *Eriogonum floridanum* seeds were recovered after controlled burns in sand pine scrub at Archbold Biological Station and at Ocala National Forest, Florida, versus number of petri dishes from which all seeds were recovered non-charred; and total number of non-charred seeds recovered. Petri dishes were placed at 0 cm and 2 cm depth in the soil, and in open and vegetated (from 0–2 m vegetation height) microsites. Each petri dish contained ten seeds.

Soil depth/microsite	Petri dishes with charred seeds	Petri dishes without charred seeds ^(a)	Total non-charred seeds
0 cm/open	17	0	0
0 cm/vegetated	16	1	10
2 cm/open	3	14	154
2 cm/vegetated	3	14	156

^(a)More petri dishes with non-charred seeds were recovered from 2 cm depth ($\chi^2 = 43.95$, $P < .001$).

although differences were not tested statistically due to small sample sizes (Table 6).

No seeds germinated during trials using non-charred seeds recovered after the fires. Tetrazolium tests on seeds that were collected at the same time as seeds used in the experimental fires indicated that viability was $34 \pm 4\%$.

3.2. Laboratory Experiments. In both *Eriogonum* and *Garberia* experiments 100°C was lethal to seeds; no seeds exposed

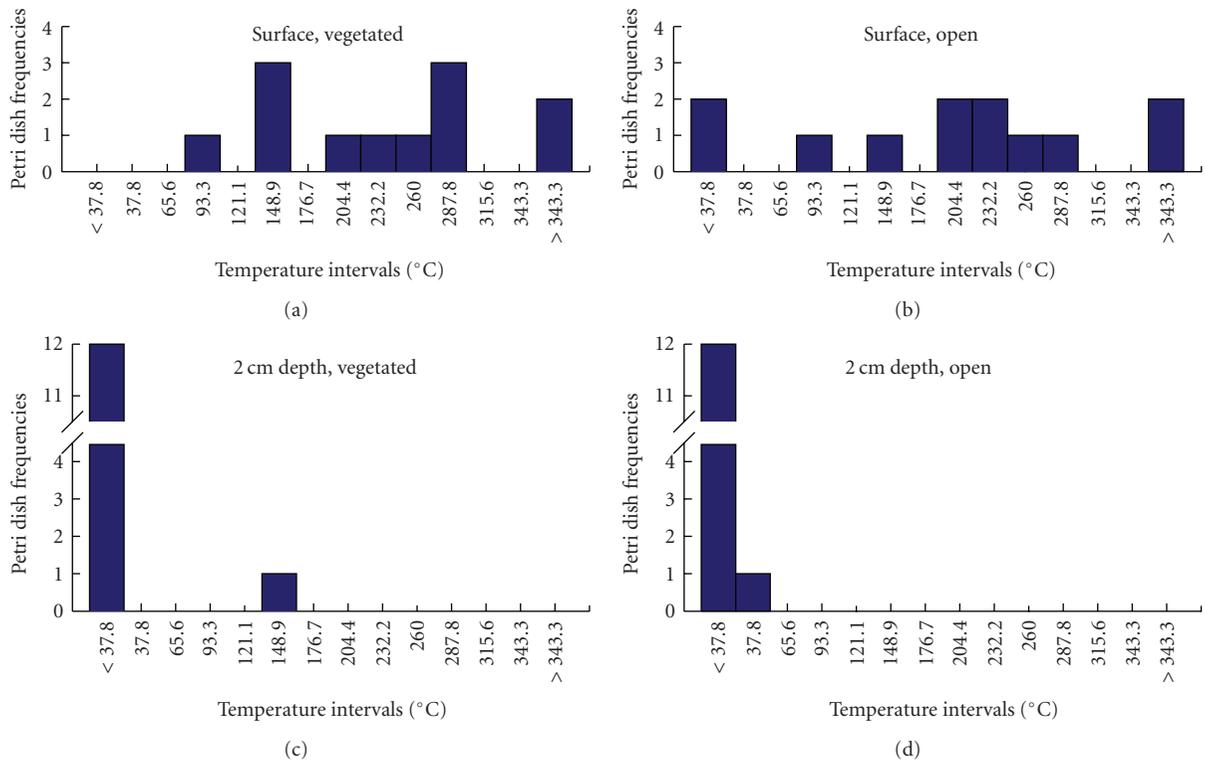


FIGURE 5: Frequency distributions of maximum petri dish temperatures during a prescribed sand pine scrub fire at Archbold Biological Station, Florida on May 25, 1993. Temperatures were quantified with temperature-sensitive paints on the petri dishes; temperature intervals for the frequency distributions represent melting points of the paints. Petri dishes were placed at the soil surface in vegetated (a) and open (b) microsites, and at 2 cm depth in vegetated (c) and open (d) microsites; each depth-microsite combination was replicated 12 times.

TABLE 7: Number of petri dishes from which *Eriogonum floridanum* (Polygonaceae) and *Garberia heterophylla* (Asteraceae) seeds germinated after being exposed to 100°C or 25°C for 5 minutes. Germination trials were conducted from December 8–17, 1993, and from December 14, 1995 to January 2, 1996 for *Eriogonum* and *Garberia*, respectively.

Seed species	Temperature (°C)	Number of petri dishes ^(a) (n = 4)
<i>Eriogonum</i>	25	4
	100	0 ^(b)
<i>Garberia</i>	25	4
	100	0 ^(b)

^(a)Each petri dish contained 20 seeds.

^(b)Fisher exact test showed a reduction in germination ($P = .0143$).

to 100°C for five minutes germinated, while seeds exposed to room temperature germinated in all petri dishes (Fisher exact test, $P = .0143$ for both species, Table 7). Seeds of both species also behaved similarly when exposed to 60°C for 30 minutes; seeds germinated from all petri dishes in both experiments, with no differences in numbers germinating between seeds exposed to 60°C and seeds exposed to room temperature (*Eriogonum*: $t = 1.27$, $P = .25$; *Garberia*: $t = 0.397$, $.5 < P < .9$; Table 8).

TABLE 8: Number (mean ± S.E.) of *Eriogonum floridanum* (Polygonaceae) and *Garberia heterophylla* (Asteraceae) seeds that germinated after being exposed to 60°C or 25°C for 30 minutes. Germination trials were conducted from December 8–17, 1993, and from December 30, 1995 to January 7, 1996 for *Eriogonum* and *Garberia*, respectively. Identical superscripts within the same species indicate no difference in germination between temperature treatments (t -test, $P > .05$).

Seed species	Temperature (°C) [†]	Germinated seeds (mean ± S.E.)
<i>Eriogonum</i>	25	15.0 ± 1.6 ^(a)
	60	11.5 ± 2.3 ^(a)
<i>Garberia</i>	25	19.0 ± 0.4 ^(a)
	60	19.3 ± 0.5 ^(a)

[†] n = 4 petri dishes, each with 20 seeds.

4. Discussion

4.1. *Soil Temperatures during Fires.* Depth in the soil has a strong influence on magnitude and variability of temperatures during Florida sand pine scrub fires, and thus influences seed survival during fires. As expected, maximum temperatures at the soil surface were higher and peak temperature durations were shorter than at 2 cm depth. Less predictable, however, were (1) effects of microsites at the soil surface on maximum temperatures; and (2) detailed

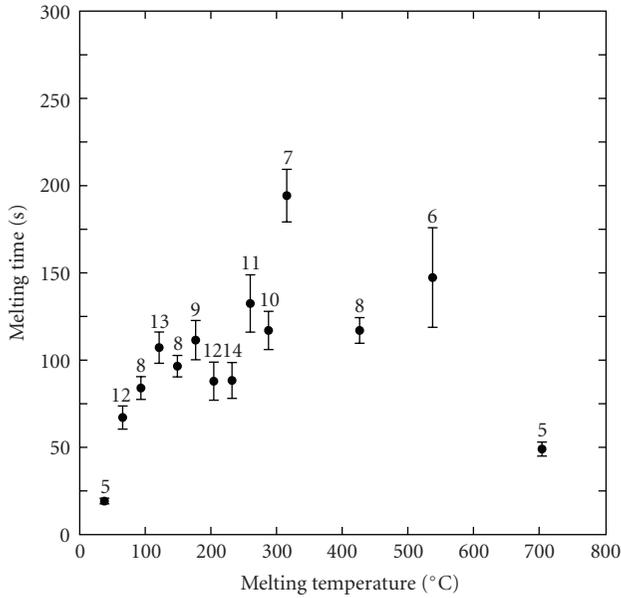


FIGURE 6: Melting times (mean \pm S.E.) of temperature-sensitive paints (Tempilaq, Tempil Division, Big Three Industries, Inc.) on glass petri dishes. The number above each symbol represents the number of melting trials conducted for that paint. In each trial a petri dish was placed in a muffle furnace set at the melting temperature of the paint on the dish, and melting time was quantified.

spatial patterns of temperatures at the soil surface, and their implications for seed survival.

The effect of microsites on soil temperatures was different from that predicted, and was different between the two fires. Differences in overstory pine species and resulting litter characteristics between the sites contributed to the different microsite effects. Sand pine, the only tree species at Ocala, produces sparse litter consisting of short needles, but south Florida slash pine has much longer and more flammable needles than sand pine, and produces more litter. Because south Florida slash pine was present only at Archbold, different types and amounts of pine litter had accumulated in open microsites at the two sites; litter in vegetated microsites consisted primarily of sclerophyllous leaves with comparatively low flammability.

During the Ocala fire, a high variance in temperatures within microsites precluded detection of a microsite effect. During the Archbold fire a microsite effect was detected, but the pattern of temperatures between open and vegetated microsites was the reverse of the expected pattern. Higher maximum temperatures in open microsites were probably due to the well-aerated, relatively flammable slash pine litter in open microsites burning more completely and at higher temperatures than the more compacted, less flammable oak and hickory litter in vegetated microsites [50]. As reported in other studies [12, 14, 15], patterns of soil temperatures during fires appear to be related more directly to litter (i.e., fuel) type and amount than to microsites defined in this study.

Not only was the effect of microsites on soil temperature unpredictable, but temperatures at the soil surface in general were variable when compared to temperatures at 2 cm depth. Soil surface temperatures, in addition to having greater variation among experimental locations than at 2 cm depth, varied widely both in time and in space within experimental locations, as demonstrated by temperatures recorded with thermocouples and with temperature-sensitive paints. Temperatures recorded by thermocouples at the soil surface generally increased to extremely high, brief maxima, thereby producing many within-location combinations of temperatures and temperature durations. As a consequence of this high variation in temperatures over time, temperature-sensitive paints on petri dishes usually underestimated maximum temperatures of adjacent thermocouples at the soil surface. The maximum temperatures recorded by temperature-sensitive paints apparently were the highest temperatures that persisted long enough to melt the corresponding paints. As might be predicted by the variation in patterns of thermocouple temperatures versus time, differences between maximum temperatures of petri dishes and adjacent thermocouples varied widely.

Differences between petri dish and adjacent thermocouple temperatures at Archbold also indicated that soil temperatures varied spatially within experimental locations. Because maximum temperatures recorded by temperature-sensitive paints often differed from those expected based on temperature patterns of adjacent thermocouples (Table 4, Figures 3 and 4), temperatures and temperature durations must have varied over a very small spatial scale.

4.2. Seed Survival during Fires. Because virtually all maximum temperatures at the soil surface were $>100^{\circ}\text{C}$ and lethal to *Eriogonum* and *Garberia* seeds, much of the variation in soil surface temperatures during fires was irrelevant to seed survival for these species. Such extremely variable but high temperatures also should be lethal to most other species of seeds; in other studies, even seeds for which germination increased after exposure to high temperatures were usually killed by temperatures between $120\text{--}150^{\circ}\text{C}$ [32]. Nevertheless, a fraction of seeds at the soil surface may survive fires in sand pine scrub, because *Eriogonum* seeds in one petri dish at the soil surface remained non-charred, and soil surface temperatures presumably were heterogeneous at a very small scale.

Seed survival is more likely and more predictable at 2 cm depth in the soil, because soil temperatures during fires were relatively low, and varied little from site to site. Although higher proportions of seeds should survive through fire at this depth in the soil, some seed mortality must occur, because lethal temperatures were occasionally reached. Surprisingly, in this study all *Eriogonum* seeds recovered after the Archbold fire from petri dishes placed at the surface and at 2 cm depth failed to germinate, even though seeds subjected to temperatures lower than 100°C in the laboratory germinated. Perhaps an unanticipated factor, possibly related to the glass petri dishes, prevented germination after the fire.

For species that rely on recruitment from seeds that survive through fire, a tradeoff exists between higher probability of survival and increasing difficulty of seedling emergence with increasing depth in the soil. Seedlings from larger seeds should emerge from 2 cm depth with little difficulty, as has been demonstrated for several legume species with seed masses near 30 mg [9, 13, 32]. *Eriogonum* and *Garberia* seeds, however, are much smaller, having an average mass of 3.7 ± 0.1 mg. Their seeds may be incapable of germination and seedling emergence from 2 cm depth, especially because litter apparently acted as a mechanical barrier to *Eriogonum* seedling emergence in another experiment [52, 53].

The extremely limited capacities for *Eriogonum* and *Garberia* seed survival through fires are consistent with postfire recruitment characteristics for these species. In a concurrent study of seedling recruitment following the experimental fires, *Eriogonum* and *Garberia* seedlings germinated from seeds produced after the fires by resprouting adults. Seeds of some species quantified as seedlings after the fires (e.g., *Calamintha ashei*, *Lupinus diffusus*, *Tephrosia chrysophylla*), however, presumably germinated after surviving the fires, as adults of the species were killed by the fires and seeds had no obvious long-distance dispersal mechanisms [51]. Although seed germination characteristics for these adult-killed species are unknown, seeds probably were capable of germinating after exposure to elevated temperatures (i.e., -60 – 100°C). Seeds germinated either at the soil surface in microsites that failed to reach lethal temperatures, or at depths beneath the soil surface from which seedlings could emerge.

This study not only showed that patterns of temperatures differ between the soil surface and 2 cm depth, but also demonstrated differences in relative strengths and weaknesses of two temperature quantification methods. Temperature-sensitive paints on petri dishes were much less precise than thermocouples in quantifying maximum temperatures; therefore, results from temperature-sensitive paints were reliable only at 2 cm depth, where temperature durations were long. Nevertheless, temperature-sensitive paints are adequate for documenting large differences in temperatures between depths in the soil, and for recording maximum temperatures beneath the soil surface, where relatively large proportions of seeds should survive fires.

In addition to maximum temperatures, temperature duration influences seed survival through fires. Since (1) variation in temperature duration and spatial variation in maximum temperatures at the soil surface are potentially relevant to seed survival and (2) thermocouples can quantify temperature duration and complex spatial patterns in temperatures, thermocouples should be used in studies of temperatures relevant to seed survival during fires to quantify temperature patterns at the soil surface.

Results from this study suggest that small-scale spatial variation in temperature exists at the soil surface during fires, and that low-temperature patches are essential for seed survival on the soil surface. Additional studies are needed to document small-scale patterns of temperatures, temperature durations, and seed survival at the soil surface during fires. Seed survival through fire and germination after fire, however, are only a small part of the process of

postfire recruitment. Future research on topics such as effects of postfire microsite conditions on seedling establishment, and the relevance of postfire microsite conditions to the evolution of seed germination characteristics, will contribute to a comprehensive characterization of postfire recruitment.

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Research Article

Physiological Effects of Smoke Exposure on Deciduous and Conifer Tree Species

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Smoke from forest fires can persist in the environment for weeks and while there is a substantial amount of literature examining the effects of smoke exposure on seed germination, the effects of smoke on leaf function are nearly uninvestigated. The objective of this study was to compare growth and primary and secondary metabolic responses of deciduous angiosperm and evergreen conifer tree species to short smoke exposure. Twenty minutes of smoke exposure resulted in a greater than 50% reduction in photosynthetic capacity in five of the six species we examined. Impairment of photosynthesis in response to smoke was a function of reductions in stomatal conductance and biochemical limitations. In general, deciduous angiosperm species showed a greater sensitivity than evergreen conifers. While there were significant decreases in photosynthesis and stomatal conductance, smoke had no significant effect on growth or secondary defense compound production in any of the tree species examined.

1. Introduction

Fire has shaped terrestrial plant communities for the last 350 million years [1]. In the Intermountain West, fire has had an integral role in structuring plant communities with typical fire return intervals between 35 and 200 years [2]. Smoke produced from fires varies with the fuel loads, intensity, and duration of burning, and can persist in the air for weeks [3]. A better understanding of the responses of plants to smoke is becoming increasingly more relevant as longer growing seasons and increased drought frequency and duration projected under future climate scenarios are expected to result in an increase in wildfires [4].

Nearly all of the studies that examine the effects of smoke on plant physiology and development have been tied to seed germination [5]. Relatively little is known about how smoke influences primary and secondary metabolism in plants. Davies and Unam [6] studied the effects of forest fires in Indonesia on photosynthesis and found that despite increases in CO₂ from the fires, photosynthetic rates were lowered. Gilbert and Ripley [7] showed that smoke exposure reduced stomatal conductance, CO₂ assimilation rate, and intercellular leaf CO₂ concentrations.

In theory, smoke could reduce photosynthesis through physical and/or chemical processes. Physically, smoke production can lead to high-vapor pressure deficits that can trigger stomatal closure [8]. Chemically, over 100 compounds have been identified in smoke [9]. Of those that have been identified, many are known to have physiologically effects on plants, including NO₂ [10], CO₂, SO₂, and O₃ [11]. O₃ has been linked to the destruction of chlorophyll [12] and has also been shown to inhibit the K⁺ channels that regulate guard cell function and in turn controls stomatal opening [13]. SO₂ reduces stomatal conductance [14], inhibits photosynthetic oxygen evolution and electron transport, and inactivates Calvin-cycle enzymes [15–17]. When combined, NO₂ and SO₂ mixtures have shown to additively inhibit photosynthesis [18]. Long-term exposures to NO₂ and SO₂ show subsequent reductions in superoxide dismutase and glutathione reductase [19], which are major antioxidant enzymes in plants [19, 20]. The disabling of antioxidant enzyme function in conjunction with high levels of ozone, a powerful pro-oxidant, may promote oxidative stress during extended smoke exposure.

Changes in environmental conditions following a fire can reduce biotic stress pressure experienced by plants. Moritz

and Odion [21] found a strong relationship between the absence of infection of *Phytophthora ramorum* and time since last burn. They suggested that fire may inhibit pathogen activity by increasing the availability of Ca, which is crucial for plant resistance to disease [22]. Drier microclimates following fire can limit fungal pathogen growth [23], and Schwartz et al. [24] proposed that the fungicidal properties of smoke reduced fungal infection and growth on leaves [24].

Smoke is a highly complex chemical cocktail with plant active compounds that can provide information to plants in ecosystems that have recently experienced fire. For example, smoke is used as a cue by seeds in some fire adapted plant species as a signal that conditions are favorable for germination, for example, [25]. Butenolide 3-methyl-2H-furo[2,3-c]pyran-2-one is a compound in smoke that induces germination [26]. It is unknown how the seed perceives the butenolide but there is evidence that it triggers germination by facilitating uptake of water [27]. As there are many changes in environmental conditions after a fire (e.g., reduction in competition, nutrient pulses in the soil and decreased pathogen loads), plants may use smoke as an environmental cue to initiate other adaptive metabolic and growth responses.

Condensed tannins and phenolic glycosides are foliar defense compounds that plants often produce in very high concentrations (up to 30% dry weight in some species) to defend themselves against herbivory and pathogen attack [28, 29]. Allocation of resources to defense chemistry production results in a tradeoff where growth potential is reduced [30, 31]. Plasticity in defense chemistry production in response to shifts in environmental conditions has been demonstrated [32, 33]. In a postfire scenario, a reduction in pathogen and insect pressure may result in a reduced need for high levels of secondary defense compounds and thereby allow for a greater resource allocation to growth and reproduction.

Here we investigate the responses of three deciduous angiosperm (*Populus tremuloides*, *Acer glabrum*, *Quercus gambelii*) and three evergreen conifer (*Pinus ponderosa*, *Pseudotsuga menziesii*, and *Picea pungens*) tree species to short-term smoke exposures. We hypothesize that: (1) exposure to smoke reduces rates of photosynthesis and stomatal conductance; (2) smoke serves as a signal that results in the allocation of seedling resources away from defense chemistry production to growth.

2. Materials and Methods

Six tree species (*Populus tremuloides*, *Acer glabrum*, *Quercus gambelii*, *Pinus ponderosa*, *Pseudotsuga menziesii*, and *Picea pungens*) in their second year of growth were used as treatment units. These species were chosen because they have adaptations that allow them to survive fire through resistance or regeneration, which indicates they have evolved in response to fire. *Populus tremuloides* (quaking aspen), *Acer glabrum* (Rocky Mountain maple), and *Quercus gambelii* (gamble oak) respond to fire with resprouting through root suckers [34–36]. Evergreen conifer species such as

Pinus ponderosa (ponderosa pine) and *Pseudotsuga menziesii* (Douglas-fir) employ a strategy of fire resistance with their thick bark [37]. *Picea pungens* (blue spruce) is not known for fire resistance but it is useful as another evergreen conifer species that regularly experiences fire. All of these species are common in the Rocky Mountains and are ecologically important species. *Populus tremuloides* was grown from wild root cuttings from a common clone, and the remaining five species were obtained from two tree nurseries (Sun Mountain growers, in Kaysville, Utah, and Plants of the Wild, Tekoa, Washington) as potted and bare root seedlings.

Prior to planting, seedling roots were washed and fresh weight plant mass was measured. Within each species, trees of uniform mass and height were used in the study. On March 26–27, 2008, each tree was transplanted into a peat/perlite (3 : 1)-based medium of 75%–80% Canadian Sphagnum peat moss with gypsum, perlite, limestone and wetting agent (Sunshine Mix #1, Sun Gro Horticulture, Bellevue, WA) in pots 23.5 cm × 11.5 cm². Four grams of Osmocote Smart Release Plant Food with 14-14-14 were added to each pot to provide necessary nutrients for growth. The trees were in a climate controlled greenhouse for the remainder of the summer and were watered to saturation twice a week.

2.1. Smoke Treatment. From May 26–30, 2008, five replicate seedlings of each species were exposed to smoke staggered across time (one replicate each day, over a five-day period). Smoke exposure occurred for 20 minutes. A second cycle of smoke exposure on the same plants occurred from June 9–13, 2008.

The smoke chamber was fabricated from a sealed plastic cooler (95 cm × 38 cm × 45 cm). Equal parts of dried leaf material obtained from each of the six tree species in the study were used to generate the smoke. The leaves were combusted in a glass funnel fitted into a flask that was connected to the top of a glass flask. The flask was cooled in an ice bath to eliminate temperature increases inside the chamber. For 25 seconds, 500 mg of leaf material mixture were burned to ash with a butane lighter and the smoke was pulled through plastic tubing into the chamber using a vacuum connected to tubing at the bottom of the cooler. A fan inside the cooler dispersed the smoke and a florescent light inside the cooler provided low light levels. Temperatures inside of the smoke chamber never exceeded 35°C, as measured by a Hobo U10-003 data logger (Onset Computer Corporation, Pocasset, MA). A second chamber identical to the first was used for control treatments. All procedures were exactly the same for the control chamber with the exception that leaf material was not placed in the glass funnel.

It is difficult to compare our smoke exposure with what is experienced in natural settings as smoke production is extremely variable in western North America [3]. This is due in part to variations in fuel load, fuel consumption, rate of emissions, and dispersion rates [38]. Mixed conifer forest fuel loads can vary from 63–112 MT ha⁻¹ and aspens forests from 20–83 MT ha⁻¹ [38]. As we used 0.03 MT ha⁻¹ (leaf

mass \times area of smoke chamber), we estimate that our smoke exposure is less concentrated than what is experienced in a forest fire.

2.2. Gas Exchange. After smoke exposure, the treated plants were removed from the smoke chamber to measure rates of photosynthesis and stomatal conductance with a gas exchange system (LI-COR 6400, Li-Cor Biosciences, Lincoln, NE). Photosynthetic measurements were taken at a photosynthetic photon flux density (PPFD) of $1200 \mu\text{mol m}^{-2} \text{s}^{-1}$ with the 6400-04 LED blue-red light source at ambient temperature and humidity. Two measurements were taken at CO_2 concentrations of 385 ppm and 1000 ppm, respectively, with CO_2 concentrations being achieved using the CO_2 mixer to distinguish whether smoke effects on photosynthesis were related to stomatal and/or biochemical limitations [39]. Measurements were initiated by sealing the leaf in the chamber on the youngest fully expanded leaf or needles of each tree. After CO_2 and water vapor concentrations in the leaf chamber reached a steady state (60–90 seconds), rates of photosynthesis and stomatal conductance were logged. Measurements were taken immediately after smoke exposure, 30 minutes after exposure, and then every 70 minutes until 310 minutes thereafter.

To calculate leaf area for leaves that did not fill the leaf chamber, leaves were traced on paper which was cut out and then measured for area with the leaf area meter (Li-Cor 3000, Li-Cor Biosciences, Lincoln, NE, USA). Needle area was calculated by scanning an image of the needles and measuring area with Scion Image for Windows (Frederick, Maryland, USA).

2.3. Growth. On July 29, 2008, the trees were harvested for growth and mass measurements. Stem height was measured and then the seedling was cut off at soil level and both roots and shoots were dried at 60°C for 72 hours to obtain dry mass using an analytical balance (GeneMate GP-600, ISC Bioexpress, Kaysville, UT, USA).

2.4. Secondary Chemistry. Leaves and needles were removed from the seedlings nine weeks after smoke exposure (July 29, 2008) and packed on dry ice before being moved to storage at -80°C for later analysis of phenolic glycosides and condensed tannins. Leaves were freeze dried and needles were oven dried at 60°C for 72 hours. Leaf and needle material was then crushed in a Wiley Mill using a no. 10 screen. Tannins were quantified for all species using a modified butanol-HCL method described in Porter et al. [40], where approximately 50 mg of leaf material were placed in 2 mL screw-cap microcentrifuge tubes suspended in 1 mL of 70% acetone-10 mM ascorbic acid solution. The samples were then vortexed on high at 4°C for 20 minutes. The liquid supernatant was then removed and the extraction was repeated. The concentration of tannins was then quantified spectrophotometrically (SpectraMax Plus 384, MDS, Toronto, Canada) using purified tannins as a standard.

The phenolic glycosides, salicortin and tremulacin, were extracted from approximately 50 mg of aspen leaf tissue (the other species do not contain significant levels of phenolic glycosides). The tissue samples were placed in 2 mL screw cap micro-centrifuge tubes and suspended in methanol. The samples were then vortexed on high for 5 minutes. The liquid supernatant was removed and the extraction was repeated. Final concentrations of salicortin and tremulacin were quantified using high-performance liquid chromatography (Agilent 1100 Series, Santa Clara, CA, USA) with a Luna 2, C18 column ($150 \times 4.6 \text{ mm}$, $5 \mu\text{m}$) at a flow rate of 1 mL/min. Compound peaks were detected using a UV lamp at a wavelength of 280 nm with purified salicortin and tremulacin standards isolated from aspen leaves [41].

2.5. Statistical Analysis. We ran a Student's *t*-test to test for differences in defense chemistry and growth. Repeated measures analysis of variance (ANOVA) was used to test the effects of smoke exposure on rates of photosynthesis from 30 minutes after exposure to 310 minutes after exposure using time as the "within" factor [42]. Homogeneity of variance and normality were tested with Shapiro-Wilk *W* statistics and equal variance tests. Data that did not meet the assumptions for the parametric tests were tested using a Wilcoxon rank sum test, while the data in the graphs and tables were untransformed. Statistical analysis was performed using JMP version 7 statistical software (SAS Institute, Cary, NC, USA).

3. Results

All of the species showed significant differences in stomatal conductance and rates of photosynthesis 30 minutes after exposure, except for Douglas-fir. Aspen and ponderosa pine showed the greatest reductions in photosynthesis (Figure 1). Douglas-fir initially showed a significant decrease in A_{max} and g_s (data not shown). Two weeks after exposure, rates of photosynthesis were measured again and there was a complete recovery in all species (data not shown).

The repeated measures analysis on rates of photosynthesis at 1000 ppm, CO_2 showed a significant time effect (*P*-value < 0.001) in which rates of photosynthesis recovered from smoke exposure as time progressed (Figure 2). At 1000 ppm there was also a significant interaction between time and species type (deciduous angiosperms and evergreen conifer) (*P*-value = .0073) with deciduous angiosperm species showing slower recovery (Figure 2). At 385 ppm CO_2 , time was the only significant effect in the repeated measures model (*P*-value = .0209). Species type was marginally significant (*P*-value = .0709).

There were no significant differences for growth, condensed tannins, or phenolic glycosides (Figure 3; data not shown for the latter).

4. Discussion

The data are consistent with our first hypothesis that smoke exposure reduces rates of photosynthesis. Comparing

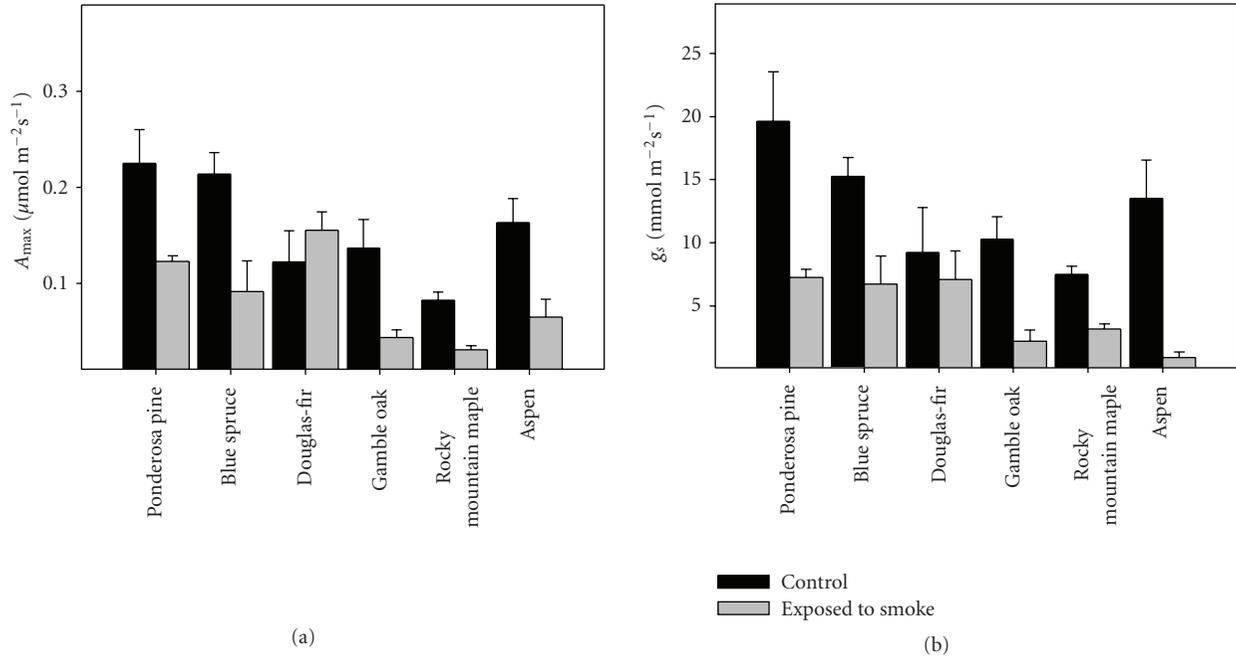


FIGURE 1: A_{max} (maximum rate of photosynthesis) and g_s (stomatal conductance) after 30 minutes of smoke exposure. The only species without significant differences between treatments (at $\alpha < 0.05$ level) was Douglas-fir.

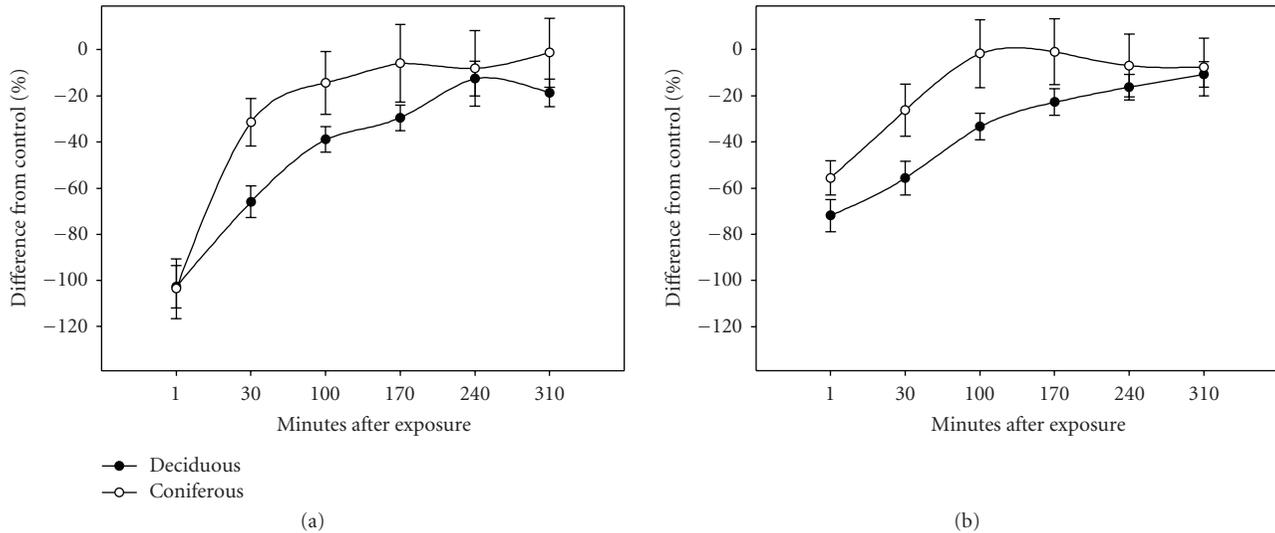


FIGURE 2: Decreased rates of photosynthesis expressed as percent difference from control at both ambient (a) (385 ppm) and saturating (b) (1000 ppm) CO_2 concentrations.

photosynthetic responses at ambient and saturating CO_2 concentrations suggests that smoke affects photosynthetic function by reducing stomatal conductance and through impairment of biochemical function (Figure 2). Our results show for the first time that photosynthetic sensitivity to smoke occurs across a diverse sampling of tree species and that there is wide-ranging variation in sensitivity between those species.

Because of the complexity of smoke constituents, it is hard to pinpoint which chemicals may be adversely affecting photosynthesis. Different compounds in smoke, such as NO and NO_2 , affect plant species to varying degrees [43]. We found that the evergreen conifers initially recovered from the smoke exposure faster than the deciduous angiosperms (Figure 2). Thirty minutes after smoke treatments had ended, only Douglas-fir had recovered completely (initial decreased

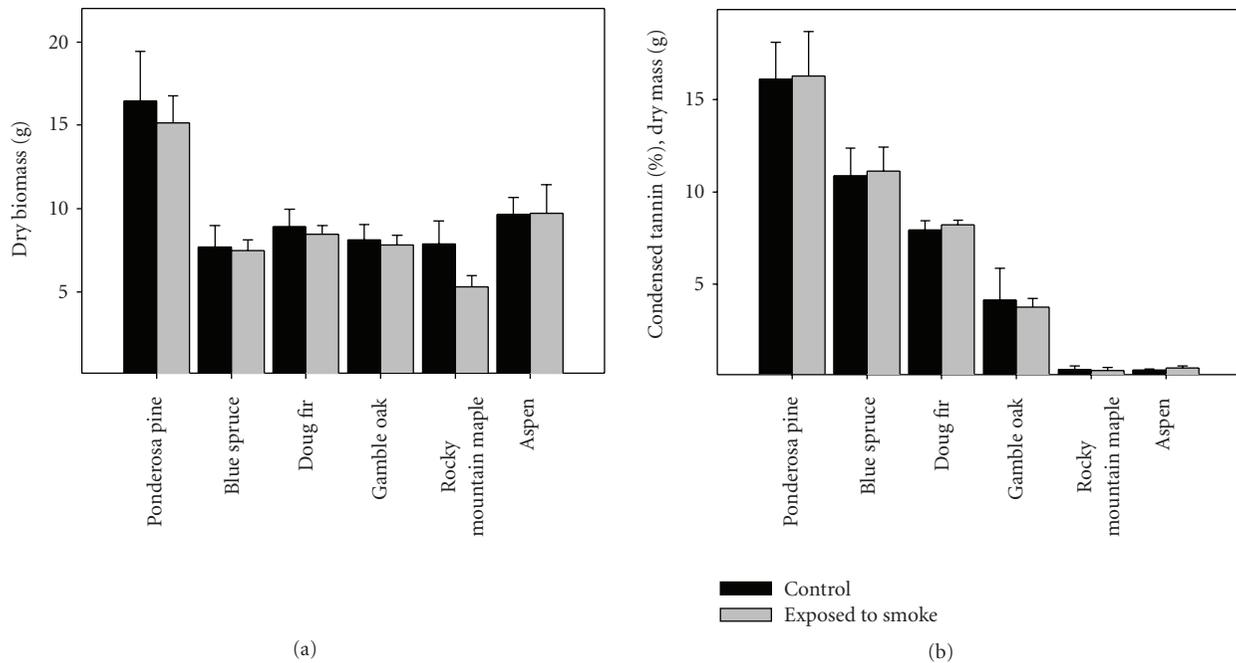


FIGURE 3: Comparisons of biomass and condensed tannins in smoke-exposed samples and controls. There were no significant differences between treatments of any species.

rates of photosynthesis not shown) (Figure 1). Though evergreen conifers recovered faster than the deciduous angiosperms, there were no changes in growth patterns or defense chemistry production in response to smoke exposures (Figure 3). This indicates that there were no long-term effects from our relatively short 20-minute smoke exposures.

Why the evergreen conifers initially recovered faster than the deciduous angiosperms is unknown. Plant species can develop tolerance to pollutants that are known to affect photosynthesis [44, 45]. The greater tolerance in evergreen conifers could be a result of the different fire strategies, in which gamble oak, rocky mountain maple, and aspen employ a survival strategy of overstory mortality followed by asexual regeneration at some later time [34–36]. In contrast, evergreen conifer species including ponderosa pine and Douglas-fir employ a strategy of fire resistance with their thick bark that allows the overstory to survive [37]. We hypothesize that species that employ a strategy of fire resistance would have a greater need to develop mechanisms of tolerance to avoid the negative effects of needle exposure to smoke for extended periods of time.

The results are inconsistent with second hypotheses that smoke alters growth patterns or allocation to defense chemistry. It is likely that two 20-minute smoke exposures are insufficient to elicit a growth response. In western North America, plants can be exposed to smoke on scales of weeks to months, as reviewed in [3]. Smoke exposures of such length are impractical in controlled studies but tree ring data could potentially be used to examine correlations between growth rates and smoke extent over the summer season if other confounding factors can be accounted for.

There are a few possible reasons why we did not find any significant differences in defense chemistry in response to smoke treatments. First, for aspen, it is known that different genotypes respond differently to environmental changes [29]. Here we only used one genotype and that could result in missing responses that occur in other aspen genotypes. Second, in contrast to seed germination, plants may not use smoke as a cue for physiological leaf responses following fire. Third, while we looked at two important defense compounds based on quantity and function, we certainly did not conduct a comprehensive survey of secondary metabolic responses. Finally, it is also possible that the signature of our smoke exposures (chemistry, timing, intensity) was not adequate for eliciting a defense response.

Because there are many compounds in smoke and we know so little about how they can affect plants, we have much to learn about the influence of smoke on plant function. The fact that different plant species can show varying responses to smoke, in addition to the potential for different plant species to produce their own complex suite of compounds, suggests there may be some intriguing roles for smoke in plant and ecosystem function.

Acknowledgment

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Research Article

Adverse Influence of Radio Frequency Background on Trembling Aspen Seedlings: Preliminary Observations

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Numerous incidents of aspen decline have been recorded in North America over the past half century, and incidents of very rapid mortality of aspen clones have been observed in Colorado since 2004. The radio frequency (RF) environment of the earth has undergone major changes in the past two centuries due to the development and use of electricity in power and communications applications, and the anthropogenic RF background continues to increase in intensity and complexity. This study suggests that the RF background may have strong adverse effects on growth rate and fall anthocyanin production in aspen, and may be an underlying factor in aspen decline.

1. Introduction

Incidents of aspen decline in North America have been observed since the mid-20th Century [1–3]. Stands at the limits of aspen's lower elevation range, on sites with poor drainage, with limited water [4] or nutrient supply [5], are more susceptible to decline. Stand age and clonal differences are also factors in susceptibility to decline [6]. Factors initiating decline include: defoliation by insects, damage caused by wildlife, severe drought, and extreme weather incidents [7]. Damage caused by these factors can diminish the vigor of affected clones and make them vulnerable to opportunistic fungal pathogens and insects [8]. The concept of forest decline has been used to describe the interaction of these various factors; however, the underlying causes of aspen decline are not well understood [9]. Since 2004, incidents of very rapid aspen clone mortality have been seen in Colorado [10]. Because the electromagnetic (EM) environment of the earth has changed radically in the past two centuries, this study investigates the possibility that anthropogenic changes in this environment, particularly in the radio frequency (RF) spectrum, are adversely affecting growth and health of aspen populations, making them vulnerable to decline.

Electromagnetic energy from the sun is essential for life on earth. Plants rely on inputs of EM energy for photosynthesis and for regulation of periodic functions (flowering, shoot and root growth, respiration, and dormancy). A plant's response to EM energy is dependant on frequency, timing, and intensity of the signal. The source of the EM input, however, makes no difference. Timing of plant processes is an important mechanism for plant protection and efficient functioning in changing day/night and seasonal environmental conditions [11]. Although photosynthesis requires fairly strong energy input in the blue and red visual frequencies (full sun/shade) [12], photoperiodic responses in plants are typically triggered by energy inputs in the red and far-red frequencies that are in the range of 10^{-4} times the energy required for photosynthesis, and even a brief flash of light during a plant's subjective night can be enough to trigger a short night response, strongly affecting plant behavior and morphology [13]. The radio frequencies, lower than 300 gigahertz, are below visual and infrared frequencies in the electromagnetic spectrum. The earth's natural RF environment has a complex periodicity that has been more or less the same within the lifespan of modern tree taxa. Before 1800, the major components of this environment were broadband radio noise from space (galactic noise), from

lightning (atmospheric noise), and a smaller RF component from the sun [14]. Because of the periodic nature of the naturally occurring RF background, plants may have evolved to use those environmental signals, as well as visible light, to regulate periodic functions, and therefore they may be sensitive to anthropogenic RF input. The intensity of the human-generated RF environment has increased gradually since about 1800. This background of RF pollution is now many times stronger than the naturally occurring RF environment. From the perspective of evolutionary time, the change can be considered sudden and dramatic [14, 15].

Many experiments have been conducted investigating possible effects of RF exposure on plants and animals. Generally, exposures to particular single frequencies at particular, usually fairly high intensities, have been used in these previous experiments [16]. However, the assumption seems to have been made that the low-level background of RF pollution has no effect on biological systems. Therefore, not only has this particular phenomenon not been studied, but it has been generally disregarded in earlier experiments designed to look for effects of RF exposure. Results of those previous experiments are often difficult to duplicate, and it may be that the anthropogenic RF background has been a confounding factor. However, for some RF effects on biological systems, consistent results have been documented in previous experiments: growth rates of plants [17] and fungi [18] can be increased or decreased by RF exposure. Exposure to RF signals can induce plants to produce more meristems [19], affect root cell structure [20, 21], and induce stress response in plant species, causing biochemical changes [22]. Effects on circadian rhythms in several animal species have been documented [23]. Some possible mechanisms of effect have been identified [24]. This experiment investigates the effects of the radio frequency background on aspen seedlings. The objective of this preliminary study was to determine if aspens respond to the current RF background in ways that result in reduced growth, or in increased susceptibility to pathogens.

1.1. Study Area. The experiment was conducted in a rural area near Lyons, Colorado: at 40.29° Latitude and -105.28° Longitude, at an altitude of 1,700 meters, and on a north-facing slope. The ecological system in the area of the experiment is Rocky Mountain Lower Montane. The site was about 400 meters below the lower elevation of aspen's natural range in Colorado. The north-facing slope was chosen as a somewhat cooler microclimate than other aspects. Vegetation included various grasses, which were mowed on the 8 × 10 m experimental plot. Vegetation in the east, south, and west directions from the experiment included: wild grasses and various low shrubs, rabbit brush (*Chrysothamnus nauseosus*), sage (*Artemisia tridentata*), wild currant (*Ribes cereum*), chokecherry (*Prunus virginiana*), yucca (*Yucca angustifolia*), and skunkbush (*Rhus trilobata*). North of the experiment, there were large cottonwood trees along the river, with grass and chokecherry undergrowth.

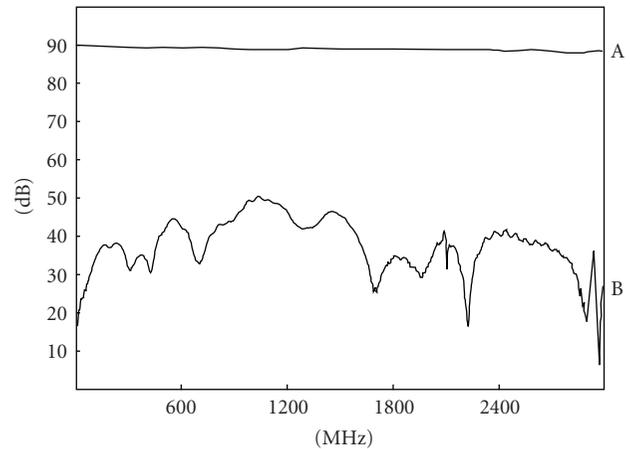


FIGURE 1: The aluminum screen material in the configuration used for this experiment was tested at NIST in Boulder, CO. From 1.0 MHz to 3.0 GHz, its effectiveness in blocking RF signals was found to vary from 40 dB to 73 dB across the entire range of frequencies. X axis = Radio frequency from 1.000 MHz to 3000.000 MHz in increments of 300.000 MHz left to right. Y axis = Decibel scale. Reference signal level was 90 dB. A = Reference signal. B = Attenuated signal.

1.2. Materials and Methods. In order to create an environment free of RF signals, a Faraday cage was built, using two layers of aluminum window screen supported by a bamboo frame. Cage dimensions were 75 cm by 75 cm by 120 cm. The aluminum screen material in the configuration used for this experiment was tested at a laboratory of the National Institute of Standards and Technology (NIST) in Boulder, CO. From 1.0 MHz to 3.0 GHz, its effectiveness in attenuating RF signals was found to vary from 40 dB to 73 dB across the entire range of frequencies (Figure 1). Theoretically, an enclosure made of this material would reduce signal intensity by a factor of 10^{-4} to $10^{-7.3}$, blocking essentially all ambient RF energy, including the naturally occurring RF background. In practice, the shielding effectiveness of a Faraday cage made of this material could be somewhat less than that of the material itself due to gaps or imperfect electrical contact at seams and closures, and to the internal RF acoustical properties of the cage. A similar cage was constructed as a control, with fiberglass screen, which is not conductive and which does not block RF signals, instead of aluminum. A transistor radio was used to test the effectiveness of the cages to block the RF background. No radio stations could be picked up inside the Faraday cage. In both the mock-Faraday cage and the uncaged area, numerous stations were received in the AM and FM bands. A sweep of RF background at the site, June 6, 2009, using an *Anritsu* spectrum analyzer, showed that field intensity ranged from -117 dBm to -87 dBm at frequencies from 1 to 1,000 MHz. Mean field intensity was -109 dBm.

On May 28, 2007, 30 aspen seedling plugs were obtained from the Colorado State Forest Service (CSFS) nursery in Fort Collins, Colorado. Seed for these seedlings came from Caffey County near Salida Colorado, approximately



FIGURE 2: October 6, 2007. Mock-shielded seedlings on the left and shielded seedlings on the right, the latter showing more total leaf area, stronger fall leaf coloration, and minimal leaf necrosis symptoms.

195 km SSW of the experiment site, at an elevation of about 2,100 meters. The seeds were germinated in June 2006 at the CSFS Nursery, and the resulting seedlings were grown in a shade house in a Styrofoam planter-block of 30 seedling plugs. The seedlings had leafed out in early spring and, when purchased on May 28, 2007, were not producing new leaves. Seedlings were transplanted into no. 1 black gallon plastic pots on June 5, 2007 using a commercial potting medium, Black Gold, composed of: 45–55% Canadian sphagnum peat moss, compost, pumice, perlite, and composted worm castings (N .05%: water soluble .006%, water insoluble .044%). Since only 27 seedlings were needed for the experiment, due to space restrictions, the three smallest seedlings were discarded. The remaining seedlings were relatively uniform in height, stem diameter, and leaf development, and the leaves appeared healthy and green. The 27 seedlings were assigned to 3 groups of 9 seedlings each, with variation in size distribution distributed equally among the 3 groups. After potting, the three groups were photographed and randomly assigned to the mock-shielded cage, the shielded cage, or to the unshielded area. The experiment began June 6, 2007. All treatments in the experiment were exposed to full sun from sunrise to late afternoon. There was a distance of three meters between treatment enclosures. All seedlings in the experiment were watered at the same time 1-2× per week, depending on the weather, using Lyons water. Seedlings were watered with a weak solution of fertilizer (5-10-5) on July 29, 2007, and otherwise were not fertilized.

Two sets of a calibrated thermometer and humidity gauge were used to compare temperature and humidity readings between cages under various weather conditions and times of day and night. The monitoring devices were placed in the middle of the monitored treatment enclosure, just above the top of the pots. A board was placed south of the devices to provide shade. A lux meter was used to measure light intensity in the treatment areas. Shielding reduced light intensity by 35% for the mock-shielded enclosure and 40% for the RF-shielded enclosure. Naturally occurring sunlight intensity was not reduced for the group that was not shielded. Except for the difference in RF background intensity, conditions in the shielded and mock-shielded enclosures were very similar. The unshielded seedlings were exposed to higher light levels (full sun), higher airflow, and generally lower humidity than



FIGURE 3: Unshielded seedling, showing green to yellow leaf coloration and gray to brown necrotic leaf tissue, Oct. 6, 2007.



FIGURE 4: Mock-shielded seedling, exhibiting yellow leaf coloration and brown lesions, Oct. 6, 2007.

the shielded and mock-shielded treatments since they were not in a screened enclosure.

1.3. Measurements. After seedlings were transplanted and placed in the three treatment enclosures in early June, they began to grow again. Because of that, there was a shoot node dividing spring growth from the summer growth phase that was easy to identify. Measurement of active leader (shoot) length was taken from the tip of the shoot down to that first shoot node, so leader length measured was only that produced after the experiment began on June 6, 2007. For leaves emerging directly from a main stem, leader length was recorded as 0.00 cm.

On July 28-29, 2007, measurements of active leader length and width of each leaf on each active leader were made on all seedlings in the experiment. Leaves had not begun to drop at that time, and the great majority of them in all treatment groups appeared healthy and green. Leaf width was converted into estimated leaf area using an algorithm (Leaf Area (cm²) = 0.637 * Leaf Diameter (cm)^{1.951}) developed by W.D. Shepperd of the USDA forest Service's Rocky Mountain Research Station [25]. After measurements were taken, all seedlings were returned to their cages. October 5-6 photos



FIGURE 5: Shielded seedling, showing red petioles and veins on light green leaf tissue, and very little leaf tissue affected by necrosis. Oct. 6, 2007.



FIGURE 7: Shielded seedling, with leaves on active leaders mainly free of necrotic lesions, and leaf veins and petioles red, Oct. 6, 2007.



FIGURE 6: Shielded seedling. Combination of red veins and green leaf tissue makes leaves look black (left side of photo), Oct. 6, 2007.



FIGURE 8: Mock-shielded seedling, showing all leaves affected by necrotic lesions to some extent, leaf veins yellow or green, and petioles light red to pink, Oct. 6, 2007.

were taken showing differences in leaf coloration, and relative leaf area affected by necrotic lesions.

2. Results

Seven seedlings in each RF-exposed group and eight seedlings in the shielded group produced active leaders and new leaves during the experiment. The RF shielded group evidenced more vigorous growth, producing 74% more total leader length and 60% more leaf area than the mock-shielded group, though the number of leaves produced by both groups was nearly the same (Table 1). The two RF-exposed groups' morphology and behavior were very similar and within the current norm for aspen, including absence of fall anthocyanin production, and extensive leaf area affected by necrotic lesions in fall senescing leaves. On active leaders, the shielded group showed fall production of anthocyanins far outside the norm, absence of fall leaf tissue necrotic lesions, and a wide range of fall colors: bright orange, yellow, green, dark red, and black (a combination of dark green

leaf tissue with red veins). Shielded leaves produced in the spring flush (before treatment), however, were similar in appearance to leaves in the two exposed groups in color, size, and incidence of lesions. All of the shielded leaves on active leaders had dark to bright red veins and petioles indicating strong anthocyanin production (Figure 2). On October 5, 2007, unshielded and mock-shielded seedlings had leaf tissue ranging in color from yellow to green, and a high percentage of leaf tissue in both exposed groups displayed necrotic lesions (Figures 3 and 4). Shielded seedlings had larger leaves, petioles and leaf veins were red, and tissue colors varied from yellow to dark green (Figure 5). Some shielded leaves looked black because of the combination of red veins and dark green tissue (Figure 6). Leaves on active leaders in the shielded group were substantially free of leaf tissue lesions (Figure 7), but unshielded and mock-shielded leaves were all affected to some extent by leaf tissue necrosis (Figure 8).

TABLE 1: Various characteristics of aspen seedlings following one of three RF treatments.

Seedling Characteristic	Treatment		
	Not-Shielded	Mock-Shielded	Shielded
No. leaders	4 (0, 6)*	2 (0, 7)	3 (0, 3)
Leader length (cm)	22 (0, 52)	17 (0, 43)	31 (0, 53)
No. Leaves	27 (0, 37)	16 (0, 34)	16 (0, 31)
Leaf area (cm ²)	87.4 (0, 165.8)	72.8 (0, 186.7)	170 (0, 219.8)
No. seedlings producing leaders and leaves	7	7	8
No. seedlings out of 9 producing anthocyanins	0	0	8

*Median (min, max) n = 9.

3. Discussion

Because only one treatment enclosure was established for each treatment, differences among groups could not be analyzed statistically. Results of this experiment do, however, suggest several possible effects of RF exposure on aspen. Those effects include reduction of shoot length and leaf area, suppression of fall anthocyanin production, and increased incidence of necrotic leaf tissue in fall senescing leaves. Reduced vigor in the two RF-exposed groups is demonstrated by lower total leader length and diminished production of leaf area relative to the shielded group. A study [26] comparing mutant nonanthocyanin-producing strains of fall anthocyanin-producing species, *Cornus sericea*, *Vaccinium elliotii*, and *Viburnum sargentii*, showed very similar results to this experiment with regard to fall color in that extensive necrotic leaf tissue was seen in nonanthocyanin-producing mutants during fall leaf senescence and leaves dropped while still green. Wild-type strains of those species, which produced anthocyanins, did not exhibit necrotic lesions. In that study, leaf tissue damage in mutant strains was shown to be caused by photooxidative stress. During fall leaf senescence photosynthetic mechanisms become vulnerable to damage by visible light. Anthocyanins shield the photosynthetic apparatus from high light levels, preventing photoinhibition and damage to leaf tissue due to light stress. Transport of foliar nutrients requires energy provided by photosynthesis [27], and since the majority of nutrients in overwintering deciduous trees are derived from foliar nutrient transport during autumn leaf senescence, differences in anthocyanin production could have major effects on plant fitness [28].

Since all leaves on active leaders in the shielded aspen group showed striking fall coloration, and since each of the seedlings was genetically distinct, it appears that the Faraday cage environment favored strong production of anthocyanins during fall leaf senescence. Five bright sunny days, Sept. 30–Oct. 4, accompanied by cool nights (~5°C) preceding the appearance of red leaf coloration, provided optimal conditions for anthocyanin production. Although shielding materials substantially reduced light levels in

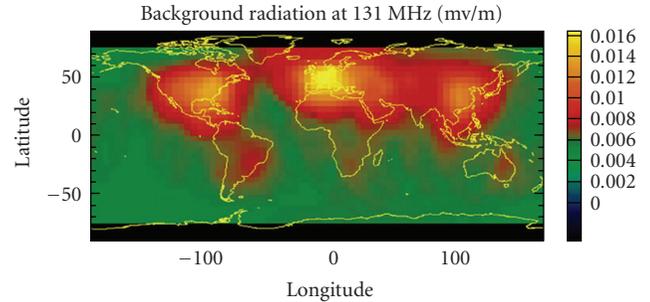


FIGURE 9: Forte Satellite: 131 MHz RF background 2000. Areas of highest radio background intensity occur in the eastern United States, central Europe, and China. Acquired by the Los Alamos National Laboratory FORTE spacecraft. Principal investigator A.R. Jacobson.

the two caged groups (mock-shielded and shielded), the behavior and appearance of the two RF-exposed groups (mock-shielded and unshielded) were most similar, both showing no apparent anthocyanin production, leaf tissue remaining light green or yellow, and a high percentage of leaf tissue affected by necrotic lesions.

3.1. Radio Frequency Environment. Beginning around 1800, EM experimentation, establishment of electrical telegraph systems, generation and distribution of electricity, and the use of broadcast signals gradually began to fill the region of the electromagnetic spectrum below 300 GHz. Currently, the RF spectrum is quite crowded, and new technologies are constantly being developed to allow more information to be transmitted on the available frequencies [29]. Unintended broadband RF noise is created as a by-product of electrical power generation, transmission, and use. These human-made RF sources create a background noise (as differentiated from signal) level generally 10 to 100 times stronger than the naturally occurring background of galactic noise and atmospheric noise at frequencies below 30 MHz [14]. Human-generated signal intensities in large regions of the RF spectrum are in the range of 10^3 – 10^6 times stronger than the naturally occurring RF background in urban areas [15]. Because terrestrial and satellite RF sources are numerous and widely dispersed globally, and since below 30 MHz radio signals can travel great distances around the earth by bouncing between the ionosphere and the earth's surface [14], currently a strong human-generated RF background exists at every point on the earth's surface, although radio field strength is relatively greater in the most populous and urbanized areas. Globally, the highest field strengths occur in central Europe, the eastern United States, and in China (Figure 9). Forest decline was first recognized and defined based on observed events in central Europe and the eastern US, and China, at this time, is experiencing rapid desertification.

3.2. Forest Decline. The first widely recognized incidents of forest decline [30] began in the late 1970s. In a European study [31], stress factors related to forest defoliation were

found to be age, altitude, drought, and various types of air pollution, in descending order of importance. Although the statistical correlation was high for some of these effects, because the number of samples was large, the effects documented were quite small and altogether could account for only 15–55% of the observed decline, depending on species. No temperature variables were found to have significant effects. In several studies, climate change was found not to be a causal agent in forest decline [32, 33]. There is evidence, however, that trees involved in forest decline are less tolerant of extreme weather conditions. Freeze damage, possibly indicating disrupted dormancy, for instance, has been noted as one symptom of forest decline where temperature and/or precipitation pattern changes were not evident [32, 34]. More recently, it has been shown that mortality rates of all dominant tree species in the western United States have been doubling every 17–29 years in old growth forests, and that recruitment of new trees is now occurring at a lower rate than mortality [35]. Since aspen decline and other tree decline incidents worldwide have similar symptoms, and since no definitive explanation has been found for those events, it seems plausible that their decline may be related to RF exposure.

Changes in health and growth rates of aspen and other plants, due to increasing RF exposure, would have been difficult to detect for two reasons: first, because the RF background is widely dispersed globally, comparisons between plant populations, even over great distances, would always have been between RF-exposed groups, even though exposure levels would vary with relative proximity to RF sources. Second, it is difficult to compare the health and appearance of plants living today to those living 200 years ago, though some comparisons can be made from previous research data, tree ring data, and pollen samples, for instance. Changes would have occurred very slowly over time, from the human perspective, and would have been widely dispersed geographically so that, at any particular time, RF-altered plant morphology and behavior would have been normal, the norm, by definition. Plants and animals have in previous experiments been shown to respond in various ways to RF exposure. Growth of organisms may be inhibited or accelerated by RF exposure, thus possibly affecting interactions at the level of communities and ecosystems from microscopic to global scales. In the case of aspen, reduced plant vigor and adverse effects on fall storage of nutrients due to RF exposure could leave seedlings vulnerable to pathogens and less able to accommodate other environmental stress.

4. Conclusions

The results of this preliminary experiment indicate that the RF background may be adversely affecting leaf and shoot growth and inhibiting fall production of anthocyanins associated with leaf senescence in trembling aspen seedlings. These effects suggest that exposure to the RF background may be an underlying factor in the recent rapid decline of aspen populations. Further studies are underway to test this hypothesis in a more rigorous way.

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