WILLIAM RUSSELL STRAW
50 Years Of Woody Succession At The Landscape Level:
An Aberrant Case In South Carolina, USA
(Under the Direction of FRANK B. GOLLEY)

Woody succession in a 235-hectare oldfield (Field 3-412), in South Carolina, USA, from 1951 through 2001, has been slower and has had different species frequencies and distributions than that predicted by southeastern U.S. ecological succession (SUSES) models. The SUSES models predicted that pines (*Pinus* spp.) would dominate Field 3-412 after about 50 years of succession, and that mixed oaks (*Quercus* spp.) and hickories (*Carya* spp.) would replace the pines and would dominate the field after about 100 to 150 years of succession. However, after 50 years of succession, only about 70 percent of Field 3-412 is wooded, with black cherry (*Prunus serotina*) and laurel oak (*Quercus laurifolia*), particularly in areas that were more than 200 m from the field's 1951—1966 field/forest edges. This and other cases of apparently aberrant woody succession suggest that ecological succession at larger spatial scales (e.g., at the landscape level) may operate differently than that predicted by current ecological succession theory and models, which were based on studies of sites that covered less than 10 hectares. If this is true, then ecological succession theory and models need to be revised to more accurately and realistically explain and predict ecological succession at larger spatial scales, because disturbances are occurring at increasingly larger scales, and revised models can used to develop more effective and efficient natural resource management applications.

INDEX WORDS: Biome, Clonal, Community, Dispersal, Disturbance, Field/Forest Edge, Forest Gap Dynamics, Forest Migration, Hard Mast, Hardwood, Individual, Invasion, Landscape Ecology, Matrix, Oldfield, Patch, Phase, Population, Restoration Ecology, Sere, Soft Mast, Softwood, Stage, Succession, Woody

50 YEARS OF WOODY SUCCESSION AT THE LANDSCAPE LEVEL: AN ABERRANT CASE IN SOUTH CAROLINA, USA

by

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numerous to name here, who have provided a myriad of valuable personal, spiritual, and intellectual lessons (big and small, direct and indirect), and who have made many contributors to our collective, albeit very limited wisdom and knowledge.

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CHAPTER 1

INTRODUCTION

THE PROBLEM

Woody succession in Field 3-412, a 235-hectare (ha) oldfield in southernmost Aiken County, South Carolina, USA, from 1951 through 2001, has been slower and has had different species frequencies and distributions than that predicted by southeastern U.S. Ecological Succession (SUSES) models (Crafton and Wells 1934, McQuilkin 1940, Oosting 1942, Keever 1950, Golley 1965, Golley *et al.* 1994). The SUSES models predicted that early stage pines (*Pinus* spp.) would dominate Field 3-412 after about 50 years of oldfield succession, and that mixed middle and late stage oaks (*Quercus* spp.) and hickories (*Carya* spp.) would replace the pines and would dominate the field after 100 to 150 years of oldfield and forest succession. However, after 50 years of oldfield and forest succession, only about 70 percent of the field is wooded, mostly notably with *Prunus serotina* Ehrh. (black cherry, rum cherry, or wild cherry) and *Quercus laurifolia* Michx. (laurel oak, Darlington oak), particularly in areas that were more than 200 m from Field 3-412's 1951—1966 field/forest edges. This phenomenon has been called "arrested succession" (Golley *et al*. 1994, Pinder *et al*. 1995). All plant species nomenclature throughout this dissertation follows Radford *et al*. 1968, except for *Quercus laurifolia*, which follows Workman and McLeod. (1990).Woody succession is generally defined as the deciduous (hardwood) and evergreen (softwood) tree and shrub components of primary and secondary ecological succession. There are no widely accepted definitions of arrested woody succession. Arrested woody succession can be defined as woody succession that is slower than ecological succession theory and models predict. Field 3-412's woody succession from 1951 through 2001 meets this definition. Arrested woody succession could also be defined as woody succession that is significantly slower than that on other sites nearby or within the same biogeographic region. However, it is noteworthy that no suitable study site analogs or replicates were known to exist in the eastern U.S. for study replication (Archer, personal communication [pers. comm.], 1994; Billings, pers. comm., 1994; Christensen, pers. comm., 1994; Clark, pers. comm., 1994; Golley, pers. comms. 1994-2001; Haines, pers. comms. 1992-2001; Lugo, A.A.L. pers. comm., 1992; Lugo, A.E. pers. comm., 1992, 1994; Odum, pers. comms., 1994-1995; Parrota, pers. comms., 1992, 1999; Peet, pers. comm., 1994; Pickett, pers. comm., 1995; Rios, pers. comms., 1994; Straw, personal observations, 1986-2001; Wein, pers. comms., 1998-2001; White, pers. comm., 1994).

Examples of apparently arrested and/or otherwise aberrant woody succession at larger spatial scales (e.g., the landscape level) have also been found at other sites around the world, including: electrical transmission line right-of-ways in the northeastern U.S. (Pound and Egler 1953, Niering and Egler 1955, Niering and Goodwin 1974, Niering *et al*. 1986, Hill *et al.* 1995); artificial land in Denmark (Andersen 1995); abandoned surface mines and pits in central Europe (Prach and Pyšek 1994); and large oldfields in Venezuela (Uhl *et al*. 1988), Brazil (Nepstad *et al*. 1990, Kolb 1993), East Africa, West Africa, Madagascar, and India (Backéus 1992).

Many of the numerous biotic and abiotic environmental factors that are associated with these different cases of apparently aberrant woody succession have been investigated at various spatial and temporal scales, from individual to landscape levels, and from several years to several decades. The environmental factors that were determined to be most significant include, but are not limited to: soil and/or microclimate conditions (Connell and Slatyer 1977, Backéus 1992); limited plant species pool diversity (Egler 1954, Parrotta 1999); large site size (McQuilkin 1940, Odum 1960, Golley 1965, Parrotta 1999, Golley *et al*. 1994, Pinder *et al*. 1995, Robinson and Handel 2000); and plant dispersal ranges that are adapted to disturbance regimes with generally less extensive natural disturbances (Connell 1961).

Apparently aberrant woody succession has been previously studied in coarser, less spatially explicit detail at the community and landscape levels in several parts of the world (Bormann 1953a, Uhl *et al.* 1988, Nepstad *et al*. 1990, Backéus 1992, Golley *et al.* 1994, Andersen 1995). However, it has not been previously studied in finer, more spatially explicit detail at the landscape level. This is apparently the first study, based upon an extensive survey of ecological and forestry literature, that explicitly examines a case of apparently arrested woody succession at the landscape level. Most previous ecological succession studies, cited in Chapter 2 (Background), surveyed and examined less than 5 ha in fine detail (less than 1m minimum polygon size). This study surveyed and examined about 25 ha in fine detail with 100% field verification (ground truthing). It also surveyed another 100 ha in coarse to moderate detail, also with 100% field verification, to obtain additional data.

Forest migration during the past 22,000 years has been studied in very coarse to coarse detail at the landscape to biome levels in North American, Europe and Asia (Wright 1981, Delcourt *et al*. 1983, Huntley and Birks 1983, Porter 1983, Wright 1983, Velichko *et al*. 1984, Davis 1987, Ritchie 1987, Ruddiman and Wright 1987, Delcourt and Delcourt 1988, Huntley and Webb 1988, Sauer 1988, Delcourt and Delcourt 1991, Clark 1998). These and other forest migration studies extend across distances of more than 1000 km. However, most previous ecological succession studies extended across distances of less than 200 m. This study goes well beyond most previous ecological succession studies by extending across distances of more than 500 m. However, this greater distance only slightly closes the physical gap between community level ecological succession studies and biome level forest migration studies.

The results of this study suggest that the Field 3-412 seed distribution curve “tail” starts somewhere between 100 and 300 m from seed sources, and that the tail declines slowly afterwards (McQuilkin 1940, Portnoy and Willson 1993, Clarke 1998). Similarly, studies of artificial seed dispersal also indicate that most seed dispersal curve tails probably start within 300 m of seed sources (Greene and Johnson 1989, 1993 and 1996). Therefore, this study may more substantially close the conceptual or theoretical gap between community level ecological succession studies and biome level forest migration studies.

Detailed background information on ecological succession theory in general, forest migration theory in general, the SUSES models specifically, Field 3-412-specific biotic and abiotic factors, and previous related Field 3-412 studies are presented in Chapter 2 (Background).

OBJECTIVES

The primary objectives of this study were to:

1. Describe Field 3-412’s woody succession rates, woody species spatial distributions, and woody interspecific associations from 1951 through 2001;
2. Develop testable (falsifiable) hypotheses of Field 3-412’s woody succession rates, woody species spatial distributions, and woody interspecific associations from 1951 through 2001;
3. Test these hypotheses through field observations (natural, non-manipulative experiments, *sensu* Diamond 1986); and
4. Provide results and conclusions that contribute to the body of knowledge of ecological succession and forest migration, and to further beneficial basic (theoretical) and applied research and development in restoration ecology, landscape ecology, conservation biology, sustainable development, and other natural resource management purposes.

The secondary objectives of this study were to:

1. Design field experiments (manipulative experiments, *sensu* Diamond 1986) to more rigorously test falsifiable hypotheses of Field 3-412’s woody succession processes and underlying mechanisms;
2. Propose a unified ecological theory and model encompassing the continuum of primary succession, secondary succession, oldfield succession, forest gap dynamics, and forest migration; and

3. Propose applications of study findings and the unified ecological theory and model in the natural resource management triad of conservation biology, sustainable development, and restoration ecology.

HYPOTHESES

Three testable (falsifiable) hypotheses (H1 through H3) were developed to characterize Field 3-412’s woody succession and examine several mechanistic factors that may explain the woody succession rates, species distribution patterns, and interspecific associations. These hypotheses were developed *a posteriori* from thousands of casual, unrecorded observations over more than 30 years, of small, isolated sites throughout the eastern U.S., Puerto Rico, Venezuela, Canada, and Europe. Each hypothesis has a corresponding null hypothesis ($H1_0$ through $H3_0$). The “Condition/s” in the natural experiments for this study are conceptually analogous to “Treatment/s” in manipulative experiments, in that they reduce the influence of confounding effects on study results. The three hypotheses and their corresponding null hypotheses, conditions, and expectations are:

H1 Soft mast tree species (e.g., *Prunus serotina*, *Melia azedarach* L. (Chinaberry, Pride of India), *Malus angustifolia* (Ait.) Michx. (southern crabapple, wild crabapple), and *Diospyros virginiana* L. (common persimmon)) and shrub species (e.g., *Crataegus* spp. L. (hawthorns), *Rhus* spp. L. (sumacs), and *Prunus* spp. L. (wild plums)) differentially establish and initially dominate most woody patches (defined as a contiguous area of woody vegetation that is at least 1 m high and covers at least 4 m^2 area) that were initially more than 200 m from the nearest woody species seed source/s (e.g., Field 3-412's 1951-1966 field/forest edges); and conversely, pines (*Pinus* spp. L.) and various hard mast tree species (e.g., *Quercus* spp. L. and *Carya* spp. L.) differentially establish and initially dominate most woody patches that were initially less than 200 m from Field 3-412's 1951-1966 field/forest edges

$H1_0$ There are no differences between woody species in the frequency of establishment and initial dominance of woody patches between 0 and 500 m from Field 3-412's 1951-1966 field/forest edge.

Condition: Woody patch's initial distance from Field 3-412's 1951-1966 field/forest edges.

Expectations: A positive correlation (direct relationship) between woody patch initial distance from the nearest field/forest edge and soft mast woody species establishment and initial dominance of these woody patches. The relationship is probably due to the soft mast woody species' dominance of medium-range (100 to 1000 m) and long-range (> 1000 m) dispersal by birds and mammals.

H2 Some woody species have positive associations and spatial correlations with other woody species. That is, some of the woody species that make up the core (defined as the initial tree or shrub of a woody patch) of the woody patch influence the species composition of the woody patch's fringe (defined as the subsequent trees and/or shrubs that establish and grow within and/or around the initial tree or shrub of a woody patch).

$H2_0$ There are no positive or negative associations and spatial correlations between pine, hard mast, and soft mast woody species

Condition: The woody patch core species composition

Expectations: Positive correlations between some woody patch core species and fringe species. The relationship will probably be observed for all core species and *Quercus* spp. fringes, and possibly between some soft mast core and soft mast fringe species. The first expectation is based upon woody succession increasing suitable habitat and cover for hard mast dispersing bird (e.g., *Cyanocitta cristata* (blue jay)) and mammal species over time, and from *Quercus* spp. and *Carya* spp. shade tolerance The second expectation is based upon known bird and mammal species behavior and feeding preferences

H3 Plot percent woody cover between 1951 and 2001 is correlated with soil albedo (surface tone or gray scale values in aerial photographs)

$H3_0$ Plot percent woody cover between 1951 and 2001 does not vary with soil Albedo

Conditions: The soil albedo in 1943 and 1951, as a proxy for soil fines (i.e., silt- and clay-sized particles) content, moisture availability, and nutrient status.

Expectation: Negative correlations (inverse relationship) between soil albedo and soil fines content, moisture availability, and nutrient status, and between soil albedo and plot percent woody cover between 1951 and 2001. These expectations were based upon previous studies where darker albedos were often associated with higher soil fines content, fertility, and moisture availability, all factors that can facilitate woody succession.

SIGNIFICANCE

Understanding how woody succession has operated in Field 3-412 can directly contribute to understanding how woody succession operates at the landscape level elsewhere in the southeastern U.S and elsewhere in the world. If woody succession at the landscape level is indeed slower than that predicted by ecological succession theory and models, then we can revise the theory and models to more accurately and realistically explain and predict woody succession at the landscape level (Levins 1966, Armour and Williamson 1988).

Furthermore, more accurate and realistic ecological succession theory and predictive models, with suitable species data bases, can be used for species selection and planting location/spacing to improve various practical natural resource management applications to assist or facilitate ecological succession to reclaim, rehabilitate, and restore large (extensive) and/or degraded, damaged or destroyed sites and ecosystems (Ewel 1980, Bradshaw 1984, Allen and Hoekstra 1987, Diamond 1987, Uhl 1987, Lugo 1988, Uhl *et al.* 1988, Westoby 1989, Luken 1990, Nepstad *et al.* 1990, Polster 1991, Parrotta 1992, Kolb 1993, McClanahan and Wolfe 1993, Robinson and Handel 1993, Brown and Lugo 1994, Prach and Pyšek 1994, Aide *et al*. 1995, Hannah and Bowles 1995, Parrotta 1995, Lugo 1997, Palmer *et al*. 1997, Parrotta *et al*. 1997a and 1997b, Shigesada and Kawasaki 1997, Aldrich and Hamrick 1998, Parrotta 1999, Prach *et al*. 1999, Toh *et al*. 1999, Robinson and Handel 2000, Prach and Pyšek 2001). Large and/or intensely disturbed sites will probably become increasingly common in the future because of increasing farm size, agricultural mechanization, and agricultural expansion into areas with forests, marginal lands, and/or more variable climates (Rotmans and Swart 1991, Dodd 1994, Golley *et al.* 1994, Milton *et al*. 1994, Hannah and Bowles 1995, Vitousek *et al*. 1997); and more widespread disturbances from surface mining (e.g., coal (lignite through bituminous), bauxite, kaolin, phosphates, sand and gravel, tar sands), waste disposal sites (landfills), exotic insect and pathogen transport and outbreaks, terrorism and warfare (biological, chemical, nuclear), and global climate change.

CHAPTER 2

BACKGROUND

INTRODUCTION

This chapter covers background information to better understand the study's purpose, context and significance, methods, results, and conclusions. This includes surveys of the broad personal context for this study; of the broader professional context, the many other researcher's previous studies that provide the basis and ancillary data sources for this study; and finally, of an even broader context, i.e., the history, basic (pure) and applied science, concepts, theory, applications, morals, ethics, and implications. Key terms and concepts are identified by bold text.

ORIGINS OF THIS STUDY – A Personal Story

As far back as I can remember, I have always had an insatiable desire to thoroughly understand how people think and work, how nature works, how we work with nature, how it does not always work out so well, how to make it work better, and how to fix what we have broken; and a compelling desire to share love, wisdom, knowledge, and good works for the benefit of all concerned. With my innate interests and attributes, it seems only natural for me to be very interested in restoration ecology, landscape ecology, seed dispersal, and woody succession, as well as to be very interested many other topics and subtopics, human and natural

While traveling across the United States of Venezuela in 1985, through extensive, deforested areas in the Coastal Range and Andes Mountains, I observed many positive and negative, direct and indirect, environmental effects of deforestation, tillage, and grazing. I particularly noticed that although the natural recovery process of ecological succession was operating, most of the woody succession was apparently arrested or inhibited, that the natural recovery process was literally an “uphill battle” on several different levels. I decided then that I would someday study arrested ecological succession and develop new and improved natural resource management applications to assist or facilitate ecological succession to reclaim, rehabilitate, and/or restore lands, waters, flora, fauna and microbes.

Between 1986 and 1994, while I was working throughout the eastern and central U.S. and also consulting with researchers from Texas to New Jersey, and New York to Venezuela (Archer, personal communication [pers. comm.], 1994; Billings, pers. comm., 1994; Christensen, pers. comm., 1994; Clark, pers. comm., 1994; Golley, pers. comms. 1994-2001; Haines, pers. comms. 1992-2001; Lugo, A.A.L. pers. comm., 1992; Lugo, A.E. pers. comm., 1992, 1994; Odum, pers. comms., 1994-1995; Parrota, pers. comms., 1992, 1999; Peet, pers. comm., 1994; Pickett, pers. comm., 1995; Rios, pers. comms., 1994; Straw, personal observations, 1986-2001; Wein, pers. comms., 1998-2001; White, pers. comm., 1994), I had identified several potentially suitable sites for this study in Venezuela, Puerto Rico, and South Carolina.

The site selection criteria used to evaluate these and other potential study sites favored larger sites with sufficient woody succession, minimal post-abandonment human-induced (artificial) disturbance (e.g., mowing, disking, plowing, grading, controlled/prescribed burns; herbicide, pesticide, and fertilizer application), many previous relevant studies, and many historic aerial photographs. The criteria and underlying rationale are discussed in more detail in the next section and in Chapter 3 (Methods).

FIELD 3-412 STUDY SITE

In late 1994, I selected Field 3-412 (South Carolina, Figures 2-1 through 2-3) to be the primary site for this study because it best met the site selection criteria that I had established:

- **Large (i.e., > 64 ha), Compact Site:** Field 3-412 is both large (141.7 ha in 1951) and compact (relatively simple margins, major-to-minor axis length ratio of about 2.0), with open barren areas that were initially at least 500 m from the nearest field/forest edges (Figure 2-4);
- **Limited Post-Abandonment Disturbance:** Field 3-412 had relatively little post-abandonment artificial disturbance (Figure 2-5). These disturbances were adequately documented so that they could be either included in or excluded from the analyses;
- **Sufficient Woody Succession:** Field 3-412 had enough post-abandonment succession (contrast Figures 2-4 and 2-6) to yield a sufficient amount of data for analyses, but not too much succession so as to be too complicated and difficult to analyze;

- **Previous Relevant Studies:** Many previous ecological succession studies were done in Field 3-412 from 1951 through the present (Odum 1960, Golley 1965, Golley and Gentry 1966, Pinder 1971, Coleman 1973, Spring *et al*. 1974, Pinder 1975, Wiegert and McGinnis 1975, Haines 1977, Pinder 1977, Haines 1978, Odum *et al*. 1984, Gabrielson 1985, Monk and Gabrielson 1985, Friebaum 1987, Collins and Pinder 1990, Golley *et al*. 1994, Pinder *et al*. 1995; Wein, pers. comms., 1998-2001; Davis, pers. comms., 1998-2001). These studies provided an extraordinary foundation for this study, with extensive data on the grass and pine phases of Field 3-412's oldfield succession;
- **Historic Aerial Photographs:** SREL's GIS Laboratory provided large-scale (> 1:50,000 scale, mostly between 1:16,000 and 1:40,000 scales) black-and-white, color, and color infrared (CIR) aerial photographs of Field 3-412 and surrounding areas for 25 different years from 1943 through 1998, which greatly facilitated this study; and
- **Research Support Facilities:** The University of Georgia, Savannah River Ecology Laboratory (SREL) provided excellent, conveniently located (about 15 km north of Field 3-412) research support facilities, including a well-appointed reference library.

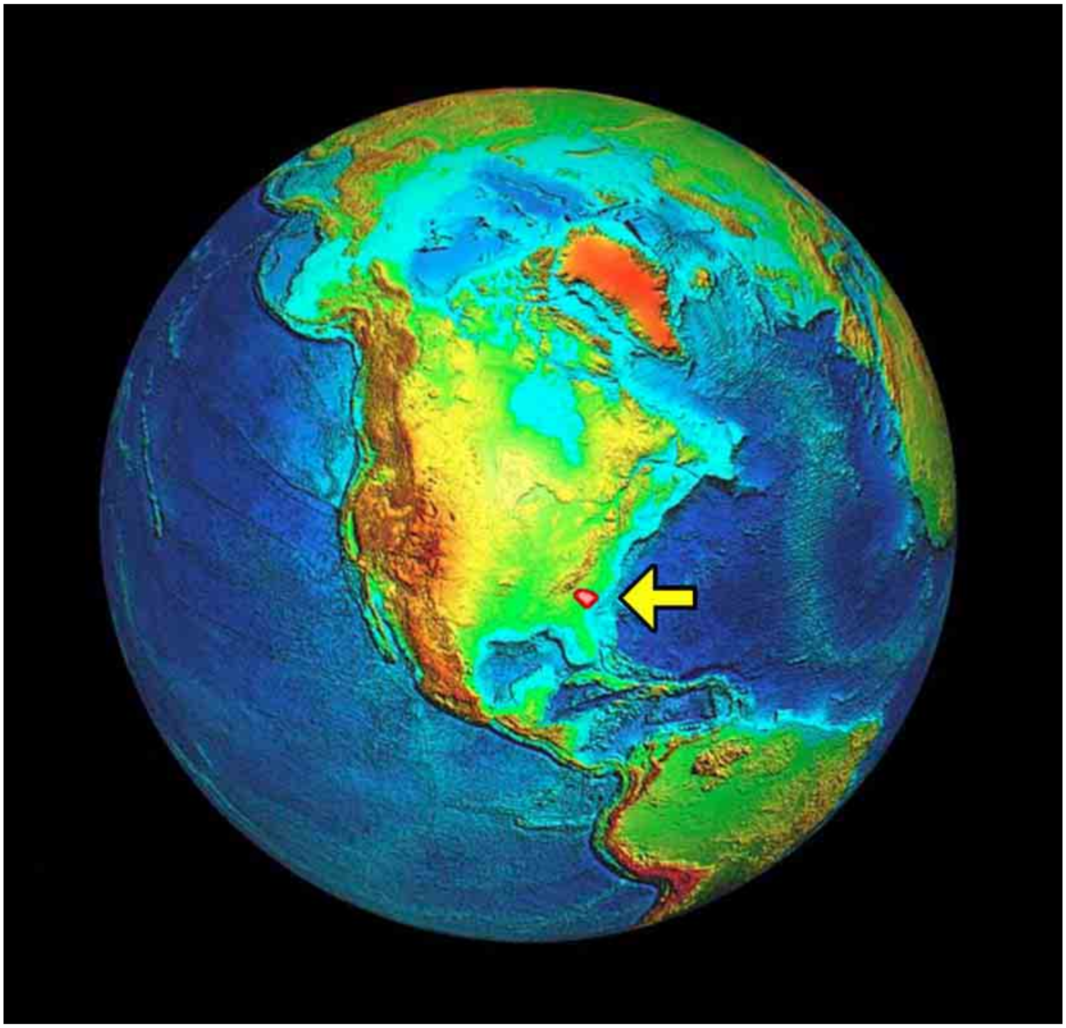

Figure 2-1. South Carolina’s location in North America (adapted from NOAA 2001).

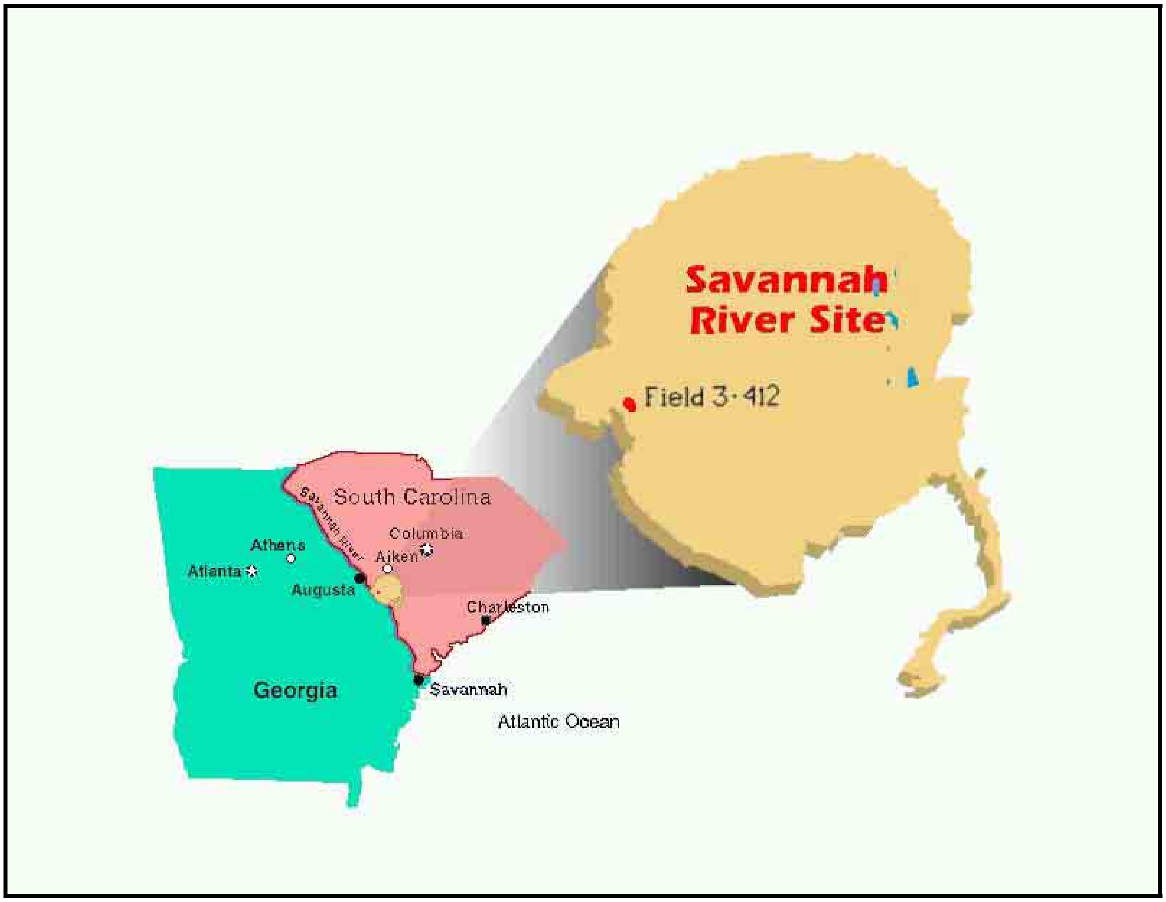

Figure 2-2. SRS's location in South Carolina (adapted from SRS 2001).

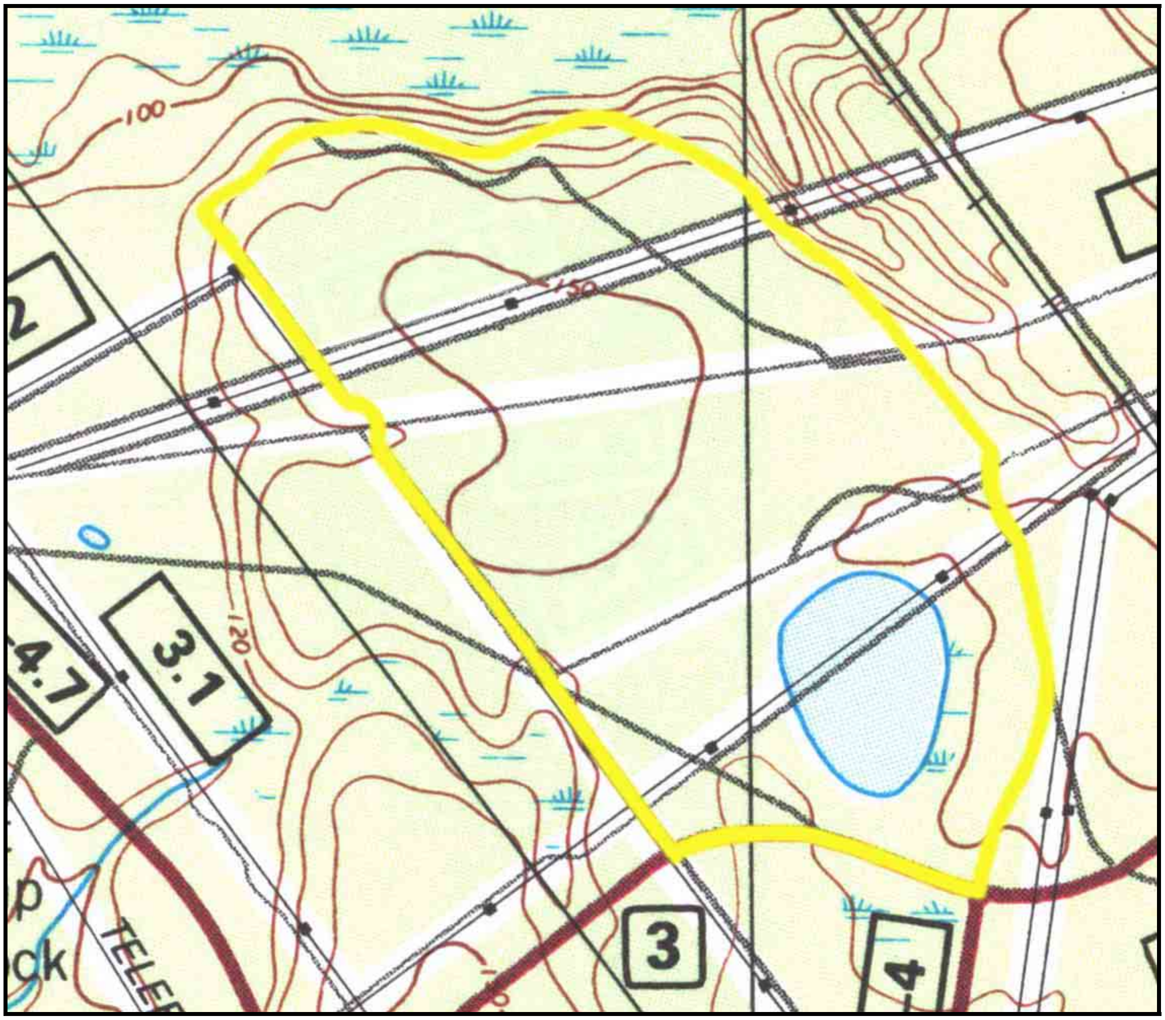

Figure 2-3. Field 3-412's approximate 1951 boundary (yellow line) and topography(USGS and USDOE 1987).

Figure 2-4. Field 3-412 and surrounding areas in 1951 (University of Georgia, Savannah River Ecology Laboratory).

Figure 2-5. Major Field 3-412 disturbance locations from 1951 through 2001. Color code: red – 1950’s, orange – 1960’s, yellow – 1970’s, green – 1980’s, and blue – 1990’s.

Figure 2-6. Field 3-412 and surrounding areas in 1998 (University of Georgia, Savannah River Ecology Laboratory).

Field 3-412 was initially a 141.7 ha oldfield in 1951, on the U.S. Atomic Energy Commission-Savannah River Operations Office's (AEC-SROO) 80,267 ha (803 km^2 or 310 mi^2) Savannah River Plant (SRP), in southernmost Aiken County, South Carolina, USA. Field 3-412 was named "SREL Reserve Area #8" in 1968. The SRP was designated as the nation's first National Environmental Research Park in 1972. The former AEC was integrated into the newly created U.S. Department of Energy (DOE) in 1977, and the SRP was renamed the Savannah River Site (SRS) in 1989.

Field 3-412 (SREL Reserve Area #8) was renamed DOE Research Set-Aside Area #1 in 1989, and was expanded with the addition of forested areas adjacent to Field 3-412, to create the present 234.6 ha ecology research reserve, which is managed under the SRS Set-Aside Program. These add-on areas were excluded from this study because of the more than 20 years of intensive, forestry-related disturbances in these areas (Davis and Janecek 1997, Davis 1998).

Before 1950, Field 3-412 was part of more than 600 ha of contiguous farm fields that usually produced cotton, corn, peanuts, peas, and beans (Figure 2-4, SREL 1951). These farm fields were agriculturally abandoned in 1951 when the AEC created the SRP (Odum 1987, Davis and Janecek 1997).

In 1951, Field 3-412's nearest woody seed sources were:

- A small cluster of hardwoods (farmstead woodlot) in the northern part of the field;
- Eight isolated hardwood trees (removed by 1955) widely scattered throughout the field; and

- Bottomland hardwood and mid-slope pine-hardwood forests to the west along an unnamed intermittent tributary of the Savannah River, and to the north and northeast along Upper Three Runs and its unnamed intermittent tributary (Figure 2-3).

Since 1951, parts of Field 3-412 have been disturbed to construct and maintain roads, water mains, power transmission lines, and their rights-of-way, and for biological and ecological field experiments (Figure 2-5).

Field 3-412 was informally “set-aside” for ecological research in 1952, and was named one of several “reserve areas” in 1963, which provided limited protection from human-induced (artificial) disturbances that would introduce additional confounding factors and influences into biological and ecological processes. Field 3-412 was formally designated as “SREL Reserve Area #8” in 1968, which provided more protection from artificial disturbances other than those from SREL-approved biological and ecological research. The SRP was designated as the nation’s first National Environmental Research Park in 1972. Field 3-412 was renamed DOE Research Set-Aside Area #1 in 1989, expanded to 234.6 ha, and subsequently managed under the SRS Set-Aside Program. The SRS Set-Aside Program objectives stipulate that the Set-Aside Areas are primarily for non-manipulative research, to protect the Set-Aside Area’s long-term research value (Hillestad and Bennett 1982, Davis and Janecek 1997).

Since the early 1960's, the U.S. Forest Service has planted, intensely managed, and harvested *Pinus taeda* and some *Pinus palustris* stands in the forest subcompartments that surround three quarters of Field 3-412 (Davis and Janecek 1997). All plant species nomenclature throughout this dissertation follows Radford *et al*. 1968, except for *Quercus laurifolia*, which follows Workman and McLeod. (1990). These managed pine stands are within 100 m of the northwest, east, southeast, south, and southwest margins of Field 3-412, and their trees have contributed to the seed rain in these adjoining margins. However, these seed rain effects are masked by roads and road right-of-way (ROW) vegetation management in the first 20 to 50 m from the pine stand edges (Figures 2-5 and 2-6).

Field 3-412's general history of woody succession from 1951 through 2001 is discussed in Chapter 4 (Results). When I started my initial dissertation fieldwork in 1994, Field 3-412's vegetation cover was about 70% woody (i.e., 25% pines and 45% hardwood trees and shrubs) and 30% herbaceous (forbs, grasses, and vines).

By 2001, after only seven years, Field 3-412's vegetation cover changed to about 80% woody (i.e., 25% pines and 55% hardwood) and 20% herbaceous. Figure 2-6 shows Field 3-412's woody cover in 1998, the most current aerial photograph available at this time. The pine cover showed no appreciable net change, with pine gains by invasion into open herbaceous areas being essentially offset by pines losses as hardwoods replace pines. The hardwood cover increased by about 22% in only seven years, mostly through forest succession, invasion into woody patches, and lateral growth from woody patches into adjacent open herbaceous areas.

FIELD 3-412 ECOLOGICAL SUCCESSION STUDIES

Field 3-412 has an incomparably large number of previous ecological succession studies. Such studies are an essential basis for any short-term study of long-term ecological succession, providing the data that are needed to make more accurate and realistic deductions about the past and present biological mechanisms and biological/ecological processes that are behind the present ecological succession patterns.

The more notable Field 3-412 ecological succession studies are Odum's work on forb succession starting in 1951, Golley's work on grass and pine succession starting in 1959, and Pinder's work on herbaceous and pine succession starting in 1968. References to these and related Field 3-412 studies include: Odum and Hight 1957, Odum 1960, Odum and Golley 1963, Golley 1965, Golley and Gentry 1966, Pinder 1971, Coleman 1973, Spring *et al*. 1974, Pinder 1975, Wiegert and McGinnis 1975, Haines 1977, Pinder 1977, Haines 1978, Odum *et al*. 1984, Gabrielson 1985, Monk and Gabrielson 1985, Friebaum 1987, Odum 1987, Collins and Pinder 1990, Golley *et al*. 1994, and Pinder *et al*. 1995.

These ecological succession studies were extremely important for their extensive data on Field 3-412's oldfield succession during the 43 years before this study's fieldwork started. These data included early stage (forb and grass phases) species composition, distribution, and interaction that cannot be obtained from non-existent plant remains (few remains after 10 years, almost no remains after 25 years), and cannot be reliably extracted from the available historic black-and-white, color, and color infrared aerial photographs.

These and about 240 other Field 3-412, SREL, and SRS studies were also important for their extensive ancillary data on many of Field 3-412's early, middle, and late stage plant species (and also the many interacting mammal, bird, insect, and microbial species). This literature includes data on the dominant and subordinate forb, grass, and woody species' life history, phenology, physiology, tolerances, reproduction, dispersal, emergence, competitive strengths and weaknesses, growth, and structure (architecture). The following discussion chronologically summarizes the previous Field 3-412 ecological succession studies that are the basis for this study. Plant species nomenclature follows Radford, Ahles and Bell (1968).

Early Stage Studies

The first sequence of Field 3-412 ecological succession studies started in the early 1950's and focused on the early stage (i.e., forb and grass phases) of oldfield succession (Odum 1960, Golley 1965, Golley and Gentry 1966, Pinder 1971, Pinder 1975, Wiegert and McGinnis 1975, Pinder 1977, Gabrielson 1985, Monk and Gabrielson 1985, Odum 1987, Collins and Pinder 1990). These studies included field observations and manipulative (e.g., species removal) experiments concerning the biological and ecological characteristics (i.e., species frequency, density, dimensions, biomass, productivity, chemical composition, nearest neighbor, litter, soil chemistry and seed bank) of the site's early stage herbaceous forb and grass species.

Field 3-412's early stage herbaceous species composition included:

Forb (annual and biennial) Phase (1 to 5 years after abandonment):

Ambrosia artemisiifolia L. (ragweed)

Aster spp. L. (aster)

Gnaphalium obtusifolium L. (rabbit tobacco)

G. purpurem L. (purple cudweed)

Haplopappus divaricatus (Nuttall) Gray (yellow aster)

Heterotheca subaxillaris (Lam) Britton and Rusby (camphorweed)

Leptilon (Erigeron) canadensis L. (horseweed)

Rumex hastatulus Baldwin ex. Ell (sheep sorrell)

Grass (perennial, clump-forming) Phase (3 to 25 years after abandonment):

Andropogon ternarius Michx. (broomsedge)

A. virginicus L. (broomsedge)

Aristida purpurascens Poiret (arrowfeather)

Cynodon dactylon (L.) Pers. (Bermuda grass)

Eupatorium capillifolium (Lam.) Small (dog fennel)

Leptoloma cognatum (Shultes) Chase (Fall witchgrass)

Lespedeza spp. Michx. (Lespedeza)

Panicum spp. L. (panic grasses)

Many remnant forbs, but in stunted form

Middle Stage Studies

The second sequence of Field 3-412 ecological succession studies started in the early 1960's and focused on the middle stage, pine phase of oldfield/woody succession (Spring *et al*. 1974, Friebaum 1987, DeSteven 1991a and 1991b, Golley *et al*. 1994, Pinder *et al*. 1995). These studies included field observations concerning the biological and ecological characteristics (i.e., dimensions, age, seed production; seedling establishment, survival, and growth; oldfield size, seed dispersal curve, arrested pine succession) of Field 3-412's pine species:

Pine Phase (10 to 75+ years):

Pinus taeda L. (loblolly pine)
P. palustris Mill. (longleaf pine)
Many remnant forbs and grasses

Middle & Late Stage Studies

The third sequence of these Field 3-412 ecological succession studies started in the mid-1990's and focuses on the middle stage, pine and hardwood phases of woody succession, and to some extant, also on the late stage woody succession and transition to forest (this study). These studies included field observations concerning the species biological and ecological characteristics (i.e., dimensions, regeneration, understory cover; oldfield size, seed dispersal curve, arrested woody succession) of Field 3-412's pine and hardwood (softmast and hardmast) species:

Early (First) Hardwood Phase (10 to 75+ years):

Crataegus spp. L. (hawthorns)
Prunus serotina Ehrh. (black cherry, rum cherry, or wild cherry)
Prunus spp. L. (wild plums)
Rhus spp. L. (sumacs)
Some remnant pines

Middle (Second) Hardwood Phase (25 to 150 years):

Quercus laurifolia Michx. (laurel oak, Darlington oak)

Quercus nigra L. (water oak)

Quercus laevis Walter (turkey oak)

Quercus stellata Wang. (post oak)

Some remnant pines and early hardwoods

Late (Third) Hardwood Phase (50 to 250+ years):

Carya glabra (pignut hickory)

Carya tomentosa (mockernut hickory)

Liquidambar styraciflua L. (sweetgum)

Liriodendron tulipfera L. (yellow poplar, tulip poplar, tuliptree)

Quercus spp. L. (more mesic oaks [*Quercus alba* {white oak}, *Quercus falcata* {southern red oak}, *Quercus velutina* {black oak}] in moister sites; more xeric oaks [*Quercus incana* {bluejack oak}, *Quercus marilandica* {blackjack oak}] in drier sites).

Some remnant early and middle hardwoods

The potential natural vegetation for Field 3-412 is complicated. Field 3-412 is on a mesic river terrace, in a transition zone between several physiographic units: The Piedmont, where southern Appalachian and Coastal Plains (includes the Aiken Plateau and Sand Hills) woody species intermingle; the Coastal Plains (includes Aiken Plateau and Sand Hills), with its generally more xeric and mesic (-) woody species; and the Southern Floodplain or Bottomland Forest , with its typically more hydric and mesic (+)

woody species (Bartram 1791, Braun 1950, Quarterman and Keever 1962; Barry 1980, Reed 1988, Kovacik and Winberry 1989, Sharitz and Mitsch 1993, Skeen *et al*. 1993, Ware *et al*. 1993, Godfrey 1997).

The potential natural vegetation of the Piedmont and Upper Coastal Plain uplands in the southeastern United States is southern mixed hardwood forest, i.e., oak-hickory associations with some green ash, white ash, American beech, flowering dogwood, winged elm, American holly, loblolly pine, persimmon, sweetgum, tulip poplar, and black walnut (Bartram 1791, Braun 1950, Quarterman and Keever 1962; Barry 1980, Kovacik and Winberry 1989, Skeen *et al*. 1993, Ware *et al*. 1993, Godfrey 1997).

The potential natural vegetation of the Southern Floodplain or Bottomland Forest in the southeastern United States is a cypress-tupelo forest association with water ash, red bay, water elm, sweetbay magnolia, and black willow (Bartram 1791, Braun 1950, Quarterman and Keever 1962; Barry 1980, Kovacik and Winberry 1989, Sharitz and Mitsch 1993, Godfrey 1997).

Field 3-412 is a mesic river terrace with woody species composition that is generally more characteristic of upland forests. However, the lower elevation northern and eastern parts of Field 3-412, as well as the inner rim of Ellenton Bay (a 11.3 ha Carolina bay in southeastern Field 3-412), have narrow zones with woody species compositions that are more characteristic of floodplain or bottomland forests. The closest likely matches to Field 3-412’s future woody species composition are suggested in several sites elsewhere on SRS and Aiken County, and are discussed in Chapters 4 (Results) and 5 (Conclusions).

OTHER STUDY SITES

Additional study sites were sought and evaluated for their suitability as replicate study sites. These additional sites would have provided a reasonable trade of space for time (Pickett 1989), to give this study greater depth and breadth. Unfortunately, of the many potential sites that were evaluated, none of them adequately met the site selection criteria.

All of these sites were either too small (< 64 ha), they had too much or too little woody succession, they were too frequently and/or intensely disturbed, their land use history was too uncertain, they were not the subject of previous ecological succession studies, and/or aerial photograph coverage was inadequate to reliably reconstruct the historic woody succession and account for the confounding factors. Nevertheless, several of these sites were partially surveyed and photographed for casual comparison with Field 3-412 data, maps, and photographs.

SRS Oak-Hickory Set-Aside Areas. Two SRS Oak-Hickory Set-Aside Areas (Area #5, a.k.a. Oak-Hickory Forest # 1; and Area #12, a.k.a. Oak-Hickory Forest # 2) are located about 15 km to the northeast of Field 3-412, in north central SRS (Figure 2-3). Their topography, soils, land use history, vegetation, and other characteristics are described at length in Davis and Janecek (1997). Both of the sites have some areas with the same soils (i.e., Blanton sands, Orangeburg loamy sands, Troup sands, and Lucy sands) that are present in Field 3-412. However, these areas are located on valley walls (sloped sides) and narrow strips of the adjacent uplands, unlike Field 3-412, which is on a river terrace.

The oak-hickory covered portions of both Oak-Hickory Set-Aside Areas have extended shapes (not being relatively compact, like Field 3-412) where the aforementioned soil areas were almost entirely within 200 m of the nearest field/forest edge. Their land use history probably involved less deforestation than Field 3-412, as few valley walls were completely deforested. The greater heights and Dbhs of trees growing on the valley walls support this conjecture. Although these Oak-Hickory Set-Aside Areas do not meet the site selection criteria, and although they have many dissimilarities with Field 3-412, as products of the local and regional species pools, they provide indications of Field 3-412's future "climax" forest species composition.

Hitchcock Woods. An approximately 800-ha, privately owned, publicly accessible recreational area in the City of Aiken, South Carolina, located about 35 km north of Field 3-412. Hitchcock Woods includes several dozen former farm fields, wooded fence lines, and woodlots (Wilds *et al*. 1998). Several Hitchcock Woods sites have the same soils as Field 3-412, but these sites are on gently rolling hills, with greater deep drainage (Way 1978, Brady and Weil 1996).

The Hitchcock Woods sites' land use histories are dissimilar to Field 3-412's land use history, with many older, smaller former farm fields that were probably within 200 m of the nearest wooded fence line or field/forest edge. This conjecture is consistent with local land uses at the time of the sites' agricultural abandonment, around 1900 (Fite 1984, Wilds *et al*. 1998). This conjecture is also supported by the observed heights and Dbhs of trees growing in and between the former farm fields.

However, unlike Field 3-412, the Hitchcock Woods sites are treated with prescribed or controlled burns for longleaf pine regeneration and wildfire management, with a 2 to 5 year burn interval (rotation) for uplands and a 4 to 8 year burn interval for slopes (Wilds *et al*. 1998; Shealy and Berger, pers. comms., 2001). Although these sites also have many dissimilarities with Field 3-412, like the SRS Oak-Hickory Set-Aside Areas, they provide an indication of Field 3-412's future "climax" forest species composition.

Several hundred other potential study sites were evaluated in Pennsylvania, Maryland, North Carolina, South Carolina, Georgia, Florida, and Louisiana during my off-duty hours while working in these States with the Federal Emergency Management Agency (FEMA). All of these sites were either too small, had too much or too little woody succession, they were too disturbed or the disturbance history could not be determined, their land use history was uncertain, they were not previous studied, and/or aerial photographs were inadequate to reliably reconstruct the historic woody succession and account for confounding factors. Therefore, these sites were not surveyed.

OTHER SITE ECOLOGICAL SUCCESSION STUDIES

Numerous biological and ecological studies from many other sites (excluding those previously described) elsewhere in the Carolinas, the U.S., and the world were researched to obtain a broad range of relevant data and concepts, covering a wide range of spatial and temporal scales, from the individual to the biome, and from the moment to the millennia (Bard 1952, Bormann 1953a, Quarterman 1957, Davis and Cantlon 1969, Buell *et al* 1971, Nicholson and Monk 1975, Christensen 1977, Whitford and Whitford 1978, Keever 1979, Peet and Christensen 1980, Werner and Harbeck 1982, Keever 1983, McDonnell and Stiles 1983, Monette and Ware 1983, Harrison and Werner 1984, Forman and Godron 1986, Guevara *et al*. 1986, McClanahan 1986, McDonnell 1986, Inouye *et al*. 1987, Archer *et al*. 1988, Hoppes 1988, Uhl *et al*. 1988, Belsky *et al*. 1989, Brown and Archer 1989, Hardt and Forman 1989, Myster and Pickett 1990, Ben-Shahar 1991, Burton and Bazzaz 1991, Facelli and Carson 1991, Gill and Marks 1991, Scanlan and Archer 1991, Skarpe 1991, Debussche and Lepart 1992, Guevara *et al*. 1992, Kellman and Kading 1992, Myster and Pickett 1992a, Myster and Pickett 1992b, Kolb 1993, McClanahan and Wolfe 1993, Myster and Pickett 1993, Robinson and Handel 1993, Archer 1994, Belsky 1994, Facelli 1994, Inouye *et al*. 1994, Orwig and Abrams1994, Ribbens *et al*. 1994, Archer 1995, Forman 1995, Li and Wilson 1998, Wilds *et al*. 1998, Duncan and Chapman 1999 , Riley and Jones 2000, Robinson and Handel 2000).

These many studies are incorporated into and cited throughout this study, with general discussion of their cumulative, “universal” relevance for broader context and deeper insight.

Although the ecological succession mechanisms and processes around the world may involve different topography, soils, climate, species (flora, fauna, and other), and other factors, the basic ecological succession concepts probably apply to them, as is generally described in the rest of this chapter. The following discussion is a summary of ecological succession concepts and theory from their probable origins to its present state, the various aspects and types of ecological succession, and the many synergistic abiotic (physical) and biotic (biological) factors that comprise ecological succession-related mechanisms, processes, and patterns around the world in general, and in Field 3-412 specifically.

ECOLOGICAL SUCCESSION THEORY

This study raises conceptual questions about the accuracy and realism of the southeastern U.S. ecological succession (SUSES) models specifically, and since the SUSES models are largely based on general ecological succession theory, this study also raises conceptual questions about the accuracy and realism of ecological succession theory and models in general. If we are to revise ecological succession theory and models so that they are more accurate and realistic, then we should thoroughly understand the concepts, history, and rationale to make sounder recommendations, cases, and judgments.

Ecological succession is generally defined as the directional change of community species composition, distribution (frequency and density), and structure over time, initiated by allogenic (external) environmental changes caused by natural and/or human agents (e.g., stresses, disturbances), and influenced by the community’s species' (i.e., flora, fauna, and others) autogenic (inherent) properties (e.g., physiology, tolerances, growth form, litter, allelopathy, defenses, reproduction, propagation). The following paragraphs discuss various aspects and types (subsets) of ecological succession.

Nature abhors vacuums. Before, during and after nature- and human-induced stresses and disturbances, individual organisms try to continue their inherent (genetically programmed) processes. The organisms’ processes are affected by their habitat, which is invariably heterogeneous to some degree, from the atomic to the landscape scales, i.e., the organisms’ environmental conditions vary spatially, from point to point, and temporally, from moment to moment (Denslow 1980, Saunders 1980, Sousa 1980, Facelli and Carson 1991, Gross *et al*. 1995, Pickett and Cadenasso 1995, Pedersen 1998).

The individual organism's processes directly and indirectly affect the individuals themselves, other individuals within their population (intraspecific interactions), other individuals within other species populations (interspecific interactions), and also their habitat (e.g., environmental conditions, biogeochemical cycling, habitat carrying capacity) (Bazzaz 1975, 1979; Belsky *et al*. 1989, Ben-Shahar 1991), Burton and Bazzaz 1991, Skarpe 1991, Belsky 1994).

Life is so persistent and tenacious that it advances as far as possible, sometimes beyond what may be practical, it retreats only when possible and seemingly necessary, and often returns afterwards, and finally, it dies in place or away if unavoidable (Connell and Sousa 1983). Life has been found in various forms in some of the most remote, inhospitable locations on Earth, as evidenced by various microbial "extremophiles" that have been found more than 10 km above the surface, more than 5 km below the ocean surface, more than 4 km below the ground surface, at temperatures from about 0ºC to 113ºC, in pHs from < 2.0 to > 10.0 , and in extremely nutrient poor (i.e., oligotrophic) habitats, (e.g., Antarctic sea ice) (Madigan and Marrs 1997).

Individual organisms synergistically push and/or pull their communities' composition along various dynamic, shifting, multidimensional (*sensu* Hutchinson 1957) successional **pathways** or **trajectories** (Cattelino *et al*. 1979, Myster and Pickett 1990), progressing or regressing towards one or more (multiple) possible steady state "climax" (Clements 1916, May 1977) or "subclimax" communities (Tansley 1935, Laycock 1991) in a non-equilibrium state, landscape level **mosaic** (Sutherland 1974, Shugart 1984, Sutherland 1990, Law and Morton 1993), over a period of time ranging from as little as a few weeks, months, or years, to as much as several decades, centuries, or millennia

(Delcourt *et al*. 1983, Urban *et al*. 1987). Succession trajectories can also be “directed” towards a selected semi-steady state climax or subclimax community (Luken 1990).

You never step into the same river twice. Considering that landscape matrices are heterogeneous at levels atomic through landscape, that organisms live in a garden-restaurant, where everything grows and is also on the menu, and with stochastic events (e.g., insolation (incoming solar radiation), precipitation, disturbances), and the practically infinite number of points and continual scales of factor values, it’s doubtful that any community would follow the exact same successional trajectory and reach the exact same end point(s) after any two comparable disturbances. Presently, I think that highly precise, predictive ecological succession models (for trajectory and end point(s)) are practically impossible to finish without inordinate cost and effort.

However, considering the strength of the ecosystem’s “Attractor”, i.e., the synergy of a community’s species’ inherent mechanisms, processes, and characteristics, and that many physical and biological factors and events tend to cancel each other out over time, and with sufficient data and algorithms (probably still very complex by some/many people’s standards), I think that “satisfactory” (accurate and realistic), general (coarse scale) predictive ecological succession models are reasonably possible. Considering humanity’s historic record and our current, collective rate of population growth and environmental degradation and destruction, time for effective action is critical, and is essential for humanity’s long-term survival and well-being.

Ecological succession may have several distinguishable, typically sequential **successional stages**, **seres**, and/or **phases** (Oosting 1942). However, community composition and structure changes during succession are usually more subtle and continual than distinct and discrete, so the successional stage and phase boundaries may be fuzzy and porous.

Succession rates usually vary temporally and spatially (Clements 1916; Gleason 1926; Tansley 1935; McQuilkin 1940, Bornkamm 1981, Pickett *et al.* 1987a). Succession rates generally are fastest under moderate environmental conditions, increase with fertility, and decrease with time (Prach *et al*. 1993, 1999). There are no standard, quantified categories or classifications of succession rates.

"**Arrested succession**" has usually been used as a relative term rather than an absolute term. Arrested succession is most frequent in areas with environmental extremes (Prach et al. 1993, 1999). Succession rates can be arrested (inhibited, retarded) naturally or artificially, as well as accelerated or facilitated naturally or artificially (Luken 1990).

Secondary succession is generally defined as a community's recovery after a disturbance, where the substrate previously supported life (e.g., oldfields, grazing/overgrazing, grass/forest fires, forest gaps, timber harvests, earthflows, mudflows). This contrasts with primary succession, where the substrate did not previously support life (e.g., some surface mines/pits/quarries, aggregate piles, covered landfills; new sand dunes, stream/river point bars, overwash fans, glacial moraines and outwash plains, volcanic eruptions, comet/meteor impacts).

Secondary succession has a continual scale or continuum of degrees. The degree in each case depends upon disturbance extent, frequency, and intensity; soil and climate characteristics, species characteristics, interspecific dynamics, community composition and structure, and other physical and biological factors. More intense, extensive disturbances can create droughty, nutrient-poor, almost seedless substrates that have secondary succession that is comparable to primary succession.

Oldfield succession is the secondary succession in abandoned agricultural fields (Crafton and Wells 1934). Oldfield plant communities can range from sparse grasslands to open savannas, and may remain stable or eventually become forests.

Woody succession is the deciduous (hardwood, soft and hard mast) and evergreen (softwood) tree and shrub component of oldfield and secondary succession.

Forest succession is the deciduous and evergreen tree component of ecological succession within a forest stand, where gap dynamics dominates, e.g., forest regeneration consists mostly of shade tolerant dominant “climax” tree species that grow slowly in the shaded understory, and quickly grow up and into gaps that are formed when canopy layer trees die and/or are damaged, destroyed, or dislocated.

ECOLOGICAL SUCCESSION THEORY HISTORY

Obscure Origins. Ecological succession concepts probably arose at least 9,000 years ago, independently in various areas around the world, from logical conclusions based upon many casual observations of “natural experiments” and possibly also from some manipulative trial and error experiments. These applied ecological concepts were probably an integral part of ancient indigenous knowledge of many cultures around the world. Hunter-gatherers may have applied such concepts in vegetation management to increase habitat carrying capacity for game species. Farmers probably applied such concepts in vegetation management to increase crop yields and control invasive, undesirable "weeds".

Although those who hunted and farmed more than 9,000 years ago probably noticed and partly understood the natural processes and patterns of what we call ecological succession, and although they probably applied their understanding to successfully direct ecological succession for better catches and crop yields, and although this understanding and its applications were probably a part of their indigenous knowledge, there are no known records of their observations, understanding, or applications. We can only indirectly deduce these observations, understanding, and applications from limited archeological evidence and from basic principles of human nature that have changed little in 9,000 years.

> What has happened before will happen again. What has been done before will be done again. There is nothing new in the whole world. ~ Ecclesiastes 1:9 (St. Jerome's Version (SJV) from Thomas Nelson 1985)

Oldest Known Records. The *Holy Bible* includes what may be the oldest known writings that have indications of what we now consider to be ecological succession, particularly oldfield succession:

> … the fields and vineyards … were full of thorn bushes and overgrown with weeds. The stone wall around them had fallen down. ~ Proverbs 24:30-31 (SJV)

> I will let it [vineyard] be overgrown with weeds. I will not trim the vines or hoe the ground; instead, I will let briers and thorns cover it. ~ Isaiah 5:6 (SJV)

> Beat your breasts in grief because the fertile fields and the vineyards have been destroyed and thorn bushes and briers are growing on my people's land. ~ Isaiah 32:12-13 (SJV)

Theophrastus (circa 300 BC) wrote about plant-environment interactions and plant community changes over time. Saint Basil the Great (circa AD 330-379) observed the sequential nature of plant community changes (McIntosh 1985). Buffon (1742) described ecological succession in French forests and noted that plants may alter their site conditions, making the site more suitable for other species (Drury and Nesbit 1973).

Darwin (1859) described plant community changes in pastures after the exclusion of grazing cattle. Thoreau (1993 [1860]) described succession in New England forests in long-unpublished manuscripts. Cowles (1899) applied the word "succession" to the concept of ecological succession, in his classic study of primary ecological succession in the Indiana Dunes.

Golden Age of Ecological Succession Theory. Clements (1916) developed the first general ecological succession theory (i.e., first approximation), the "organismal" concept, replete with his original terminology. The Clementsian organismal concept was of a multi-stage ecological succession process where earlier stage species modified the environment, made the environmental conditions more favorable for later stage species and less favorable for themselves, which ultimately lead to a single climax community, a self-reproducing "superorganism."

Gleason (1917, 1926) proposed the first opposing general ecological succession theory (i.e., second approximation), the "individualistic" concept, which emphasized stochastic processes and opportunistic species.

The Clementsian organismal concept dominated ecology until the 1950s, when the Gleasonian individualistic concept became and has since remained dominant. However, Clementsian elements persist in ecological succession theory (e.g., Connell and Slatyer 1977), although little of Clements’ original terminology remains in regular use. Here, I have retained Clements’ terms “sere” and “climax” species.

Tansley (1935) developed the first second-generation general ecological succession theory (i.e., third approximation), a holistic synthesis of compatible Gleasonian and Clementsian concepts that included much of Tansley’s original thought.

Subsequent general ecological succession theories (Whittaker 1953, Egler 1954, Drury and Nesbit 1973, Connell and Slatyer 1977, Connell *et al*. 1987, Huston and Smith 1987; Pickett *et al*. 1987a, 1987b; Pickett and McDonnell 1989, McCook 1994) are generally synthetic theory (i.e., variations of and expansions upon the third approximation), essentially Tansleyian syntheses of many Gleasonian elements and some Clementsian elements. These theories have served as the conceptual basis for numerous field and laboratory observational and experimental studies on all types of ecological succession.

Golden Age of Oldfield Succession Theory. Widespread agricultural field abandonment in the U.S. during the 1920s and 1930s lead to the first systematic studies of oldfield succession (Golley *et al.* 1994). Crafton and Wells (1934) may have been the first to publish using the term "oldfield" in the context of ecological succession.

Crafton and Wells (1934), McQuilkin (1940), Oosting (1942), and Keever (1950) developed several similar word models of oldfield succession in the southeastern U.S. These models state that plants usually invade oldfields in three stages (early (forb and grass phases), middle (pine and early hardwood phases), and late (middle and late hardwood phases)(Figure 2-7); gradually reestablish a mixed mesic hardwood forest in about 150 to 200 years, unless disturbances divert, arrest, or setback the oldfield succession process.

Table 2-7. Field 3-412 ecological succession stages and phases.

STAGE	**EARLY**		**MIDDLE**	**LATE**	
PHASE	FORB (1 to 5 Years)	GRASS (3 to 25 Years)	PINE (10 to 75+ Years) EARLY HARDWOOD (10 to 75+ Years)	MIDDLE HARDWOOD (25 to 150 Years)	LATE HARDWOOD (50 to 250+ Years)

These southeastern U.S. ecological succession (SUSES) models (Golley, pers. comm., 1995), have been cited as the classic example of oldfield succession in many widely used ecology textbooks for decades (Odum 1953, 1959, 1971; Smith 1980, 1990; Colinvaux 1986, 1993; Barbour *et al*. 1987; Ricklefs 1990). These SUSES models are also the most frequently cited example of oldfield succession on Internet web sites.

The SUSES model collectively includes most of the relevant aforementioned biotic and abiotic factors and mechanisms. However, it is based upon studies of oldfields that covered less than 10 ha, with study plots of less than 0.1 ha, mostly within 100 m of field/forest edges. The SUSES model realistically predicts succession for southeastern

U.S. oldfields that cover less than 10 ha. However, we may not be able to extrapolate the SUSES model predictions to accurately predict succession in larger oldfields, i.e., those covering more than 50 ha, and for plots that are more than 150 m from the nearest field/forest edges.

Odum started studying SRS in general, and Field 3-412 specifically, in 1951. He speculated that natural reforestation would be slow because of large field sizes, poor soil conditions, and absence of natural seed sources (Odum 1960). Golley started studying Field 3-412 in 1959. He found that the pine succession was indeed slower than predicted by SUSES models, and suggested that “large” (size undetermined) oldfields may have temporary arrested stable states (Golley 1965).

Silver Age of Ecological Succession Theory. Since the 1930s, researchers have generally borrowed from and built upon earlier works to develop their later-generation general ecological and oldfield succession theories (i.e., variations of the third approximations) and word models (Watt 1947, Spurr 1952, Whittaker 1953, Egler 1954, Drury and Nesbit 1973, Holling 1973, Sutherland 1974, Horn 1975, Pickett 1976, Connell and Slatyer 1977, MacMahon 1981, Pickett 1982, Connell *et al*. 1987, Huston and Smith 1987, Pickett *et al*. 1987a, 1987b, Bornkamm 1988, Pickett and McDonnell 1989, Facelli and Pickett 1990, Sutherland 1990, Farrell 1991, Fekete 1992, Huston 1992, McCook 1994, Ludwig *et al*. 1997, Prach *et al*. 1997, Turner *et al*. 1998, McIntosh 1999, Prach and Pyšek 1999, Young *et al*. 2001).

Connell and Slatyer's (1977) model states that arrested succession commonly occurs in large, intensely disturbed landscapes. However, their model provides few details on relevant factors and mechanisms. Other general word models (citations in previous paragraph) include plant history, seed dispersal, disturbance extent and intensity, and other factors and mechanisms. However, these word models do not explain how these factors and mechanisms operate in large, intensely disturbed landscapes such as Field 3-412.

General ecological succession theories and word models usually lack one or more significant site-specific factors that influence ecological succession, e.g., disturbance regime, seed distribution/dispersal curves, and food web structure.

Furthermore, most of the world lacks adequate site-specific databases. As such, ecological succession models that rely on these inadequate databases may produce inaccurate and/or unrealistic predictions, particularly for large, intensely disturbed landscapes, such as Field 3-412.

Now that we have covered the history and highlights of general ecological succession theory and word models, we will review the abiotic and biotic factors that influence ecological succession. We will generally discuss each factor or group of factors as they apply worldwide, and we will specifically discuss them as they apply to Field 3-412. These factors are arbitrarily separated into categories and subcategories to facilitate discussion. Of course, these factors are actually synergistic, so the discussions of factors will have some necessary redundancy.

ECOLOGICAL SUCCESSION FACTORS: ABIOTIC

Introduction. Abiotic (geological, edaphic, climatalogical, meteorological, and hydrological) factors can directly affect plants, animals, and microbes; and thus, abiotic factors can indirectly affect community species composition, distribution, and structure;

ecological succession rates, trajectories, and end point(s); and the resulting landscape patterns (Connell 1978, White 1979, Denslow 1980, Schmidt 1988).

Geological Factors. Geological processes, structures and bedrock composition directly affect landforms, elevation, slope, and aspect (Lobeck 1939); indirectly affect climate and microclimate characteristics (Critchfield 1983, Rosenberg *et al*. 1983), soil characteristics (Birkeland 1984, Fanning and Fanning 1989), and surface and subsurface hydrology (Way 1978, Brady and Weil 1996); and thus, can indirectly affect ecological succession (Rohdenburg 1989).

Field 3-412 Geology. Field 3-412 is on a Savannah River terrace, known as the Ellenton Terrace (Siple 1959, 1967) or the Sunderland Terrace (Colquhoun 1965), in the Upper Coastal Plain physiographic province (Odum 1960). This terrace was probably formed during the early to middle-Holocene from ca. 8,500 to 2,500 B.C., when rising sea levels raised the hydrologic base level and reduced the river gradient, thus creating a more depositional environment (Sassaman *et al*. 1990).

Field 3-412 is underlain by about 250 m of coastal plain sediments, which rest upon metamorphic gneisses and granitic intrusions similar to those in the Piedmont about 35 km to the northwest (King 1955; Siple 1959, 1967; Nystrom and Willoughby 1992; Nystrom *et al.* 1992). Geological structure and bedrock composition were not considered further in this study because of their depth below the surface.

Field 3-412's surface elevations are between 135 and 155 m above mean sea level (amsl, 1927 North American Datum). The topography is flat to gently rolling (Figure 2-3), with many imperceptible depressions and several 1 to 2 m-deep gullies in northern Field 3-412. Most slopes range between 0% and 2%, except in the north, where slopes are between 2% and 10%. Elevation, slope and aspect were not considered further in this study because of the low degree of relief and gentle slopes.

Edaphic (Soil) Factors. Soil texture, structure, permeability, drainage, chemistry, and moisture and nutrient availability directly affect surface and subsurface hydrology (Way 1978, Brady and Weil 1996), plants (Howard and Mitchell 1985), and some microbes (Theophrastus ca. 300 BC; Blackman 1905; Clements 1920; Barbour *et al*. 1987); directly and indirectly affect insects, wildlife, and other microbes (Shelford 1913, Schlesinger 1991); and thus, soil factors can indirectly affect ecological succession (Clements 1916, Billings 1938, Oosting 1942, Odum 1960, Golley 1965; Haines 1977 and 1978; Robertson and Vitousek 1981, Tilman 1986, Inouye and Tilman 1988; Myster and Pickett 1990, 1994; Leps *et al*. 2000).

Field 3-412 Soils. Field 3-412's soils (excluding those in Ellenton Bay and inclusions elsewhere) have moderately thick to thick sand surface and subsurface layers, deep sandy loam subsoils, are well to somewhat excessively drained, have low soil moisture availability, moderate to very strong acidity with rapid leaching, low fertility and organic matter (OM) content (Rogers and Herren 1990), and relatively light soil albedos (SREL 1943 and 1951). Ellenton Bay (a Carolina bay in southeastern Field 3-412), and small **inclusions** elsewhere in Field 3-412, have soils with higher soil fines (i.e., silt- and clay-sized particles) content, that are moderately to poorly drained, and have low to moderate moisture availability, low to moderate fertility and OM content (Rogers and Herren 1990), and relatively dark soil albedos (SREL 1943 and 1951).

Many of these inclusions are in areas that may have been incipient Carolina bays, ancient meander and oxbow scars, and drainage ways that feed into ephemeral tributaries of the Savannah River, Upper Three Runs, and their tributaries (perennial, intermittent, and ephemeral).

Soil droughtiness and low fertility, mostly the result of low soil fines content through pedogenesis and past farm practices in Field 3-412, may be strong contributing factors to the arrested woody succession in Field 3-412. Therefore, soil albedo, fines content, and moisture and nutrient availability (except carbon (C) and nitrogen (N) because of their inherently weak correlations between 1951 and 2001 conditions) were considered further in this study.

Climatological and Meteorological Factors. Insolation, radiation, temperature, growing season length, humidity, dew, frost, rime, precipitation, actual evapotranspiration (AET), and wind speed, direction, frequency and duration can directly and indirectly affect soil characteristics (Way 1978, Fanning and Fanning 1989), surface and subsurface hydrology (Way 1978, Brady and Weil 1996); microbe, plant, and animal habitat, physiology, survival, reproduction, and dispersal (Elton 1927, Ridley 1930, Daubenmire 1974, Murray 1986, Greene and Johnson 1989, Monteith and Unsworth 1990, Greene and Johnson 1993, Ribbens *et al*. 1994); species geographic range (Willdenow 1792, Humboldt and Bonpland 1807, De Candolle 1855, Warming 1895, Thornthwaite 1933, Holdridge 1967); and thus, can indirectly affect ecological succession.

Field 3-412 Climate and Weather. Field 3-412's climate is classified as humid subtropical (Cfa) in the Köppen classification system (Trewartha 1968). Latitudinal and elevational climatic factors were not considered further in this study because of Field 3-412 covers only 235 ha and has only a 20 m elevation range.

Winters are mild with an average temperature of 9°C. Summers are hot with an average temperature of 27°C. The frost-free period is about 240 days. Annual rainfall (1952 to 1982) averaged 120 cm, ranging from as little as 5.9 cm in November to as much as 13.1 in March (Workman and McLeod 1990). Thunderstorms occur about 55 days every year (Rogers and Herren 1990).

A late hard frost in March 1996 killed about 80% of Field 3-412's wild plum blossoms, which substantially decreased wild plum seed dispersal that year. This probably had little effect on 1996 wild plum clonal propagation, but it undoubtedly reduced 1996 wild plum establishment beyond the clonal propagation range.

The SRS wind rose shows similar wind frequencies in all eight cardinal compass sectors, i.e., there is no annual prevailing wind direction. However, there are some monthly prevailing high velocity wind directions (WebMet 2001). Field 3-412's highest velocity winds tend to be from the northwest in December through January, which probably would asymmetrically skew pine seed rain shadows towards the southeast (Golley, pers. comms., 1994, 2001).

Rot-weakened trees are more vulnerable to wind damage. Wind damage has contributed to tree fall (a.k.a., blowdown, tip-up, or wind throw) and patch and forest gap formation in Field 3-412. Wind thrown tree directions may be most frequent towards the southeast.

Lightning more frequently strikes taller trees than surrounding open areas and shorter trees. Several tall pioneer loblolly pine trees in Field 3-412 were apparently killed by lightning during my 1994-2001 fieldwork, as evidenced by burn marks and shattered wood. Invariably, the surviving, surrounding trees were mostly younger, shorter, middle stage *Quercus laurifolia*.

Field 3-412's mean annual precipitation is 121 cm, with 8.9 to 13.2 cm/month from December through September, and 5.8 to 6.4 inches/month in October and November. Mean annual snowfall is 3 cm, with no snow accumulation on the ground in some years (Rogers and Herren 1990). Precipitation was considered relatively even over time, and was not considered further in this study.

Microclimatological Factors. Microclimate insolation, radiation, temperature, wind, humidity, and actual evapotranspiration (AET) are well-understood. These factors directly affect plant physiology; indirectly affect seed germination and plant growth, survival, structure, and reproduction; and thus, microclimate factors indirectly affect ecological succession (Daubenmire 1974, Critchfield 1983, Rosenberg *et al*. 1983, Monteith and Unsworth 1990).

Conversely, vegetation cover, structure, leaves, and albedo differentially affect microclimate radiation, temperature, wind, humidity, and AET. This creates notable microclimate differences between grasslands (drier, more variation), woody patches, open forests, and closed forests (moister, less variation); and between north- (cooler, moister) and south-facing (warmer, drier) edges of woody patches and forests (Watts 1957, Daubenmire 1974, Critchfield 1983, Rosenberg *et al*. 1983, Monteith and Unsworth 1990).

Field 3-412 Microclimate Factors. Vegetation cover, structure, leaves, and albedo differences in Field 3-412 have undoubtedly contributed to microclimate differences between the grasslands, woody patches, open forests, closed forests, and between the north- and south-facing edges of woody patches and forest stands in Field 3-412. Microclimate factors and effects were not considered to be sufficiently significant to include in this study.

Hydrological Factors. Soil moisture, groundwater, and surface water quality, quantity, and movement directly and indirectly affect plant, animal, and microbial habitat, physiology, growth, survival, structure, and reproduction (Daubenmire 1974, Kramer and Kozlowski 1979, Larcher 1995); indirectly affect plant community species composition, structure, and distribution (Clements 1920, Barbour *et al.* 1987); and thus, hydrological factors indirectly affect ecological succession.

Potential soil moisture availability is generally higher in soils with moderate fines and/or OM content (Fanning and Fanning 1989, Brady and Weil 1996), which generally increases plant community NPP and facilitates ecological succession (Prach et al. 1993, 1999).

Field 3-412 Hydrology. Field 3-412, except for Ellenton Bay, has sandy, well-drained, droughty (low soil moisture availability) soils that allow most precipitation to infiltrate to depths below most Field 3-412 plant feeder roots (Rogers and Herren 1990). Selected parts of Field 3-412 were excluded from this study to reduce the likely confounding effects of poor soil drainage.

Savannah River's normal level is 45 to 55 m below Field 3-412 (Figure 2-3, USGS and USDOE 1987), and the river has not flooded Field 3-412 in recorded history (Weins, pers. comm., 1998; Davis, pers. comm., 1999). Upper Three Runs flows west-southwest, several hundred meters north of Field 3-412. Savannah River and Upper

Three Runs have negligible influence on Field 3-412 soil moisture availability and were not considered further in this study.

ECOLOGICAL SUCCESSION FACTORS: BIOTIC

Introduction. Biotic factors can also directly affect plants, animals, and microbes; and thus, biotic factors can indirectly affect community species composition, distribution, and structure; ecological succession rates, trajectories, and end point(s); and the resulting landscape patterns (Alvarez *et al*. 1974, Connell 1978, White 1979, Denslow 1980, Schmidt 1988).

Biotic factors that affect ecological succession rates, trajectories, and endpoints include, but are not limited to:

- Species adaptations: r-selected (ruderal or weedy; low stress, high disturbance regimes), K-selected (competitive; low stress, low disturbance regime), and S-selected (stress-tolerant; high stress, low disturbance regimes) (Grime 1977, Brown 1992);
- Species environmental tolerances (Theophrastus ca. 300 BC, Willdenow 1792, Humboldt and Bonpland 1807, De Candolle 1855, Blackman 1905, Clements 1920, Thornthwaite 1933, Hutchison 1957, Holdridge 1967, McIntosh 1967, Daubenmire 1974, Kramer and Kozlowski 1979, Larcher 1995);
- Biotic and abiotic (human and non-human) disturbances (Connell 1978; Denslow 1980; Pickett et al. 1987a, 1987b);
- Species pool composition (Egler 1954, Hanski 1982);

- Reproduction and genetics (Pianka 1970, Hamrick and Nason 1996);
- Propagule dispersal (Darley-Hill and Johnson 1981 (blue jay hypothesis), Harrison and Werner 1984, Burrows 1986, Johnson and Adkisson 1986, Levey 1986, Greene and Johnson 1989, Johnson and Webb 1989, Willson 1992, Howe 1993, Greene and Johnson 1993, Johnson *et al*. 1993, Robinson and Handel 1993, Willson 1993, Johnson *et al*. 1997, Robinson and Handel 2000);
- Herbivory, frugivory and granivory (Martin *et al*. 1951, Brown 1985, Price and Jenkins 1986, Howe and Westley 1988, Rankin and Pickett 1989, Jordano 1992, Bowers 1993, Davidson 1993, Inouye *et al*. 1994);
- Safe Sites (Harper *et al*. 1961, Fowler 1988, Schupp 1995);
- Seed germination (Billings 1938, McQuilkin 1940; Keever 1950, 1979; Howe and Smallwood 1982, Fenner 1985, Fowler 1988, DeSteven 1991a);
- Resource competition (Bormann 1953a, MacArthur and Wilson 1967, Horn 1974, Pinder 1975, Whitford and Whitford 1978, Tilman 1986, Huston and Smith 1987, Carson and Barrett 1988, Tilman 1991, Belsky 1994, Gross *et al*. 1995);
- Mycorrhizal associations (Allen 1991, Collins-Johnson 1991, Haselwandter and Bowen 1996);
- Seedling establishment (Billings 1938, McQuilkin 1940; De Steven 1991*b*), Golley *et al* 1994);
- Plant growth and survival (Clark 1990, Gleeson and Tilman 1990, Pinder *et al*. 1995);

- Litter (Golley 1960, Gabrielson 1985, Monk and Gabrielson 1985, Fowler 1988, Carson and Peterson 1990, Facelli and Carson 1991, Facelli and Pickett 1991, Myster and Pickett 1993, Facelli 1994); and
- Allelopathy (Rice 1974, Jackson and Willemsen 1976, Rice 1979)
- Intra- and inter-specific interactions, generally categorized as: mutualism, commensalism, predation/parasitism , or competition (Cooper 1926, Clements *et al*. 1929, Elton 1958, Harper 1961, Pimm 1984, Golley 1998, Csillag *et al*. 2000);
- Community Assembly Rules (Diamond 1975, Conner and Simberloff 1979, Lawton 1987, Drake 1990, Pimm 1991, Luh and Pimm 1993, Morton *et al*. 1996, Lockwood 1997, Lockwood *et al*. 1997, Young *et al*. 2001)

These biotic factors directly and indirectly affect individuals and populations, and thus, also indirectly influence community ecological succession, community species composition, and landscape patterns (Bazzaz 1979, MacMahon 1981, Huston and Smith 1987). Each biotic factor's effects depend on a wide variety of site-specific, synergistic biotic and abiotic factors. The significance of these factors varies over time: diurnally, seasonally, annually, and longer time periods. The significance of these factors also varies spatially, at all levels from individual through landscape (Allen and Hoekstra 1992).

As previously discussed, Field 3-412 species-specific biotic factors have been extensively studied, particularly the forb and grass phase species (Crafton and Wells 1934; Keever 1950, 1979; Odum 1960, Golley 1965, Golley and Gentry 1966, Pinder

1971, Pinder 1975, Wiegert and McGinnis 1975, Pinder 1977, Gabrielson 1985, Monk and Gabrielson 1985, Collins and Pinder 1990), as well as the pine phase species (Billings 1938, McQuilkin 1940, Oosting 1942; Keever 1950, Radford *et al.* 1968, Schopmeyer 1974, Keever 1979, Kramer and Kozlowski 1979, Little 1980, Duncan and Duncan 1988, Hightshoe 1988, Brown and Kirkman 1990, Burns and Honkala 1990a, Dirr 1990, Hamel 1992, Young and Young 1992, Little 1993, Harrar *et al*. 1996, Odenwald and Turner 1996, Flint 1997; Spring *et al*. 1974, Friebaum 1987, DeSteven 1991a and 1991b, Golley *et al.* 1994, Pinder *et al*. 1995).

Although the hardwood phase species have also been studied, they are somewhat less well understood, particularly the non-commercial species (Radford *et al.* 1968, Schopmeyer 1974, Kramer and Kozlowski 1979, Little 1980, Duncan and Duncan 1988, Hightshoe 1988, Brown and Kirkman 1990, Burns and Honkala 1990b, Dirr 1990, Gill and Marks 1991, Hamel 1992, Young and Young 1992, Little 1993, Harrar *et al*. 1996, Odenwald and Turner 1996, Flint 1997; Golley *et al.* 1994).

The following paragraphs examine various general ecological succession concepts that incorporate the aforementioned biotic factors that affect ecological succession. The discussion includes much of the cited author’s original terminology.

Anthropogenic (Artificial) Disturbances. Field 3-412 and the river terrace upon which it rests show physical evidence of human settlement and activities from about 8,000 B.C. through 1950 (Sassamen *et al*. 1990). European settlement of the study area essentially started during the 1730’s and continued until 1951, when the 803 km^2 (310 mi^2) SRS was established and the residents were relocated elsewhere (Sassaman *et al.* 1990). Farming in the study site, Field 3-412, probably started in the 1750’s and continued until 1951 (Brooks and Crass 1991). Most of Field 3-412 was practically devoid of woody vegetation for about 200 years.

Written records, aerial photographs, and field evidence reveal that although some farms covered more than 200 ha, the individual field sizes were typically less than 20 ha, with most fields being separated by fences with little or no woody vegetation (SREL 1943—1998, Sassaman *et al*. 1990, Brooks and Crass 1991, Cabak and Inkrot 1997).

Since SRS's complete agricultural abandonment in 1951, parts of Field 3-412 have been disturbed to construct and maintain roads, water mains, power transmission lines, and their rights-of-way, and for biological and ecological field experiments (Figure 2-5).

Initial Floristic Composition (*Being there is 90% of success*). Initial oldfield plant community species composition often corresponds more closely with the local plant (floristic) species composition (local species pool) than with the regional plant species composition (regional species pool) (*sensu* Egler 1954). Things tend to be more similar to other things that are closer by than to other things that are not.

Field 3-412's species composition has closely corresponded with the local species pool composition throughout the field's successional history to date. However, the species proportions have differed over time, as expected by SUSES and general ecological succession theory and models, where many local species are present through all successional stages, but only a few species are dominant during any particular stage.

Safe sites. Safe sites are generally defined as a microsite suitable for germination and establishment (Harper *et al*. 1961, Fowler 1988). That definition varies with species, depending on tolerance and physiology, and over time, with variable environmental conditions and events.

Generally, woody species establishment rates are highest on areas with moderate soil fertility and moisture availability conditions, and decline toward extreme conditions (Prach et al. 1993, 1999). Oldfield open areas can have more “safe sites” (Facelli 1994) than some closed forests, particularly for middle stage woody species seeds to germinate and for subsequent tree and shrub growth, survival, and reproduction. However, some grasses may significantly inhibit woody succession within their cover (Buell *et al*. 1971, Li and Wilson 1998, Duncan and Chapman 1999).

Some Field 3-412 woody species seeds do best with bare or almost bare mineral soil surfaces (e.g., *Pinus palustris*), or under high light conditions (e.g., *Pinus taeda*) Other woody species do best under an organic litter layer and low to moderate light conditions (e.g., *Quercus laurifolia* in *Prunus* spp. (wild plum) and *Rhus* spp. (sumac) woody patches).

Perches. Trees, shrubs, fences, posts, poles, and other perches play a larger role in oldfield succession than in subsequent forest succession, by increasing seed rain density under and immediately around the perches. The type of perch may influence seed rain species composition by attracting birds and mammals with various selective feeding preferences (McDonnell and Stiles 1983; Holthuijzen and Sharik 1985a, 1985b; Howe 1986, McDonnell 1986, Izhaki *et al*. 1991, Myster and Pickett 1992b, Howe 1993, McClanahan and Wolfe 1993, Robinson and Handel 1993, Ne'eman and Izhaki 1996, Verdú and García-Fayos 1996, Robinson and Handel 2000).

Some evidence of perch effects accelerating or facilitating woody succession has been found throughout Field 3-412. This remains a matter for future study.

Nucleation or Succession Loci (*Success builds upon success*). Pioneer trees and shrubs (hereafter, pioneers) are predominantly middle stage woody species. The first pioneers in oldfields can serve as succession loci or nuclei, i.e., centers for locally accelerated or facilitated succession (Yarranton and Morrison 1974, Hubbell 1979, Whittaker *et al*. 1979, Guevara *et al*. 1986, McClanahan 1986, Archer *et al*. 1988, Uhl *et al*. 1988, Scanlan and Archer 1991, Skarpe 1991, Debussche and Lepart 1992, Kellman and Kading 1992, Kolb 1993, McClanahan and Wolfe 1993, Robinson and Handel 1993, Verdú and García-Fayos 1996, Li and Wilson 1998, Toh *et al.* 1999, Robinson and Handel 2000).

This ecological succession concept has analogs in coral atoll establishment and development (Darwin 1842), human settlement patterns (Christaller 1933), land use and economic location theory (von Thünen 1826, Weber 1909, Burgess 1925, Hoyt 1939, Harris and Ullman 1945, Zipf 1949, Lösch 1954, Alonso 1964), “hierarchical” diffusion of culture (Ratzel 1897) and innovations (Hägerstrand 1952, Gould 1969), and in shorter-range (contagious, more deterministic) and longer-range (more stochastic) diffusion of diseases (Cliff *et al*. 1981, Keeling *et al*. 2001).

Pioneers inherently modify their habitat, albeit gradually, by locally increasing soil OM content and nutrient availability (Billings 1938, Coleman 1973, Kellman 1979, Fanning and Fanning 1989, Carson and Peterson 1990, Monk and Gabrielson 1991, Ko and Reich 1993, Myster and Pickett 1993), increasing soil moisture availability (Barbour *et al*. 1987), and reducing microclimate stresses (Connell and Slatyer 1977, Werner and Harbeck 1982, Rosenberg *et al*. 1983, Tilman 1986, Belsky 1994).

Pioneers may direct succession with allochthonous seed rain by bearing fruit that attract birds and mammals with selective feeding habits (Odum 1950, Martin *et al*. 1951, Smith 1975, Hubbell 1979, Howe and Smallwood 1982, McDonnell and Stiles 1983, Strong 1983, Harrison and Werner 1984, Guevara *et al*. 1986, Howe 1986, Levey 1986, McClanahan 1986, McDonnell 1986; Hoppes 1987, 1988; Myster and Pickett 1992a, 1992b; Stiles 1992, McClanahan and Wolfe 1993, Robinson and Handel 1993, DaSilva *et al*. 1996, Ne'eman and Izhaki 1996, Li and Wilson 1998, Robinson and Handel 2000); serving as perches that attract birds regardless of their selective feeding habits; and by providing protective cover from predators (Herrera 1984, Hoppes 1987, Howe and Westley 1988, Izhaki *et al*. 1991, Debussche and Lepart 1992, Debussche and Issenmann 1994, Herrera *et al*. 1994, Verdú and García-Fayos 1996, Alcántara *et al*. 2000).

Nurse Plants. By modifying their habitat, most pioneers facilitate ecological succession by gradually altering their habitat conditions so that the conditions are less suitable for establishment, growth and survival, and regeneration of early and middle stage species such as themselves, and more suitable for establishment, growth and survival, and regeneration of late stage species (Niering *et al*. 1963, Werner and Harbeck 1982, Franco and Nobel 1988, Vetaas 1992, Kolb 1993, Verdú and García-Fayos 1996, Li and Wilson 1998).

Field 3-412 has an overwhelming body of evidence that *Prunus* spp. (wild plums), *Rhus* spp. (sumacs), *Crataegus* spp., *Prunus serotina*, and *Diospyros virginiana* commonly serve as nurse plants for *Quercus laurifolia*, and occasionally serve as nurse plants for *Pinus* spp., *Prunus serotina*, and several other *Quercus* spp. More details are in Chapter 4 (Results).

Resistant relicts. However, by primacy and persistence, some pioneers may arrest ecological succession for decades to centuries, through space (i.e., light, water, and/or nutrient) competition or competitive exclusion (Bormann 1953a, MacArthur and Wilson 1967, Pinder 1975, Whitford and Whitford 1978, Huston and Smith 1987, Belsky 1994), tolerance, allelopathy (Rice 1974, Jackson and Willemsen 1976, Rice 1979), damage by wind-blown branches (Golley *et al*. 1994, Pinder *et al*. 1995), and burial by litter (e.g., *Pinus* spp.).

Keystone Species. Woody species that particularly attract certain bird and mammal species with selective or preferential feeding habits (Hubbell 1979, McDonnell and Stiles 1983, Harrison and Werner 1984, Guevara *et al*. 1986, McClanahan 1986, McDonnell 1986, Myster and Pickett 1992a, Myster and Pickett 1992b, McClanahan and Wolfe 1993, Robinson and Handel 1993, Li and Wilson 1998, Robinson and Handel 2000), may serve as keystone-species (Mill *et al*. 1993) that influence communities' ecological succession trajectories (Luken 1990).

Pinus taeda, *Quercus laurifolia*, *Prunus serotina*, *Prunus* spp. (wild plums), and *Crataegus* spp. (hawthorns) have been dominant species in Field 3-412. They have been the woody matrix for each stage, paving the way for the next stage's dominant woody species. Most other woody species have been subordinate, and they have followed the keystone species' lead, with few exceptions.

Adaptive Geometry and **Tree Architecture**. Tree and shrub structure (architecture) can provide reliable physical evidence of a woody patch's growth history

(Watts 1957, Horn 1971, Henry and Swan 1974, Hallé and Oldeman 1975). Structure was used in this study whenever it was a suitable substitute for more invasive or damaging field data collection methods.

Relay Floristics. During ecological succession, later stage plant species seem to invade as earlier stage species disappear in "relay floristics" (Egler 1954). However, although individual species may appear and disappear in a sequence, not all species do, and they rarely do so as groups (Gleason 1917, Whittaker 1953).

As previously mentioned, many plant species have been present in Field 3-412 throughout all stages and phases, but often very few and very widely scattered. These species have usually been underrepresented in studies that cover only very small portions of Field 3-412.

Species Arrival Sequence. The sequence that species arrive in an oldfield can affect ecological succession rates and pathways, and thus affect species spatial distribution and landscape pattern (Egler 1954, Robinson and Dickerson 1987, Myster and Pickett 1990, Vankat and Snyder 1991).

Field 3-412 has several areas where the sequence of species arrival has affected the succession. Specifically, the many pines that first invaded the northwestern part of Field 3-412, and the many *Quercus laurifolia* that first invaded the northeastern part. Northwestern Field 3-412’s pine patches and forest stands facilitated succession to *Quercus laurifolia*, most likely because of the many long-range, wind dispersed pines that served as nurse trees. However, northeastern Field 3-412’s *Quercus laurifolia* patches had slower succession to *Quercus laurifolia* stands, most likely because of the relatively few short-range, gravity and mammal dispersed *Quercus laurifolia* that could serve as nurse trees. These were few long-range, bird dispersed *Quercus laurifolia* during the first few decades of Field 3-412's succession. Other woody species had to become established, and grow to provide perches and protective cover, for *Quercus laurifolia* to become a larger proportion of the seed rain and decades later become the leading dominant woody species in Field 3-412.

The former peach orchards in the western part of Field 3-412 were quickly invaded by *Prunus serotina*, within 100 m of mesic oak-hickory forest edges, which makes this aberration even more conspicuous. The former orchard also has extensive bird-dispersed vine species, which have damaged, killed, and downed many trees and shrubs in this area.

Succession Resistant Subclimax Communities. Some plant species can form an invasion or succession resistant subclimax community that may last for decades (Pound and Egler 1953, Niering and Egler 1955, Niering *et al*. 1974, Niering *et al*. 1986, Niering 1987, Hill *et al*. 1995, Fike and Niering 1999). Community resistance to invasion probably varies during the dominant species' life history and with environmental changes, which in turn could alter population processes, community succession direction, and landscape patterns (Abugov 1982).

Field 3-412 has several persistent early stage communities, composed almost completely of dominant *Lespedeza striata* (annual lespedesia), *Rubus* spp. (blackberry), *Lonicera japonica* (Japanese honeysuckle), and *Campsis radicans* (trumpet creeper). These persistent communities have probably inhibited woody invasion through competitive exclusion, literally smothering and downing other species, as evidenced in aerial photographs and seven years of field observations.

Community Convergence. As oldfield succession progresses, and the vegetation modifies the habitat as previously described, the between site differences of soil, microclimate, hydrology, and community species compositions generally decrease (West *et al*. 1981, Finegan 1984, Shugart 1984, Inouye and Tilman 1988).

Field 3-412's woody cover was a matrix with a roughly even mixture of five dominant woody species (*Pinus taeda*, *Quercus laurifolia*, *Prunus serotina*, *Prunus* spp. (wild plums), and *Crateagus* spp.) in the 1970s and 1980s. However, *Quercus laurifolia* has been expanding throughout the field at a disproportionately fast rate, such that *Quercus laurifolia* became the leading dominant woody species in Field 3-412 during the 1990's, and it may cover most of Field 3-412 within about another 50 years.

ECOLOGICAL SUCCESSION FACTORS: SPACE

Community ecological succession factors, processes, and patterns are known to vary spatially (Oosting 1942, Golley 1965, MacArthur and Wilson 1967, Davis and Cantlon 1969, Forman and Godron 1986, Guevara *et al*. 1986, McClanahan 1986, Augspurger and Franson 1987, Urban *et al*. 1987, Pulliam 1988, Hardt and Forman 1989, Greene and Johnson 1989, Magnuson 1990, Armesto *et al*. 1991, Debussche and Lepart 1992, Guevara et al 1992, Facelli and Carson 1991, Levin 1992, Myster and Pickett 1992b, Myster and Pickett 1993, Robinson and Handel 1993, Golley *et al*. 1994, Prach and Pyšek 1994, Bartha *et al*. 1995, Forman 1995, Hill *et al*. 1995, Pinder *et al*. 1995, Meiners and Gorchov 1998, Robinson and Handel 2000). However, our understanding of how space (distance) affects community ecological succession rates, species composition, frequency and density, and the resulting landscape pattern is not well known.

Field 3-412 is an optimal site to study the effects of space on ecological succession, for the many aforementioned reasons. Such a study requires considerable time and effort given the scale of the site, which is at least one order of magnitude larger than almost all other ecological succession study sites. I think that the value of the knowledge gained from such as study is well worth the time and effort, not only for the sake of knowledge, but also for the sake of the potentially beneficial application.

CHAPTER 3

METHODS

INTRODUCTION

This chapter covers this study's methods to collect field data, to generate synthesized data, and to analyze the field and synthesized data.

STUDY SITE

Study Site Selection. The site selection criteria that I established for this study favored larger, less vegetated, more isolated sites to emphasize and more rigorously evaluate relevant species and distance factors at the landscape level. The site selection criteria also favored sites with minimal within-site topographic, edaphic, and climatic variation, and minimal artificial (anthropogenic) post-abandonment disturbance to reduce confounding factors; maximum historic aerial photograph coverage to reduce fieldwork and it's costs and adverse environmental effects (collateral damage); and more previous related ecological succession studies for broader, deeper context and applicability.

The 3-year (1992 to 1994) study site search covered most of the eastern U.S., Puerto Rico and Venezuela. The search focused on sites that covered more than 100 ha. The search included inquiries with academic and government researchers from Texas to New Jersey, and New York to Venezuela, for site recommendations and referrals to other researchers for their site recommendations; and extensive ground and aerial surveys to identify and evaluate sites (Archer, personal communication [pers. comm.], 1994; Billings, pers. comm., 1994; Christensen, pers. comm., 1994; Clark, pers. comm., 1994; Golley, pers. comms. 1994-2001; Haines, pers. comms. 1992-2001; Lugo, A.A.L. pers. comm., 1992; Lugo, A.E. pers. comm., 1992, 1994; Odum, pers. comms., 1994-1995; Parrota, pers. comms., 1992, 1999; Peet, pers. comm., 1994; Pickett, pers. comm., 1995; Rios, pers. comms., 1994; Straw, personal observations, 1986-2001; Wein, pers. comms., 1998-2001; White, pers. comm., 1994).

Only one large site, Field 3-412 in Savannah River Site, Aiken County, South Carolina, adequately met the site selection criteria. Other large sites were identified in Venezuela, Puerto Rico, North Carolina, South Carolina, and Tennessee. However, these sites were deemed to be unsuitable because they either had too little vegetation for evaluation, too much vegetation that would confound evaluation; and/or too much disturbance or undeterminable past land use/disturbance history (e.g., cattle grazing, harvesting, mowing, disking and plowing, chemical (fertilizer, herbicide, and/or pesticide) treatments, prescribed (controlled) burns that would preclude or confound evaluation.

No other large eastern U.S. sites are known that could be suitable for study replication (Archer, pers. comm., 1994; Billings, pers. comm., 1994; Christensen, pers. comm., 1994; Clark, pers. comm., 1994; Golley, pers. comms. 1994-2001; Haines, pers. comms. 1992-2001; 1994; Odum, pers. comms., 1994-1995; Peet, pers. comm., 1994; Pickett, pers. comm., 1995; Straw, personal observations, 1986-2001; Wein, pers. comms., 1998-2001; White, pers. comm., 1994).

The study site search also included smaller, highly isolated sites with minimal topographic, edaphic, and climatic variation, and minimal artificial post-abandonment disturbance. Such small sites could be suitable for limited study of relevant species and distance factors at the landscape level. However, like most of the larger sites considered for this study, all of the smaller sites that were evaluated were found to be unsuitable because they did not adequately meet the various site selection criteria.

Field 3-412 Size and Shape. Field 3-412 is both large and compact. Field 3-412 is at least one order of magnitude larger (141.7 ha in 1951) than most other previously studied oldfields (Chapter 2, Background). The studied area covers about 142 ha (major axis (NW-SE) is about 2.0 km long, minor axis (SW-NE) is about1.0 km long), has relatively simple margins, and a major-to-minor axis length ratio of about 2.0. Field 3-412 had open barren areas that were initially at least 500 m from the nearest field/forest edge (Figure 2-4). This larger size makes Field 3-412 suitable for studying woody succession at the landscape level. With all other topological variables held equal, larger older field sites would have greater distances from field/forest edges, so any distance effects on plant community species composition are more likely to be apparent.

Field 3-412 Topography. Field 3-412 ground surface elevations range from between 39 and 47 m above mean sea level (amsl) (Figure 2-3, USGS 1987). The world mean dry adiabatic lapse rate is about 0.98°C/100 m, the wet (moist) adiabatic lapse rate is about 0.49-0.55-0.60°C/100 m, and the average lapse rate is about 0.65°C/100 m. With an elevation range of about 8 m, elevation and corresponding adiabatic effects (about 0.05°C range) were considered to be insignificant factors in Field 3-412 oldfield succession, and therefore, were not further evaluated in this study.

Field 3-412 ground slopes generally range from zero to three percent (0° to 1°21’), except for the Upper Three Runs valley walls (sloped sides) and the inner rim of Ellenton Bay, where slopes are usually between three and ten percent (1°21’ to 4°30’). Ground slope was considered to be an insignificant factor in Field 3-412 oldfield succession, and thus, was not further considered in this study.

Field 3-412 ground aspect is well distributed throughout all eight compass azimuth cardinal sectors (e.g., N, NE, E, …). Ground aspect directly affects insolation (incoming solar radiation) rates, and thus, indirectly affects surface and near surface air temperature and humidity.

At a latitude of about 33°13’ N, with the earth axis declination of about 23°30’, and with ground slopes of generally less than three percent (1°21’), and rarely greater than ten percent (4°30’), ground slope, ground aspect, and their corresponding temperature effects were considered to be insignificant factors in Field 3-412 oldfield succession, and therefore, these factors were not further evaluated in this study.

Field 3-412 Soils. Most Field 3-412 soils have similar spectral, textural, structural, hydrological, and chemical characteristics, except for the soils in Ellenton Bay and some unmapped soil inclusions elsewhere throughout Field 3-412 (Rogers and Herren 1990). More specifically, soil factors include drainage, moisture availability, and nutrient status. Soil factors were considered to be potentially significant in Field 3-412 oldfield succession, and thus, were further considered in this study.

Field 3-412 Climatic and Microclimate. Field 3-412’s major axis (NW-SE) is about 2.0 km long, and its minor axis (SW-NE) is about 1.0 km long. Therefore, climate factors (e.g., continentality, maritime influences, general storm tracks, insolation, reradiation, temperature, wind direction and velocity, humidity, precipitation, potential evapotranspiration, CO_2 concentration, etc.) were considered to be very similar throughout the site over time, and therefore, were not further evaluated in this study.

Field 3-412's vegetation composition, density, and structure directly and indirectly affect microclimate factors (insolation, reflectance, absorption, reradiation, temperature; wind direction, velocity, and turbulence; humidity, precipitation, potential evapotranspiration), to a much greater extent than the site's elevation, slope and aspect. These biogenic microclimate factors were considered to be potentially significant in Field 3-412 oldfield succession (e.g., during forb, grass, pine, and early hardwood phases), and thus, were further considered in this study, albeit briefly.

Field 3-412 Post-Abandonment Disturbance. Field 3-412's limited post-abandonment disturbance, particularly anthropogenic disturbances, reduces the effects of this confounding factor. All road and utility right-of-ways (ROWs) are mown several times annually, so they were excluded from this study. ROW edge effects were considered when evaluating nearby woody patches. Post-1951 disturbed research plots were included in this study, as younger oldfields dated from the year of their last study disturbance.

Field 3-412 Aerial Photographs. Twenty-five years of aerial photographs, taken between 1943 and 1998 inclusive, provided extensive photographic data on past woody succession in Field 3-412 (SREL 1943-1998). Photographic data collection (extraction) significantly reduced the need for expensive, time-consuming field data collection. It also substantially reduced the need for invasive, destructive vegetation data collection methods (Diamond 1986, Farnsworth and Rosovsky 1993).

Field 3-412 Ecological Studies. Ecologists have studied Field 3-412 continuously since its agricultural abandonment in 1951. Their studies provide a substantial body of data on the forb, grass, and pine succession stages in Field 3-412. This dissertation study relies upon these earlier studies for a more comprehensive evaluation of Field 3-412's oldfield succession in general, and it's woody succession specifically. These earlier studies are summarized in Chapter 2 (Background).

REMOTE SENSING

Aerial Photographs. The University of Georgia (UGA) Savannah River Ecology Laboratory (SREL) provided the aerial photographs that were used for this study. Various contractors acquired these photographs for the USDA SCS (U.S. Department of Agriculture Soil Conservation Service (now Natural Resources Conservation Service (NRCS)), AEC (Atomic Energy Commission), DOE (U.S. Department of Energy), USFS (U.S. Forestry Service), and UGA SREL.

These aerial photographs included the years: 1943, 1951, 1953, 1955, 1956, 1961, 1966, 1971, 1973, 1974, 1975, 1977, 1978, 1979, 1981, 1982, 1984, 1985, 1986, 1987, 1989, 1990, 1991, 1996 and 1998 (SREL 1943-1998). The photographs' ground resolutions range from about 1.0 to 5.0 m in the pre-1970 photographs, to about 0.3 to 2.0 m in the post-1970 photographs.

The aerial photographs used for this study were from 1943, 1951, 1961, 1974, 1982, 1990, and 1998 (Appendix A), for the closest goodness of fit to a 10-year interval. The data extracted from the aerial photographs included, but was not limited to: soil albedo (surface tone or reflectance in aerial photographs), vegetation cover, ROWs and ecological study plot disturbances.

GEOGRAPHIC INFORMATION SYSTEM (GIS)

GIS Layer Creation. The selected aerial photographs were digitally scanned at between 600 and 2,400 dots per inch (dpi) to create TIFF image files. The TIFF files were digitally resampled, using Adobe Photoshop® 5.0, and resaved at a ground resolution of between 0.5 and 2.0 m. The modified TIFF files were imported into ERDAS Imagine® 8.3.1 to create GIS raster layers (.img files).

Field Map Production. A ground position system (GPS), Trimble Pro-XL®, mobile receiver and base station receiver were used to obtain centimeter precision ground control points (GCPs). GCPs with horizontal error of less than ±2 m were used in ERDAS Imagine® 8.3.1 to orthorectify the GIS raster layers. The orthorectified GIS raster layers were then used to produce field maps and map overlays.

FIELD PLOTS

Field Plot Purposes. Field plots were used to evaluate the possible relationships between plot distance from Field 3-412's 1951 field/forest edge and each woody patch's initial (core, pioneer or primary) species composition, and any possible interspecific associations or correlations between the core tree/shrub species and the surrounding secondary tree and shrub species composition.

Field Plot Selection. Field plots were selected by random, stratified sampling (Bordeau 1953, Bormann 1953b, Phillips 1959, Whittaker 1962, Grieg-Smith 1965, Krebs 1989). Recommended plot sizes for sites with a patch mosaic of trees, shrubs, and open areas are 0.01 ha (Oosting 1956, Bonham 1989), 0.1 ha (Küchler and Zonneveld

1988), or 0.04 to 0.25 ha (Kent and Coker 1992). I selected plots covering ≥1.0 ha for comparisons with other studies with plots covering ≥1.0 ha.

Field 3-412 was divided into four quadrants (NE, SE, SW and NW) that meet at the approximate center of the field. One field plot, covering 1.0 to 2.5 ha, was randomly selected from each quadrant 100 m interval from the nearest 1951 field/forest edges, for a total of 17 field plots (Figure 3-1). The southwest field quadrant 0-100 m plot (Plot #10) was excluded because of potential confounding factors from the adjacent peach orchards and disproportionately high amount of road right-of-ways. The 17 selected field plots cover about 24.5 ha, which is an approximately 17% sample of Field 3-412.

Field Plot Data Collection. Woody patches were defined for this study as one or more trees and/or shrubs ≥ 1 m high and covering ≥ 4 m^2 ground surface area. All woody patches within each field plot were delineated on orthorectified field maps. Woody species identification from aerial photographs proved inadequate (Sayn-Wittgenstein 1961, Heller *et al*. 1964, Avery 1978, Sayn-Wittgenstein 1978, Paine 1981, Lo 1986). Therefore, woody patches were 100% field verified and delineated on field maps using species-specific colors (Figures 3-3 and 3-4).

> **Woody Patch:** One or more contiguous woody plants that are at least one meter tall and cover at least four meters square. This definition excludes small, isolated shrubs (mostly wild plum and sumac) that often lived for less than 20 years. These small shrubs either died and contributed little or nothing to Field 3-412's woody succession, or lived and grew large enough to become a woody patch. This definition also excludes blackberry and vine patches that could be misidentified as wild plum or sumac patches. Smaller woody plant(s) are very

difficult to distinguish from blackberry and vine patches in pre-1975 aerial photographs.

Woody cover in each field plot was delineated on field map overlays for the years 1951, 1961, 1974, 1982, 1990, and 2001 (Figure 3-3). The overlays were created using scanned aerial photographs, Adobe Photoshop® 5.0, and archival quality pens and mylar sheets. Each overlay was registered to the enlarged scanned aerial photographs by aligning key ground features on both the overlay and the photographs.

Tree and shrub architecture (Watts 1957, Horn 1971, Henry and Swan 1974, Hallé and Oldeman 1975), dead tree and shrub snags, debris, and other remains were also used to reconstruct tree, shrub, and woody patch history (Henry and Swan 1974, Drahn and 1988, Hoadley 1990). Unique tree and shrub structure were recorded using species-specific colored symbols within applicable map polygons, and in field map marginal notes (marginalia).

Percent woody cover in each field plot was determined for the years 1951, 1961, 1974, 1982, 1990, and 2001 by placing a 6.25 x 6.25 cm grid over each woody cover field map overlay, estimating the woody cover in each grid cell to the nearest 0.1 cells, and dividing the total woody cover cell count by the corresponding total cell count.

Field Plot Data Analysis. The field plot data were analyzed using descriptive statistical methods (details in Chapter 4, Results); and Chi-Square and Fisher’s Exact Test for Hypotheses One and Two.

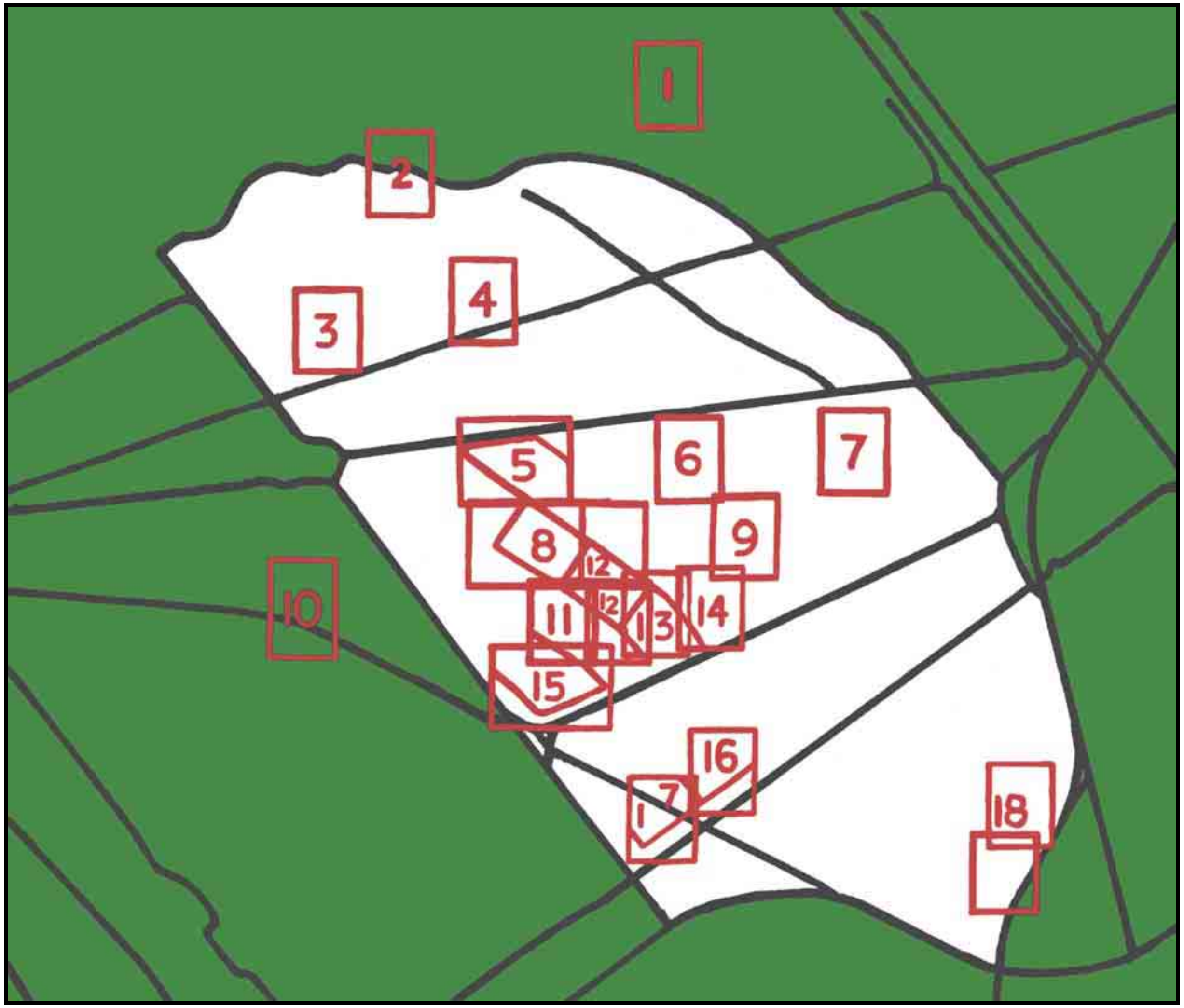

Figure 3-1. Field plots.

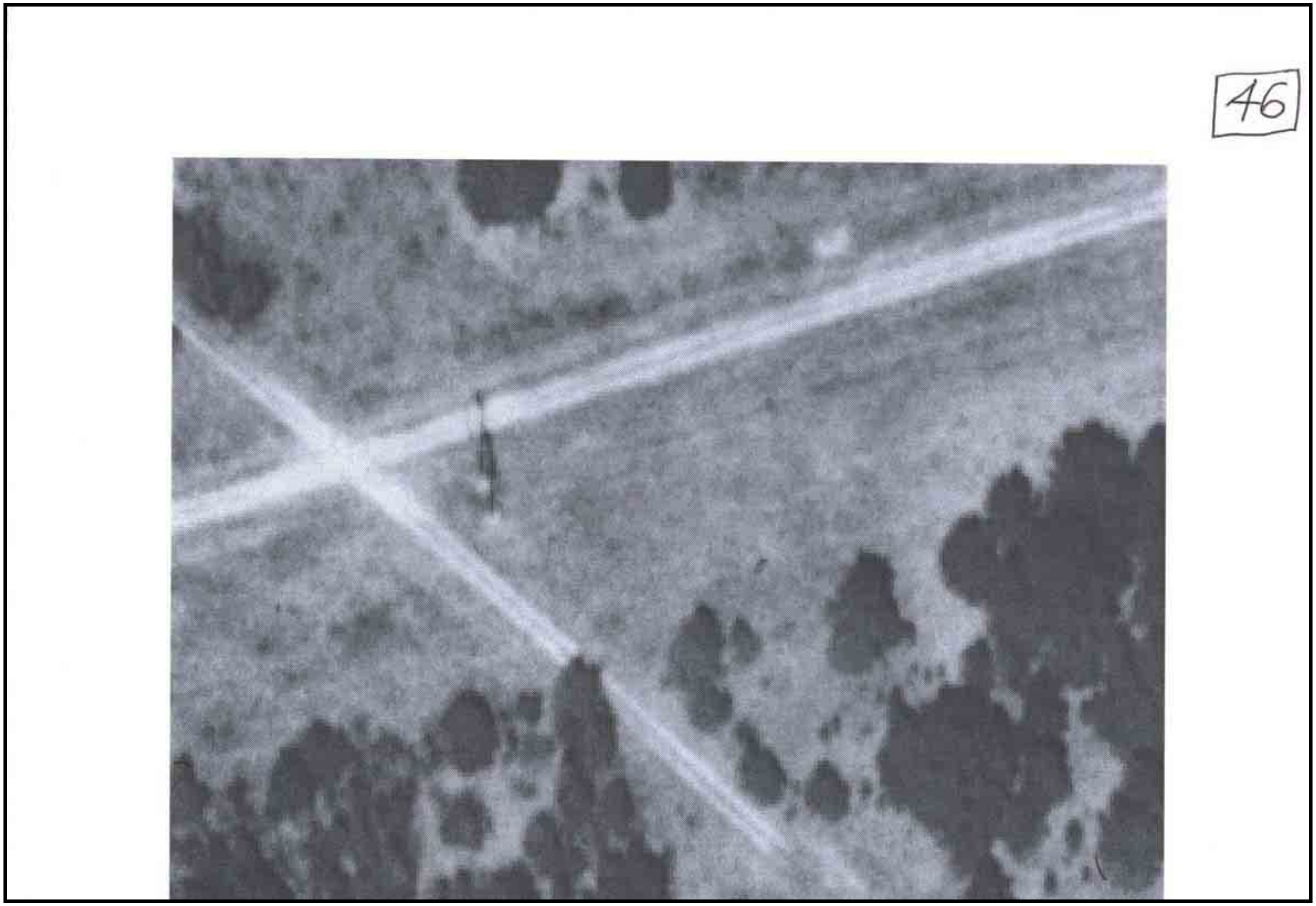

Figure 3-2. Field map (upper half).

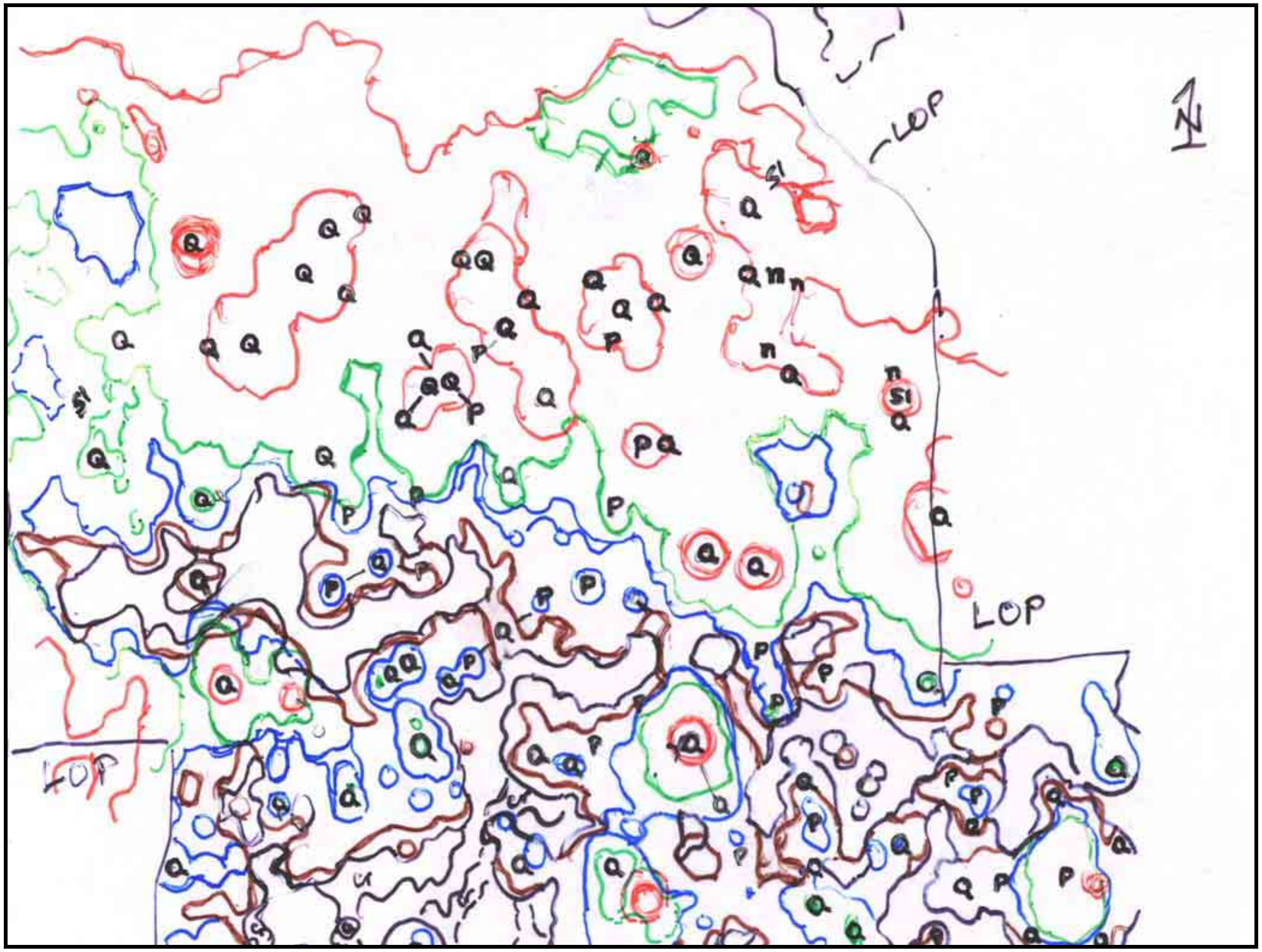

Figure 3-3. Field plot woody cover overlay (upper half, Field Plot #1) . Woody patch boundary color code: red – 1951, orange – 1961, green – 1974, blue – 1982, brown – 1990, and black – 2001.

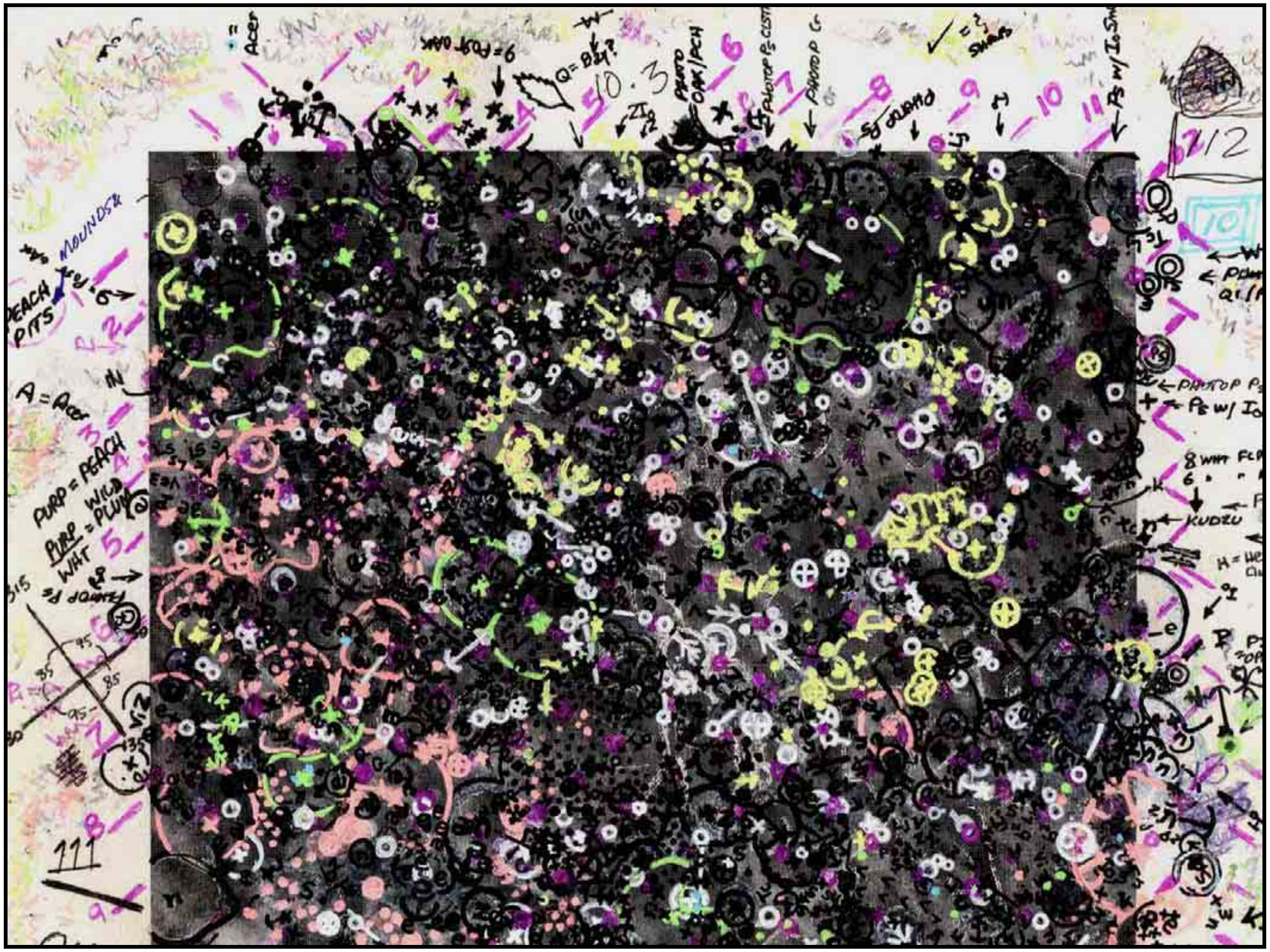

Figure 3-4. Completed field plot map (upper half, Field Plot #10).

FIELD TRANSECT PLOTS

Field Transect Purpose. Field transects were used to evaluate possible relationships between distance from the 1951 field/forest edge and the 1st generation (i.e., pioneers) woody species composition. Field transect data were compared with corresponding field plot data.

Field Transect Plot Selection. Field transects were surveyed extending true N, S, E, and W from the approximate field center to the 1951 field/forest edges (Figure 3-5). Field transect plot center points were surveyed at 50 m intervals, from the approximate field center, along each transect. Plot quadrants (NE, SE, SW and NW), 25 x 25 m (625 m^2), were then surveyed from each field transect plot center point (Figure 3-6).

Field Transect Plot Data Collection. The species name, Dbh, and height of the oldest tree or shrub (Dbh >10 cm, height >2 m) was collected within each field transect plot quadrant (Avery and Burkhart 1994). The oldest tree or shrub was identified when apparent in the field and/or aerial photographs. Dead tree and shrub snags, debris, and other remains were also used to reconstruct tree, shrub, and woody patch history as needed (Henry and Swan 1974).

Woody Volume Data Synthesis. Relative woody volume was roughly approximated using Dbh, height, and plain, evenly tapered stems. Accurately estimated volume was not needed for comparisons in this study.

Field Transect Plot Data Analysis. The field transect plot data were analyzed using descriptive statistical methods for comparison with the corresponding field plot descriptive statistical results.

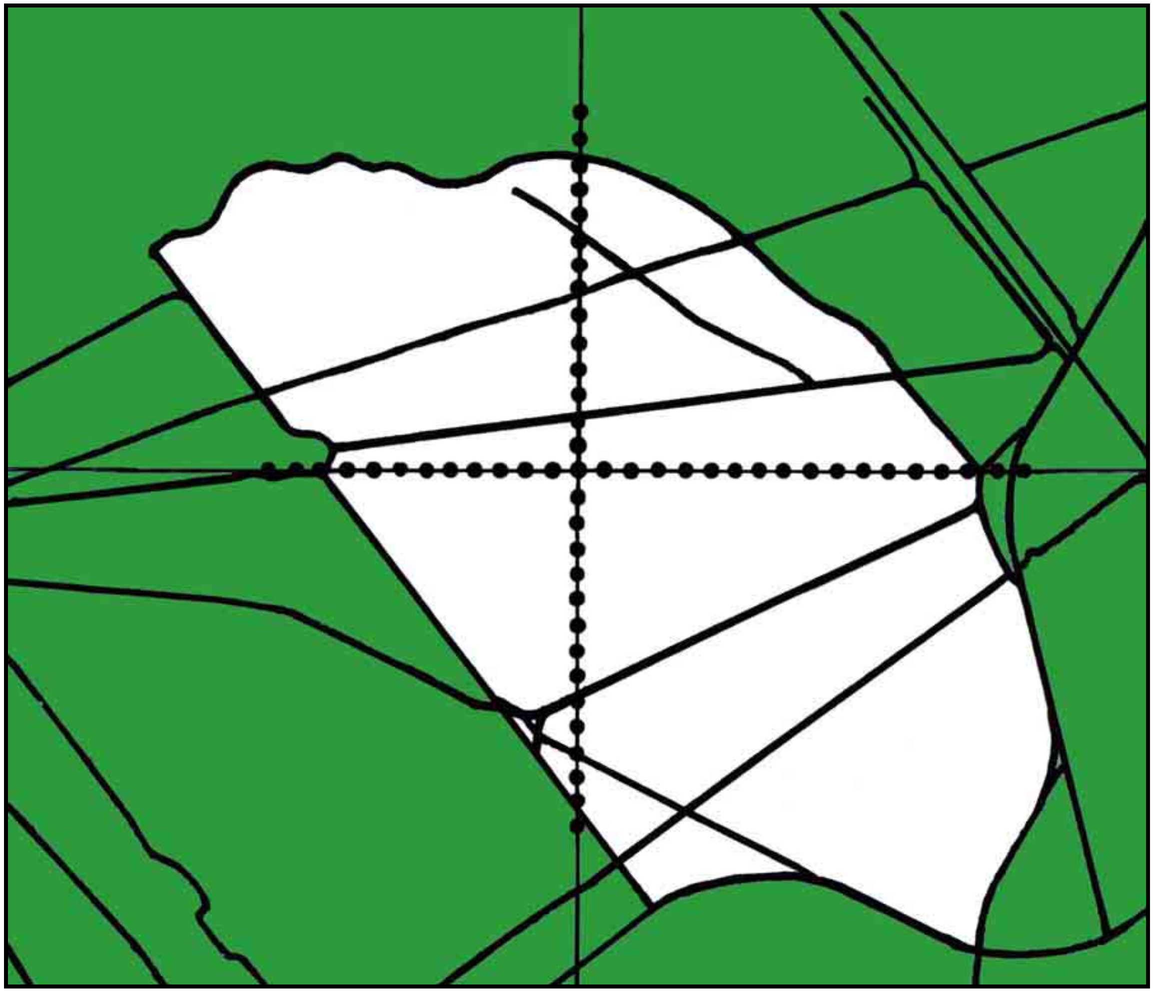

Figure 3-5. Field transect plots.

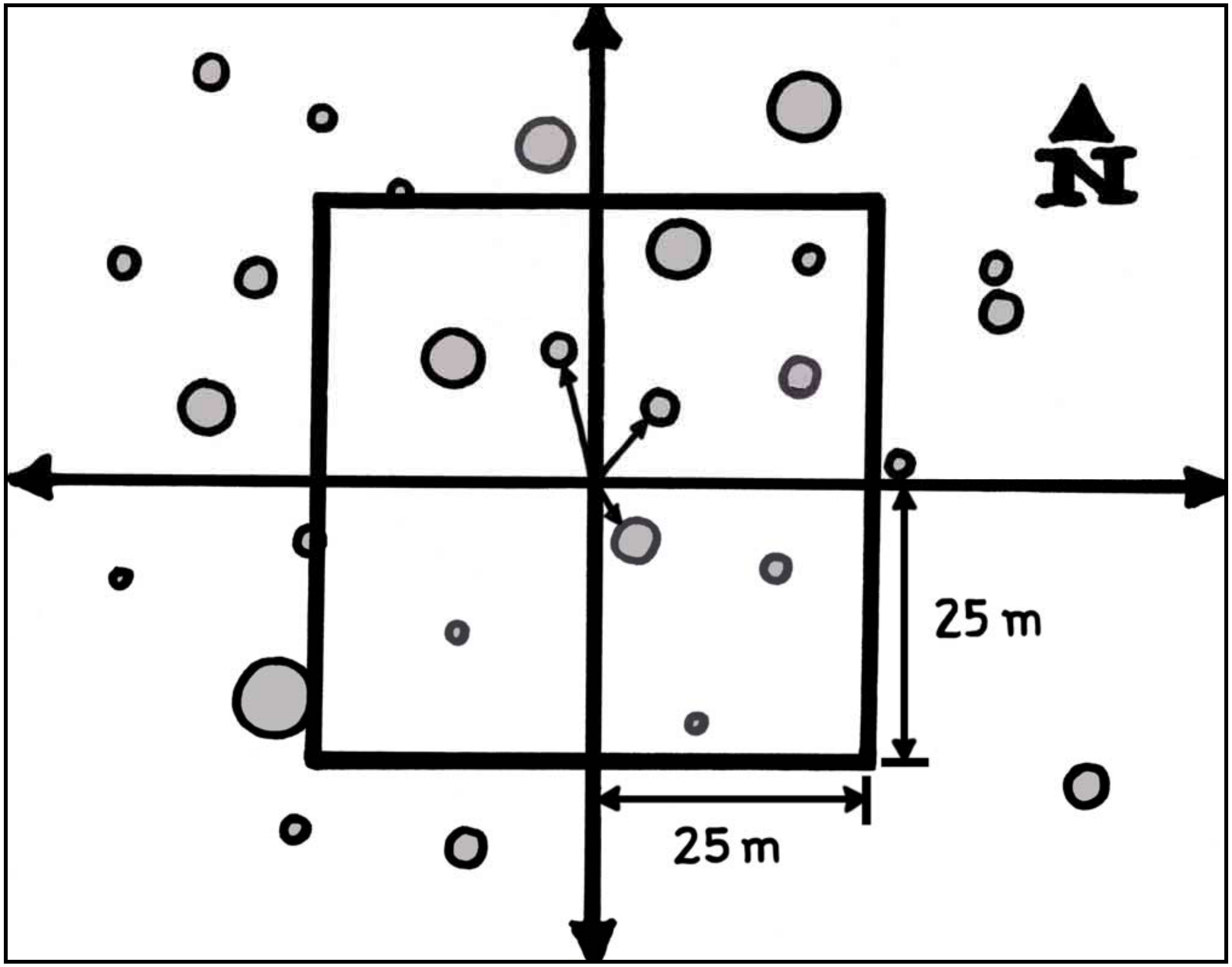

Figure 3-6. Sample field transect plot

WOODY PATCH PLOTS

Purpose of Woody Patch Plots. Woody patch plots were used as natural experiments (*sensu* Diamond 1986) in lieu of long-term field experiments. Older woody patches are the result of decades of natural processes, where the effects of positive and negative interspecific correlations are more apparent in the surviving vegetation. These decades exceed the time available for this study’s fieldwork and experiments.

These woody patch plots, like the field plot woody patches, were also used to evaluate possible interspecific relationships between the core tree and shrub species and the surrounding secondary tree and shrub species.

Woody Patch Selection. Discrete, relatively isolated woody patches (<50 m diameter) were identified in aerial photographs, and their suitability for this study was verified in the field. The patch’s core tree or shrub must have originally been more than 20 m from the nearest neighbor tree or shrub for the patch to be considered suitable. These selection criteria were set to reduce potential confounding effects from neighboring trees and shrubs. Only 30 woody patches met these selection criteria (Figure 3-7).

Woody Patch Data Collection. Woody patch core trees and shrubs were identified using photographic and field evidence, including woody patch and individual tree and shrub structure. Dead tree and shrub snags, debris, and other remains were also used to reconstruct tree, shrub, and woody patch history (Henry and Swan 1974).

Species name, Dbh, height, and main bole base to main bole base distance from, and magnetic direction to, the core tree or shrub were determined for every surrounding secondary tree and shrub (Dbh ≥ 1 cm, height ≥ 2 m) within 5.0 m of the center of the core tree or shrub’s main bole base figure (Figure 3-8).

Woody Patch Data Analysis. Woody patch tree and shrub data were analyzed using descriptive statistical methods (details in Chapter 4, Results), for comparison with other data analysis results, and Fisher’s Exact Test and Linear Regression (general linear model) for Hypothesis Two.

SOIL ALBEDO PLOTS

Soil Albedo Purpose. Soil albedo (surface tone or gray value in aerial photographs) was used to evaluate possible relationships between soil characteristics and woody succession rate. Darker soil albedos may correspond to soils with higher fines content (i.e., percent clay and silt-sized particles), OM (organic matter) content, nutrient status, and/or soil moisture availability (Lobeck 1939, Way 1978, Birkeland 1984, Howard and Mitchell 1985, Brady and Weil 1996).

Soil Albedo Analysis. The parts of Field 3-412 that had the 10% darkest soil albedos, approximated with adjustments for crop litter, were delineated from 1943 and 1951 aerial photographs (Figure 3-9). The percent of woody cover was then measured in 20 paired 0.5 ha plots, with 10 plots in the areas with darker soil albedo, and 10 matching plots in nearby areas with lighter soil albedo.

Figure 3-7. Woody patch plots.

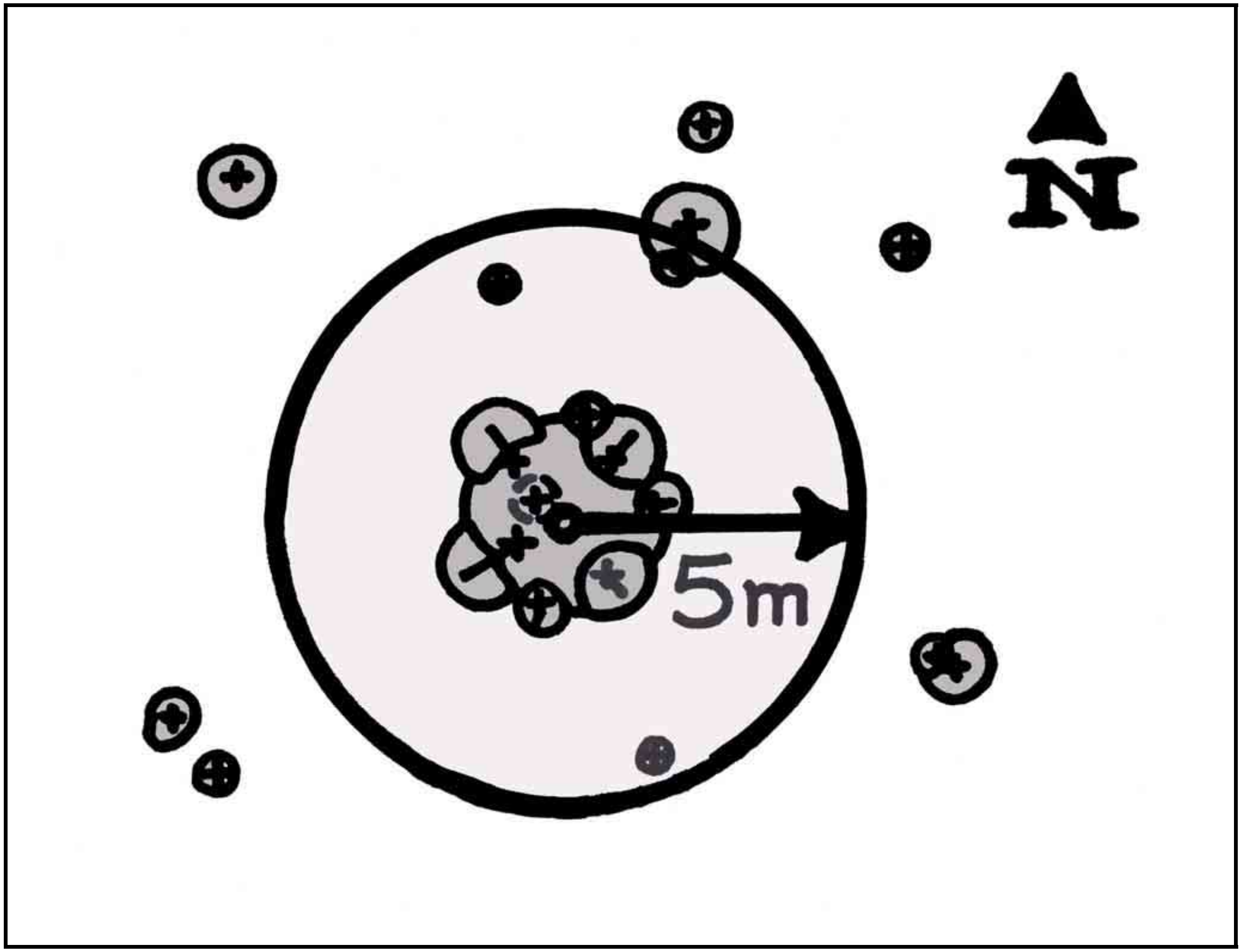

Figure 3-8. Sample woody patch plot

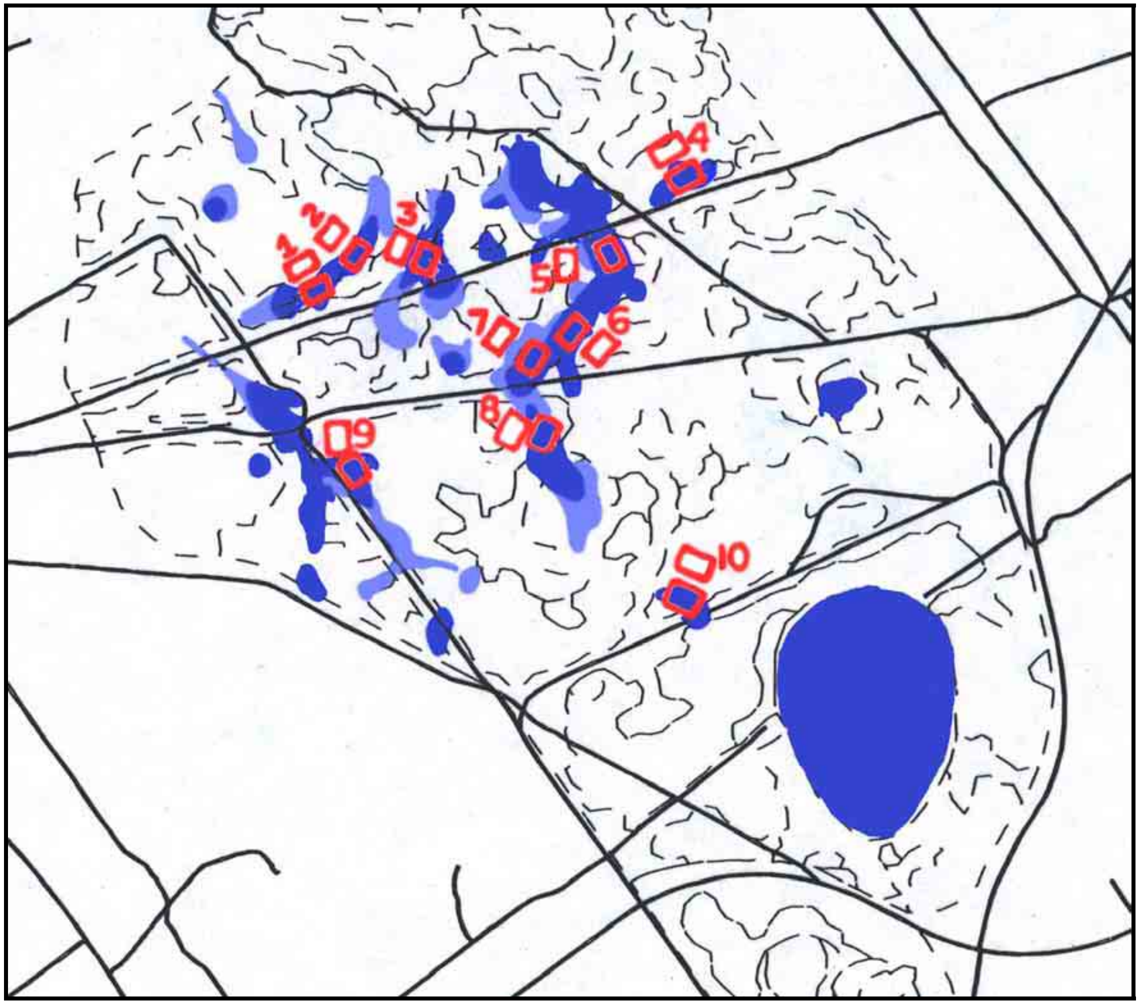

Figure 3-9. Soil plots.

These woody cover data were collected for 1951, 1961, 1974, 1982, and 1990, from aerial photographs, and for 2001 from aerial photographs and field surveys, using the same woody cover measurement methods used to measure field plot percent woody cover. These woody cover data were analyzed using an Unpaired t-Test, two-tailed, for Hypothesis Three

OTHER SITES

Savannah River Site Oak-Hickory Sites. Two SRS oak-hickory forest ecological research set-aside sites (SRS O-H sites), located in the northeast quadrant of SRS, have mostly secondary growth oak-hickory-yellow poplar forest stands between about 50 and 150 years old. Field 3-412 woody patches and forest stands are between a few years to about 100 years old. SRS O-H woody patches and forest stands were considered as possible study replicates to extend the SRS woody succession trajectory model from about 100 to about 150 years.

However, SRS O-H sites have predominantly different soils, landscape positions (mostly valley walls), topological configuration (extended rather than compact shape), and land use histories and legacies (selectively logged, secondary growth forest stands in 1951) than Field 3-412 (Davis and Janecek 1997). Therefore, the SRS O-H sites were not considered suitable for extrapolating Field 3-412’s woody succession trajectory.

Hutchison Woods. Hutchison Woods (HW), is an approximately 800-ha forested reserve in southwest Aiken, in Aiken County, South Carolina, located about 35 km north of Field 3-412. HW’s woody patches and forest stands are from less than 5 years to more than 200 years old. These patches and stands were considered as possible study replicates to extend the SRS woody succession trajectory model to about 200 years.

Like Field 3-412 and surrounding SRS, HW has many similar soils, landform positions, and a various pine, mixed pine-hardwood, and hardwood woody patches and forest stands. Unlike Field 3-412, HW patches and stands are treated with prescribed (controlled) burns for longleaf pine regeneration and wildfire management, with a 2 to 5 year burn interval (rotation) for uplands and a 4 to 8 year burn interval for slopes (Wilds *et al*. 1998; Shealy and Berger, pers. comms., 2001).

Controlled burns alter succession trajectory, most notably, early and mid-sere community species composition. However, the native woody species are sufficiently fire resistant that they eventually dominate the community, so that the burns may not substantially alter old growth forest woody species composition.

HW plots used for descriptive comparison with Field 3-412 plots and patches, with caveats concerning fire treatment effects and HW plot applicability to extrapolate Field 3-412's woody succession trajectory. Possible interspecific relationships between core tree species and the surrounding secondary trees and shrubs were to be casually evaluated.

Distinctly isolated, larger core trees were identified in the field. The core tree must have been more than 20 m from the nearest neighbor core tree for the plot to be suitable for this study. This selection criterion was set to reduce potential confounding effects from neighboring trees. Eight plots were selected for descriptive comparison with Field 3-412 plots and patches.

Relatively isolated core trees were identified in the field by their distinctly larger size and structure characteristic of core trees. Dead tree and shrub snags, debris, and other remains were used to forensically reconstruct plot history (Henry and Swan 1974).

Species name, Dbh, height, and main bole base to main bole base distance from and magnetic direction to the core tree were determined for every surrounding secondary tree and shrub (Dbh ≥ 1 cm, height ≥ 2 m) within 5.0 m of the center of the core tree's main bole base.

HW Plot tree and shrub data from eight plots were descriptively compared with corresponding data from Field 3-412.

Other Southeastern U.S. Woody Patch Plots. Woody patches in North Carolina, South Carolina, Georgia, and Florida were evaluated in 2000 and 2001 as potential study plots. These patches were to be replicates for the Field 3-412 woody patches, additional natural experiments (*sensu* Diamond 1986) in lieu of long-term field experiments. This would extend the applicability of this study's conclusions to a much larger biogeographical area.

The other woody patches, like the Field 3-412 woody patches, were to be used to evaluate possible interspecific relationships between the core tree and shrub species and the surrounding secondary tree and shrub species.

Discrete, relatively isolated woody patches (<50 m diameter) were evaluated in the field. The core tree or shrub must have originally been more than 20 m from the nearest neighbor tree or shrub for the patch to be considered suitable. Furthermore, the patch must have relatively affected by artificial disturbances. These selection criteria were set to reduce potential confounding effects.

Although several hundred of these woody patches were evaluated, none were considered suitable for this study for various reasons, including: heavy livestock grazing, trampling, chemical (i.e., fertilizer, herbicide, pesticide) treatment, mowing, pruning, and/or watering.

CHAPTER 4

RESULTS

INTRODUCTION

This chapter covers the data and descriptive statistics concerning Field 3-412 woody succession from 1951 through 2001, and the test statistics concerning the three study hypotheses of various spatial and temporal aspects of this succession. Discussion of these results would benefit from the following additional background information, best discussed here rather than in Chapter 2 (Background).

Definitions and Descriptions

First, there are no standard definitions for some of this study's subjects. Special definitions were established for these subjects in order to make this study more rigorous and feasible. These special definitions were partly based upon standard international (SI) unit measurements to facilitate comparisons of the study results.

Standard definitions used in this study include, but are not limited to:

> **Woody Plants:** Photosynthetic organisms that have one or more ligneous stems, reproduce sexually and/or asexually, and disperse propagules via seeds, rhizomes, stolons, fragments, and other means.

Woody Cover: Ground surface (area) covered by woody plants, with leaves on, as viewed from directly above (perpendicular to) the surface.

Special definitions established for this study are:

Succession Stages (Seres):

Early Stage: Herbaceous grass (graminoids) and forb (annuals and perennials) species are dominant. Note that species growth form and ecological function, rather than time (years) after abandonment, is used as the classification criteria.

Middle (or Mid) Stage: Pioneer (pine and early hardwood phases) and subclimax (middle hardwood phase) tree and shrub species are dominant.

Late Stage: "Climax" (late hardwood phase) tree and shrub species are dominant.

Woody Patch: One or more contiguous woody plants that are one or more meters tall and cover four or more meters square of ground surface area. Note that smaller woody plant(s) are indistinguishable from blackberry and vine patches in pre-1975 aerial photographs. More than

80% of Field 3-412’s woody plants that were too small to meet these “woody patch” criteria were shrubs, mostly wild plums and sumacs, which typically die within 20 years, usually from pathogen outbreak, and leave little trace after another 10 years. However, these smaller woody plants often serve as nurse plants for *Quercus laurifolia*, and sometimes for *Prunus serotina* and *Pinus taeda*.

Isolated Woody Patch: A woody patch that was established at least 5.0 m from the nearest tree or shrub crown. This reduces confounding effects from older woody patches in the area.

Distance from Field/Forest Edge: Straight-line distance from the nearest edge between oldfield and woody patch or forest stand, which is usually a woody species seed source. Field 3-412’s 1951-1966 field/forest edges were combined for the purposes of this study, to account for seed rain from the U.S. Forest Service post-1951 *Pinus taeda* and *Pinus palustris* plantings, as well as for the seed rain from the pre-1951 forest stands and woody patches. Some of these edges may be abrupt, with cleared area extending under the tree drip line. Other field/forest edges may be gradual, with several meters of scrub/shrub buffer between the cleared area and the tree drip line.

Near Plots: Plots that are within 100 m of a field/forest edge. These plots are relatively close to the field/forest edge, where most wind-dispersed seeds, most bird- and mammal-caching dispersed seeds, most bird- and mammal-defecation dispersed seeds, and all gravity-dispersed seeds are deposited. Therefore, we would expect to find relatively more pioneer pine and hard mast, and fewer pioneer soft mast trees and shrubs per unit of area in the near plots than in the mid and far plots.

Mid Plots: Plots that are 100 to 200 m from a field/forest edge. The 200 m distance from field/forest edges represents a natural break in many seed dispersal curves, as suggested in this and other studies (Chapter 2, Background). Here, some wind-dispersed seeds, some bird-caching and bird- and mammal-defecation dispersed seeds, almost no mammal-caching dispersed seeds, and no gravity dispersed seeds are deposited. Thus, we would expect to find relatively fewer pine, even fewer pioneer hard mast, but more pioneer soft mast trees and shrubs per unit of area in mid plots than in near plots.

Far Plots: Plots that are more than 200 m from a field/forest edge. Here, few wind-dispersed seeds, some bird-caching and bird- and mammal-defecation dispersed seeds, and no mammal-caching or gravity dispersed seeds are deposited. Therefore, we would expect to find relatively fewer pioneer pine, about the same amount of pioneer hard mast, but relatively more pioneer soft mast trees and shrubs per unit of area in far plots than in mid plots. Comparing the relative dispersal ranges of bird-caching (synornithochory), mammal-caching (synmammalochory) and mammal defecation (endomammalochory), soft mast seeds are typically carried further than hard mast seeds, so we could expect hard mast woody species frequency/density to generally decrease with distance from the seed source (e.g., field/forest edges for oldfields), and soft mast woody species frequency to generally increase with distance (up to several hundred meters) from the seed source.

Short Range Seed Dispersal: Seed dispersal <100 m. Relatively heavy to moderate seed rain. Includes all clonal and most gravity and synmammalochory dispersed seed distributions.

Mid Range Seed Dispersal: Seed dispersal 100 to 1000 m. Relatively moderate to light seed rain. Includes most wind (anemochory) and synornithochory dispersed seed distributions, and probably much/most water (hydrochory) and endomammalochory dispersed seed distribution. This corresponds with the first, more deterministic part of the so-called "fat" or "long" tail of seed distribution curves, particularly for the lighter wind-borne seed bearing species (e.g., *Populus deltoids*, eastern cottonwood) (Portnoy and Willson 1993, Clark *et al*. 1999).

Long Range Seed Dispersal: Seed dispersal >1000 m. Relatively light to very light seed rain. Includes some wind, bird-caching, and bird- and mammal-defecation dispersed seed distributions. This corresponds with the remaining, more stochastic part of the so-called “fat” or “long” tail of seed distribution curves (Clark *et al*. 1999).

Short lived: Woody species individuals that usually live less than 100 years.

Medium Lived: Woody species individuals that usually live between 100 and 200 years.

Long Lived: Woody species individuals that usually live more than 200 years before they begin to decline.

Slow growing: Woody species individual apical meristem (leader) annual growth increment of less than 30 cm.

Medium growing: Woody species individual apical meristem annual growth increment of between 30 and 60 cm.

Fast growing: Woody species individual apical meristem annual growth increment of more than 60 cm.

Woody Species Characteristics

Second, five woody species and woody congeneric species groups comprise about 90% of Field 3-142's woody cover: *Pinus* spp. (i.e., loblolly pine and longleaf pine), *Quercus laurifolia* (laurel oak), *Prunus serotina* (black cherry), *Prunus* spp. (wild plums), and *Crataegus* spp. (hawthorns). About 25 other woody species play various roles in Field 3-412's ecological succession, usually as less active, non-influential followers rather than as more active, influential leaders. The following list summarizes growth and dispersal characteristics of woody species that are present in Field 3-412 and in Aiken County, South Carolina (Fowells 1965, Radford *et al.* 1968, Schopmeyer 1974, Kramer and Kozlowski 1979, Little 1980, Duncan and Duncan 1988, Hightshoe 1988, Brown and Kirkman 1990, Burns and Honkala 1990a and 1990b, Dirr 1990, Workman and McLeod 1990, Hamel 1992, Young and Young 1992, Little 1993, Harlow *et al*. 1996, Odenwald and Turner 1996, Flint 1997).

Pines And Other Softwood Species

Pinus taeda L. (loblolly pine):

Structure: Evergreen tree; up to 35 m tall; conical to rounded or ovoid spreading crown; fusiform (*Cronartium quercuum* f. sp. *fusiforme*) rust prone, trunks and branches with fusiform rust-induced cankers are more vulnerable to wind breakage

Dispersal: 7.5 to 15 cm cone with twenty to two hundred, 20 to 25 mm long samaria; October through December; wind dispersed

Tolerances: Shade intolerant, drought tolerant

Succession Role: Early woody stage (pine phase); many woody patch cores and fringes; medium lived, fast growing

Pinus palustris Mill. (longleaf pine):

Structure: Evergreen tree; up to 45 m tall; conical to open, irregular, spreading crown

Dispersal: 10 to 25 cm cone with fifteen to fifty, 35 to 45 mm long samaria; October through November; wind dispersed

Tolerances: Very shade intolerant, drought tolerant, very fire tolerant

Succession Role: Early woody stage (pine phase); some woody patch cores; medium lived, fast growing after 3 to 5 years

Juniperus virginiana L. (eastern redcedar):

Structure: Evergreen tree, up to 35 m tall; very dense, conical (pyramidal) or almost columnar crown

Dispersal: 5 to 10 mm berrylike cone with one to four seeds; February through March; gravity, bird, and mammal dispersed; susceptible to cedar apple rust (blight) (*Gymnosporangium juniperi-virginianae*), which with heavy infection can inhibit reproduction

Tolerances: Shade tolerant in youth, very shade intolerant with maturity; drought tolerant, fire intolerant

Succession Role: Early and middle woody stages; few woody patch cores; long lived, slow growing

Softmast Hardwood Species

Prunus spp. L. (wild plums):

Structure: Deciduous small tree or patch-forming shrub, up to between 6 and 11 m tall, rounded crown

Dispersal: 10 to 15 mm plum with single stone and seed; May through July; clonally, gravity, bird, and mammal dispersed

Tolerances: Shade intolerant, drought tolerant

Succession Role: Early woody stage (early hardwood phase); many woody patch cores and fringes; common nurse shrub for *Quercus laurifolia*; short lived, medium to fast growing

Other: Most wild plums in Field 3-412 are *Prunus angustifolia* Marshall (Chickasaw plum), *Prunus americana* Marshall (wild plum), *Prunus umbellata* Ell. (hog plum), and their hybrids. These sub-congeneric species were combined, because of their many physical and ecological similarities, to facilitate analyses

Prunus serotina Ehrh. (black cherry, rum cherry, or wild cherry):

Structure: Deciduous tree, up to 35 m tall; medium to open, ovoid or rounded crown; canker (black knot) prone, canker-weakened branches are very vulnerable to breakage by wind and climbing vines

Dispersal: 10 mm drupe with single stone and seed; gravity, bird, and mammal dispersed

Tolerances: Shade intolerant, drought tolerant

Succession Role: Early woody stage (early hardwood phase); many woody patch cores and fringes; dominant or co-dominant tree up to 100 years age; common nurse tree for *Quercus laurifolia*; medium lived, fast growing

Crataegus spp. L. (hawthorns):

Structure: Deciduous small tree or patch-forming shrub; up to between 7 and 9 m tall; dense, rounded crown

Dispersal: 12 mm pome, 1 to 5 nutlets; May through June; gravity, bird, and mammal dispersed

Tolerances: Shade intolerant, drought tolerant

Succession Role: Early hardwood stage (early hardwood phase); woody patch core and fringe; short lived, slow growing

Other: This genus is confused taxonomically, with many species and hybrids (Radford *et al.* 1968). Most hawthorns in Field 3-412 are probably *Crataegus flava* Ait. (southern haw). All hawthorn were summarily taxonomized, and because of the congeneric species' many physical and ecological similarities, were combined to facilitate analyses

Rhus spp. L. (sumacs):

Structure: Deciduous small tree or patch-forming shrub, up to 12 to 15 m tall; open, spreading crown

Dispersal: 3 to 5 mm single nutlets; June through October; bird, mammal, and gravity dispersed

Tolerances: Very shade intolerant, drought tolerant

Succession Role: Early woody stage (early hardwood phase); some woody patch cores and fringes; short lived, fast growing

Celtis occidentalis L. (common hackberry):

Structure: Deciduous tree, up to 35 m tall, ovoid or rounded crown

Dispersal: 6 to 12 mm drupe with single seed; October through January; gravity, bird, and mammal dispersed

Tolerances: Intermediate shade tolerance, drought tolerant

Succession Role: Early woody stage (early hardwood phase); some woody patch cores and fringes; medium lived, medium growing

Diospyros virginiana L. (common persimmon):

Structure: Deciduous tree, up to 40 m tall; ovoid crown, sometimes irregular; branches vulnerable to stem borer

Dispersal: 2 to 4 cm plum-like berry with 3 to 8 flat seeds; September through November; gravity, bird, and mammal dispersed

Tolerances: Shade intolerant, drought tolerant

Succession Role: Early hardwood stage (early hardwood phase); woody patch cores and some fringes; some in forest stands, particularly the more mesic sites; short lived, slow growing

Malus angustifolia (Ait.) Michx. (southern crabapple, wild crabapple):

Structure: Deciduous small tree or patch-forming shrub, up to 14 m tall; open, rounded spreading crown

Dispersal: 2 to 2.5 cm fleshy pome with 5 to 10 seeds; August through October; clonally, gravity, bird, and mammal dispersed

Tolerances: Shade intolerant, drought tolerant

Succession Role: Early hardwood stage; some woody patch cores and fringes; short lived, medium growing

Melia azedarach L. (Chinaberry, Pride of India):

Structure: Deciduous small tree and patch-forming shrub, up to 15 m tall; open, rounded or umbrella-shaped crown

Dispersal: 15 mm drupe with one stone containing 3 to 5 seeds; September through January; gravity and bird dispersed

Tolerances: Shade intolerant, drought tolerant

Succession Role: Early hardwood stage (early hardwood phase); some woody patch cores and fringes; short lived, fast growing

Prunus caroliniana (Mill.) Ait. (Carolina laurelcherry, cherry-laurel):

Structure: Evergreen shrub or small tree, up to 14 m tall; dense, conical to ovoid or rounded crown

Dispersal: 6 to 12 mm drupe with single stone and seed; September through March; gravity and bird dispersed

Tolerances: Shade intolerant

Succession Role: Early woody stage (early hardwood phase); few woody patch cores; short lived, fast growing

Sassafras albidum (Nutt.) Nees (common sassafras):

Structure: Deciduous tree or patch-forming shrub, up to 30 m tall; irregular conical to irregular round or ovoid crown

Dispersal: 10 to 12 mm berry with single seed; September through October; clonally, bird, gravity, and mammal dispersed

Tolerances: Shade intolerant, drought tolerant, fire intolerant

Succession Role: Early woody stage (early hardwood phase); some woody patch cores and fringes; short lived, medium growing; allelopathic

Cornus florida L. (flowering dogwood):

Structure: Deciduous small tree, up to 15 m tall; open, rounded or spreading crown

Dispersal: 10 to 15 mm drupe with stone containing one or two seeds; September through November; gravity, bird, and mammal dispersed

Tolerances: Very shade tolerant, intermediate drought tolerance

Succession Role: Late woody stage (late hardwood phase); usually in forest stand understory to mid-story, few in woody patch fringes, may live up to 125 years, medium to fast growing

Hardmast Hardwood Species

Quercus laurifolia Michx. (laurel oak, Darlington oak):

Structure: Nearly evergreen (semi-evergreen or tardy deciduous) tree, up to 40 m tall; dense, conical or rounded crown; poorly self-pruning

Dispersal: 12 mm acorn (nut); September through October; gravity, water, bird, and mammal dispersed

Tolerances: Shade tolerant, drought tolerant, fire intolerant

Succession Role: Early and middle woody stages (early and middle hardwood phases); many woody patch cores and very many fringes; allelopathic or water competition zone around many trees, with reduced biodiversity; short lived, fast growing

Other: Many authors refer to *Quercus laurifolia* as *Quercus hemisphaerica* Bartram ex Willd., which they define as an upland oak species, and they consider *Quercus laurifolia* (swamp laurel oak, diamond leaf oak) to be a lowland oak species. These were combined into a single species: *Quercus laurifolia*

Carya illinoensis (Wang.) K. Koch (pecan):

Structure: Deciduous tree, up to 35 m tall; open, rounded crown

Dispersal: 3 to 5 cm nut, thin husk and shell; August through October; gravity, water, bird, and mammal dispersed

Tolerances: Shade intolerant, intermediate drought tolerance

Succession Role: Early hardwood stage; some woody patch cores, few woody patch fringes; long lived, slow growing

Quercus spp. L. (oaks):

Structure: Deciduous trees, up to between 15 and 40 m tall (scrub oaks are the shorter spp., mesic oaks are the taller spp.), rounded crowns

Dispersal: 1 to 3 cm acorn; September through October; gravity, water, bird, and mammal dispersed

Tolerances: Intermediate shade tolerance to shade intolerant; all drought tolerant

Succession Role: Middle and late woody stages (middle and late hardwood phases); usually in forest stands; scrub oaks (*Quercus incana* (bluejack oak), *Quercus laevis* (turkey oak), *Quercus marilandica* (blackjack oak), *Quercus stellata* (post oak)) more common on drier soils, mesic oaks (*Quercus alba* (white oak), *Quercus falcata* (southern red oak), *Quercus velutina* (black oak}) more common on moister soils; mesic oaks are long lived, slow growing

Carya spp. (Nutt.) (hickories):

Structure: Deciduous trees, up to between 35 and 45 m tall, ovoid to rounded crown

Dispersal: 2.5 to 5 cm nut, thin to thick husks and shells; August through October; gravity, water, bird, and mammal dispersed

Tolerances: *Carya cordiformis* (Wangenh.) K. Koch (bitternut hickory), and *Carya glabra* (Mill.) Sweet (pignut hickory) have intermediate shade tolerance (shade intolerant in Kramer and Kozlowski 1979); *Carya tomentosa* (mockernut hickory) is shade intolerant; all are drought tolerant

Succession Role: Late hardwood stage; usually in forest stands, rarely in woody patches; long to very long lived, slow growing

Liquidambar styraciflua L. (sweetgum):

Structure: Deciduous tree, up to 38 m tall; conical, ovoid, or rounded spreading crown

Dispersal: 2.5 to 3 cm fruiting head (“ball”) of beaklike capsules (“spikes”) with one or two, 8 to 12 mm long samaria (carpel) per capsule; September through November; gravity and wind dispersed

Tolerances: Shade intolerant, intermediate drought tolerance

Succession Role: All hardwood stages, most in early hardwood stage; usually in more open forest stands, some in woody patch fringes; long lived, medium to fast growing

Liriodendron tulipfera L. (yellow poplar, tulip poplar, tuliptree):

Structure: Deciduous tree, up to 38 m tall; epicormic branching, good self-pruner; conical to columnar, ovoid or rounded spreading crown

Dispersal: 4 to 5 cm “cone” of 80 to 100 overlapping, one- or two-seeded, 15 to 25 mm long samaria; October through November; wind dispersed

Tolerances: Intermediate shade tolerance, drought intolerant

Succession Role: Late woody stage (late hardwood phase); usually in more open forest stands; quick vertical and lateral growth to fill forest canopy gaps; long lived, medium to fast growing

Quercus nigra L. (water oak):

Structure: Deciduous tree, up to 32 m tall; conical or rounded crown; rot prone; soft/weak wood, larger branches are moderately vulnerable to wind breakage

Dispersal: 10 to 15 mm acorn; September through October; gravity, water, bird, and mammal dispersed

Tolerances: Intermediate shade tolerance

Succession Role: Late woody stage (late hardwood phase); usually in forest stands; short lived, fast growing

Species Groupings For Analyses

Third, many of Field 3-412's woody plant species have similar growth form (structure or architecture), bark, leaves, flowers, fruit, physiology, tolerances, ecosystem functions, and roles in ecological succession. Some of these species are so similar that botanists disagree of the number of species and hybrids, e.g., *Crataegus* spp. (hawthorns) (Radford *et al*. 1968).

Two Field 3-412 woody species were studied as separate species; all others were studied as groups of similar species, based upon their apparent roles in ecological succession:

- *Quercus laurifolia* and *Prunus serotina* were studied as two separate species;
- All other hard mast woody species were studied as one group;
- *Pinus palustris* and *Pinus taeda* were studied as a second group; and
- All other soft mast woody species were studied as a third group.

FIELD 3-412 WOODY SUCCESSION FROM 1951 THROUGH 2001

The SUSES models predict that southeastern U.S. oldfields, without reference to oldfield size, would be completely covered by young pine forest after about 25 years; that hardwoods would gradually invade the understory, where canopy shade favors hardwoods over pines; and that hardwoods would gradually replace pines after about 100 years and eventually dominate the forests after about 150 years (Crafton and Wells 1934, McQuilkin 1940, Oosting 1942, Keever 1950). However, Field 3-412's observed woody succession between 1951 and 2001 has differed significantly from the SUSES model predicted woody succession (Golley 1965, Golley *et al.* 1994). Let's discuss some of the features of this "aberrant" woody succession.

General Photointerpretation Results: None of the 152 (0%) points (on a regular hexagonal grid) throughout Field 3-412 had woody cover in 1951. The number of points with woody cover increased to 6 (4%) in 1961, 23 (15%) in 1974, 58 (38%) in 1982, 98 (64%) in 1990, and 120 (79%) in 2001 (Table and Figure 4-1). Field 3-412's overall plant cover in 2001 is approximately 25% pines, 55% hardwoods (soft and hard mast trees and shrubs), and 20% grasses, forbs, and vines. The change of species composition over this 50-year period could not be determined because many trees and shrubs could not be identified to the species on the aerial photographs.

These results are consistent with ecological succession theory and models, where woody primary production, biomass, and cover generally increase over time after disturbances. The woody cover percent (frequency) curve is sigmoidal, with descending inflection at about the year 1990. The woody cover curve will probably peak between the

Table 4-1. Field 3-412 woody cover plot count and total percent woody cover in 1951, 1961, 1974, 1982, 1990, and 2001.

Year	Woody Cover Plots	Percent Woody Cover
1951	0	**0**
1961	6	**4**
1974	23	**15**
1982	58	**38**
1990	98	**64**
2001	120	**79**

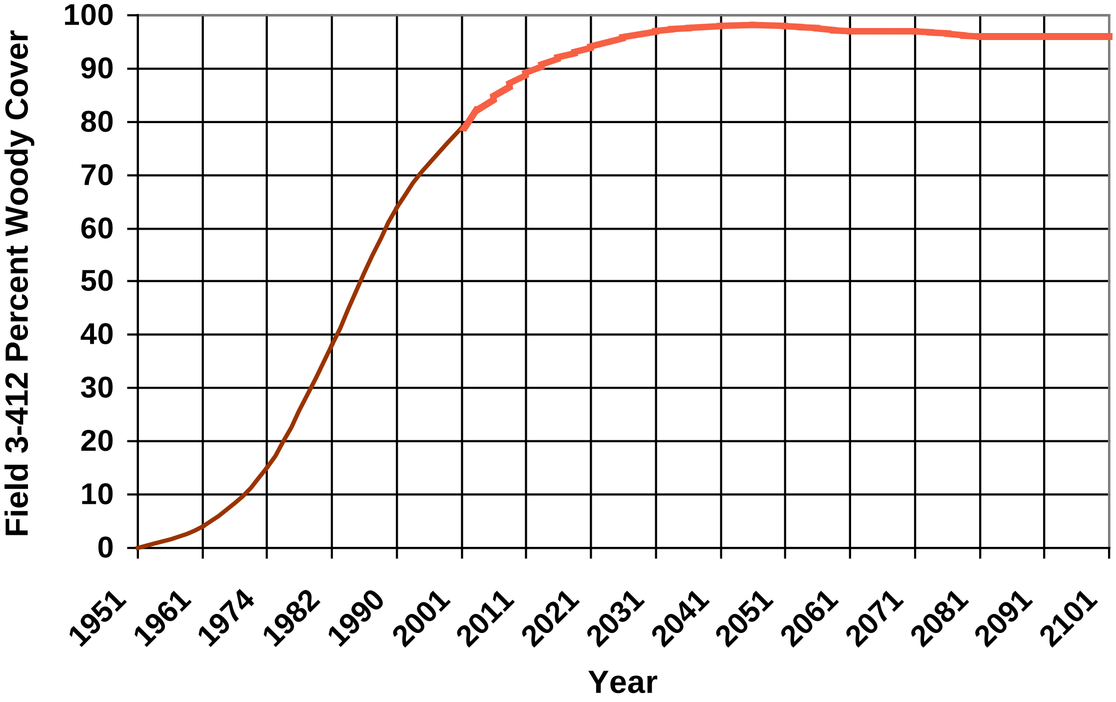

Figure 4-1a. Field 3-412 total percent woody cover in 1951, 1961, 1974, 1982, 1990, and 2001. Brown line represents the observed percent woody cover, red line represents the predicted (projected) percent woody cover.

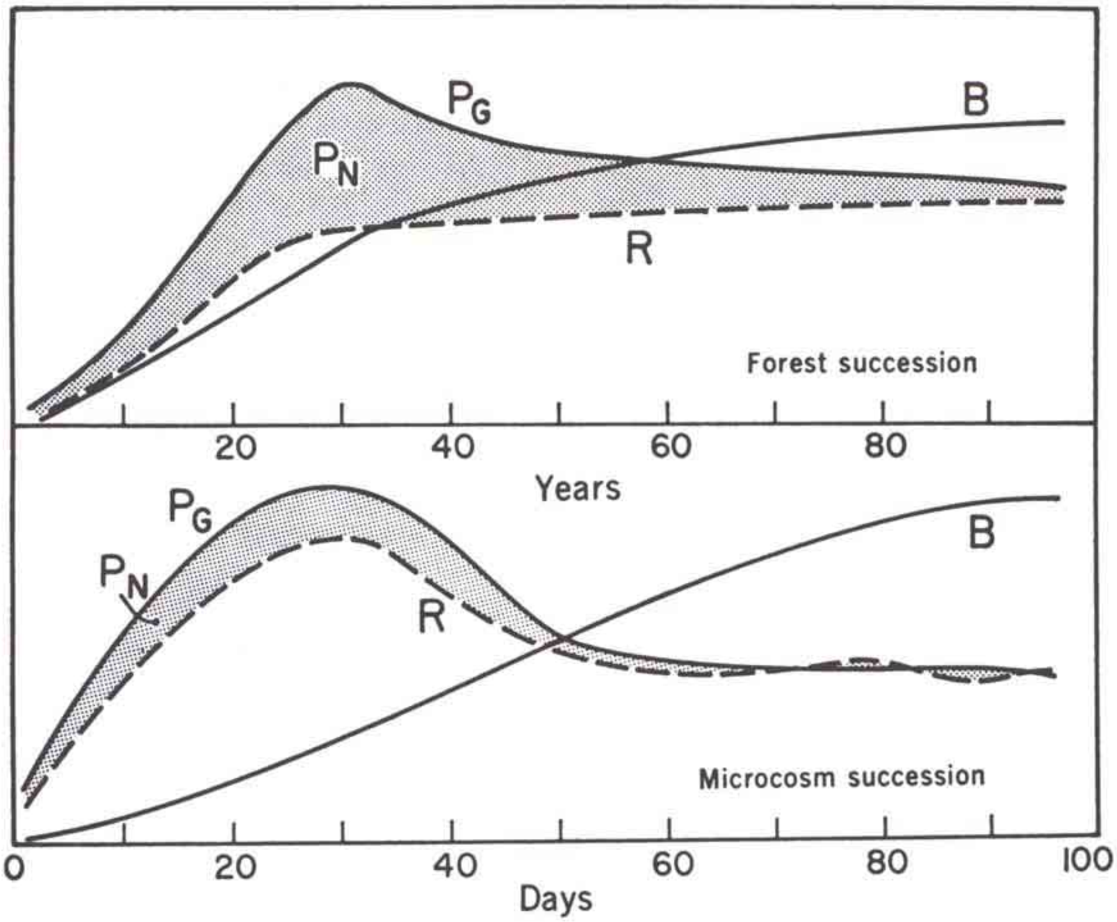

Figure 4-1b. Ecosystem succession and corresponding gross and net primary productivity (P_G and P_N) and biomass (B) changes over time (Odum 1969).

years 2040 and 2060, decline slightly for several decades after the peak (overshoot), much like the forest gross primary productivity as modeled by Eugene Odum (Figure 4-1b, 1969), then level off with minor irregular fluctuations until the next major disturbance(s).

Detailed Photointerpretation Results: The 17 Field 3-412 field plots (covering 1.0 to 2.5 ha each, totaling about 24.5 ha (17%) of Field 3-412's 142 ha) also provide data on overall woody cover. These plots had 0% woody cover in 1951, 3% in 1960, 13% in 1974, 26% in 1982, 49% in 1990, and 62% in 2001. These compare with 4% in 1961, 15% in 1974, 38% in 1982, 64% in 1990, and 79% woody cover in 2001, from the photo-interpretation results that cover the entire field (Table and Figure 4-1). The detailed results, like the general results, are consistent with ecological succession theory and models, with woody biomass and cover increasing over time.

The 17 field plots were used to describe woody cover over space. Percent cover was compared at five distance intervals from the field/forest edge, over six years from 1951 to 2001 (Table 4-2). The effect of the edge on woody cover is obvious throughout all years. However, the results from plots between 101 and 300 m from the field/forest edge did not form a regular transition between distance classes. The 101 to 200 m plots had later and slower woody succession as expected from seed dispersal models, but it was unexpectedly slower than the woody succession in the 201 to 300 m plots (Figures 4-2a and 4-2b). These irregularities are probably not unusual considering the study sample size and typical environmental heterogeneities over time and space.

Table 4-2. Percent of field plot woody cover grouped by year at different distances from Field 3-412's 1951-1966 field/forest edge, and weighted mean woody cover percentage for all distances.

	Plot Distance from 1951-1966 Field/Forest Edge					**Weighted Mean for All Distances**
	0 to 100 m	**101 to 200 m**	**201 to 300 m**	**301 to 400 m**	**401 to 550 m**	
1951	0	0	0	0	0	**0**
1961	7	2	2	0	0	**3**
1974	22	8	16	2	2	**13**
1982	40	15	28	14	13	**26**
1990	75	38	40	28	29	**49**
2001	88	57	47	40	42	**62**

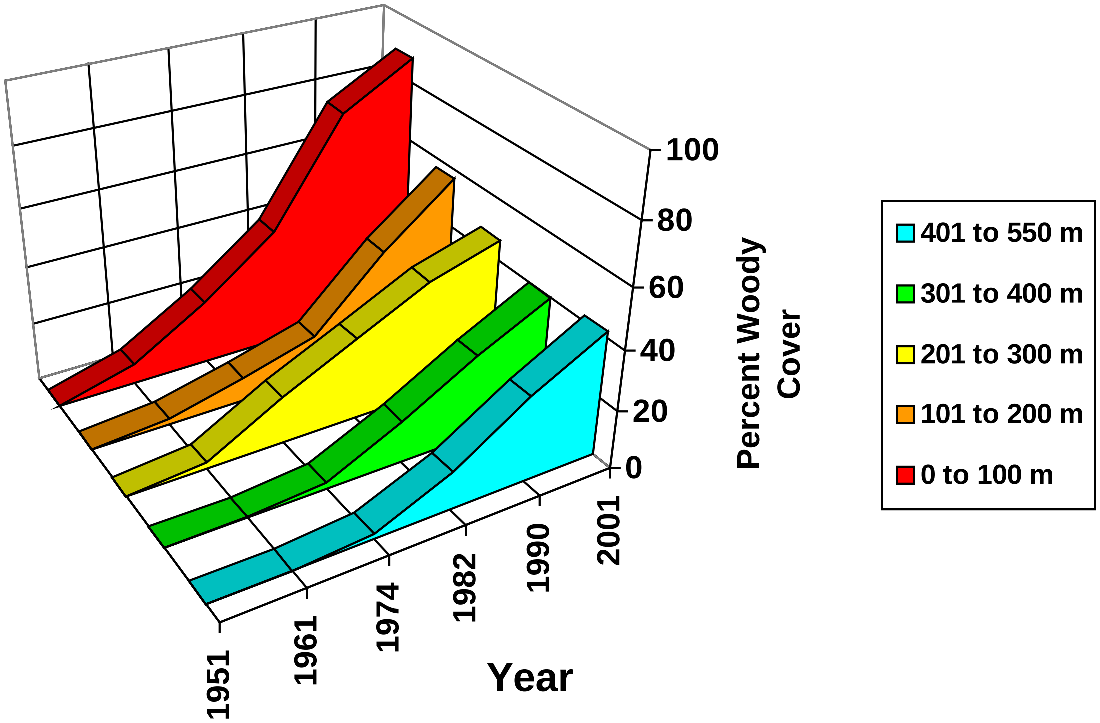

Figure 4-2a. Percent of field plot woody cover grouped by year at different distances from Field 3-412's 1951-1966 field/forest edge.

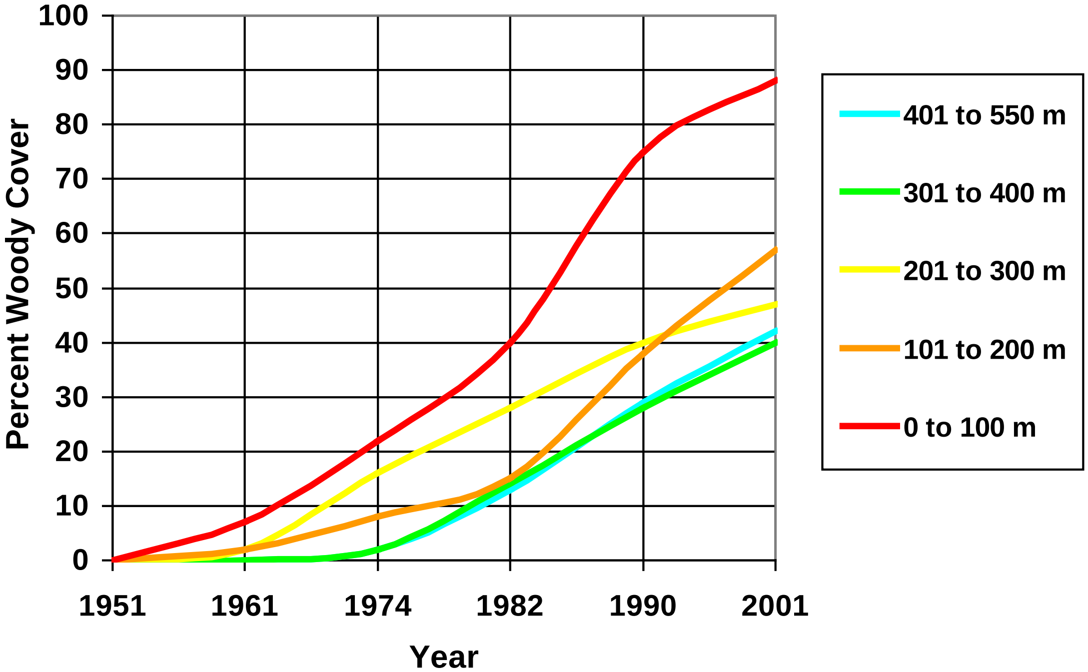

Figure 4-2b. Percent of field plot woody cover grouped by year at different distances from Field 3-412's 1951-1966 field/forest edge.

The weighting factors used to calculate the weighted means in Table 4-2 are proportional to the percentage of Field 3-412 that is covered by each corresponding 100 m zone (0.34 for 0 to 100 m, 0.26 for 101 to 200 m, 0.21 for 201-300 m, 0.14 for 301-400 m, and 0.05 for 401-500 m).

HYPOTHESIS ONE

Hypothesis One concerns relationship(s) between the distance of isolated woody patches from field/forest edges and the corresponding woody patch core species composition. Null Hypothesis One is that isolated woody patch core species composition remains constant (does not vary, there is no difference) with distance from the field/forest edge. The SUSES models predict that pines would substantially dominate isolated woody patch core species composition, without reference to distance from the field/forest edge.

Specifically: Field 3-412 soft mast tree species (*Prunus serotina* (black cherry), *Prunus carolinia* (laurel or Carolina cherry), *Melia azedarach* (Chinaberry), *Pyrus coronaria* (crabapple), and *Diospyros virginiana* (persimmon)) and shrub species (*Crataegus* spp. (hawthorn), *Rhus* spp. (sumac), and *Prunus* spp. (wild plum)) were expected to dominate the core species composition of most isolated woody patches that were >200 m from Field 3-412's 1951-1966 field/forest edges. This expectation arose from exploratory observations of woody plant patterns (distributions) made throughout Field 3-412, and from the general likelihood of bird- and mammal-dispersed seed dominance of seed rain at these distances.

Table 4-3. Number of isolated woody patches grouped by core woody species at different distances from Field 3-412's 1951-1966 field/forest edge.

Patch Core Woody Species	**Patch Distance from 1951-1966 Field/Forest Edge**				
	0 to 100 m	**101 to 200 m**	**201 to 300m**	**301 to 400 m**	**401 to 550 m**
Quercus laurifolia	82	70	44	29	15
Other Hard Mast Spp.	6	6	6	9	2
Pinus Spp.	34	61	25	42	25
Prunus serotina	13	47	71	47	24
Other Soft Mast Spp.	0	22	68	23	20

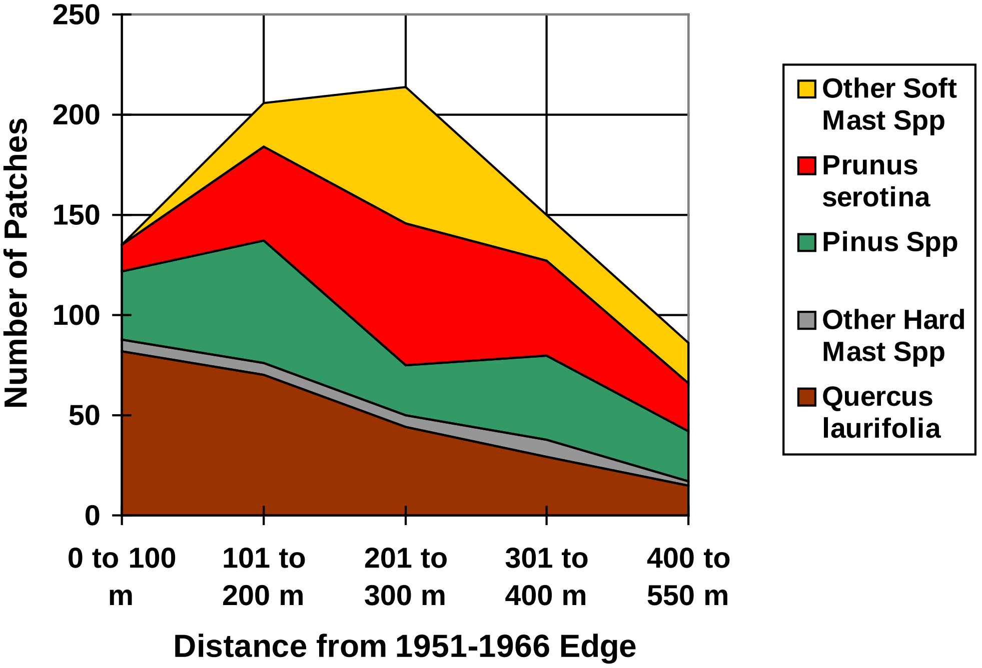

Figure 4-3. Number of isolated woody patches grouped by core woody species at different distances from Field 3-412's 1951-1966 field/forest edge. The upper curve represents the total number of observed woody patches from Table 4-3.

Table 4-4. Percent of isolated woody patches by core woody species at different distances from Field 3-412's 1951-1966 field/forest edge.

Patch Core Woody Species	**Patch Distance from 1951-1966 Field/Forest Edge**				
	0 to 100 m	**101 to 200 m**	**201 to 300m**	**301 to 400 m**	**401 to 550 m**
Quercus Laurifolia	61	34	21	19	17
Other Hard Mast Spp.	4	3	3	6	2
Pinus Spp.	25	30	12	28	29
Prunus serotina	10	23	33	31	28
Other Soft Mast Spp	0	11	32	15	23

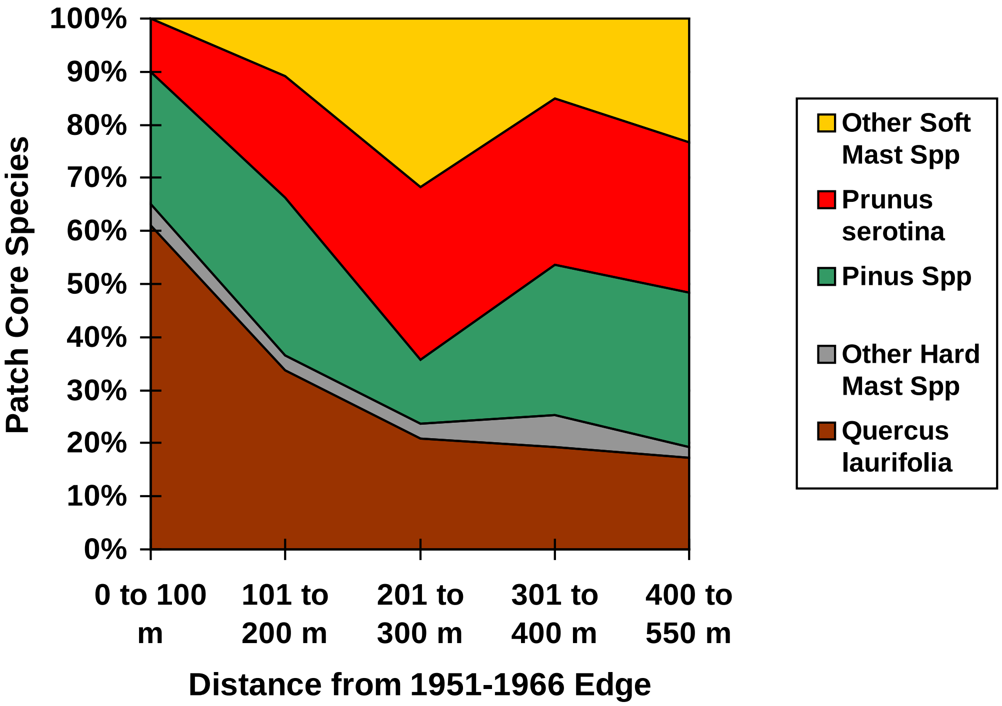

Figure 4-4. Percent of isolated woody patches by core woody species at different distances from Field 3-412's 1951-1966 field/forest edge.

Field Plot Results: Two hundred and fifty three out of the 450 (56%) field plot isolated woody patch cores that were >200 m from Field 3-412's 1951-1966 field/forest edges were dominated by soft mast woody species, 92 (20%) by pine species, and 105 (23%) by hard mast woody species (Tables and Figures 4-3 and 4-4). This contrasts with 24% soft mast, 28% pine, and 48% hard mast for patches <200 m from the field/forest edges.

The Chi-square test of the field plot data shows a positive association ($\chi^2 = 3.849$ with degrees of freedom (d.f.) = 1) between isolated woody patch distance from Field 3-412's 1951-1966 field/forest edges and soft mast woody species dominance of the patch cores. This was statistically significant, with a P value of 0.0498.

These findings support rejection of Null Hypothesis One and are generally inconsistent with SUSES model predictions that pines would dominate isolated woody patch cores that were >200 m from Field 3-412's 1951-1966 field/forest edges. However, there were cases that were consistent with SUSES model predictions:

> Several extensive pine patch clusters, predominately *Pinus taeda*, were established at >200 m from Field 3-412's 1951-1966 field/forest edges. These pine patches grew, coalesced, and now cover only about 25% of Field 3-412 in 2001, 50 years after abandonment, rather than the entire field as predicted by SUSES models.

The scarcity of suitable replicate study sites and the time and expense required to find and study these sites precluded determining whether Field 3-412 is a rare case of relatively unaltered atypical arrested succession at the landscape level, or a rare case of relatively unaltered typical succession at the landscape level.

Several thousand casual (informal, not anecdotal), unrecorded observations and evaluations (since early 1970's) of plant communities throughout the eastern U.S., Puerto Rico, Venezuela, Canada, and Europe have lead me to conclude that Field 3-412 is most likely a rare case of relatively unaltered typical succession at the landscape level, i.e., bird and mammal dispersed soft mast woody species establish and initially dominate most woody patches that were initially >200 m from the nearest woody species seed source/s, e.g., Field 3-412's 1951-1966 field/forest edges.

Long-range dispersal (>1000 m) of soft mast woody species seeds by birds (e.g., *Crataegus* spp., *Diospyros virginiana*, *Melia azedarach*, *Pyrus coronaria*, *Rhus* spp.) (McDonnell and Stiles 1983, McDonnell 1986, Howe and Westley 1988, DeGraaf *et al.* 1991, Hamel 1992, McClanahan and Wolfe 1993, Robinson and Handel 1993) and mammals (e.g., *Odoccoileus virginianus* (white-tailed deer), *Procyon lotor solutus* (raccoon), and *Sus scrofa* (feral swine)) (Golley 1962, 1966; Howe and Westley 1988, Cothran *et al.* 1991, is the most likely explanation for soft mast woody species dominance of isolated woody patch core species composition of patches >200 m from Field 3-412's 1951-1966 field/forest edges.

Conversely: Field 3-412 pines (*Pinus taeda* (loblolly pine), *Pinus palustris* (longleaf pine)) and hard mast woody species (*Cornus florida* (flowering dogwood), *Liquidambar styraciflua* (sweetgum), *Liriodendron tulipfera* (yellow or tulip poplar), *Quercus laurifolia*, *Quercus nigra* (water oak), assorted scrub *Quercus* spp., *Carya* spp. (pecan and hickories)) were expected to dominate isolated woody patch core species composition within 200 m of Field 3-412's 1951-1966 field/forest edges. This expectation arose from local species pool species composition and the species' seed distribution curves, and was reinforced by exploratory observations of woody plant distribution throughout Field 3-412.

Field Plot Results: Ninty-five out of the 341 (28%) field plot isolated woody patch cores that were <200 m from Field 3-412's 1951-1966 field/forest edges were dominated by pines, 164 (48%) by hard mast woody species, and 82 (24%) by soft mast woody species (Tables and Figures 4-3 and 4-4). This contrasts with 20% pine, 23% hard mast, and 56% soft mast for patches >200 m from the field/forest edges.

Chi-square test results show a negative association ($\chi^2 = 32.075$ with d.f. = 1) between isolated woody patch distance from Field 3-412's 1951-1966 field/forest edges and hard mast woody species dominance of the patch cores, statistically significant with a P value of 0.0001.

These findings also support rejection of Null Hypothesis One, but they are less inconsistent with SUSES model predictions that pines would dominate woody patch cores that were <200 m from Field 3-412's 1951-1966 field/forest edges.

Several cases were inconsistent with SUSES model predictions:

> Mixed hardwood forest stands surrounded Field 3-412 in 1951, to the west, north and east (Figure 2-4). These stands were mostly in mesic

swales and included: *Quercus* spp. (mostly *Quercus laurifolia* and *Quercus nigra*), *Carya* spp., *Liquidambar styraciflua*, *Liriodendron tulipfera, Magnolia* spp. (magnolias), and *Cornus florida*. The woody patch cores that established in the adjacent oldfields, within about 200 m of these stands, were dominated by *Quercus laurifolia* (Tables and Figures 4-3 and 4-4). This *Quercus laurifolia* dominance is inconsistent with the SUSES model predictions. However, it is consistent with the local species pool composition (*sensu* Egler 1954) and *Quercus laurifolia*'s competitive advantage from its higher tolerance of more stressful oldfield soil and microclimate conditions.

Short-range dispersal (<100 m) of hard mast woody species seeds by wind, gravity, birds (e.g., *Cyanocitta cristata* (blue jay), *Sitta carolinensis* (white breasted nuthatch), *Bombycilla cedrorum* (cedar waxwing), *Colinus virginianus* (bobwhite)) (McDonnell and Stiles 1983, McDonnell 1986, Howe and Westley 1988, DeGraaf *et al.* 1991, Hamel 1992, McClanahan and Wolfe 1993, Robinson and Handel 1993), and mammals (e.g., *Conepatus* spp. (skunk), *Didelphis virginiana* (opossum), *Procyon lotor* (racoon), *Sciurus carolinensis* (gray squirrel), *Sciurus niger* (fox squirrel), *Sylvilagus floridanus* (eastern cottontail rabbit), *Tamias striatus* (eastern chipmunk), and *Vulpes vulpes* (red fox)) (Golley 1962 and 1966, Howe and Westley 1988, Cothran *et al.* 1992), are the most probable explanations for hard mast woody species dominance of woody patch core species composition <200 m from Field 3-412's 1951-1966 field/forest edges.

A *Quercus laurifolia* woody patch, 1.4 ha of open canopy around a farm/ homestead, was in eastern Field 3-412 in 1951 (Figure 2-4). These trees dominated the seed rain in and immediately around this woody patch, so that this part of Field 3-412 was eventually dominated by *Quercus laurifolia* rather than by pines as predicted by SUSES models. Part of this 1.4 ha patch was clear cut during the 1960's, and was quickly reforested with *Quercus laurifolia* by natural regeneration from the seed bank and stump sprouts, as evident from subsequent aerial photographs, and as still evident from the tree trunk morphology in 2001.

Quercus laurifolia dominates 247 of the 821 (30%) woody patches and 247 of the 277 (89%) hard mast woody patches. Other hard mast woody species dominate 30 of the 821 (3.7%) of the studied woody patches, and 30 of the 277 (11%) hard mast woody patches.

Long range seed dispersal from secondary growth, mixed oak-hickory forests on and around the Savannah River Site, should eventually reestablish native, late stage oak and hickory species (e.g., *Carya glabra* (pignut hickory), *Carya tomentosa* (mockernut hickory), *Quercus alba* (white oak), *Quercus falcate* (southern red oak), *Quercus incana* (bluejack oak), *Quercus marilandica* (blackjack oak), and *Quercus velutina* (black oak)) in Field 3-412 (Bartram 1791, Braun 1950, Quarterman and Keever 1962; Barry 1980, Eyre 1980, Jones *et al*. 1981, Whipple *et al*. 1981, Reed 1988, Kovacik and Winberry 1989, Sharitz and Mitsch 1993, Skeen *et al*. 1993, Ware *et al*. 1993, Godfrey 1997).

This is expected to occur as it has in the many aforementioned secondary growth, mixed oak-hickory forests, which were oldfields themselves at one time or another during the past 150 years (Davis and Janecek 1997, Wilds *et al*. 1998). These late-stage oak and hickory species gradually establish in forest understories, where they often slowly grow until they are released by gap formation, whereupon they quickly grow towards and eventually reach the canopy layer, and with sufficient time, they will dominate the canopy layer. Because of Field 3-412's extraordinarily large size and the lack of older replicates, it would be highly conjectural to estimate how many years it would take for reestablishment of these late stage oak and hickory species.

Quercus nigra and *Liquidambar styraciflua* are slowly invading the 20 to 50 year old *Quercus laurifolia* stands in northern Field 3-412 (Plots #1 and

#2). They are growing towards the canopy layer, and dominate increasing portions of the plot's understory woody species composition (i.e., regeneration for future generations). Unless there are significant disturbances, *Quercus nigra* and *Liquidambar styraciflua* are expected to eventually dominate parts of northern Field 3-412, as they are dominant in similar landscapes elsewhere throughout SRS.

The eight Aiken County, South Carolina oldfield sites that were evaluated as possible replicate study sites range from 30 to about 100 years older than Field 3-412. These sites offered the possibility to extend Field 3-412 woody succession model from 50 years to 150 years, using physical evidence rather than extrapolation. However, because these other oldfield sites were about one order of magnitude smaller, and some had relict oaks and hickories in and around the oldfields, they were not considered to be reliable replicates. The same can be said of most other former oldfield sites, given past land use practices, typical pre-1950 farm field sizes, and insufficient historical, physical and photographic evidence. Therefore, extrapolation of the Field 3-412 woody succession model beyond 100 years would be highly conjectural.

Peach (*Prunus persica* cultivar) orchards covered about 4 ha of western Field 3-412 in 1951 (Plot #10, Figure 3-1). Although these orchards were within 100 m of the mixed mesic hardwood forest edge to the west, very few of these hardwoods have been established in the former orchards after 50 years. Rather, *Prunus serotina* is the most common woody species in the former orchards, but it is a subordinate species (i.e., it has cover of more than 1% and less than 25%).

Bird-dispersed *Lonicera japonica* (Japanese honeysuckle), *Parthenocissus quinquefolia* (Virginia creeper), *Rhus radicans* (poison ivy), *Smilax* spp. (greenbriar), and *Vitis rotundifolia* (muscadine) have dominated the former peach orchards since the early 1950's and have successfully suppressed, damaged, and killed many invading trees, particularly *Prunus serotina*, with its often canker-infested and weakened branches.

The most likely explanation for these obvious aberrations is that the peach trees disproportionally attracted birds and mammals that predominantly dispersed soft mast woody species seeds, such as *Prunus serotina*. The former orchards were partially surveyed and mapped in detail, and because of their confounding affect on woody succession on adjacent oldfield plots, the orchards and nearby areas were set-aside for separate study of the peach tree effects on woody succession, which is beyond the scope of this study.

Table 4-5. Number of transcect plots grouped by dominant woody species (by cover) at different distances from Field 3-412's 1951-1966 field/forest edge.

Dominant Plot Woody Species	**Transect Plot Distance from 1951-1966 Field/Forest Edge**				
	0 to 100 m	**101 to 200 m**	**201 to 300m**	**301 to 400 m**	**400 to 550 m**
Quercus laurifolia	7	2	4	2	1
Other Hard Mast Spp.	0	0	0	0	0
Pinus Spp.	7	2	6	2	1
Prunus serotina	2	3	4	8	1
Other Soft Mast Spp.	0	0	1	0	0

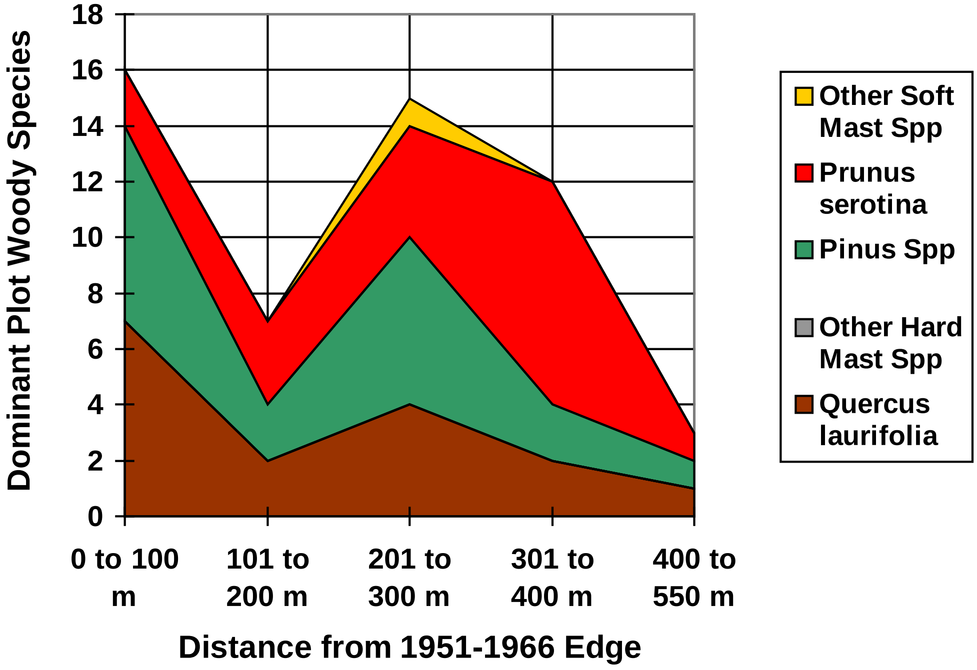

Figure 4-5. Number of transect plots grouped by dominant woody species (by cover) at different distances from Field 3-412's 1951-1966 field/forest edge.

Table 4-6. Percent of transect plots grouped by dominant woody species (by cover) at different distances from Field 3-412's 1951-1966 field/forest edge.

Dominant Plot Woody Species	**Transect Plot Distance from 1951-1966 Field/Forest Edge**				
	0 to 100 m	**101 to 200 m**	**201 to 300m**	**301 to 400 m**	**400 to 550 m**
Quercus laurifolia	44	29	27	17	33
Other Hard Mast Spp.	0	0	0	0	0
Pinus Spp.	44	29	40	17	33
Prunus serotina	13	43	27	67	33
Other Soft Mast Spp.	0	0	7	0	0

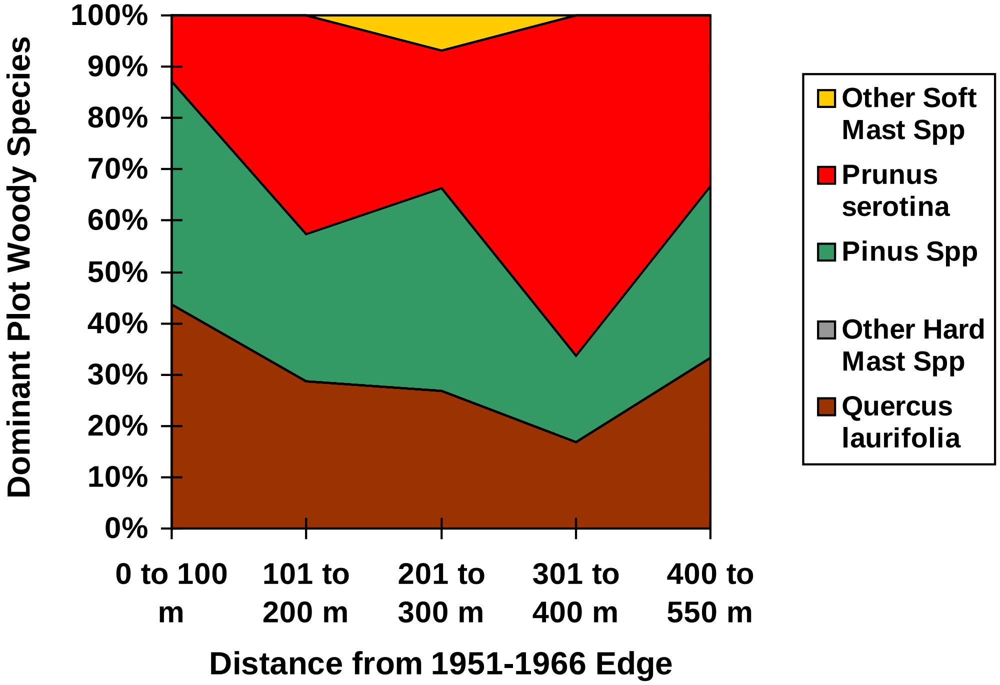

Figure 4-6. Percent of transect plots grouped by dominant woody species (by cover) at different distances from Field 3-412's 1951-1966 field/forest edge.

Field Transect Woody Cover Results: The woody cover in 14 out of the 30 (47%) transect plots that were >200 m from Field 3-412's 1951-1966 field/forest edges was dominated by soft mast woody species, 9 (30%) by pine species, and 7 (23%) by hard mast woody species (Tables and Figures 4-5 and 4-6). This compares with 56% soft mast, 20% pine, and 23% hard mast from the field plot woody patch core results.

Field Transect Woody Volume Results: The relative woody volume in 11 out of The woody cover in 9 out of the 23 (39%) transect plots that were <200 m from Field 3-412's 1951-1966 field/forest edges was dominated by pines, 9 (39%) by hard mast woody species, and 5 (22%) by soft mast woody species (Tables and Figures 4-4 and 4-5). This compares with 28% pine, 48% hard mast, and 24% soft mast from the field plot woody patch core results the 30 (37%) transect plots that were >200 m from Field 3-412's 1951-1966 field/forest edges was dominated by soft mast woody species, 13 (43%) by pine species, and 6 (20%) by hard mast woody species (Tables and Figures 4-7 and 4-8). This compares with 47% soft mast, 30% pine, and 23% hard mast from the field transect woody cover results.

The relative woody volume in 11 out of the 23 (48%) transect plots that were <200 m from Field 3-412's 1951-1966 field/forest edges was dominated by pines, 8 (35%) by hard mast woody species, and 4 (17%) by soft mast woody species (Tables and Figures 4-7 and 4-8). This compares with 39% pine, 39% hard mast, and 22% soft mast from the field transect woody cover results.

Table 4-7. Number of transect plots grouped by dominant woody species (by relative volume) at different distances from Field 3-412's 1951-1966 field/forest edge.

Dominant Plot Woody Species	**Transect Plot Distance from 1951-1966 Field/Forest Edge**				
	0 to 100 m	**101 to 200 m**	**201 to 300m**	**301 to 400 m**	**400 to 550 m**
Quercus laurifolia	6	2	3	1	1
Other Hard Mast Spp.	0	0	1	0	0
Pinus Spp.	9	2	8	4	1
Prunus serotina	1	3	2	7	1
Other Soft Mast Spp.	0	0	1	0	0

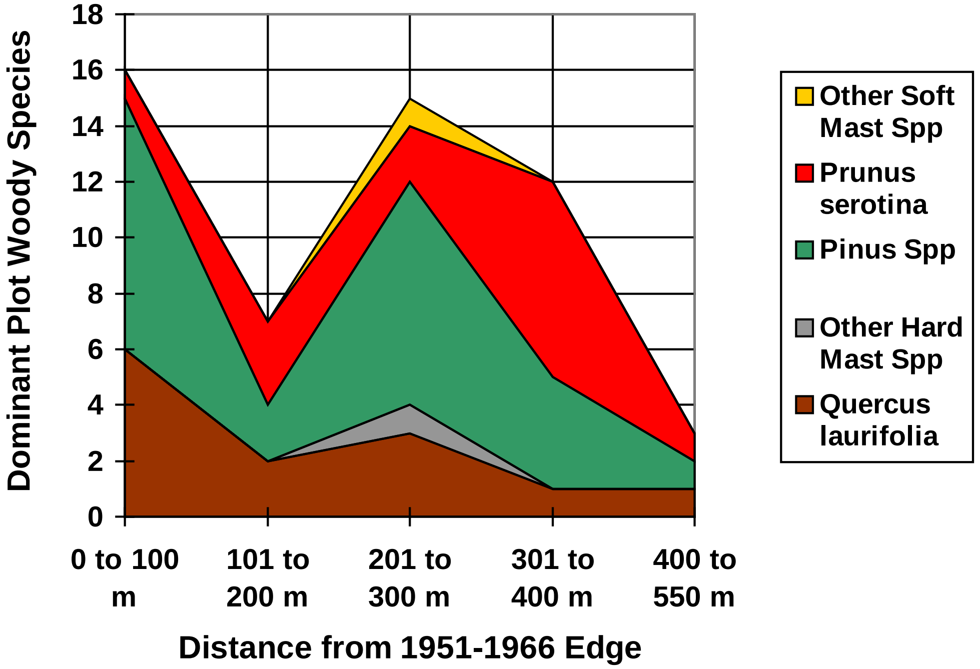

Figure 4-7. Number of transect plots grouped by dominant woody species (by relative volume) at different distances from Field 3-412's 1951-1966 field/forest edge.

Table 4-8. Percent of transect plots grouped by dominant woody species (by relative volume) at different distances from Field 3-412's 1951-1966 field/forest edge.

Dominant Plot Woody Species	**Transect Plot Distance from 1951-1966 Field/Forest Edge**				
	0 to 100 m	**101 to 200 m**	**201 to 300m**	**301 to 400 m**	**400 to 550 m**
Quercus laurifolia	38	29	20	8	33
Other Hard Mast Spp.	0	0	7	0	0
Pinus Spp.	56	29	53	33	33
Prunus serotina	6	43	13	58	33
Other Soft Mast Spp.	0	0	7	0	0

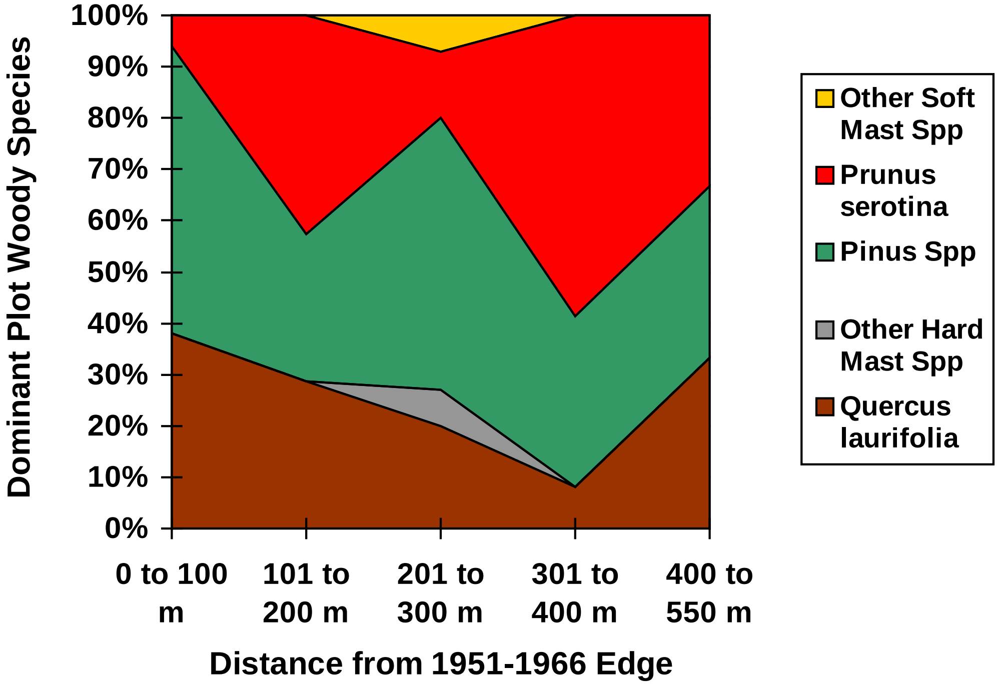

Figure 4-8. Percent of transect plots grouped by dominant woody species (by relative volume) at different distances from Field 3-412's 1951-1966 field/forest edge.

The following table summarizes and compares the percent of woody cover by grouped woody species (Pine spp; All Hard Mast spp.; and All Soft Mast spp.), at different distances from Field 3-412's 1951-1966 field/forest edges, using four different measurement methods (Transect Plot Quadrant Woody Cover, Transect Plot Quadrant Relative Volume, Field Plot Woody Patch Core, and Field Plot Woody Patch Fringe Cover).

Table 4-A. Comparison of woody cover percentages by dominant grouped woody species, at different distances from the nearest field/forest edge, using different measurement methods.

Dominant Woody Species Group	**Measurement Method**						
	Transect Cover < 200 m	Transect Volume < 200 m	Field Plot Patch Core < 200 m	Transect Cover > 200 m	Transect Volume > 200 m	Field Plot Patch Core > 200 m	Field Plot Patch Fringe At All Distances
Pine Spp.	39	48	28	30%	43	20	15
Hard Mast Spp.	39	35	48	23%	20	23	67
Soft Mast Spp.	22	17	24	47%	37	56	17

The transect plot quadrant woody cover and relative volume results differed for plots <200 m and >200 m from Field 3-412's 1951-1966 field/forest edges. Volume results were higher for pines and lower for both the hard and soft mast species. The differences between woody cover and volume results are possibly the consequence of tree architecture differences between pines and hardwoods (both soft and hard mast), where hardwood crowns typically spread more broadly than pine crowns, such that hardwoods cover more ground per unit of total volume.

The field plot woody patch core results differ considerably from both transect plot method results, but are closer to transect plot quadrant woody cover results than to transect plot quadrant relative volume results. The closer similarity is probably because it is a comparison between measures of woody cover rather between measures of woody cover and volume.

The field plot woody patch fringe method results (Table 4-B, right column, from Hypothesis Two) differ even more from both transect plot method results, differ less from the field plot woody patch core results, particularly for woody patches <200 m from the field/forest edges. The closest similarity probably arises from dissimilar causes (processes) with similar effects (results). The closer woody patches probably have a higher percentage of *Quercus laurifolia* because of the species' short wind and gravity dispersal range, and bird and mammal preference for shorter dispersal ranges for caching. The woody patch fringes, regardless of their distance from the field/forest edge, probably have a higher percentage of *Quercus laurifolia* because of the competitive advantage of the species' relatively high shade tolerance.

The transect plots were intended to be a second set of woody succession measurements, for comparison with field plot method results. The differences between the transect plot results and the field plot results (Table 4-B) are more likely the result of the transect plot data set’s relatively small sample size, and as such, the transect plot results should be considered with greater caution. There were only 30 1-ha transect plots, which finely sampled only 4 trees/shrubs per plot, for a total of about 115 countable trees/shrubs overall. This contrasts with the 17 field plots that covered 1.0 to 2.5 ha, which coarsely sampled all trees/shrubs for a total of at least 15,000 countable tree/shrubs overall.

The field plot results, although based on coarser sampling, are probably more rigorous and reliable than the transect plot results because of the sample size that was at least two orders of magnitude greater. Additional sets of transects are needed to determine whether or not the transect plots are a faster and cheaper suitable alternative to the field plot method.

HYPOTHESIS TWO

Hypothesis Two concerns possible relationships between the isolated woody patch core species composition and the corresponding woody patch fringe species composition. Null Hypothesis Two is that the isolated woody patch fringe species composition frequency does not vary with the corresponding woody patch core species composition. The SUSES models predict that pines would dominate isolated woody patch fringe species composition, as well as the original woody patch core species composition, between 25 and 50 years after agricultural abandonment.

Specifically: Field 3-412 hard mast tree species (mostly *Quercus laurifolia* and some *Quercus nigra*, other *Quercus* spp., *Carya illinoisensis* (pecan), other *Carya* spp. (hickories), *Liriodendron tulipfera*, *Liquidambar styraciflua*, *Sassafras albidum* (sassafras)), were expected to dominate the fringe species composition of most formerly isolated woody patches, regardless of the patches' initial core species composition. This expectation arose from exploratory observations of woody plant patterns (distributions) throughout Field 3-412.

Furthermore: Field 3-412 soft mast tree species (*Prunus serotina*, *Prunus carolinia*, *Melia azedarach*, *Pyrus coronaria*, and *Diospyros virginiana*) and shrub species (*Crataegus* spp., *Rhus* spp., and *Prunus* spp. (wild plum)) were expected to preferentially establish within and immediately adjacent to woody patches with soft mast woody species cores. This expectation also arose from the aforementioned exploratory observations.

Field Plot Results: The woody cover in 406 out of the 602 (67%) field plot isolated woody patch fringes in 2001 was dominated by hard mast woody species, 92 (15%) by pines, and 104 (17%) by soft mast woody species (Tables and Figures 4-9 and 4-10).

Hard mast species dominate woody patch fringe species compositions as expected by SUSES model predictions. However, *Quercus laurifolia* unexpectedly accounted for more than 95% of the woody patch fringe hardwood dominance.

There is a positive relationship between woody patch age and hard mast species dominance of woody patch fringe cover, as patches grow and coalesce, and patch species compositions converge towards expected “climax” community species compositions over time, barring catastrophic disturbances and human manipulation of succession trajectory (e.g., timber harvests).

Hard mast woody species dominance of woody patch fringe cover increased from 56% after 27 years to 73% after 50 years. Pine dominance of woody patch fringes remained almost constant, going from 16% to 17%, and as expected, soft mast fringe dominance decreased from 29% to 9% over the same time interval.

These findings are consistent with SUSES model predictions, that oaks and hickories (late to “climax” stage species) would invade pine patches and stands and eventually dominate what would become “climax” old growth forest stands.

The Chi-square test of these data showed a positive association ($\chi^2 = 56.366$ with d.f. = 16) between *Quercus laurifolia* and all species. This was statistically significant (P value = 0.0032), which was expected with *Quercus laurifolia*’s universal dominance. However, this does not indicate any unique species-specific positive interspecific associations.

Fisher’s Exact test of Table 4-9 data, which groups hard mast and soft mast species, excluding pines, yielded a P value of < 0.0001, indicating significant associations between the two grouped hard mast and all soft mast species, including *Prunus serotina*.

Table 4-9. Number of isolated woody patches grouped by dominant fringe woody species and the corresponding core woody species.

Dominant Patch Fringe Woody Species	**Patch Core Woody Species**				
	Quercus laurifolia	*Pinus* Spp.	*Prunus serotina*	Other Soft Mast Spp.	Other Hard Mast Spp.
Quercus Laurifolia	77	112	105	78	26
Other Hard Mast Spp.	4	4	0	0	0
Pinus spp.	21	30	15	14	12
Prunus serotina	5	17	16	13	10
Other Soft Mast Spp.	0	7	14	9	13

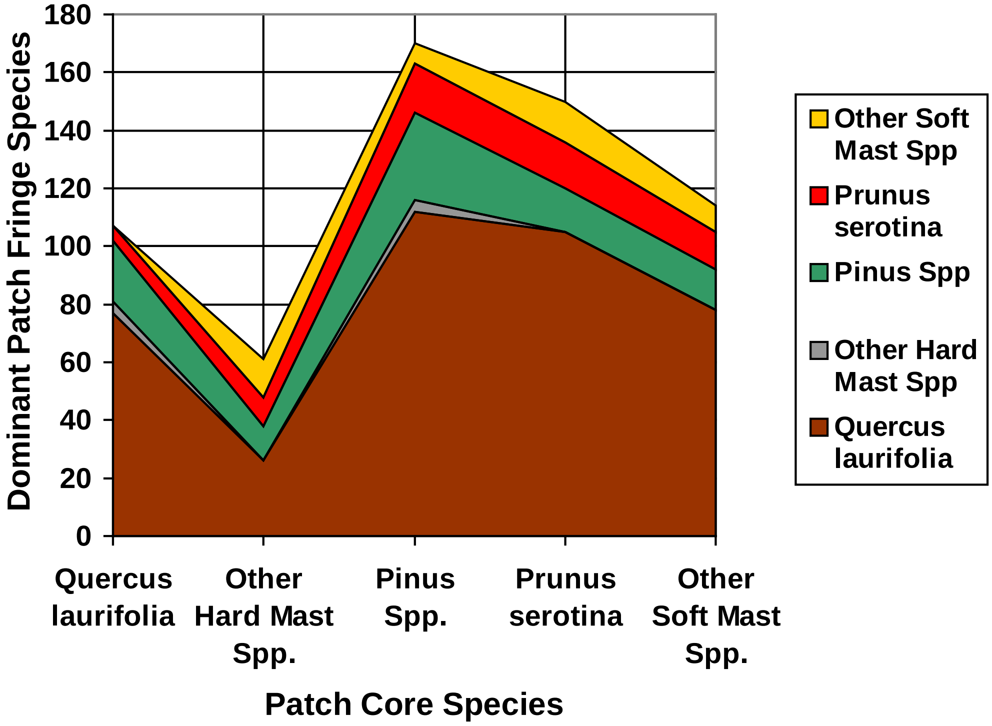

Figure 4-9. Number of isolated woody patches grouped by dominant fringe woody species and the corresponding core woody species.

Table 4-10. Percent of isolated woody patches grouped by dominant fringe woody species and corresponding core woody species.

Dominant Patch Fringe Woody Species	**Patch Core Woody Species**				
	Quercus laurifolia	*Pinus* Spp.	*Prunus serotina*	Other Soft Mast Spp.	Other Hard Mast Spp.
Quercus Laurifolia	72	66	70	68	43
Other Hard Mast Spp.	4	2	0	0	0
Pinus spp.	20	18	10	12	20
Prunus serotina	5	10	11	11	16
Other Soft Mast Spp.	0	4	9	8	21

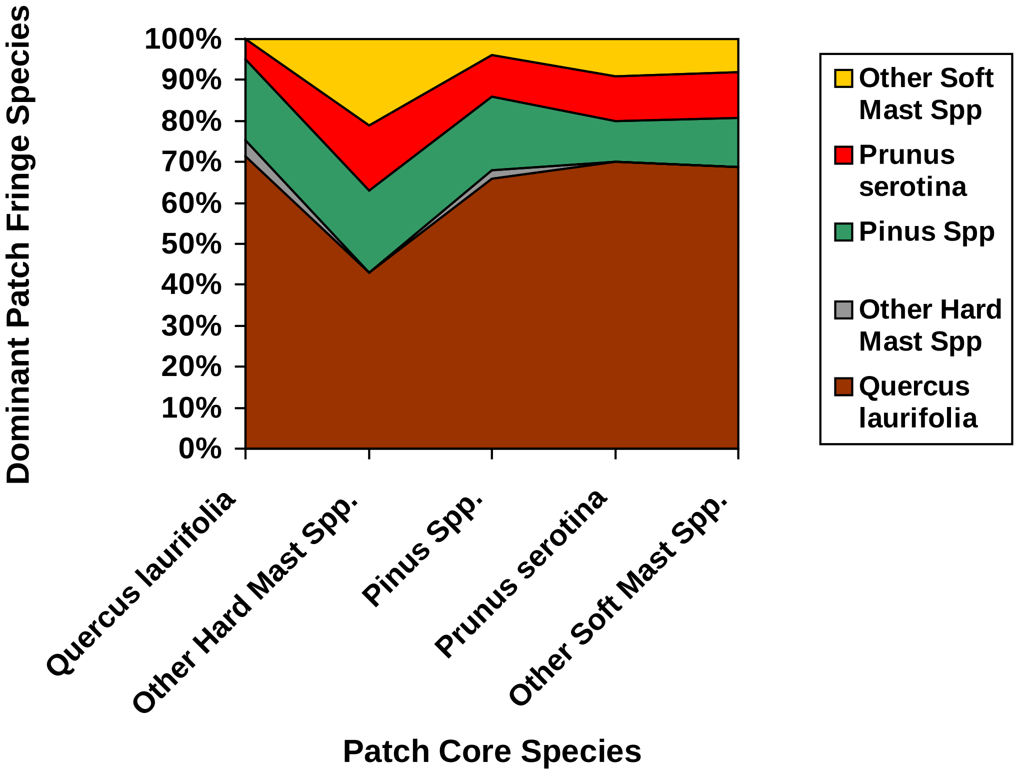

Figure 4-10. Percent of isolated woody patches grouped by dominant fringe woody species and corresponding core woody species.

Tree Plot Results: Eight out of the 30 (27%) isolated tree plot cores in 2001 were dominated by hard mast woody species, 5 (17%) by pines, and 17 (57%) by soft mast woody species (Tables and Figures 4-11 and 4-12). This compares with 23% hard mast, 20% pine, and 56% soft mast from the field plot woody patch core results for patches >200 m from Field 3-412's 1951-1966 field/forest edge. However, it contrasts with 48% hard mast, 28% pine, and 24% soft mast from the field plot woody patch core results for patches that were <200 m from the field/forest edge (Tables and Figures 4-3 and 4-4).

These findings suggest that isolated woody patches, regardless of distance from Field 3-412's field/forest edge, have core species compositions more like the woody patch cores >200 m from that edge than cores <200 m from that edge. This was expected since most remaining open areas, where most remaining isolated woody patches would be, are >200 m from the 1951-1966 field edge.

Twenty-two out of the 30 (73%) isolated tree plot woody fringes in 2001 were dominated by hard mast woody species, 4 (13%) by pines, and 4 (13%) by soft mast woody species (Tables and Figures 4-11 and 4-12). This compares with 67% hard mast, 15% pine, and 17% soft mast from the field plot isolated woody patch fringes throughout Field 3-412 in the year 2001 (Tables and Figures 4-9 and 4-10).

These isolated tree plot woody fringe test results (Table and Figure 4-12), like the field plot woody patch fringe test results, show that hard mast species dominate the woody patch fringes. This was expected based upon the exploratory field observations. However, *Quercus laurifolia* unexpectedly dominated 73% of the woody patch fringe cover, and >95% of the fringe hardwood cover.

Table 4-11. Number of isolated woody patches grouped by dominant fringe woody species and corresponding core woody species.

Dominant Patch Fringe Woody Species	**Patch Core Woody Species**				
	Quercus laurifolia	*Pinus* Spp.	*Prunus serotina*	Other Soft Mast Spp.	Other Hard Mast Spp.
Quercus Laurifolia	4	4	6	7	1
Other Hard Mast Spp.	0	0	0	0	0
Pinus spp.	2	1	1	0	0
Prunus serotina	1	0	0	0	0
Other Soft Mast Spp.	0	0	2	1	0

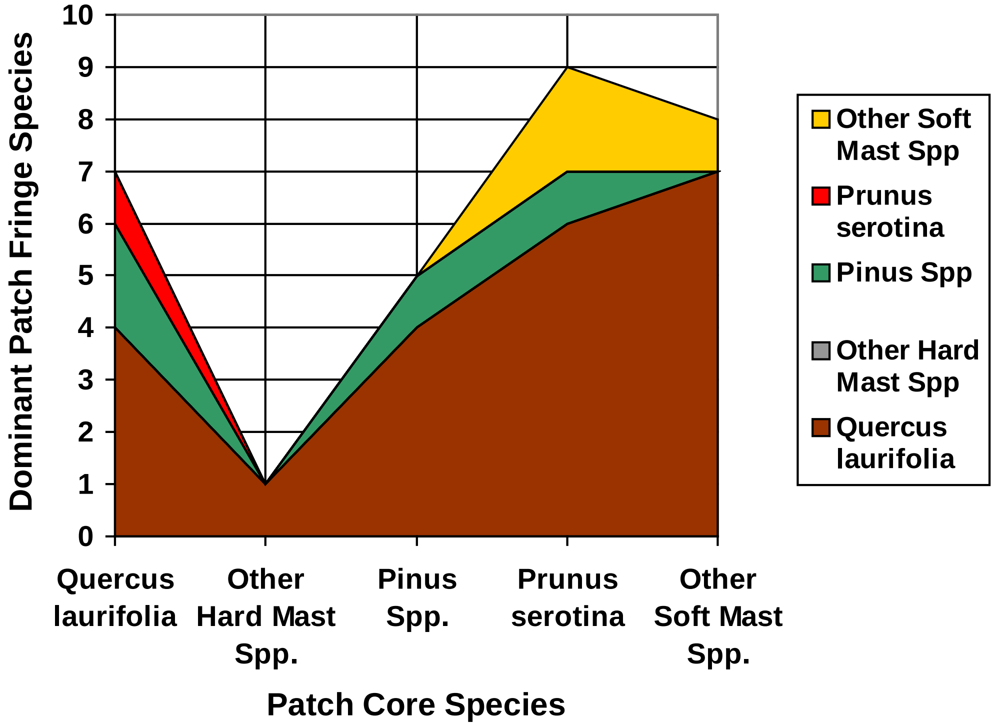

Figure 4-11. Number of isolated woody patches grouped by dominant fringe woody species and corresponding core woody species.

Table 4-12. Percent of isolated woody patches grouped by dominant fringe woody species and corresponding core woody species.

Dominant Patch Fringe Woody Species	**Patch Core Woody Species**				
	Quercus laurifolia	*Pinus* Spp.	*Prunus serotina*	Other Soft Mast Spp.	Other Hard Mast Spp.
Quercus Laurifolia	57	80	67	88	100
Other Hard Mast Spp.	0	0	0	0	0
Pinus spp.	29	20	11	0	0
Prunus serotina	14	0	0	0	0
Other Soft Mast Spp.	0	0	22	12	0

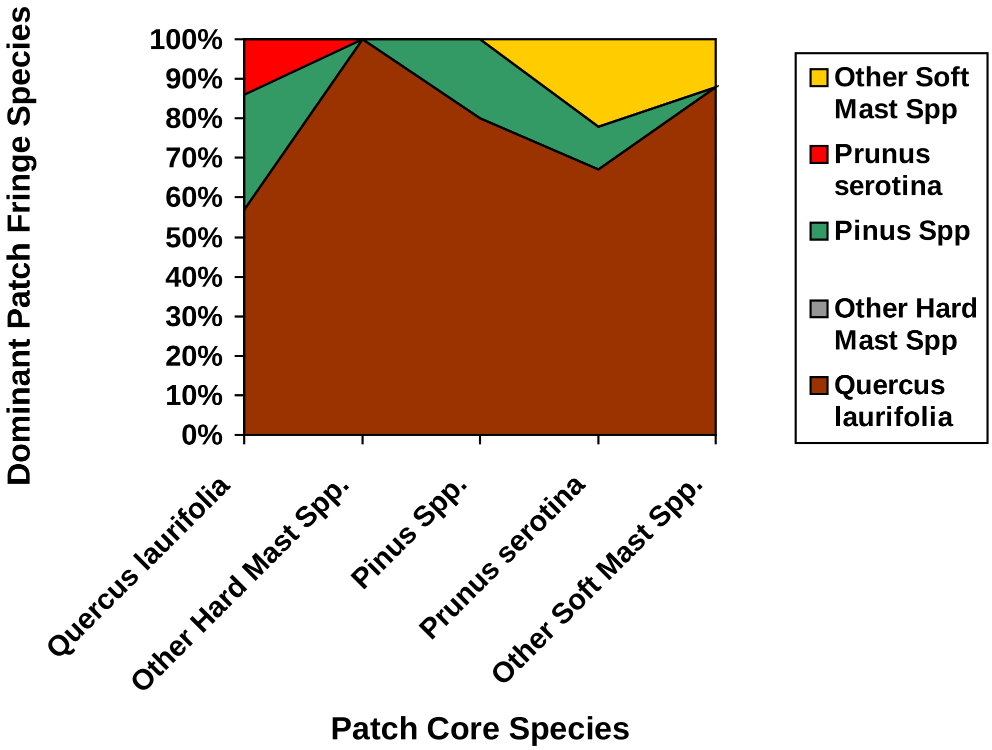

Figure 4-12. Percent of isolated woody patches grouped by dominant fringe woody species and corresponding core woody species.

Linear regression (general linear model) of the *Prunus serotina* and all other soft mast species data yielded an r^2 value of 0.9099, with a P value of 0.0118, which is considered significant.

Selected tree plot core and fringe woody species combinations were casually analyzed for possible interspecific associations (Table 4-13). The casual findings to date include:

> *Crataegus* spp.: Pioneer shrub/tree, open savannas, and patches (closed clusters). Common nurse shrub/tree for *Quercus laurifolia*.

> *Diospyros virginiana*: Pioneer tree and open clusters. Possible positive spatial association with *Prunus serotina*. Occasional nurse shrub/tree for *Quercus laurifolia*.

> *Juniperus virginiana*: Pioneer tree.

> *Pinus taeda*: Pioneer tree, open and closed clusters. Common nurse tree for *Quercus laurifolia* and some *Prunus serotina*.

> *Prunus serotina*: Pioneer tree and open clusters. Common nurse shrub/tree for *Quercus laurifolia*, some *Pinus* spp. and privet spp. Many trees have blackberry understory (bird dispersed), which when sufficiently dense, apparently inhibits woody species establishment

Melia azedarach: Pioneer tree and closed clusters. Nurse tree for some *Quercus laurifolia*, *Pinus taeda*, and *Diospyros virginiana*.

Quercus laurifolia: Middle and late stage tree. Lower incidence of woody fringes, possibly the consequence of allelopathy, water competition, and/or nurse tree branches killing woody fringe seedlings/saplings.

Medium-range (100 to 1000 m) and long-range dispersal of hard mast woody species seeds by birds (e.g., *Cyanocitta cristata* (blue jay), *Sitta carolinensis* (white breasted nuthatch), *Melanerpes erythrocephalus* (red-headed woodpecker)) (McDonnell and Stiles 1983, McDonnell 1986, Howe and Westley 1988, DeGraaf *et al.* 1991, Hamel 1992, McClanahan and Wolfe 1993, Robinson and Handel 1993), and by mammals (e.g., *Sciurus carolinensis* (eastern gray squirrel) and *Sciurus niger* (eastern fox squirrel)) (Golley 1962 and 1966, Howe and Westley 1988, Cothran *et al.* 1992), are the most likely explanations for hard mast woody species' invasion and subsequent dominance of most Field 3-412 woody patches, regardless of the patch core's species composition.

The tree plot findings build upon SUSES models and predictions, by adding details of species composition, frequency, density, and interspecific associations. Frugivorous and omnivorous bird and mammal species behavior and feeding preferences are the most likely explanations for the observed positive interspecific associations and spatial correlations between soft mast woody species in Field 3-412 (Martin *et al.* 1951, MacMahon 1981, McDonnell and Stiles 1983, McClanahan 1987, Hamel 1992, McClanahan and Wolfe 1993).

HYPOTHESIS THREE

Hypothesis Three concerns possible relationships between soil albedo (tone or gray value in aerial photographs) and corresponding woody succession (woody patch establishment and growth) rates. Null Hypothesis Three is that woody succession rates do not vary with soil albedo and associated soil characteristics. The SUSES models do not include soil effects.

Specifically: Field 3-412 woody succession rates between 1951 and 1989 were expected to be negatively correlated with the 1943 soil albedo, with higher rates in the areas with the darkest 10% of the soil albedos (Figure 3-9). This expectation arose from several thousand casual, unrecorded observations and evaluations (since the early 1970’s) of site soils and plant communities throughout the eastern U.S., Puerto Rico, Venezuela, Canada, and Europe between 1983 and 1992.

Soil Plot Results: The lighter soil albedo (approximated highest 90% of Field’s albedos) plots had 0% woody cover in 1951, 0% in 1961, 6% in 1974, 34% in 1982, 65% in 1990, and 75% in 2001. The darker soil albedo (approximated lowest 10% of Field’s albedos) plots had 0% woody cover in 1951, 0% in 1961, 10% in 1974, 31% in 1982, 61% in 1990, and 79% in 2001 (Table 4-14, Figures 4-14a and 4-14b).

These results compare closely with the general photointerpretation woody cover results for the entire field. Interestingly, the general photointerpretation method is about ten times more detailed than the soil plot photointerpretation method, yet the results are very similar. This suggests that the simpler soil plot photointerpretation method was reasonably adequate for estimating woody cover.

The unpaired t-Test, two-tailed P value was 0.9933, strongly suggesting acceptance of Null Hypothesis Three, that the soil albedo and associated soil characteristics did not affect the rate of woody succession.

Table 4-14. Percent woody cover in the soil plots and the entire field.

Year	**Lighter Soil Plots**	**Darker Soil Plots**	**Entire Field**
1951	**0**	**0**	**0**
1961	**0**	**0**	**4**
1974	**6**	**10**	**15**
1982	**34**	**31**	**38**
1990	**65**	**61**	**64**
2001	**75**	**79**	**79**

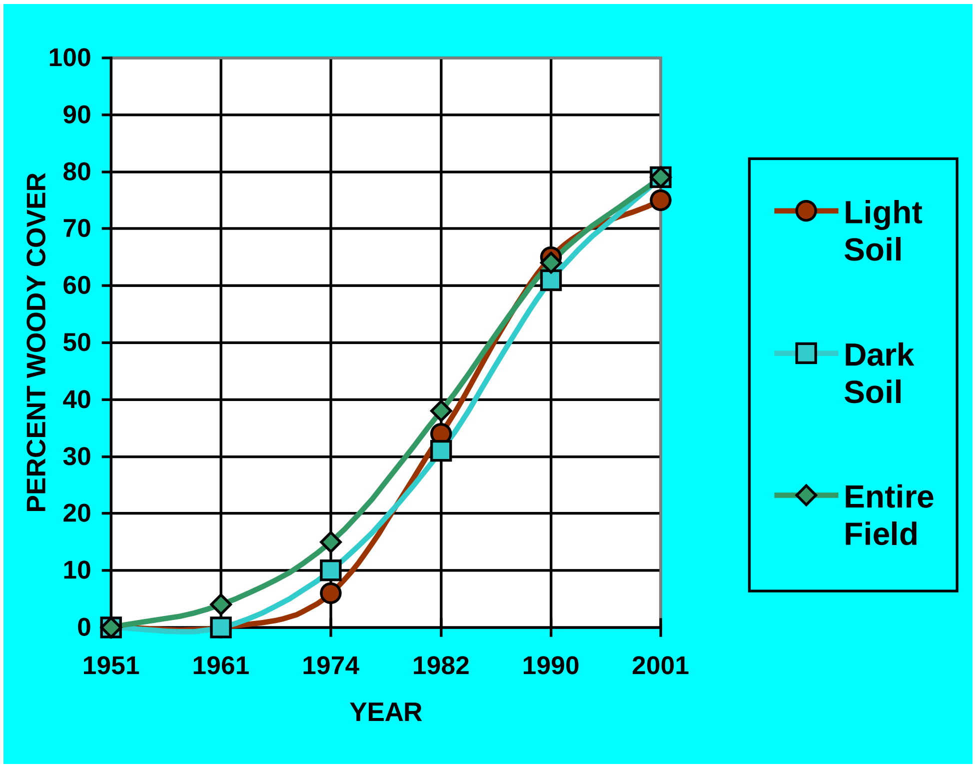

Figure 4-14a. Percent woody cover in the soil plots and the entire field.

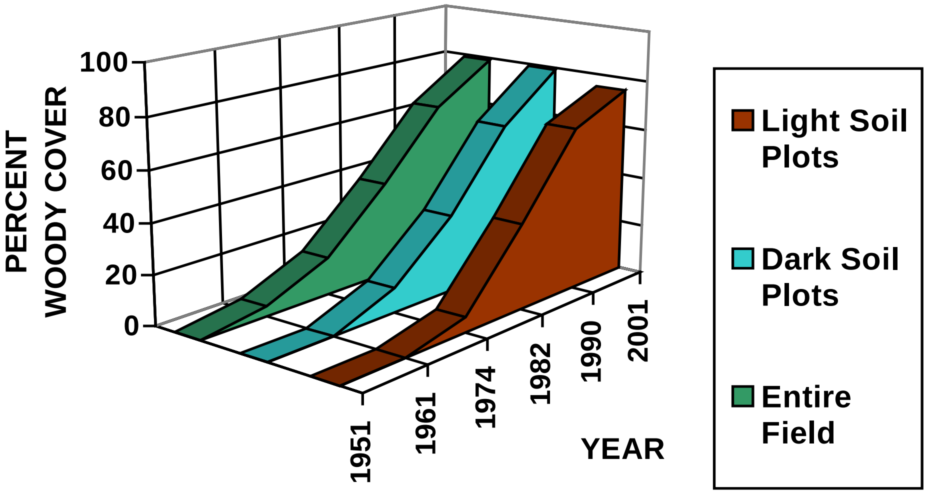

Figure 4-14b. Percent woody cover in the soil plots and the entire field.

CHAPTER 5

CONCLUSIONS

INTRODUCTION

This chapter discusses the conclusions of this study. It starts with the narrower context of the site-specific processes and patterns in Field 3-412; proceeds to the broader context of the general ecological succession theory, models, and applications that can be extended to the southeastern U.S. and elsewhere worldwide; and ends with general consideration of future research, basic (pure) and applied.

Field 3-412's woody succession began in 1951 as a few remaining fencerow trees and trees surrounding the field released seeds that dispersed into *Leptilon (Erigeron)* spp. (horseweed) and *Heterotheca subaxillaris* (camphorweed) dominated fields that the year before were occupied by agricultural crops. Tree seeds rarely germinated and grew within the forb and grass patches that dominated most of the field for the first 15 years after abandonment. Only in a few peripheral sites did *Pinus taeda* (loblolly pine) disperse from adjacent mature trees to build local patches of young trees. The field as a whole remained mostly an open area occupied by grasses, forbs, and field adapted animal species.

Gradually, individual tree seeds reached "safe sites", grew, and became visible above the *Andropogon* spp. (broomsedges) and *Eupatorium capillifolium* (dog fennel). These were predominantly gravity dispersed *Quercus laurifolia* (laurel oak) and wind-dispersed *Pinus taeda* closer to the field/forest edges, and mammal-dispersed *Prunus* *serotina* (black cherry) and *Prunus* spp. (wild plums) farther from the field/forest edges. These *Prunus* species attract birds and mammals because of their fruit. These animals disperse the *Prunus* species more widely throughout the field so that these species become more common.

In addition, *Prunus* individual trees and shrubs provide perches for birds. Birds that fly across the oldfield to these isolated pioneer trees and shrubs may carry seeds in their beaks or gastro-intestinal tract, seeds that come from other tree species in the surrounding forests. This process of attraction of birds and deposition of seeds carried by these birds results, over time, in a fringe of younger, smaller trees and shrubs around the pioneer individual trees and shrubs. These groups form woody patches that can easily be observed in the SREL aerial photographs (1943-1998).

Quercus laurifolia is the most common woody patch fringe species in Field 3-412. This was a surprising finding! Field 3-412 is near the limit of *Quercus laurifolia*'s natural geographic range. However, it is a popular shade tree in Aiken and in Aiken County. Field 3-412's nearest and most substantial local *Quercus laurifolia* seed source was the farmstead woodlot in the northeastern corner of Field 3-412. Most of Field 3-412's laurel oaks may have descended from these trees. This is a good example where a unique case is at the source of an ecological principle (Golley, pers. comm., 2001).

Quercus laurifolia are highly sun and drought tolerant, after they have been established under shaded conditions. Since they are also shade tolerant, they eventually crowd out most other woody patch trees and shrubs.

Most woody patches grow in size and coalesce, forming larger patches and forest stands. These larger patches recreate forest environmental conditions, including shade, microclimate, litter, humus, nutrient cycling, soil moisture availability, and species richness. Many plants and animals disperse to the large woody patches (Adams 1908, Odum 1950), find new habitat, and eventually the former oldfield is transformed into a heterogeneous forest of older and newer patches reflecting its successional history. Trees die and create gaps, opportunities for invasion, often best suited for forest-adapted (K-selected) species, except in the largest gaps (Phillips and Shure 1990).

Field 3-412 is not at this forest stage, contrary to southeastern U.S. ecological succession (SUSES) model predictions models. After 50 years, about twenty percent of Field 3-412's land area is still free of trees and shrubs. But succession continues at a rapid pace and probably the forest will be complete in about 25 more years. Although *Quercus laurifolia* will probably cover more of Field 3-412 than any other woody species during most of the next 50 years, it is a short-lived tree and shorter than the more shade tolerant, long-lived late stage oak, hickory, and other mesic hardwood species.

Liquidambar styraciflua (sweetgum) and *Liriodendron tulipfera* (tulip poplar) started invading Field 3-412's margins, and the inner rim of Ellenton bay, from the adjacent pre-1951 mixed mesic hardwood forests. The regional species pool's more diverse variety of "climax" oaks and hickories have had much further distances to travel than the sweetgum and tulip poplar. Nevertheless, given sufficient time and no major disturbances, the climax oaks and hickories will probably dominate "Site" 3-412 by between about 200 and 300 years from present.

This is the general pattern of Field 3-412's woody succession. Now, let us consider some of the species feature's of Field 3-412's woody succession.

FIELD 3-412 PROCESSES AND PATTERNS

Field 3-412 Historic Woody Succession. Field 3-412's observed woody succession from 1951 through 1976 was about 80% slower than the predicted woody succession: only about 20% of the field had woody cover, rather than 100% as predicted by the SUSES models (Crafton and Wells 1934, McQuilkin 1940, Oosting 1942, Keever 1950, Golley 1965, Golley *et al.* 1994).

Field 3-412's observed woody succession from 1951 through 2001 also had very different species composition than the predicted woody succession (Tables and Figures 4-3 through 4-8):

> Field 3-412 had about 25% early middle sere pine cover, rather than about 100% pine cover as predicted by the SUSES models;
>
> Field 3-412 had about 20% early middle sere soft mast woody (tree and shrub) species cover, rather than about 0% as predicted when pines were to crowd out early sere scrub/shrub species.
>
> Field 3-412 had about 35% middle sere *Quercus laurifolia* (laurel oak) cover, rather than any of the late sere oak, hickory, or other hardwood species that are predicted to be present after about 50 years and dominant after about 100 to 150

years. Nevertheless, these predicted late sere woody species still may dominate Field 3-412 after about 150 years, as suggested by the understory species composition in some oldest stands in the field (e.g., Field Plot #1 and the former farmstead woodlot, both in northeaster Field 3-412).

H1 The 1st wave. Distance from field/forest edge clearly affects woody patch's initial species composition. Woody patches within 200 m of the field/forest edge were initially dominated by pines (28%) and hard mast woody species (48%) (Tables and Figures 4-3 through 4-6). This species composition is contrary to the SUSES model predictions that pines would dominate (almost 100%) after about 50 years (Crafton and Wells 1934, McQuilkin 1940, Oosting 1942, Keever 1950,). However, this species composition is relatively consistent with the initial floristic composition (local species pool) concept (*sensu* Egler 1954).

This suggests that the SUSES models can be revised to include the local species pool concept to more accurately predict the woody species composition over a range of at least 500 m from the nearest field/forest edges.

Woody patches more than 200 m from the field/forest edge were dominated by soft mast woody species (56%), with pines (20%) and hard mast species (23%) being subordinate (Tables and Figures 4-3 through 4-6). Soft mast dominance may actually have been more than 80%, as most hard mast species are initially established in soft mast woody patches (i.e., *Prunus* spp. (wild plums) and *Rhus* spp. (sumacs) shrubs) that could not be distinguished in older, smaller scale aerial photographs. Notably, in 2001, more than 80% of the observed *Quercus laurifolia* seedlings and saplings, that were established more than 10 m from *Quercus laurifolia* trees, were established within *Prunus* spp., *Crataegus* spp. (hawthorns), and *Rhus* spp. woody patches.

H2 The 2nd wave. The woody patch's initial (core) woody species composition influenced the subsequent (fringe) woody species composition. This influence can be partially explained by the core tree or shrubs' own seed dispersal, resulting in autocorrelated tree or shrub fringes (Tables and Figures 4-9 through 4-12). Field 3-412's results (e.g., an acorn never falls far from its tree (anonymous)) are consistent with the generally accepted initial floristic composition (local species pool) concept (*sensu* Egler 1954).

This influence can also be explained by the core or tree's fruit attracting birds and mammals with feeding preferences and more frequently disperse these seeds around their preferred trees and shrubs. This relationship is complicated by the fact that animals may frequent some trees and/or shrubs for foraging, but other trees and/or shrubs for feeding and caching.

Soft mast species other than *Prunus serotina* (i.e., *Crataegus* spp., *Diospyros virginiana, Melia azedarach, Prunus carolinia*, *Prunus* spp. (wild plum), *Pyrus coronaria*, *Rhus* spp.,) were about twice as likely to establish around hard mast species other than *Quercus laurifolia*, yet they never established around *Quercus laurifolia* (Tables and Figures 4-9 through 4-12). A possible explanation is animal behavior. Most of the "other hard mast" trees were *Carya illinoensis* (pecan), which have a moderately open, deciduous canopy that is more suitable for birds to enter, stop, and drop seeds. Conversely, *Quercus laurifolia*, has a dense, semi-evergreen crown, and as a poor self-pruner, it retains so many more branches than all other woody species in Field 3-412. *Quercus laurifolia*'s leaves and branches probably inhibit bird movement within the tree crown, such that birds favor more open crowns that provide sufficient cover from their natural enemies (i.e., predators) (Howe 1979).

However, soft mast species other, than *Prunus serotina*, established around *Prunus seroti*na only slightly more frequently than the average for all species (Tables and Figures 4-9 through 4-12). Considering that *Prunus seroti*na, like *Carya illinoensis*, has a moderately open, deciduous canopy, one might expect more frequent establishment of other soft mast species around *Prunus seroti*na. Although this was not the case in the 150, mostly older *Prunus serotina*-cored patches (Tables and Figures 4-9 and 4-10) in the field plots, it was notable in the nine younger isolated patches (Tables and Figures 4-11 and 4-12). These observations suggest that *Prunus seroti*na actually does attract birds and mammals that disperse other soft mast species, and that the woody patch fringe growth, which is most frequently *Quercus laurifolia*, crowds out the other soft mast species. The physical evidence of this interspecific relationship typically decays within 10 to 20 years after the death of shrubs and small trees.

The former peach (*Prunus persica* cultivar) orchards, originally in western Field 3-412 in 1951 (Plot #10, Figure 3-1), are a very interesting case, but beyond the scope of this study. Although the orchards were within 100 m of the mixed mesic hardwood forest edge, very few of these hardwoods have been established after 50 years. Rather, *Prunus serotina* is the most common woody species in the former orchards, but it is a subordinate species (i.e., it has cover of more than 1% and less than 25%).

Bird-dispersed vines (i.e., *Campsis radicans* (Trumpeter creeper or trumpet vine), *Lonicera japonica* (Japanese honeysuckle), *Parthenocissus quinquefolia* (Virginia creeper), *Rhus radicans* (poison ivy), *Smilax* spp. (greenbriar), and *Vitis rotundifolia* (muscadine) have dominated the former peach orchards since the early 1950's and they have successfully suppressed, damaged, and killed many invading trees, particularly *Prunus serotina*, with its canker-infested and weakened branches.

The SUSES models can be revised to include known "subclimax" woody species phases to more accurately predict the woody species composition over a range of 500 m from the nearest field/forest edges. This revision could probably be extended to several kilometers, based upon many studies of Holocene forest migration (Wright 1981, Delcourt *et al*. 1983, Huntley and Birks 1983, Porter 1983, Wright 1983, Velichko *et al*. 1984, Davis 1987, Ritchie 1987, Ruddiman and Wright 1987, Delcourt and Delcourt 1988, Huntley and Webb 1988, Sauer 1988, Delcourt and Delcourt 1991, Clark 1998).

H3 The Soil Effects. Comparison of plot soil albedo (indicator or proxy for soil texture, fine content, and nutrient and/or moisture availability) and the corresponding rate of woody succession suggests that Field 3-412's soil characteristics did not notably affect the overall rate of woody succession from 1951 through 2001 (Table 4-14 and Figures 4-14a and b).

> However, soil characteristics apparently had a substantial affect on early woody succession, from 1951 through 1974, with darker soil plots having woody succession rates that were about 60% faster than that in the lighter soil plots. This notable difference disappeared by 1982.

This pattern suggests that soil characteristics probably do affect early woody succession rates, with faster rates in the moderate (middle) soil condition regimes, and slower rates in the extreme soil condition regimes (e.g., xeric and hydric, oligotrophic and eutrophic). This concept, if it is valid, would correspond with the moderate disturbance regime concept for higher community species diversity (Denslow 1980).

The underlying mechanisms and processes involving soil characteristics and corresponding woody succession rates were beyond the scope of this study.

Field 3-412 Predicted Woody Succession (500+ years). Field 3-412 is unlike any other SRS sites in that its barren areas were relatively extensive at the time of agricultural abandonment 50 years ago (SREL Aerial Photographs 1951), and it is located on a mesic river terrace that has not been flooded by the adjacent river in recorded history (Wein, pers. comms., 1998-2001).

Small, narrow portions of other SRS sites (i.e., Research Area #6, a Hardwood-Beech Forest Set-Aside Area about 1 km northwest of Field 3-412, and Research Areas #5 and #12, Oak-Hickory Set-Aside Areas about 15 km northwest of Field 3-412 (Figure 2-3)), have the same soils as Field 3-412 (Rogers and Herren 1990). However, these are in different landform positions and have different deep drainage (Way 1978, Birkeland 1984, Fanning and Fanning 1989). Furthermore, these other sites' land use histories are very different, with much smaller oldfield sizes, and adjacent woodlots and treelines that were selectively logged (Davis and Janecek 1997), thus altering the local species pool and site seed rain woody species composition.

Large, broad portions of several Hitchcock Woods sites also have the same soils as Field 3-412. However, like the other SRS sites, the Hitchcock Woods sites are located on different landform positions, and have different drainage, and they have different land use histories, i.e., much smaller oldfield sizes, and adjacent woodlots and treelines that were selectively logged (Wilds *et al*. 1998). Unlike the SRS sites, the Hitchcock Woods sites are treated with prescribed burns, at 2 to 8 year rotations, which can substantially alter the forest stands' woody species composition.

Field 3-412 is not only unique to Aiken County. It is also unique to the southeastern U.S. for the same reasons: its large size, compact shape, soils, landscape position, drainage, and land use history. Moreover, Field 3-412's uniqueness is enhanced by its location in the transition zones between Piedmont and Coastal Plain forest communities, and between the upland and bottomland forest communities (Bartram 1791, Braun 1950, Quarterman and Keever 1962; Barry 1980, Reed 1988, Kovacik and Winberry 1989, Sharitz and Mitsch 1993, Skeen *et al*. 1993, Ware *et al*. 1993, Godfrey 1997).

Q: What will Field 3-412's future forest stand woody species compositions be if ecological succession progresses without any major stresses or disturbances?

A Prolog: The answer is relatively speculative because of Field 3-412'a many aforementioned unique characteristics, the lack of studies of similar landscape level cases, and uncertainties concerning global climate changes. The answer is based upon limited Best Available Data (BAD) and upon generally accepted findings and concepts from many previous studies of the local species pool, applicable woody species' physiologies, life histories, spatial distribution, and seed dispersal; bird and mammal behavior affecting these species' seed dispersal; soil development, microclimate, soil hydrology, mycorrhizal associations, nutrient cycling, stresses and disturbances, granivory, herbivory, pathogens, intra- and interspecific competition, and forest gap dynamics.

A: 2001-2051: During the next 50 years of Field 3-412's ecological succession, early middle sere *Quercus laurifolia* will probably expand to cover 70 to 80% of the former oldfield, with the remaining areas covered mostly by relict early middle sere pines (*Pinus taeda* (loblolly pine) and *Pinus palustris*(longleaf pine)), early middle sere oak (*Quercus nigra* [water oak]) in the moister soil areas, and early arrived, local late sere mixed mesic hardwoods in a continued hierarchical pattern of woody succession (Yarranton and Morrison 1974).

The local species pool's late sere mixed mesic hardwoods include: *Cornus florida* (flowering dogwood), *Fagus grandifolia* (American beech), *Ilax opaca* (American holly), *Liquidambar styraciflua* (sweetgum), *Liriodendron tulipfera* (tulip poplar), *Magnolia virginiana* (sweetbay magnolia), and *Ulmus alata* (winged elm).

The primary mixed mesic hardwood seed sources for Field 3-412 are the local species pool, i.e., the pre-1951 hardwood stands immediately to the west, north, and east of the field. These stands have been selectively harvested during the past 200 years, so their species composition is altered.

A 2051 through 2151: During the second century of Field 3-412's ecological succession, the local species pool's late sere mixed mesic hardwoods will probably invade much further (i.e., more than 100 m) into the former oldfield, and through replacement during forest gap dynamics, will probably dominate Field 3-412 towards the end of this century. Other late sere mesic hardwood species, from the more diverse regional species pool, will probably establish a firm foothold in parts of Field 3-412, which would be more aptly named "Site 3-412" by then.

The regional species pool's late sere mixed mesic hardwoods include, in addition to the local pool species: *Carya cordiformis* (bitternut hickory), *Carya glabra* (pignut hickory), *Carya tomentosa* (mockernut hickory), *Fraxinus pennsylvanica* (green ash), *Fraxinus americana* (white ash), *Juglans nigra* (black walnut), *Quercus alba* (white oak), *Quercus falcata* (southern red oak), *Quercus incana* (bluejack oak), *Quercus laevis* (turkey oak), *Quercus marilandica* (blackjack oak), *Quercus stellata* (post oak), and *Quercus velutina* (black oak).

A 2151 through 2451: During the third through fifth centuries of Site 3-412's forest succession, the regional species pool's late sere mixed mesic hardwoods would probably invade much of the site, and dominate parts of the site, with community woody species compositions varying according to soil regime differences.

These within-site soil regime differences should diminish over the centuries. If the soil A-horizon builds at the net rate of about 2.5 cm/annum, then towards the end of this period, then the A-horizon should be close to its pre-European settlement conditions as William Bartam described for parts of the region.

A 2451 through 2951: Site 3-412's forest community woody species composition differences, relicts of the earlier, more substantial soil regime differences, will probably gradually diminish as the longer-lived relict trees are very gradually replaced.

This will probably be much slower than the Holocene forest migration rates, which were faster because of less "resistance" from existing community species. The within-site forest stand or community convergence would meet considerable resistance from the previous forest canopy layer occupants, and competition from the previous occupants’ contributions to the seed bank and surrounding understory and mid-story layers (i.e., seedlings, saplings, and short trees).

Barring any significant stresses or disturbances, Site 3-412’s “climax” forest stand or community woody species composition will probably be dominated by regionally-common mixed mesic hardwood species, with the more mesic species being more frequent than the less mesic species, in a fuzzy mosaic created by opportunistic responses to the opening of new forest gaps.

ECOLOGICAL SUCCESSION THEORY AND MODELS

Field 3-412’s “aberrant” ecological succession is probably typical of large oldfields in the southeastern U.S. However, subsequent land uses had erased the evidence elsewhere. Nevertheless, the same mechanisms and processes also operate elsewhere in the southeastern U.S. Although these other sites may have somewhat different local and regional species pool compositions, many of the dominant species in any stage may be ecologically equivalents, such that similarly complex woody succession sere stages and patterns would exist on these sites if the succession had operated without human stresses and/or disturbances.

If the basic biological and ecological principles apply in Field 3-412, which they do, then these same basic principals would also apply elsewhere in the southeastern U.S. If Field 3-412’s ecological succession is in fact typical of large, barren sites in the southeastern U.S., then the SUSES theory and models can be revised to more accurately and realistically predict woody succession in much of the southeastern U.S.

Field 3-412 is neither tropical, nor montane, and its species composition differs greatly from that of the Venezuelan Andes and Coastal Range, where in 1985, I decided to embark on this particular line of research.

If the same basic biological and ecological principles apply throughout most of the southeastern U.S., then they would probably also apply elsewhere around much of the world. If this is true, then we should find cases where some bird- and mammal dispersed woody species function as pioneer nurse trees, the beginning of hierarchical woody succession in large barren sites. Such cases have been found elsewhere around the world (Pound and Egler 1953, Niering and Egler 1955, Niering and Goodwin 1974, Galvin *et al*. 1979, Niering *et al*. 1986, Uhl *et al*. 1988, Nepstad *et al*. 1990, Backéus 1992, Kolb 1993, Prach and Pyšek 1994, Andersen 1995, Hill *et al.* 1995). (I have personally observed similar woody succession mechanisms, processes, and patterns across the U.S., Canada, Venezuela, and western and southern Europe during the past 30 years). These study findings suggest that general ecological succession theory and models can also be revised to more accurately and realistically predict woody succession worldwide.

These findings and speculations suggest the need for minor, but fundamental revisions of general ecological succession theory and models. This would be another third approximation of ecological succession, integrating more factors into the much larger equation, leaving the existing factors in place with more "conditions," to provide more accurate and realistic predictions of woody succession worldwide.

Ecology lacks a rigorous “unified” succession theory, which would be the basis for a more accurate, realistic, and predictive general ecological succession model (*sensu* Levins 1966, Thom 1974). The results and conclusions of this and related studies of ecological succession, forest migration, and other biological and ecological subjects could probably be synthesized and eventually lead to a “unified” ecological theory that encompasses primary succession, secondary succession, oldfield succession, forest gap dynamics and succession, and tree migration.

The value of accurate, realistic predictive ecological succession models and other model sub-routines, and of good site-specific databases, for natural resource management is evident by the development of many natural resource management models and related databases (Noble and Slatyer 1980, Diamond 1987, Armour and Williamson 1988, Huston *et al*. 1988, Huston 1991, Kosko 1993, Lockwood and Lockwood 1993, Schuster et al 1993, Schupp and Fuentes 1995).

Modeling is one of many steps in the cycle of basic and applied research. Subsequent steps include applications, monitoring, and feedback for further research and associated theory and model creation, revision, and demolition. Applications are essential to perpetuate the research and other cycles.

NATURAL RESOURCE MANAGEMENT APPLICATIONS

The need for and the value of more efficient and effective natural resource management methods increases as human populations increase and/or as their demands for higher standard of living increase. More accurate, realistic predictive models of ecological succession can help natural resource/ecosystem/watershed managers (e.g., farmers, foresters, groundskeepers; landfill, mine, and pit operators and owners; landscape architects, planners, property owners, and wildlife specialists) to meet part of these needs, as well as save time and/or money.

Many people can benefit from understanding and applying ecological theory and models, including those of ecological succession, in Best Management Practices (BMPs) for sustainable development; biological conservation, and ecological restoration (i.e., also reclamation and rehabilitation of degraded, damaged, and destroyed ecosystems).

Known model applications include development, conservation, and restoration for a wide variety of purposes in:

- Forestry
    - Reforestation
    - Afforestation (*sensu* Seuss 1971)
- Agriculture & Agroforestry
    - Microclimate
    - Soil fertility
    - Wind breaks
- Mining
    - Surface pit, mine, and spoils reclamation
- Transportation and Utilities
    - Rights-of-Way (ROWs) (Galvin *et al*. 1979)

- Landscape Architecture
    - Plant selection (purposes and suitability)
- Military
    - Maneuver area rehabilitation/restoration
- Urban and Regional Planning
    - Air quality improvement
    - Heat island effect
- Waste Management
    - Landfill closure
- Wildlife Management
    - Species conservation and recovery
    - Habitat conservation and restoration
    - Fish and game

My primary intended application of ecological succession theory and models is for what has been referred to as "accelerated," "assisted," or "facilitated" succession (Ewel 1980, Allen and Hoekstra 1987, Lugo 1988, Uhl *et al.* 1988, Luken 1990, Nepstad *et al.* 1990, Parrotta 1992, Kolb 1993, McClanahan and Wolfe 1993, Robinson and Handel 1993, Brown and Lugo 1994, Aide *et al*. 1995, Lugo 1997, Parrotta *et al*. 1997a and 1997b, Parrotta 1999, Toh *et al*. 1999, Robinson and Handel 2000). The objectives are to use a wide variety of methods and materials, biotic and abiotic, to complement selected natural succession mechanisms and processes to "guide" sites' ecological succession along desired pathways towards one or more stable climax and/or subclimax communities.

Ecological succession theory and models can also be used in low- reforestation or afforestation where owners cannot afford more costly methods, and no state or national subsidies are available. Limited planting of selected species at optimal site locations and spacing intervals can preferentially attract selected birds and mammals that drop seeds and fertilizer of desired woody species. This is essentially a trade-off of time for money. The reforestation or afforestation may take longer, but it would be feasible and more likely realized, than more costly methods that may not be realized.

FURTHER RESEARCH

Additional landscape level studies of ecological succession, similar to this study, can be conducted elsewhere in the southeastern U.S. and around the world to determine if the conclusions of this study also apply elsewhere, i.e., is woody succession at the landscape level usually hierarchical with nucleation and nurse plants? Unfortunately, suitable sites are rare, and even if they were less rare, the study methods are cost- and time-prohibitive for one researcher.

Therefore, I recommend a series (i.e., at least 30 plots per dominant species) of small (i.e., about 100 m^2 or 0.01 ha), isolated (i.e., 500 m to 10+ km from the nearest tree or shrub), single tree or shrub study plots in extensive, open, protected areas, to observe the natural woody succession around the trees and shrubs to more closely examine woody interspecific relationships. These sites are also relatively rare, and the study would be cost- and time-prohibitive for one researcher.

Sidebar: I discourage more intrusive, manipulative study methods for this particular research (Diamond 1986, Farnsworth and Rosovsky 1993). Although these methods would lead to more detailed understanding of the underlying mechanisms, I doubt that the additional details would notably improve the theory and model accuracy and realism (Ockham’s razor). Furthermore, these methods can be prohibitively costly and time-consuming on a large scale, and the additional results may have diminishing returns with a very low cost-benefit ratio (i.e., less than 0.1).

The proposed study of a series of smaller sites can be feasible if done in collaboration with other interested researchers around the world (Pickett 1989). Much of this work could be done by selected students in botany, biology and ecology, with appropriate investigator guidance and supervision. This could substantially reduce the total study costs and time required, and would provide a spatially broader, more species-diverse data set.

I further recommend theoretical work, if needed and justified, to revise predictive models to more accurately and realistically predict woody succession outcomes. This work would include model validation through comparisons with the results of related empirical works on woody succession.

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APPENDIX A

AERIAL PHOTOGRAPHS

Figure A-1. Field 3-412 in 1951 (SREL 1951)

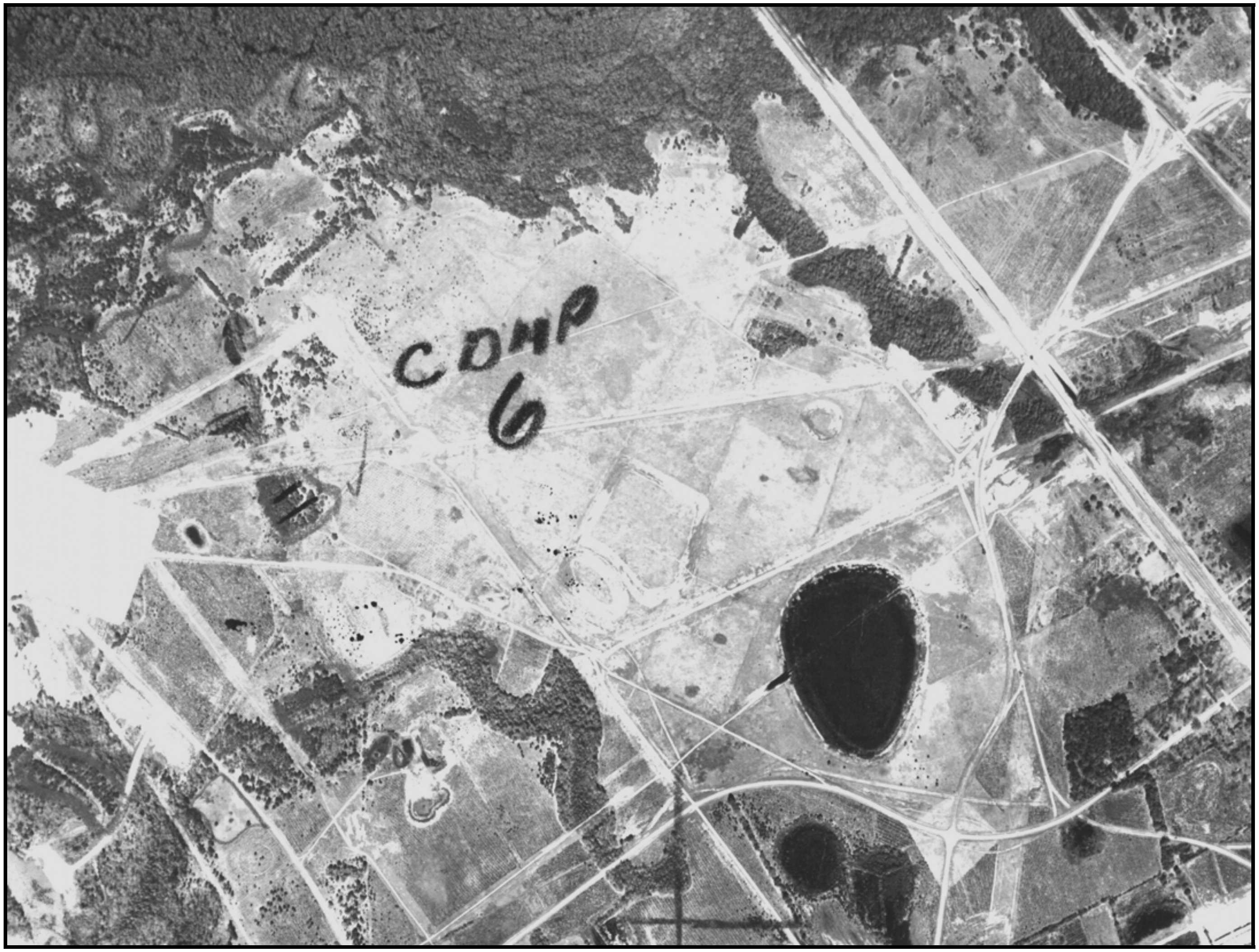

Figure A-2. Field 3-412 in 1961 (SREL 1961)

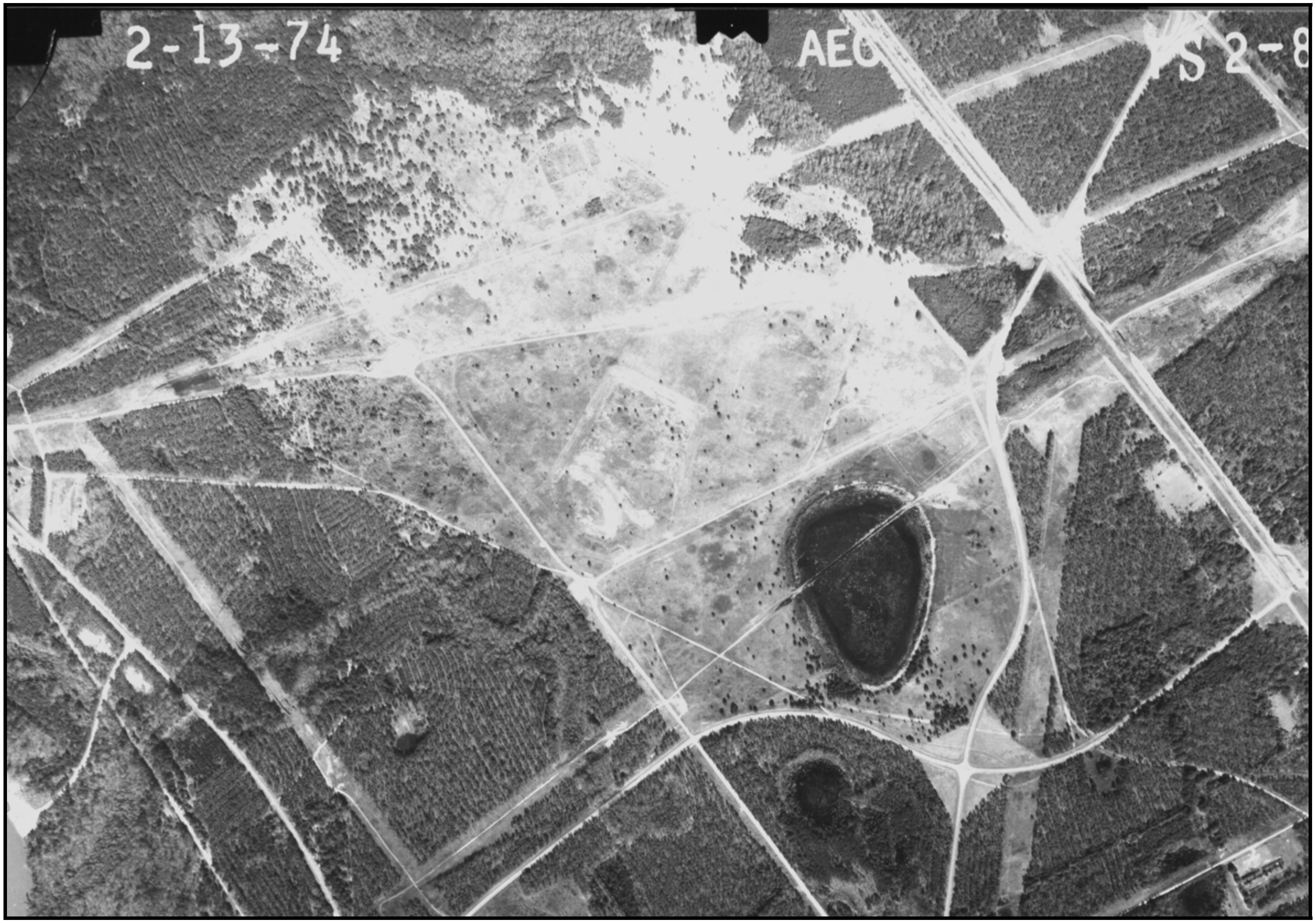

Figure A-3. Field 3-412 in 1974 (SREL 1974)

Figure A-4. Field 3-412 in 1982 (SREL 1982)

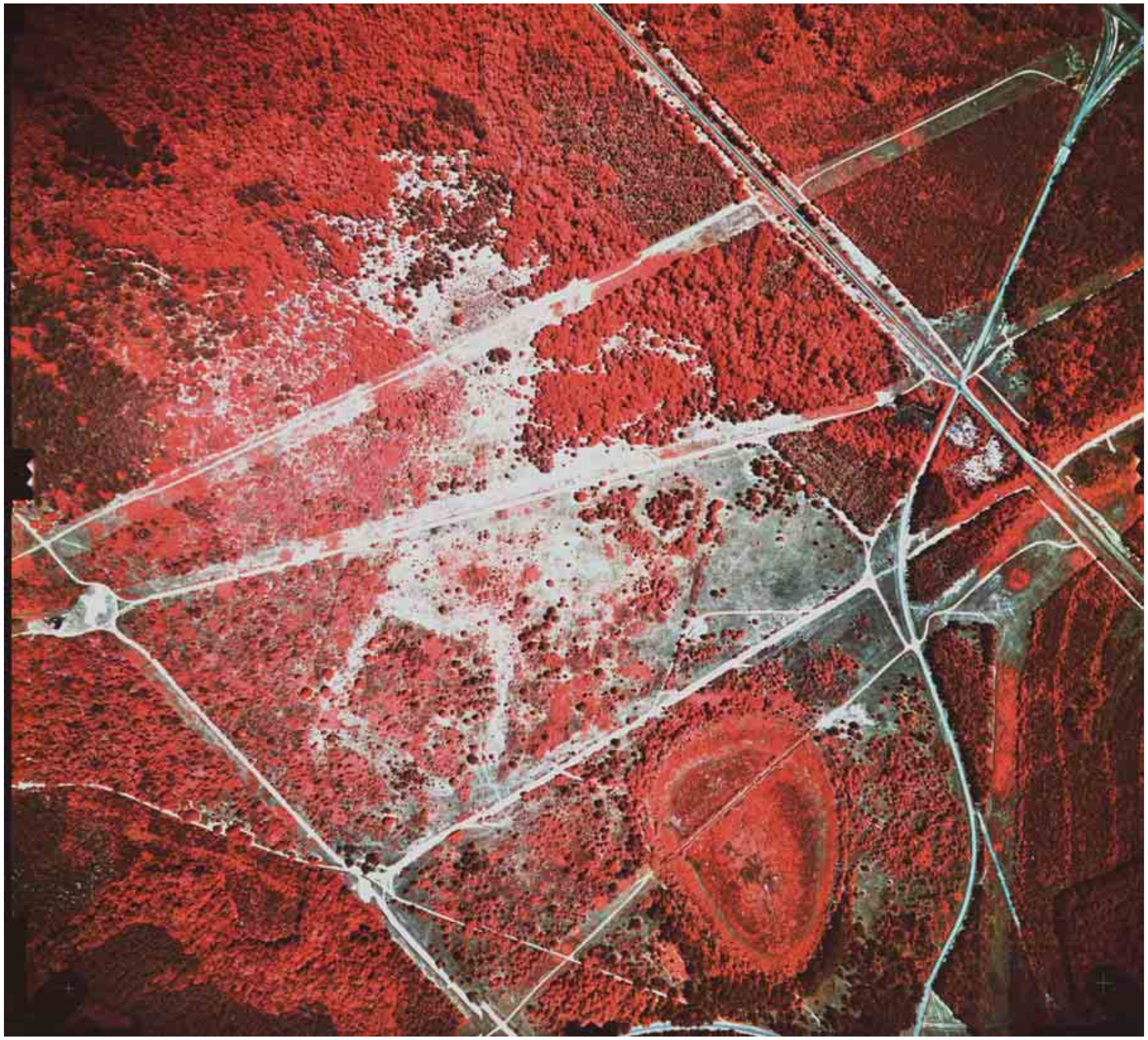

Figure A-5. Field 3-412 in 1990 (SREL 1990)

Figure A-6. Field 3-412 in 1998 (SREL 1998)

APPENDIX B

FIELD PLOT DATA

FIELD PLOT #1

1951	**1961**	**1974**	**1982**	**1990**	**2001**
0	15	28	37	62	85

Figure B-1. Percent woody cover in Field Plot #1, 1951-2001.

Core Species	**Fringe Species**						
	Quercus laurifolia	***Pinus* Spp.**	***Prunus serotina***	**Other Soft Mast Spp.**	**Other Hard Mast Spp.**	**None**	Subtotals
Quercus Laurifolia	29	1	0	0	1	13	44
***Pinus* spp.**	7	1	0	0	0	5	13
Prunus serotina	0	0	0	0	0	0	0
Other Soft Mast Spp.	0	0	0	0	0	0	0
Other Hard Mast Spp.	3	0	0	0	0	0	3
Subtotals	39	2	0	0	1	18	**Total: 60**

Table B-2. Isolated woody patches in Field Plot #1, 1951-2001, by core and corresponding dominant fringe species composition