Chapter 2: Literature Review

2.1 Introduction

This chapter provides an ecological background for *Pinus palustris*. In Section 2.2, I begin with the life history and ecology of *Pinus palustris* and then discuss the importance of fire as a disturbance in shaping this ecosystem in Section 2.3. I then provide insight into the role of *Pinus palustris* in Virginia by discussing its history (Section 2.4) and its current status (Section 2.5). This is followed by a literature review (Section 2.6) on the dendrochronology of this species. The background on the boundary-line growth method as it will be applied to *Pinus palustris* is discussed in the last section (Section 2.7).

2.2 Life History and Ecology of *Pinus palustris*

Pinus palustris is a shade-intolerant, fire-dependent, yellow southern pine occurring in various sites and conditions ranging from sandy, wet, and poorly drained areas on the coast to xeric upland ridges and sand hills in the southern plain and southern coastal plain of Virginia (Boyer 1990; Frost 1993). Production of large seeds limits dispersal of this species; for example, 71% of seed is dispersed around the base of parent *Pinus palustris* within a radius of 20 m (Croker & Boyer 1975; Landers et al. 1995). There are no known organisms that aid in the dispersal of *Pinus palustris* seeds; dispersal is limited to the effects that gravity and wind have on the seeds. After *Pinus palustris* seeds are dispersed, germination begins but requires a fully exposed mineral soil shaped by fire or site preparation and abundant sunlight, usually provided by canopy gaps (Boyer 1990). After germination, pine seedlings enter the “grass” stage that can last 3–15 years depending upon competition and sunlight (Barbour et al. 1980). During that time, *Pinus palustris* concentrates its growth on developing a strong and supportive taproot structure, whose length is determined by the distance to the water table (Platt et al. 1988; Kush & Meldahl 2000). The needles produced during the grass stage protect the meristematic region and hence the terminal bud from heat damage in a fire (Barbour et al. 1980). Fire is essential to the vitality of *Pinus palustris* at this stage. It holds back competing species allowing *Pinus palustris* to grow and controls the often fatal brown leaf spot disease, which is spread by the *Scirrhia acicola* Dearn. fungus, (Croker & Boyer 1975). Once past the grass stage, the pine tree begins to spend its energy on growth of the tissues above ground, thus entering the “juvenile” stage.

Juvenile *Pinus palustris* are susceptible to fire due to their short height (~0.6–0.9 m) and thin bark. Surface fires usually kill juveniles (Boyer 1990). For those pines that survive surface fires, use of resources promotes lateral limb growth after height gain and signals the “non-reproductive” stage (Cipollini 2002). Once cone production begins, the pines have finally reached the last stage of development, the reproductive stage. At this point, the trees are able to resist fire, insect damage, and fungal diseases, while maintaining a slow and steady growth. *Pinus palustris* is valuable as a timber species because it is able to resist disease and fire better than other southern pines, such as *Pinus taeda* Linnaeus (loblolly pine). Fires keep competitors at bay, allowing *Pinus palustris* to attain dominance within stands, while maintaining the herbaceous species that play an important role in the ecosystem. The maintenance by fire of these herbaceous plant species is also important for providing food and shelter for the fauna that make up this ecosystem.

2.3 The Role of Fire in the *Pinus palustris* Ecosystem

The *Pinus palustris* ecosystem contains high biotic diversity including an estimated 1200 vascular plant species. Members of the family Poaceae, specifically *Aristidia stricta* Michaux (wiregrass), *Aristidia simpliciflora* Chapman (southern three-awned grass), and *Schizachyrium spp.* (bluestem*)* in association with *Pinus palustris* define the landscape-mosaic in the southeast (Frost 1993; Hilton 1999). Many of these plants are pyrophytic, requiring fire to sustain their places in the plant community. In particular, wiregrass and bluestem are major understory components of the *Pinus palustris* ecosystem and are vital in restoration efforts in areas where they naturally occur in this ecosystem (Outcalt et al. 1999). Due to fragmentation, fire suppression, and habitat modification, wiregrass has been extirpated in many areas. To restore wiregrass, Outcalt et al. (1999) recommended distribution of viable seed into such areas and, once seedlings are established, the inclusion of fire management to ensure species success. Restoration of this species is important to ecosystem function because the combination of wiregrass and fallen *Pinus palustris* needles provides fuel for ignition of fire.

Fire also prevents the establishment and inhibits the growth of many oak species that compete with *Pinus palustris* (Outcalt et al. 1999). A variety of oak species occur within *Pinus palustris* ecosystems, such as *Quercus margaretta* Ashe (sand post oak) and *Quercus laevis* Walt (turkey oak). They, along with other species of pines and hardwoods, compete with *Pinus palustris* when fire suppression occurs. *Pinus palustris* forests experiencing fire suppression for at least a decade increase in the size and abundance of hardwood stems (Heyward 1939). In order to maintain *Pinus palustris* communities, *Quercus* species must be controlled by fire or removal (Greenberg & Simmons1999).

Fire is essential in maintaining the natural composition and structure of *Pinus palustris* forests by promoting fire-adapted species while limiting competition. Without proper fire regimes, both floral and faunal species are at risk of becoming endangered or extinct. Unfortunately, due to current practices in fire suppression and other anthropogenic factors, many plant and vertebrate species that reside in, or are endemic to, this ecosystem are threatened or endangered; 27 species are currently federally listed and 99 are of special concern (Hilton 1999). The reintroduction of fire in *Pinus palustris* management areas is therefore necessary to restore ecosystem function and dynamics.

2.4 The History of the *Pinus palustris* Ecosystem in Virginia

The decline of the *Pinus palustris* ecosystem in Virginia was caused by a variety of anthropogenic events tracing back to the establishment of the Jamestown Settlement in 1607. Jamestown was financed by the Virginia Company, under charter of King James I, with the intent of exploiting the people and the natural resources of the land (Frost 1993). A dependence on water for travel and trade focused English settlement to lands along the streams, rivers, and coast of Virginia. This dependence on water also prevented the settlements from making the most of its timber resources with uses limited to fencing, housing, manufactured items, and the beginnings of the naval stores industry in the southeast (Hart 1979; Frost 1993). Land was either cleared of its timber for use in fencing and housing or was burned to make way for agriculture. Fencing prevented livestock from destroying crops and provided access to an open range for grazing purposes. Cattle, horses, mules, sheep, and goats were introduced, along with feral hogs, which in particular decimated *Pinus palustris* seedlings. The taproot of the seedlings offered the hog a nutritious diet and as the English settlements expanded the hog decimated any chances of *Pinus palustris* reclaiming its former habitat in the state (Croker 1987; Frost 1993).

A second factor that would decimate the *Pinus palustris* ecosystem arose from the burgeoning naval stores industry. The naval store industry consisted of the production, shipping, and sales of tar, pitch, rosin, and turpentine (collectively called naval stores) from pine trees. Naval stores were used to grease wagon axles, waterproof cordage and sails, and to caulk leaks and coat hulls of ships and boats to prevent shipworm infestation (Frost 1993). Two methods, described in detail by Croker (1987) and Frost (1993), were used to extract gum from pine trees: the use of the tar kiln and boxing. Naval stores consisted of longleaf and small quantities of *Pinus elliottii* Engleman (slash pine), *Pinus echinata* Miller (shortleaf pine), and *Pinus taeda* (loblolly pine) (Frost 1993). Naval stores were produced along the Elizabeth and Nansemond Rivers and consumed locally until the 1700s (Frost 1993). Local consumption and the exportation of naval stores to various regions of the world, especially England, led to the end of the naval store industry in Virginia. By 1803, Virginia was unable to fulfill the demand for naval stores because of the disappearance of *Pinus palustris* (Frost 1993). After1840, the naval store industry ceased and no further naval store production was reported from Virginia (Frost 1993). After the elimination of *Pinus palustris* from the Virginia area, the naval store industry eventually took advantage of the vast supply of presettlement *Pinus palustris* available throughout the rest of the southeast (Frost 1993). Frost and Mussleman (1987) noted that prior to European settlement the extent of *Pinus palustris* in Virginia was unknown. However, Little (1971; Figure 1.1) estimated the botanical range of *Pinus palustris* as far north as Isle of Wight

County. Frost (1993; Figures 1.2 and 2.1) extended this range as far north as the Eastern Shore in Maryland, covering 15 counties within Virginia or 607,000 ha in pure or mixed stands, based on historical records, location of naval stores and tar kilns, herbarium specimens, and living *Pinus palustris* reported by foresters from 1960 to 1994. A survey conducted by Frost (1993) determined that 11 of the 15 counties in Virginia no longer contain *Pinus palustris*. Frost (1993) found only 50 mature remnant *Pinus palustris* in the counties of Isle of Wight, Southampton, Suffolk, and Greensville counties. Fernow (1892), a Harvard Forester and Chief of the Division of Forestry for the United State Agriculture Department, reported that *Pinus palustris* "is almost extinct and replaced by *Pinus taeda*." He surveyed the area in 1893, stating that "In Virginia the *Pinus palustris* is, for all practical purposes, extinct (Frost 1993, p.26)."

Frost and Mussleman (1987) examined the floristic history of the Zuni Pine Barrens, also known as the Blackwater Ecological Preserve (Figure 2.2), by looking at botanical surveys conducted throughout most of the 19th and 20th centuries and through surveys that the authors conducted themselves. These surveys shed light on the historical vegetation and provided clues as to what the area might have looked like prior to European settlement. The authors also mentioned the former importance of *Pinus palustris* in the Coastal Plain province of Virginia and the role of fire in maintaining the *Pinus palustris* ecosystem. Frost & Mussleman's (1987) survey documented two relict pyrophytic communities at the Blackwater Ecological Preserve: 1) "*Pinus palustris*/*Quercus laevis/*mixed ericads on a sand ridge or *Pinus serotina/Pinus serotina-Quercus laevis/*mixed ericads, or 2) *Pyxidanthera barbulata* (flowering pixiemoss) on a moist sand flat." After predation by feral hogs on grass stage *Pinus palustris*, small scale harvesting of *Pinus palustris* for timber, and the naval stores industry prior to 1840, *Pinus palustris* habitat in Virginia continued to dwindle down to it present size. The most recent reduction came about through fire suppression and removal of seed trees and stands established between the late 1800s and the 1920s for timber (Frost & Mussleman 1987).

2.5 The Present Status of *Pinus palustris* in Virginia

Sheridan et al. (1999) surveyed the remnants of *Pinus palustris* in Virginia finding 4,432 *Pinus palustris* and 121 seedlings left on about 81 ha (four sites) within the counties of Isle of Wight and Southampton and the City of Suffolk (Figure 2.2). Sheridan et al. (1999) survey was based on the studies by Frost & Mussleman (1987), Frost (1993), Sheridan (1993), and his own unpublished fieldwork. In the Blackwater Ecological Preserve, the site where Frost and Mussleman (1987) documented two relict pyrophytic communities, Sheridan et al. (1999) found a total of 2,139 *Pinus palustris* and nine seedlings (Figure 2.3).

The Blackwater Ecological Preserve was clear cut and burned between 1955 and 1957 according to Union Camp, a timber harvesting company who owned the land prior to donating it to the Nature Conservancy (Plocher 1999; Sheridan et al. 1999). A quarter of the land was replanted with *Pinus palustris* of Louisiana and Georgia stock (Sheridan et al. 1999). The planting of non-Virginian *Pinus palustris* in Virginia soil concerned Sheridan. His opinion was that either outbreeding depression or heterosis (hybrid vigor) could occur as a result of reproductive mixing of Virginia longleaf and southern *Pinus palustris* leading to several differing possible scenarios. The first scenario involved the idea that outbreeding depression could result in diminishing the overall fitness of this species (Lynch 1997; Sheridan et al. 1999). This decline in fitness could cause the extinction of *Pinus palustris* at the Blackwater Ecological Preserve or at all sites in the state if mixing occurred due to reproductive failure. The other scenario could lead to the creation of “superior coadapted gene complexes.” Sheridan suggested that native *Pinus palustris* should be identified at this site and the South Quay site, another site which may have had non-native *Pinus palustris* planted on it (personal communication, Bob Herren, retired forester, via tree coring and dendrochronological analysis). Sheridan et al. (1999) suggested that native *Pinus palustris* could be determined by identifying pines that predate the clearing and planting of the southern stock. Sheridan (2001) examined core samples of the *Pinus palustris* at the Blackwater Ecological Preserve and estimated tree age by counting rings to confirm Union Camp’s operations at the site back in the 1950s.

Sheridan et al. (1999) surveyed but did not core trees at the South Quay site and found 2,251 *Pinus palustris* adults and 112 seedlings (Figure 2.3). Of the eight stands at this site, two have since been clear cut, thereby eliminating 149 *Pinus palustris* from the area. With the exception of one stand, the other five stands at this site are dominated by *Pinus taeda* with *Pinus palustris* intermixed in the midstory and understory as juveniles. The other stand is an enigma because it is consists of a *Pinus palustris*-dominated stand intermixed with *Pinus taeda*, though it has not burned in over fifty years. The South Quay site was owned by Union Camp, but is now owned and managed by International Paper.

Seacock Swamp was reported to have 45 individuals of *Pinus palustris*, 16 of which were producing cones, and no seedlings in a mixed stand of *Pinus taeda* and oak (Sheridan 1993). The *Pinus taeda* found on this site are successional due to fire suppression and forestry practices. Another site with similar conditions is the Everwoods site. The ownership of this site shares similar history with the South Quay site and was surveyed by Sheridan and Chuck Peoples of International Paper in 2002 (Figure 2.4). This site was not reported by Sheridan et al. (1999) in their 1998 field census. Everwoods contains a mixed stand of *Pinus taeda* and oaks dominating the canopy along with 34 codominant *Pinus palustris* (one is the state champion *Pinus palustris* tree) and no *Pinus palustris* seedlings. This site has not been burned under the management of International Paper or under Union Camp (personal communication, Harvey Darden, International Paper Forester). Both the Seacock Swamp and Everwoods sites lack *Pinus palustris* seedlings due to low light conditions on the canopy floor, fire suppression, and timber harvest practices however, *Pinus palustris* seedlings and saplings of Virginia stock have been planted by Meadowview Biological Station at a portion of the Everwoods site that had been cleared (Sheridan personal communication).

2.6 Dendrochronology of *Pinus palustris* in the southeastern U.S.A

2.6.1 Introduction

Meldahl et al. (1999) noted that research on the dendrochronology of *Pinus palustris* with a focus on how climate affects annual ring growth has been "erratic and contradictory." The earliest research publications on the dendrochronology of *Pinus palustris* date back to the 1930s and continued until 1940. No further research on this topic appears in the literature until 1988 (Table 2.1). The research dating back to this first period lacked the more sophisticated methodologies employed by modern dendrochronologists in properly dating *Pinus palustris* cores (Stokes & Smiley 1968; Fritts 1976; Holmes 1983; Phipps 1985; Cook & Kairiukistis 1990; Yamaguchi 1991; Grissino-Mayer et al. 1997).

Dendrochronology was established in the 1920s by Andrew Ellicott Douglass, widely considered the "father" of dendrochronology. Because this was a new field, many researchers in dendrochronology were still trying to establish a set of methodologies to locate the proper place on the bole to core a tree, to standardize dates for tree cores, and to show relationships between climate patterns and tree ring growth; this is evident in one of the early publications on *Pinus palustris* (Lodewick 1930). The author developed his own methodology to extract cores and date them. He used statistical methods to determine which climatic variables influenced *Pinus palustris* growth; however his techniques and those of other early dendrochronologists lacked the sophistication to draw strong conclusions on climatic influence on tree growth. Small sample sizes may also have weakened these early studies. These problems illustrate why research from this period produced “erratic and contradictory” results, as noted by Meldahl et al. (1999).

Research after Platt et al. (1988) study on the population dynamics of *Pinus palustris* differ from prior research on this species, because they incorporated some of the standardization techniques that are now commonly used in the field of dendrochronology (Stokes and Smiley 1968; Holmes 1983; Phipps 1985; Cook 1990; Yamaguchi 1991; Grissino-Mayer et al. 1997). These techniques include taking duplicate cores from individual trees, always on opposing sides and perpendicular to the slope; “skeleton-plot” crossdating for archaeological specimens (Stokes and Smiley 1968; Cook 1990); and the list year method of crossdating (Yamaguchi 1991) for live trees. Also, with the advent of the personal computer, statistical techniques have been standardized and are easier to perform. Microscopes, fine-resolution tree-ring measurement systems, and computers have now been linked to allow detailed analyses of dendrochronological patterns using statistical techniques (Grissino-Mayer et al. 1997).

It is important to note that a review of the literature did not turn up any studies that involved the use of dendroecology to determine disturbance regimes and release events; the only types of studies that were encountered deal with the dendroclimatology of the species. Meldahl et al.

(1999) speculate on the disturbance history at their site in Flomaton Natural Area, Alabama but did not analyze the chronologies to determine if their idea on the matter could be validated.

2.6.2 Wood anatomy

A study by Pillow (1931) showed evidence of compression wood formation due to crown bending in *Pinus palustris* as a result of a 1926 hurricane that passed through western Florida. Pillow provides photographic examples of compression wood and explains how and where on the *Pinus palustris* it formed. Stone (1940) reported on the observations of frost rings in *Pinus palustris* from southern Mississippi. These rings came from second growth stands and the frost rings dated to 1932. February of that year was the warmest on record, with temperatures 10° higher than normal. Temperatures of -6°C and -4°C respectively on March 9th and 10th produced a “conspicuous yellow-to tan-colored zone” in the earlywood of the 1932 annual ring, interpreted as a “frost” ring. Microscopic analysis showed that rays were laterally displaced, xylem elements were distorted, and parenchyma was short-celled, features typical of frost injury.

2.6.3 Population dynamics

Platt et al. (1988) studied *Pinus palustris* in an old growth 80 ha upland stand known as the Wade Tract, located in Thomas County, Georgia in the Tallahassee Red Hills region of the southeastern coastal plain. Managers of this tract practiced prescribed burning annually or biennially during the late winter or early spring. These researchers surveyed and gridded a 39.4 ha plot within the Wade Tract and established 36 quadrates within it of one ha^2. They found

9340 trees, 6905 of which were *Pinus palustris* and the rest belonging to 17 other species of the genus *Quercus* (oak). Ninety percent of the oaks were <10 cm diameter at breast height (DBH). Their research on the population dynamics of *Pinus palustris* focused on age-size relationship, population demography, and spatial dispersion. Regarding population demography, the researchers took cores at breast height and measured the height of 399 *Pinus palustris* that were > 2 cm DBH. These trees were randomly selected accounting for 5.8% of the total *Pinus palustris* in the study area. The cores were only used to assess the age of the trees sampled, which was done by counting the number of rings and not by the currently accepted method of crossdating. The ages of the trees ranged from 1–244 years, with two thirds of the trees <50 years of age. Platt et al. (1988) then took the ages from this sample to calculate a 95% confidence interval for the number of individuals in each successive 25-year age class. According to the authors, the error for this calculation is unknown because the numbers of trees in each age class were not independent. There was a strong nonlinear relationship between the age and the size of *Pinus palustris* based on Spearman rank-correlation (r = 0.964 and 0.961). The research of Platt and others (1993) provided valuable insight into the ecology and natural history of old growth *P. palustris*; however, further study of the samples from this site using modern dendrochronological techniques may yield valuable information on the ecology and natural history of this stand from both a dendroclimatological and dendroecological perspective.

2.6.4 Dendroclimatology

Lodewick (1930) investigated the effects of climate on annual growth rings in western Florida. Lodewick examined 57 *Pinus palustris* samples in the Choctawhatchee National Forest located in western Florida, 80.5 km east of Pensacola and 11.3 km from the Gulf of Mexico. *Pinus palustris* at this site grew on Norfolk sand with an annual rainfall of around 152.4 cm. The early spring months were the driest and precipitation peaked during July and August. Lodewick focused on the effects of climate on crown volume and annual radial growth between 1916 and 1927. No correlations were found for temperature or crown volume, however summer precipitation (March 16–October 15) accounted for 89% of growth after adjustments were made for a heavy seed year that occurred in 1920. Earlywood production was constant and irrespective of precipitation, but mid-June to mid-October precipitation had significant impact upon latewood growth.

Working at the same site as Lodewick (1930), Paul & Marts (1931) experimented with *Pinus palustris*. They were interested in determining if irrigation could be used to increase the production of latewood (summerwood) and if commercial fertilizers could increase earlywood and latewood production. Paul & Marts (1931) showed a reasonably close correlation between the soil water supply and latewood production prior to irrigation, and that irrigation increased the growth of latewood. Fertilizers also positively influenced latewood and earlywood production, but not to the extent that irrigation did.

Coile (1936) examined the effects of climatic parameters on annual radial growth for four pine species in the southeast, including *Pinus palustris*. *Pinus palustris* cores were taken from two different stands: 1) a stand 19 miles north of Waycross, Georgia with climatic data coming from Waycross with an average age of 17 years old, and 2) a stand 18 miles south of Cordele, Georgia with an average age of 20 years old. His climatic data came from the Americus weather station 30 miles northwest of the stand. Coile (1936) analyzed 10 *Pinus palustris* cores from each stand and determined tree ages and their diameter at breast height (DBH, the diameter of a tree at breast height, typically 1.4 meters above ground). Coile (1936) found that rainfall in early spring (February–April) affected the annual growth of *Pinus palustris*, and average temperature from the current summer (June–August) had a negative correlation with growth.

Shumacher & Day (1939) also looked at the effects of precipitation on annual ring growth of a variety of tree species specific to the eastern United States. Their study included *Pinus palustris* from three locations in Florida: Lake City, (12 *Pinus palustris*, average age 32 years); Gainesville (18 *Pinus palustris*, average age 50 years); and Jacksonville (12 *Pinus palustris*, average age 58 years). For all of the sites, the authors used regression analysis, with the ring widths as the dependent variable and monthly precipitation over a 15 month period as the independent variable. A regression equation calculated from the combination of annual growth rings and precipitation data was used to express that annual growth of tree-rings is a function of average monthly precipitation or aggregate over a 15 month period (Shumacher & Day 1939). The authors determined that only 3–12 % of the trees were influenced by precipitation. Specifically, *Pinus palustris* from the Gainesville site were not affected by precipitation while those at the other two sites were. I speculate that other factors other than precipitation may have had an effect on the Gainesville site. Such factors could have been edaphic differences between sites or the effects that slope or elevation.

The development of longer and older chronologies or larger sample depth for the studies by Lodewick (1930), Coile (1936), and Schumacher and Day (1939) may have produced stronger, more verifiable results for correlating or regressing tree ring growth with climatic variables. Current dendrochronological methods usually employ trees that are older than 30 years old to determine what affects tree-ring growth through correlation and to predict or reconstruct climate from tree ring growth using regression. Schumacher and Day (1939) had trees that were 32 to 58 years old, old enough to interpret climatic influences in tree ring growth, but they only had 12 to 18 cores respectively for their two sites. Lodewick (1930) and Coile (1936) had *Pinus palustris* that were less than 20 years old—not old enough by today's standards to interpret climatic variables from tree ring growth especially because competition and canopy gaps could have had more of an influence on the growth of these *Pinus palustris*. Lodewick (1930) did however have a statistically significant sample size of 57, while Coile did not have a significant sample size for his two sites, a sample size of 10 for each site. Research after 1988 does differ greatly from these early research articles because they employ currently accepted dendrochronological methods when relating climatic variables to tree ring growth.

In later research with updated techniques, Zahner (1989) investigated the effects of stand and environmental conditions on annual growth rings of *Pinus palustris* in two stands on the Escambia Experimental Forest (EEF) in Escambia, Alabama. The two stands are situated on Troup fine sand and Benndale sandy loam with 2–6 % slopes; both soils are well drained. Management at the EEF burned these two stands at two to three year intervals and the both stands were thinned to maintain desired basal areas. Zahner (1989) cored the two largest *Pinus palustris* at breast height from these two stands and then qualitatively selected sample *Pinus palustris* based on healthy dominant crown classes. The ring width average for each site was regressed against an aggregate of seven variables: age, site, basal area, climate, fire regime, stand differences, and error. The results indicated that basal area of the stand, prescribed winter burns, and current summer weather conditions (favorable or unfavorable) affect tree ring growth. Specifically, reduction in basal area (from thinning) for the stands increased ring widths for *Pinus palustris* 20–28 years old because more light was available for growth. Prescribed winter fires resulted in a 13% decrease in ring widths for *Pinus palustris* of the same age, which further declined to 28% with the occurrence of drought years or unfavorable weather. Summer weather also affected ring growth, with favorable summer weather positively affecting rings by 12% and unfavorable summer weather negatively affecting rings by 15% for trees of the same age.

Devall et al. (1991) published research on the dendroecology of *Pinus palustris* based on increment cores collected from the 72.9 ha Harrison Research Natural Area located within the De Soto National Forest in Mississippi. The authors split the site into eight equal areas. They cored the four largest *Pinus palustris* in each area, taking two cores from each tree at breast height on opposite sides of the pines and perpendicular to the slope. One core from each tree was used in crossdating and a chronology was developed from the average of the cores. The average age of the *Pinus palustris* at this site was 55 years with a standard error of 1.8. Accounting for the biological growth trend of their cores, the authors were able to use the cores to determine the effect of climatological variables on ring growth. Monthly precipitation and temperature and the Palmer Drought Severity Index (PDSI) were the variables used. Current year August precipitation, September temperature, and February PDSI had the greatest influence on tree growth. The PDSI is a regional index developed by Palmer (1965) to measure the loss of the moisture supply. It is based on precipitation, temperature, and available water content of the soil and provides an index of water balance for the area being investigated. The index ranges from -6.0 to +6.0, with -6.0 representing extreme drought and +6.0 representing extremely wet conditions. PDSI provides a measurement of the irregularity of weather for a region, allows for current weather patterns to be put into perspective with past conditions, and provides a spatiotemporal representation of the droughts in the region (Alley 1984).

Meldahl et al. (1999) studied an old growth *Pinus palustris* stand at the Flomaton Natural Area in Escambia County, Alabama. They described the climate at this site as humid and mild with precipitation distributed plentifully throughout the year. The authors created a 60 m x 80 m grid, 30m away from the edge of the site, and circular 0.08 ha plots within the grid. The authors collected *Pinus palustris* data for trees >1.25 cm in DBH on each plot: azimuth and distance from plot center, DBH, crown height, and total height. They collected cores at 1.22m height from 100 trees >7.6 cm DBH from a height of 1.22 m. The authors measured ring widths to 0.001 mm resolution, while the separation of earlywood and latewood were estimated visually. They cross-dated the cores, validating them using COFECHA (Holmes 1983). They created tree-ring chronologies for earlywood, latewood, and total ring width, and used ARSTAN (Cook 1985) to standardize the series and remove the effects of stand disturbances to provide a better climatological signal. The authors found 10 trees dating back to 1817 with an average age of 107 years, an earlywood chronology consisting of 10 cores dating back to 1920, and a latewood chronology consisting of 10 cores dating back to 1900.

Meldahl et al. (1999) used chronologies for earlywood, latewood, and total ring widths to develop correlation coefficients with seasonal and monthly precipitation, minimum and maximum temperature, and the Palmer Hydrological Drought Index (PHDI). The PHDI is an adaptation of the PDSI and is based on the inflow, outflow, and storage of moisture (Karl and Night 1985). Current growing season precipitation from March – October and monthly precipitation in March and September positively affected tree ring growth. They found a strong negative correlation between maximum temperatures for current year months from February to

April and earlywood growth, and a positive correlation between maximum temperatures of the previous year and latewood and total ring growth. PHDI from both Alabama and Florida had positive correlations with Alabama showing a stronger relationship. The authors concluded that that the relationship between climate and growth is strong and complex and could be attributed to the unique life history of this species (Meldahl et al. 1999).

Meldahl et al. (1999) also examined the effects of disturbance on this stand. The authors compared the ring count (age) in years to tree diameter in centimeters and found some interesting features. Their results suggested *Pinus palustris* to be more shade-tolerant than previously thought. The *Pinus palustris* at this stand were overtopped and suppressed, some for 50–75 years or more. The authors saw a number of growth releases and declines in the stand data, but were not able to determine the causes. They suggested that growth declines may have resulted from competition of fire-intolerant species invading the stand due to fire suppression.

Foster and Brooks (2001) focused on shortleaf pine and *Pinus palustris* at the University of South Florida's Ecological Research Station just north of Tampa, Florida. They were interested in how climate, water flow, and location of trees with respect to a hydrological gradient (mesic, transition between mesic and xeric, and xeric) could affect annual ring width growth for both species. They sampled 21 *Pinus palustris* from xeric and transition zone areas dating from 1941–1997. Their analysis concluded that *Pinus palustris* growth in this site was not affected by a hydrologic gradient. Positive correlations were found between PDSI, precipitation, and water flow during the spring and summer and growth of *Pinus palustris* at both areas. PDSI and water flow were positively correlated with growth throughout the whole year, while precipitation had stronger correlations when based on seasonally aggregated data instead of monthly. The *Pinus palustris* in the transition zone were influenced by previous summer rainy season water availability, while those in the xeric zone were not dominantly influenced by any one particular variable. A regression analysis indicated that seasonal climate variables could explain 17.5% of the variation in growth patterns in the xeric area and 15.8% for the transition area.

2.6.5 Disturbance History

Meldahl et al. (1999) study on an old growth stand of *Pinus palustris* in Flomaton Natural Area, Alabama revealed a complex relationship between climate and growth. The authors also speculated on the disturbance history of the stand. The chronologies for these stands had significant growth declines that occurred during the last half of the 20th century. They thought that the growth declines were attributed to below ground competition from fire-intolerant species due to fire suppression of the stand. As fire-intolerant species began to move into the stand, they competed for soil nutrients with *Pinus palustris.* These species had extensive root systems, which may have caused the decline. They also stated that competition rather than climate may have been influencing the growth of *Pinus palustris* within this stand.

Although Meldahl et al. (1999) speculated on the effects of competition from fire-intolerant species for soil nutrients, they conducted no analysis to validate or refute this idea. The boundary-line growth method (Black and Abrams 2003) of determining growth releases and disturbance history may have the potential to validate or refute the assumptions of Meldahl et al. (1999). Development of multiple boundary-line growth patterns for the competing fire-intolerant species coupled with that of *Pinus palustris* would yield valuable insight into the release events for competing tree species at this site and may help to validate or refute the assumption that fire-intolerant tree species are competing with *Pinus palustris* at that site.

Dendrochronological studies focusing on the dendroecology and the disturbance history of *Pinus palustris* are lacking in the literature, aside from the speculations by Meldahl et al. (1999). A study by Devall et al. (1991) of the dendroecology of this species in Mississippi focused on climatic effects on growth, but did not address disturbance. Past dendrochronological research has focused mainly on the dendroclimatology of *Pinus palustris* in the central part of its range, specifically Alabama, Florida, Georgia, and Mississippi. Dendrochronological studies of *Pinus palustris* appear to be lacking for the extremes of its range, specifically at its northern range located in southeastern Virginia, and may yield useful information on the ecology of *Pinus palustris*. The effects of stand disturbance and canopy gaps on annual ring growth is another aspect of tree-ring research that has not been studied regarding *Pinus palustris*. This thesis will contribute to the understanding of the dendroecology of *Pinus palustris,* and to the ecological knowledge of *Pinus palustris* in Virginia.

2.7 The Boundary-Line Growth Method

The boundary-line growth method, developed by Black and Abrams (2003), identifies releases from suppressions through pulses in percent growth change as dictated by prior growth in a tree-ring chronology. This study differs from past research that investigated releases from suppressions because their methodologies may have overly generalized the response of a tree to a disturbance event. The reason for this overgeneralization was due to the application of a fixed growth-change threshold to diameter, age, and crown class (Black & Abrams 2003). This method does not involve the use of age, diameter, or crown class in assessing release from suppression because they are artifacts of the more important relationship between release and prior growth.

A boundary line is developed from the relationship of release and prior growth and major and moderate releases are defined and used to construct the disturbance history for the species being investigated.

This method can be implemented using the following steps (Black & Abrams 2003). Percent growth change and prior growth for trees at a site is determined from annual ring width measurements. Percent growth change is the 10 year mean subsequent growth of a tree (M2) minus the 10 year mean prior growth of a tree (M1) divided by the 10 year mean prior growth of a tree, or M2-M1/M1. Prior growth is the mean raw growth of a tree over the prior 10 years (Black & Abrams 2003). The boundary line is created by dividing the dataset into 0.5 mm segments of prior growth, with the top ten points of percent-growth change averaged from each segment. The segments with positive averaged values are fitted to linear, power, logarithmic, and exponential curves and the function with the highest R^2 value (a negative exponential function) is retained and used in creating the upper boundary line. The boundary line is then taken at 50% to determine which annual rings had major releases and at 20% to determine which annual rings had moderate releases.

This method can be applied to a variety of tree species because it is species specific thereby allowing for further investigations of multiple tree species in a forest and developing different disturbance histories for each species. This allows for determining the differences in release potential across different species in a forest and could provide an in depth understanding of the disturbance dynamics of a forest and the release response of a different tree species in that forest to a disturbance event.

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Chapter 2 Figures

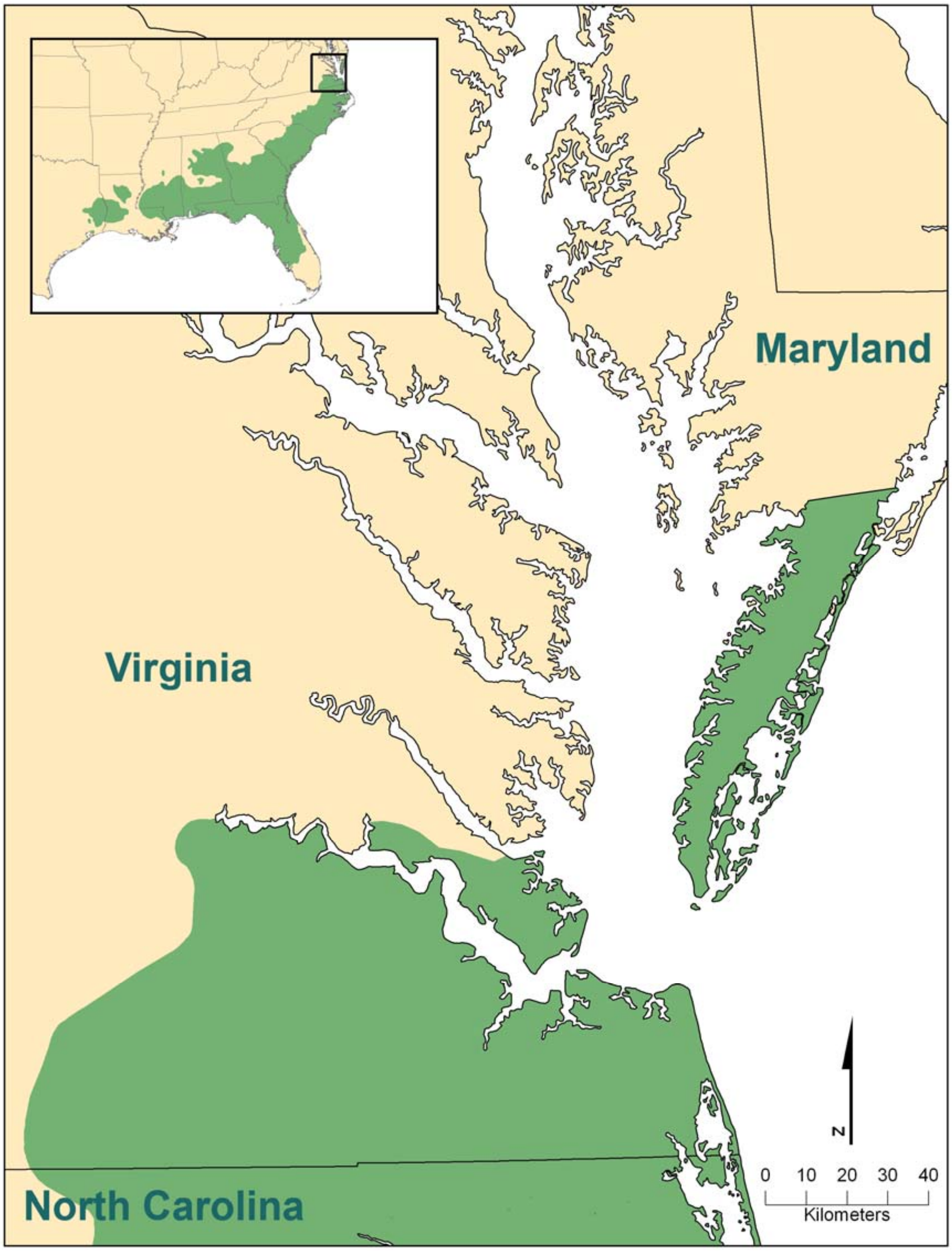

Figure 2.1. The range of *Pinus palustris* in Virginia. (Modeled after Frost 1993; Sheridan et al. 1999).

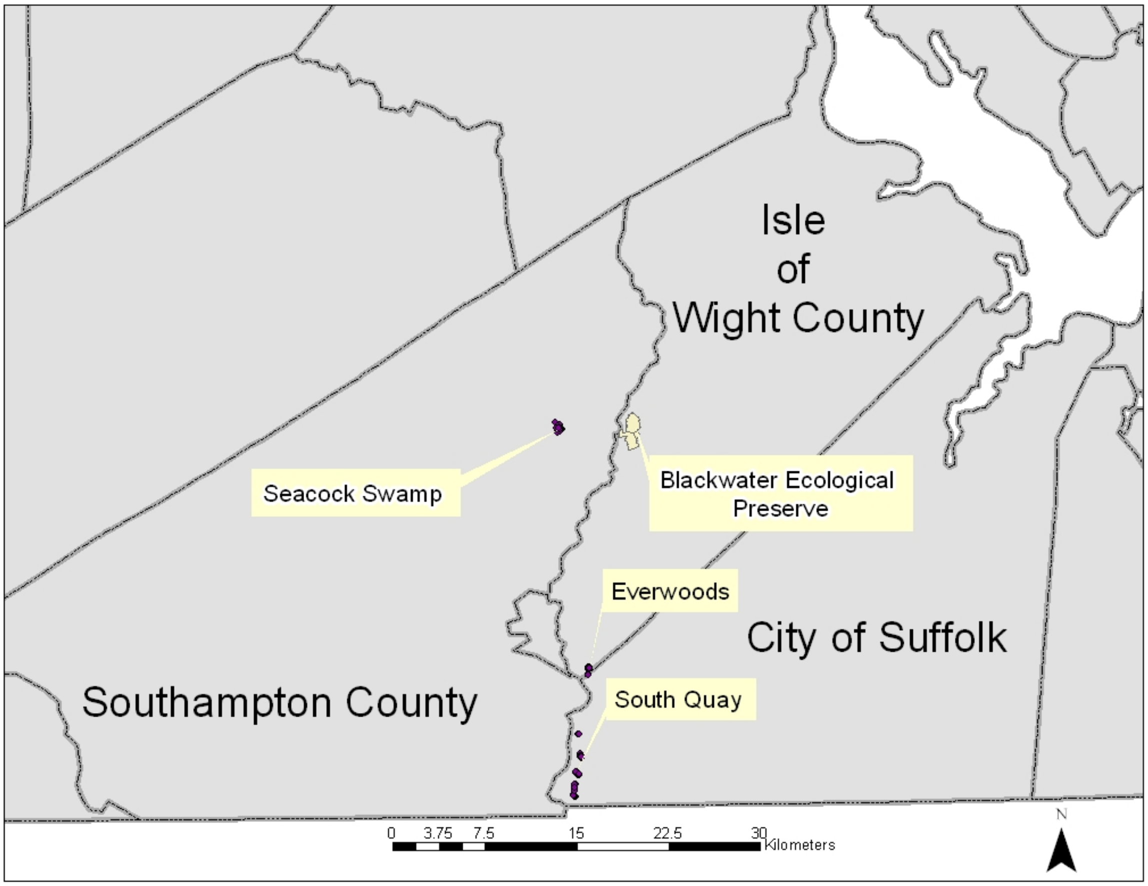

Figure 2.2. Four of the five sites containing extant *Pinus palustris* in southeastern Virginia (Kume and Surry site not shown).

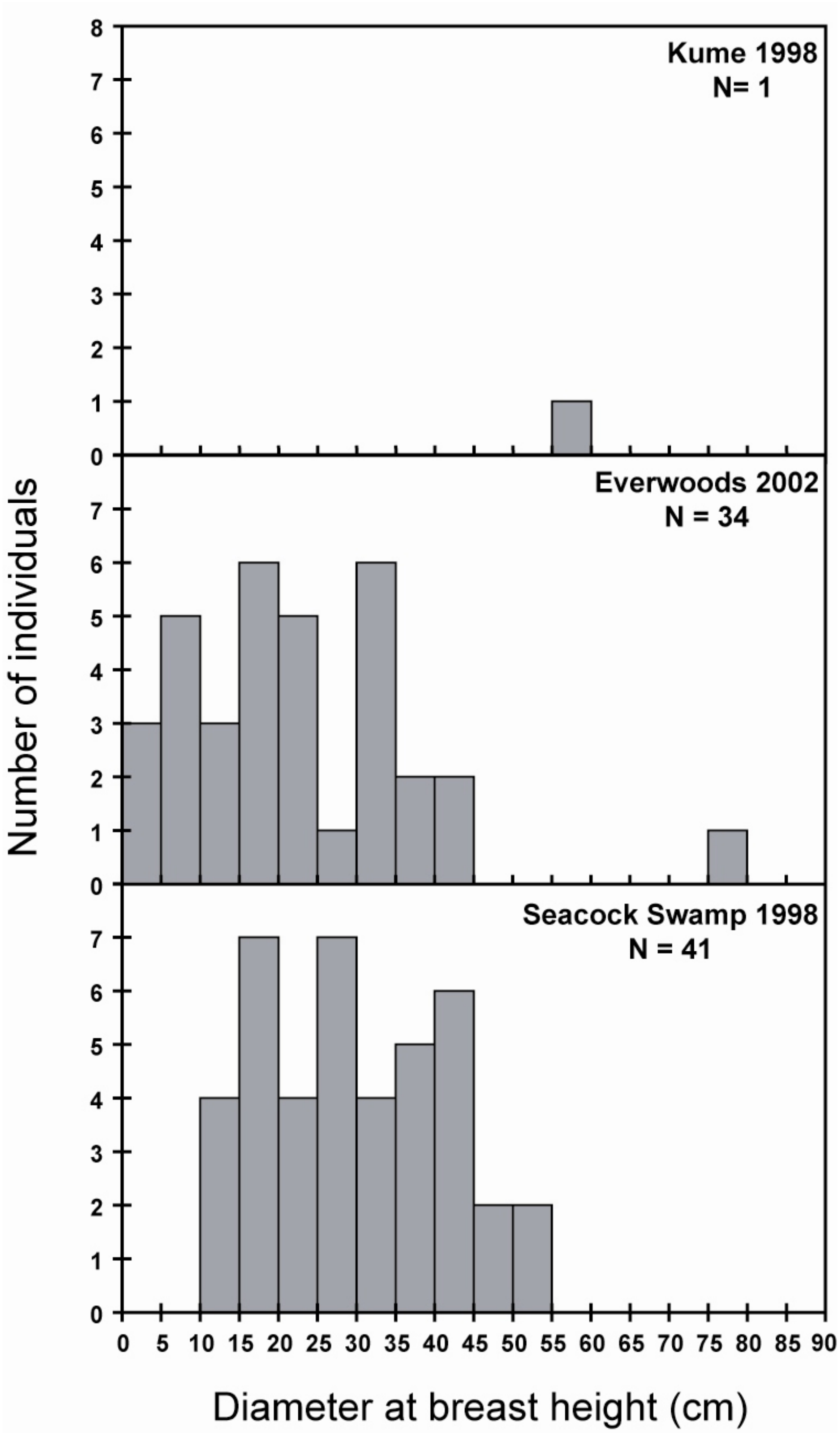

Figure 2.3. Size distribution of *Pinus palustris* at the Kume, Everwoods, Seacock Swamp, Blackwater Ecological Preserve, and South Quay. Data are from census surveys conducted by Sheridan et al. (1999) and unpublished data (personal communication, P. Sheridan).

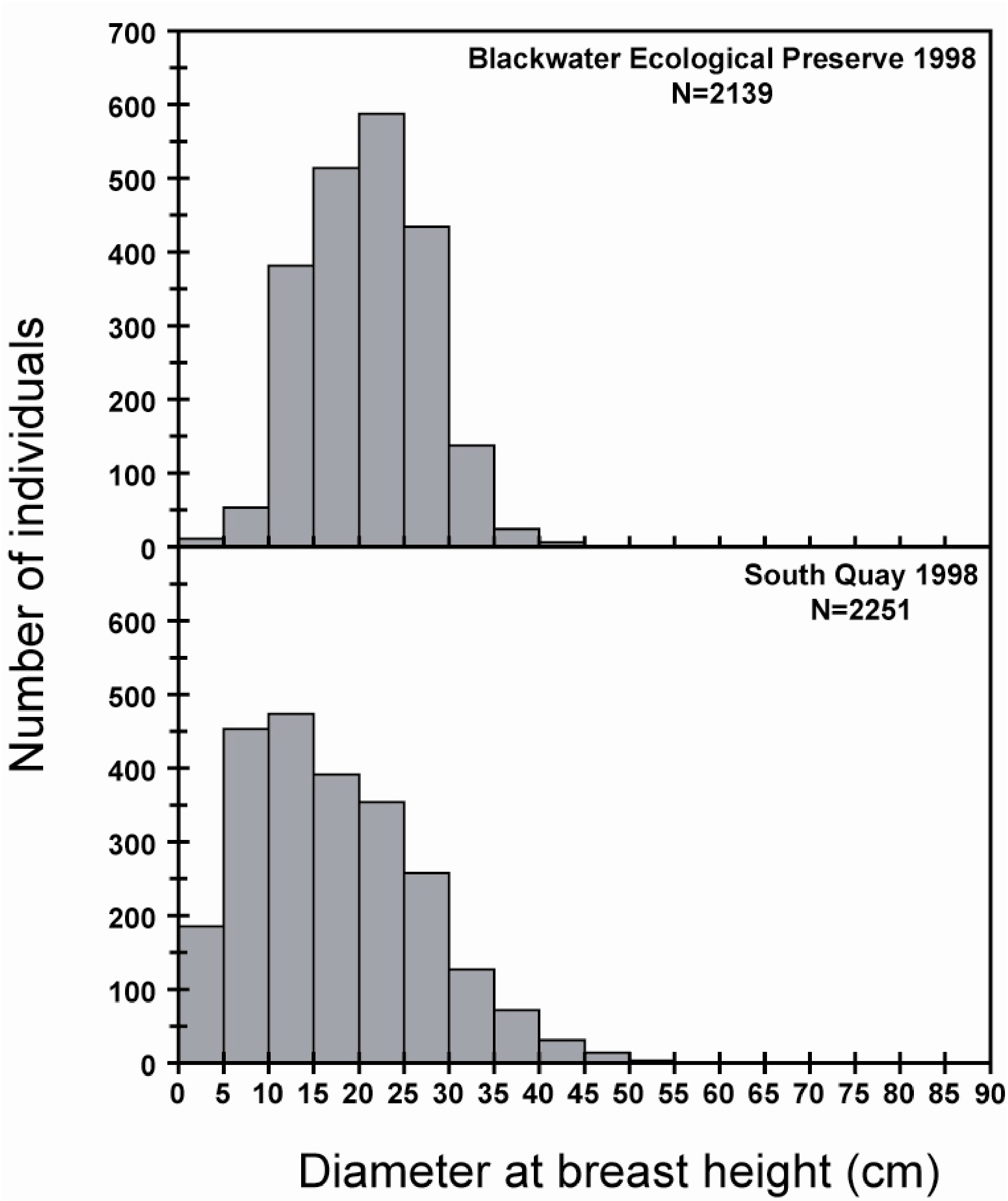

Figure Figure 2.3 continued