DEVELOPING MANAGEMENT AND RESTORATION REGIONS FOR ATLANTIC WHITE-CEDAR BASED ON PATTERNS OF GENETIC VARIATION

Kristin A. Mylecraine[1], George L. Zimmermann[2], John E. Kuser[3], Lena Struwe[4] and Peter E. Smouse[5]

[1]Department of Ecology, Evolution and Natural Resources, Rutgers, The State University of New Jersey 14 College Farm Road, New Brunswick, NJ 08901. Current address: Wildlife Biologist, Ohio Division of Wildlife, ODNR, Olentangy Wildlife Research Station, 8565 Horseshoe Road, Ashley, OH 43003

[2]Professor, Natural and Mathematical Sciences, Richard Stockton College of New Jersey, P.O. Box 195, Pomona, NJ 08240

[3]Associate Professor Emeritus, Department of Ecology, Evolution and Natural Resources, Rutgers, The State University of New Jersey, 14 College Farm Road, New Brunswick, NJ 08901

[4]Associate Professor, Department of Ecology, Evolution and Natural Resources and Department of Plant Science, Rutgers, The State University of New Jersey, 14 College Farm Road, New Brunswick, NJ 08901

[5] Professor, Department of Ecology, Evolution and Natural Resources, Rutgers, The State University of New Jersey, 14 College Farm Road, New Brunswick, NJ 08901

Abstract--Atlantic white-cedar (*Chamaecyparis thyoides*; AWC) is an important wetland tree species occurring along the Atlantic and Gulf of Mexico coasts. The economic and ecological importance of AWC, coupled with significant population decline, has led to increasing interest in its management and restoration. The geographic distribution of genetic variation is an important consideration for developing management and restoration strategies. We present an overview of rangewide genetic variation within AWC, including allozyme, provenance, cpDNA, and morphological variation, and combine this information with ecological and geographic data to identify suggested management regions within the species. We identified three major geographic regions: (1) Atlantic coast, (2) Florida peninsula, and (3) Gulf of Mexico coast, with further division of Regions 1 and 3 each into three subregions. This pattern of variation should be taken into account when identifying populations for conservation, developing management and restoration plans, and selecting propagules for regeneration and restoration purposes.

Keywords: Atlantic white-cedar, *Chamaecyparis thyoides*, genetic variation, morphology, provenance, management, distribution, Atlantic Coast region, Peninsular Florida, Gulf Coast

INTRODUCTION

Atlantic white-cedar (*Chamaecyparis thyoides*; AWC) is a wetland tree species, occurring in freshwater swamps and bogs along the Atlantic and Gulf coasts of the United States. It is a highly valued timber species (Korstian and Brush 1931), although the amount harvested has declined significantly over the past several decades, due to reduced supply and increased protection of remaining stands. Ecologically, AWC creates a unique habitat that supports a wide variety of plant and wildlife species (Mylecraine and Zimmermann 2000). Since European settlement, there has been a significant decline in the area occupied by AWC, due to overharvesting, conversion to agriculture and development, ditching and draining of wetlands, changing fire regimes, and excessive browsing by white-tailed deer (Frost 1987, Kuser and Zimmermann 1995, Mylecraine and Zimmermann 2000). The ecological and economic importance of AWC, coupled with these declines, have led to increasing interest in the species' conservation, management and restoration (Wicker and Hinesley 1998, Mylecraine and Zimmermann 2000, Smith 2003, Zimmermann and Mylecraine 2004).

Genetic variation should be an important consideration when developing restoration and management plans. Genetic diversity within populations is important for maintaining the species' ability to adapt to variable environments over space and time, reducing vulnerability to pests, and providing material for any potential breeding programs (Ledig 1986). Patterns of variation among populations may be used to infer the historical biogeography of the species, as well as to identify genetically homogenous regions of utility for management and conservation plans. For example, conservation plans should support the protection of representative populations in each unique genetic region, in order to maximize genetic variation in future generations. Such regions are also important for developing guidelines for seed and propagule movement. The geographic source of propagules should be a major consideration for restoration projects (Montalvo and others 1997, Lesica and Allendorf 1999), as the ultimate success of a restoration may depend on choosing genetically adapted material. If genetic material is not adapted to the local climatic, edaphic and biotic environments, heavy mortality and regeneration failure may result (Millar and Libby 1989).

A series of recent studies have examined geographic patterns of genetic variation in AWC (Kuser and others 1997, Eckert 1998, Haas and Kuser 1999, Dugan and Kuser 2003, Mylecraine and others 2004, Mylecraine and others 2005). In this paper, we summarize information based on neutral genetic markers (allozymes and sequences from non-coding regions of cpDNA), morphology, and adaptive traits (provenance trials). We combine this information with geographic and ecological data to suggest a number of unique management regions.

METHODS

Current Distribution

To determine the current geographic distribution of Atlantic white-cedar, we examined the published literature, examined herbarium specimens, and conducted field observations, while collecting samples for genetic studies (Mylecraine 2004, Mylecraine and others 2004, Mylecraine and others. 2005). We used this information to produce an updated range map, including all counties in which we were able to document the species' presence.

Sample Collection

We collected foliage samples from a total of 52 populations throughout the range of AWC between 1999 and 2001. Samples ranged from 44°20'N south to 29°12'N, spanning the full latitudinal range of the species. Detailed descriptions of collection methods and sampled locations are presented in Mylecraine (2004).

Genetic Methods

To examine rangewide patterns of genetic variation, we conducted allozyme analyses, DNA sequencing, morphological examination, and provenance testing. We analyzed 31 populations (n~30-50 per population) for variation at eleven allozyme loci. Detailed lab and data analysis methods are presented in Mylecraine and others (2004). We examined 43 populations for morphological variation, including foliage, seed cone and seed characters. Detailed methodology is presented in Mylecraine (2004). We also sequenced two non-coding regions of chloroplast DNA, *trn*D-*trn*Y intergenic spacer and *trn*L intron for individuals from 25 populations (Mylecraine 2004). To examine patterns of provenance variation, we rooted cuttings from 34 populations and planted them in three common garden plantations: two in New Jersey and one in North Carolina. We monitored growth and survival through the first two growing seasons. Detailed provenance methodology is presented in Mylecraine and others (2005).

RESULTS

Current Distribution

We present an updated range map (figure 1a-e), including all known counties of occurrence, based on the published literature, herbarium specimens and field observations during this study. Atlantic white-cedar is found along the Atlantic coast, from southern Maine to central Florida, and along the Gulf of Mexico coast, from Florida to

Mississippi. There is a large disjunction between the Atlantic and Gulf coastal populations, with only a few populations in the sandhills of western Georgia. The northernmost known population is located at Appleton bog, Knox County, Maine (44°20'N), while the southernmost population is located in Ocala National Forest, Marion County, Florida (29°12'N). The easternmost population is located at Northport, in Waldo County, Maine (69°01'W), and the westernmost population is found along Juniper Creek in Pearl River County, Mississippi (89°33'W). Korstian and Brush (1931) state that the distribution extended to eastern Louisiana along the Pearl River valley, but there is no recent evidence to support this (Little 1950, Clewell and Ward 1987, Ward and Clewell 1989). The only known populations in Louisiana have been planted (McCoy and others 2003).

Within its range, the distribution is patchy and disjunct, depending on the occurrence of suitable wetland habitat (Little 1950). In general, it is found within a narrow coastal belt, 80 to 160 km wide, and decreases in abundance with increasing distance from the coast. The species occurs from sea level to 457m elevation, but the majority of stands are found below 50m (Laderman and others 1987). Southeastern New Jersey, North Carolina, and northwestern Florida contain the largest natural areas occupied by this species (Kuser and Zimmermann 1995).

Summary of Patterns of Genetic Variation

AWC exhibits significant genetic variation in allozymes (Kuser and others 1997, Eckert 1998, Mylecraine and others 2004), cpDNA sequences (Mylecraine 2004), morphology (Mylecraine 2004) and adaptive traits (Haas and Kuser 1999, Dugan and Kuser 2003, Mylecraine and others 2005). Different classes of traits exhibit different geographic patterns of variation, a common finding among conifer species, which may be attributable to different evolutionary forces (Wheeler and Guries 1982, Libby and Critchfield 1987). Among AWC populations, neutral genetic markers, such as allozymes, exhibit regional patterns of variation, often associated with range disjunctions, a pattern that may have resulted from decreased gene flow and increased genetic drift, over long periods of geographic isolation. In contrast, adaptive traits, such as survival, height growth, and foliage color, exhibit clinal variation, a pattern that is likely to have developed from local adaptation to climatic conditions at the latitude of origin. In this section, we summarize results of these studies for each set of traits that have been examined.

Allozymes--AWC exhibits significant population differentiation, with an overall 'population structure' criterion Φ_{PT} = 0.12. Patterns of variation suggest three distinct geographic regions, which correspond with natural disjunctions in the species range: (1) Atlantic coast, (2) peninsular Florida, and (3) Gulf coast. Within the Gulf coast, three genetically homogenous subregions are apparent: (3a) central Florida panhandle, (3b) western Florida panhandle, and (3c) southern Mississippi (Mylecraine 2004, Mylecraine and others 2004). These patterns may have resulted from decreased gene flow and increased genetic drift, over long periods of isolation, associated with range disjunctions, suggesting the possibility of at least three refugial areas during Pleistocene glaciations. Among Atlantic coastal populations, there is a significant negative latitudinal relationship for both measures of genetic diversity (mean number of alleles per locus and proportion of polymorphic loci), consistent with a loss of rare alleles as populations spread northward from a southern refugium (Critchfield 1984).

Morphological variation--Several authors have suggested that AWC populations along the Gulf Coast are morphologically distinct, and have recognized them as a separate species (*Chamaecyparis henryae*, Li 1962) or varieties (*Chamaecyparis thyoides* var. *henryae*, Little 1966, Clewell and Ward 1987, Ward and Clewell 1989). Analysis of rangewide patterns of morphological variation strongly suggests separation of the species into two distinct groups, corresponding to the geographic delineation of two subspecific varieties by Clewell and Ward (1987, Ward and Clewell 1989). *Chamaecyparis thyoides* var. *henryae* is restricted to the western Florida panhandle and Alabama (figure 1a), and *C. t.* var. *thyoides* occurs throughout the rest of the species range. The varieties are distinguished by the presence or absence of resin glands on the facial leaves (figure 2a). Both varieties may have resin glands on the main axis (figure 2b), but *C. t.* var. *thyoides* individuals also have resin glands on all facial leaves (Figure 2a and 2b), whereas *C. t.* var. *henryae* individuals lack these facial glands (figure 2a). Despite some degree of overlap in seed cone characteristics, *C. t.* var. *henryae* typically has smaller cones, with a lower length/width ratio (figure 2c), five total unfused scales and three ovules per scale, whereas *C. t.* var. *thyoides* typically has slightly longer cones, a greater length/width ratio (figure 2d), and two (sometimes three) ovules per scale (Mylecraine 2004).

In addition to discrete varietal differences, AWC populations exhibit a wide range of morphological variation. For example, a latitudinal cline is apparent in foliage color, with northern populations (on average) exhibiting bluish-green foliage with a greater mean hue, lower mean value and lower mean chroma than southern populations having lighter green foliage (Mylecraine 2004). Several other conifers exhibit bluer or grayer foliage in drier or harsher environments (Wright 1976), which may be an adaptation for cold hardiness and/or decreased water loss. The occurrence of bluer foliage among both northern (Jull and others 1999, Mylecraine 2004) and high elevation (Dugan and Kuser 2003) AWC populations suggests that this trait may contribute to winter hardiness.

Chloroplast DNA variation--Sequence variation in two non-coding regions of chloroplast DNA suggests patterns of variation similar to allozymes and morphology. The geographic distribution of haplotypes (unique DNA sequences) of the *trn*L intron suggests a split between Atlantic and Gulf coastal populations, with four haplotypes restricted to Atlantic coastal populations and four different haplotypes restricted to Gulf coastal populations. The ninth and final haplotype was identified throughout both regions. Two haplotypes of the *trn*D-*trn*Y intergenic spacer region were found, which correspond completely with the distribution of the two varieties, based on morphology. Haplotype 2 was detected among all individuals of the western Florida panhandle and Alabama, coincident with the range of *Chamaecyparis thyoides* var. *henryae*; all other individuals contained haplotype 1 (Mylecraine 2004).

Provenance variation--In common garden plantings, AWC populations exhibit significant variation in survival, height growth and growth phenology (Haas and Kuser 1999, Dugan and Kuser 2003, Mylecraine and others 2005). In general, this variation is correlated with latitudinal climatic variation. Northern Atlantic coastal populations, planted in New Jersey and North Carolina, tend to exhibit increased winter hardiness, slower growth rates, and they complete a greater proportion of their total height growth early in the spring. By contrast, southern Atlantic populations exhibit slightly reduced winter hardiness in New Jersey, but have faster growth rates, and they complete a greater proportion of their growth later in the growing season. Florida and Gulf coastal populations outgrew more northern populations under ideal greenhouse conditions (Mylecraine 2004), but exhibited significantly reduced survival and growth in New Jersey and North Carolina (Mylecraine and others 2005). In addition to growth and survival traits, provenance variation has been identified in stratification requirements for seed germination (Jull and Blazich 2000), seedling temperature optima (Jull and others 1999), and possibly flowering phenology (Mylecraine 2004).

AWC occurs within a narrow range of elevations, from sea level to 457 m, with most stands occurring below 50 m (Laderman and others 1987). Elevation may also have a significant influence on adaptive variation. Individuals from the highest elevation stand at High Point, NJ (457 m) grew significantly less than other New Jersey sources in a central New Jersey planting (Haas and Kuser 1999). High elevation adaptation notwithstanding, climatic variation associated with latitude appears to be the dominant force influencing patterns of adaptive variation within this species.

DISCUSSION

Suggested Management Regions

Among AWC populations, different sets of traits exhibit varying geographic patterns, but several trends are recurrent among the different markers and traits that have been examined to date. In this section, we combine the available genetic information with ecological and geographic information to suggest three major management regions, and then further divide two of these regions into three subregions.

Region 1: Atlantic Coast

Atlantic coastal populations should be managed as a distinct region, based on patterns of allozyme, cpDNA and provenance variation. In this region, AWC occurs along the coast from southern Maine to Richmond County, Georgia. It typically forms dense monospecific stands (Korstian and Brush 1931), which may be even-aged or uneven-aged (Zimmermann and others 1999), but is often found in mixed stands with a variety of hardwood species (Mylecraine and Zimmermann 2000). AWC is largely confined to areas of organic peat overlying a sandy subsoil, often with a pH between 3.5 and 5.5 (Korstian and Brush 1931, Little 1950), but can also be found on poorly drained mineral soils (Korstian and Brush 1931, Mylecraine and Zimmermann 2000).

Clinal variation is apparent among Atlantic coastal populations, suggesting that populations that are geographically distant are more genetically distinct. For example, we see a relationship between geographic and genetic separation

(Mylecraine and others 2004). We also see clinal variation in provenance traits, including height growth and growth phenology (Mylecraine and others 2005). We have divided this region into three subregions, but the boundaries between regions are somewhat artificial, given the clinal pattern of variation in this region.

Region 1a: New England--New England populations (figure 1b) exhibit reduced growth rates, compared to other Atlantic populations, when planted in New Jersey and North Carolina. They also complete a greater proportion of their growth earlier in the spring and cease height growth earlier in the fall (Mylecraine and others 2005). On average, they have darker green or bluish foliage (Mylecraine 2004), which may be an adaptation for enduring harsher winters. AWC is often associated with glacial features, including glacial kettles or old lake beds (Laderman 1989). It is commonly found with red maple (*Acer rubrum*), blackgum (*Nyssa sylvatica*), white pine (*Pinus strobus*), eastern hemlock (*Tsuga canadensis*), and in some areas more boreal species such as black spruce (*Picea mariana*) red spruce (*Picea rubens*), and gray birch (*Betula populifolia*) (figure 3a, Lynn 1984, Golet and Lowry 1987, Laderman and others 1987, Stockwell 1999). AWC occurs in portions of central and southern Maine, reaching its northern limit at Appleton Bog, in Knox County, ME (figure 1b). It also occurs in five counties of southern New Hampshire, with a total of approximately 193 ha containing at least 25 percent AWC (Sperduto and Ritter 1994), as well as several counties of Rhode Island and Connecticut, and portions of New York. Prior to human development, AWC forests dominated much of Long Island; many of these stands have been drained and cleared for development, harvested, and lost due to lowered water tables associated with damming of streams. Few New York populations remain outside of Long Island; these include Sterling Forest State Park (Lynn 1984), and a few small remnant individuals or populations in Orange County (Karlin 1997). This region will be addressed in greater detail by Laderman (this volume).

Region 1b: Mid-Atlantic Coast--Mid-Atlantic populations (figure 1c) are characterized by intermediate growth rates and phenology patterns (Mylecraine and others 2005). In this region, AWC occurs in New Jersey, Delaware and Maryland (figure 1c). In New Jersey, it occurs mainly in the southern unglaciated portion of the state, with most stands in the New Jersey Pinelands. A few stands are found in the northern part of the state, including the highest elevation population (457 m) at High Point State Park, in Sussex County. Populations occur on both Delaware and Maryland portions of the Delmarva Peninsula, but represent only a small portion of the species' former range in this area (Dill and others 1987). In addition, a number of small, isolated populations occur on the western shore of Maryland (Sheridan and others 1999b). AWC commonly forms dense, monospecific stands (figure 3b) or occurs in mixed stands with red maple, blackgum, sweetbay magnolia (*Magnolia virginiana*) and pitch pine (*Pinus rigida*). Williams (this volume) will address this region in more detail.

Region 1c: Southern Atlantic Coast--In general, southern Atlantic populations (figure 1d) grow faster and exhibit a greater proportion of growth later in the season, in New Jersey and North Carolina plantations. In this region, AWC occurs from southeastern Virginia to Richmond County, Georgia. Historical records suggest a relatively continuous population in this area, but hydrologic disruption, intense logging, and alteration of the fire regime have greatly reduced the area occupied by the species. The original acreage in the Carolinas alone has been reduced by more than 90% (Frost 1987). AWC occurs in pure stands or mixed with red maple, blackgum, baldcypress (*Taxodium distichum*), sweetbay magnolia, loblolly pine (*Pinus taeda*), and redbay (*Persea borbonia*) (Laderman 1989).

Region 2: Peninsular Florida

AWC populations in the Florida peninsula (figure 1e) should be identified as a unique management unit, based on both genetic and ecological distinctiveness (Mylecraine and others 2004). Morphologically, they appear similar to remaining *Chamaecyparis thyoides* var. *thyoides* populations. One population from this region was included in provenance trials in New Jersey and North Carolina, and exhibited reduced survival in New Jersey and reduced growth in North Carolina (Mylecraine and others 2005), despite faster growth rates under ideal greenhouse conditions (Mylecraine 2004). Some early distribution maps have identified AWC throughout northern Florida and extending half-way down the eastern peninsula (Korstian and Brush 1931, James 1961). However, these maps were likely based on unsubstantiated reports (Ward 1963), and only two populations are currently known from peninsular Florida. Both are found along spring-fed streams that discharge ultimately into the St. Johns River. The southernmost population occurs along Juniper Creek and its tributary, Morman Branch, in Ocala National Forest, Marion County (Ward 1963, Clewell and Ward 1987). The second population is found along a portion of Deep Creek in Putnam County. Unlike the acidic streams generally associated with AWC in many other parts of the range (Little 1950), these streams are neutral to mildly alkaline (Collins and others 1964, Clewell and Ward 1987).

Associated species include red maple, cabbage palmetto (*Sabal palmetto*), sweetbay magnolia, swamp tupelo (*Nyssa biflora*), loblolly bay (*Gordonia lasianthus*), swampbay (*Persea palustris*), slash pine (*Pinus elliottii*), and three oak (*Quercus*) species (figure 3c, Ward and Clewell 1989).

Region 3: Gulf Coast

We have identified the Gulf coast as the third region (figure 1e), based on genetic evidence. There is also a large disjunction between Atlantic and Gulf coastal populations, with only a few populations in the sandhills region of western Georgia (Sheridan and others 1999a, Sheridan and Patrick 2003). Historical records indicate that this disjunction predates early exploitation in these areas (Frost 1987) and is a natural pattern of occurrence. Gulf coast populations form a distinct cluster based on allozymes (Mylecraine and others 2004), and exhibit a number of cpDNA haplotypes that are not found in Atlantic coastal populations (Mylecraine 2004). Little is known about provenance variation in this region, because none of these populations reached their full potential in New Jersey and North Carolina plantations (Mylecraine and others 2005). AWC populations along the Gulf coast have received little scientific study, and their distribution has not been well documented (Clewell and Ward 1987, Ward and Clewell 1989). AWC is found from Gadsden, Libery and Franklin counties in the central Florida panhandle west to southeastern Mississippi. The easternmost population is nearly 300 km from the peninsular Florida populations (Ward and Clewell 1989). Western Georgia populations are approximately 225 km to the north of these coastal populations, but are included in this region, because they are within the Gulf of Mexico watershed, and are found along streams that eventually flow into the Apalachicola River (Ward and Clewell 1989). In contrast to the dense, monospecific stands typical of many Atlantic coastal populations (Korstian and Brush 1931), AWC along the Gulf coast is found in mixed stands with pondcypress (*Taxodium distichum* var. *imbricàrium*), slash pine, and a number of hardwood species (figure 3e, Ward and Clewell 1989).

Within this region, we have identified three subregions (figure 1e), based on allozymes, cpDNA, and morphological variation, which correspond with three distinct distribution centers along the Gulf coast.

Region 3a: Central Florida panhandle--We separated the central Florida panhandle from the rest of the Gulf coast region, because we found a unique *trn*L haplotype (haplotype 7) in this region (Mylecraine 2004), and because this region is morphologically distinct from the western Florida panhandle *C. t.* var. *henryae* populations. This cluster of populations includes stands along Telogia Creek and other tributaries of the Ochlockonee River, in Gadsden and Liberty Counties; along the New River of Liberty and Franklin Counties; tributaries of the Apalachicola River, Liberty, Franklin, Gulf and Calhoun Counties; and streams directly entering the Gulf of Mexico at St. Vincent Sound and St. Joseph Bay, Gulf County. The scattered populations in several counties of western Georgia are included in this region, because they occur along streams that feed into the Apalachicola River, and are genetically similar to other populations of this region (Mylecraine and others 2004).

Region 3b: Western Florida panhandle--Populations along the western Florida panhandle and Alabama coast exhibit distinct morphological characteristics and a unique cpDNA haplotype. These *C. t.* var. *henryae* populations lack resin glands on the facial leaves, and generally have smaller cones than *C. t.* var. *thyoides* populations. In this region, AWC occurs from just east of the Choctawatchee Bay, southern Walton County, FL, west to Mobile County, AL. Some of the largest living AWC individuals occur in this area (figure 3d, Ward and Clewell 1989).

Region 3c: Mississippi Coast--The division between *C. t.* var. *henryae* populations and *C. t.* var. *thyoides* populations occurs near the Alabama/Mississippi state line. Populations in Alabama, along streams draining into Mobile Bay have characteristics of *C. t.* var. *henryae*, while those in Mississippi, along streams draining into the Gulf further west have characteristics of *C. t.* var. *thyoides* (Mylecraine 2004). McCoy and Keeland (2006, this volume) have identified several locations of *C. t.* var. *thyoides* individuals or populations in coastal Mississippi, with the westernmost known stand along Juniper Creek, in Pearl River County.

Management Recommendations and Research Needs

We have identified broad geographic regions based on current information on geographic patterns of genetic variation. We suggest the following management guidelines for these regions:

1. Representative populations from each region and subregion should be targeted for long-term protection and management, to maximize the amount of genetic variation present in future generations.

2. Propagules for restoration and regeneration should be obtained within the region and/or subregion of interest to maintain the natural genetic structure among regions. In some cases, propagules may be moved between subregions, but this should be done with appropriate caution. For example, trees from Region 3c (southern Atlantic coast) have been shown to survive and outgrow native stock in New Jersey plantations, but there is increased risk of winter damage, and long-term data on the survival and fitness of these individuals is currently lacking.

3. Propagules for restoration and regeneration can likely be moved northward within regions and subregions without negative consequences. However, data on microgeographic adaptation (i.e. for different soil types or water regimes) is minimal (but see Summerville and others 1999) and should be explored in future studies.

4. In general, propagules should not be moved southward for regeneration and restoration, even within a region or subregion. Populations originating from the north of a planting site will probably grow slower than native and more southerly sources, probably due to phenological differences that do not allow them to take advantage of the full growing season in more southern locations.

The research summarized here provides baseline genetic information for AWC managers, based on genetic markers, morphology and adaptive traits, but there are a number of research questions and needs that remain. For example, provenance plantings should be expanded to include sites in New England and along the Gulf coast. Little is known about provenance variation among Florida and Gulf coast populations, but we suspect that such differences exist because of the extent of genetic and morphological variation in this region. We also know little about adaptation to microgeographic habitat variation within the broad geographic regions identified here. Summerville and others (1999) examined ecotypic variation among North Carolina populations and found only slight differences between populations on mineral and organic soils, but this is a matter that warrants further study. Variation among individual families may also become important for selecting desirable traits. There is evidence of family-to-family variation within AWC populations (Summerville and others 1999), and the matter needs further exploration.

ACKNOWLEDGEMENTS

We would like to thank numerous individuals and organizations for assistance in locating and sampling AWC populations throughout the species' range. Several individuals also helped in the planning, establishment and maintenance of provenance plantations, and provided valuable assistance in the laboratory.

LITERATURE CITED

Clewell, A.F.; Ward, D.B. 1987. White cedar in Florida and along the northern Gulf Coast. In: Laderman, A.D., ed. Atlantic white cedar wetlands. Boulder, CO: Westview Press: 69-82.

Collins, E.A.; Monk, C.D.; Spielman, R.H. 1964. White-cedar stands in northern Florida. Quarterly Journal of the Florida Academy of Sciences. 27: 107-110.

Critchfield, W. B. 1984. Impact of the Pleistocene on the genetic structure of North American conifers. In: Lanner, R. M., ed. Proceedings of the 8th North American Forest Biology Workshop. Logan, UT: Utah State University: 70-118.

Dill, N.H.; Tucker, A.O.; Seyfried, N.E.; Naczi, R.F.C. 1987. Atlantic white cedar on the Delmarva Peninsula. In: Laderman, A.D., ed. Atlantic white cedar wetlands. Boulder, CO: Westview Press: 41-55.

Dugan, C.P.; Kuser, J.E. 2003. Provenance variation in Atlantic white-cedar (*Chamaecyparis thyoides*) planted in Jackson, New Jersey. The Bulletin of the New Jersey Academy of Science. 48: 7-11.

Eckert, R.T. 1998. Population genetic analysis of Chamaecyparis thyoides in New Hampshire and Maine, USA. In: Laderman, A.D., ed. Coastally Restricted Forests. New York, NY: Oxford University Press: 171-184.

Frost, C.C. 1987. Historical overview of Atlantic white-cedar in the Carolinas. In: Laderman, A.D., ed. Atlantic white cedar wetlands. Boulder, CO: Westview Press: 257-264.

Golet, F.C.; Lowry, D.J. 1987. Water regimes and tree growth in Rhode Island Atlantic white cedar swamps. In: Laderman, A.D., ed. Atlantic white cedar wetlands. Boulder, CO: Westview Press: 91-110.

Haas, M.J.; Kuser, J.E. 1999. Effects of propagule type, geographic origin, and fertilization on first-year performance of Atlantic white-cedar (*Chamaecyparis thyoides*) in New Jersey. In: Shear, T.H.; Summerville, K.O, eds. Proceedings of the Atlantic white-cedar: ecology and management symposium. Gen. Tech. Rep. SRS-27. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station: 22-26.

James, C.W. 1961. Endemism in Florida. Brittonia. 13: 225-244.

Jull, L.G.; Blazich, F.A. 2000. Seed germination of selected provenances of Atlantic white-cedar as influenced by stratification, temperature, and light. HortScience. 35: 132-135.

Jull, L.G.; Ranney, T.G.; Blazich, F.A. 1999. Heat tolerance of selected provenances of Atlantic white-cedar. Journal of the American Society for Horticultural Science. 124: 492-497.

Karlin, E.F. 1997. The Drowned Lands' last stand: an inland Atlantic white cedar peat swamp in Orange County, New York. Journal of the Torrey Botanical Society. 124: 89-97.

Korstian, C.F.; Brush, W.D. 1931. Southern white cedar. Tech. Bull. No. 251. Washington, DC: U.S. Department of Agriculture, Forest Service. 76pp.

Kuser, J.E.; Zimmermann, G.L. 1995. Restoring Atlantic white-cedar swamps: techniques for propagation and establishment. Tree Planters' Notes. 46: 78-85.

Kuser, J.E.; Meagher, T.R.; Sheely, D.L.; White, A. 1997. Allozyme frequencies in New Jersey and North Carolina populations of Atlantic white-cedar, Chamaecyparis thyoides (Cupressaceae). American Journal of Botany. 84: 1536-1541.

Laderman, A.D. 1989. The ecology of Atlantic white-cedar wetlands: a community profile. Biological Report 85(7.21). Washington, DC: U.S. Department of Interior, Fish and Wildlife Service. 113pp.

Laderman, A.D.; Golet, F.C.; Sorrie, B.A.; Woolsey, H.L. 1987. Atlantic white cedar in the glaciated northeast. In: Laderman, A.D., ed. Atlantic white cedar wetlands. Boulder, CO: Westview Press: 19-34.

Ledig, F.T. 1986. Conservation strategies for forest gene resources. Forest Ecology and Management. 14: 77-90.

Lesica, P.; Allendorf, F.W. 1999. Ecological genetics and the restoration of plant communities: mix or match? Restoration Ecology. 7: 42-50.

Li, H.-L. 1962. A new species of *Chamaecyparis*. Morris Arboretum Bulletin. 13: 43-46.

Libby, W.J.; Critchfield, W.B. 1987. Patterns of genetic architecture. Annales Forestales. 13: 77-92.

Little, E.L. 1966. Varietal transfers in *Cupressus* and *Chamaecyparis*. Madroño. 18: 161-192.

Little, S. 1950. Ecology and silviculture of white cedar and associated hardwoods in southern New Jersey. Yale University School of Forestry Bulletin. 56: 1-103.

Lynn, L.M. 1984. The vegetation of Little Cedar Bog, southeastern New York. Bulletin of the Torrey Botanical Club. 111: 90-95.

McCoy, J.W.; Keeland, B.D. 2006. Locations of Atlantic white cedar in the coastal zone of Mississippi. In: Burke, M.K.; Sheridan, P., eds. Proceedings of the Atlantic white cedar: ecology, restoration, and management: Proceedings of the Arlington Echo Symposium. Gen. Tech. Report SRS-91. Millersville, Maryland: U.S. Department of Agriculture, Forest Service, Southern Research Station: 44-53.

McCoy, J.W.; Keeland, B.D.; Allen, J.A. 2003. Survival and growth of Atlantic white cedar plantings in Louisiana and Mississippi. In: Atkinson, R.B., Belcher, R.T., Brown, D.A., Perry, J.E., eds. Proceedings of the Atlantic white cedar restoration ecology and management symposium. Newport News, VA: Christopher Newport University: 263-270.

Millar, C.I.; Libby, W.J. 1989. Disneyland or native ecosystem: genetics and the restorationist. Restoration and Management Notes. 7: 18-24.

Montalvo, A.M.; Williams, S.L.; Rice, K.J.; Buchmann, S.L.; Cory, C.; Handel, S.N.; Nabham, G.P.; Primack, R.; Robichaux, R.H. 1997. Restoration biology: a population biology perspective. Restoration Ecology. 5: 277-290.

Mylecraine, K.A. 2004. Geographic variation in Atlantic white-cedar, *Chamaecyparis thyoides*: Implications for management, restoration and biogeography. New Brunswick, NJ: Rutgers University. 349p. Ph.D. dissertation.

Mylecraine, K.A.; Zimmermann, G.L. 2000. Atlantic white-cedar: Ecology and Best Management Practices Manual. Trenton, NJ: New Jersey Department of Environmental Protection, New Jersey Forest Service. 84 p.

Mylecraine, K.A.; Kuser, J.E.; Smouse, P.E.; Zimmermann, G.L. 2004. Geographic allozyme variation in Atlantic white-cedar, *Chamaecyparis thyoides* (Cupressaceae). Canadian Journal of Forest Research 34: 2443-2454.

Mylecraine, K.A.; Kuser, J.E.; Zimmermann, G.L.; Smouse, P.E. 2005. Rangewide provenance variation in Atlantic white-cedar (*Chamaecyparis thyoides*): Early survival and growth in New Jersey and North Carolina plantations. Forest Ecology and Management. 216: 91-104.

Sheridan, P.; Orzell, S.; Bridges, E. 1999a. Some noteworthy vascular plant records from Atlantic white-cedar, *Chamaecyparis thyoides* (L.) B.S.P., habitats of western Georgia. In: Shear, T.H.; Summerville, K.O, eds. Proceedings of the Atlantic white-cedar: ecology and management symposium. Gen. Tech. Rep. SRS-27. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station: 49-60.

Sheridan, P.; Underwood, K.; Muller, R.; Broersma-Cole, J.; Cole, R.; Kibby, J.R. 1999b. A census of Atlantic white-cedar, *Chamaecyparis thyoides* (L.) B.S.P., on the western shore of Maryland. In: Shear, T.H.; Summerville, K.O, eds. Proceedings of the Atlantic white-cedar: ecology and management symposium. Gen. Tech. Rep. SRS-27. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station: 61-65.

Sheridan, P.M.; Patrick, T.S. 2003. A rare plant survey of Atlantic white cedar habitats of western Georgia. In: Atkinson, R.B., Belcher, R.T., Brown, D.A., Perry, J.E., eds. Proceedings of the Atlantic white cedar restoration ecology and management symposium. Newport News, VA: Christopher Newport University: 101-112.

Smith, S.B. 2003. Atlantic white cedar ecosystem restoration: Dare County Bombing Range, North Carolina. In: Atkinson, R.B., Belcher, R.T., Brown, D.A., Perry, J.E., eds. Proceedings of the Atlantic white cedar restoration ecology and management symposium. Newport News, VA: Christopher Newport University: 295-302.

Sperduto, D.D.; Ritter, N. 1994. Atlantic white cedar wetlands of New Hampshire. Boston, MA: U.S. Environmental Protection Agency, Wetlands Protection Section - Region 1.

Stockwell, K.D. 1999. Structure and history of the Atlantic white-cedar stands at Appleton Bog, Knox County, Maine, USA. Natural Areas Journal. 19: 47-56.

Summerville, K.O.; Gardner, W.E.; Bardon, R.E.; Myers, R.J. 1999. Ecotypic variation in Atlantic white-cedar in eastern North Carolina. In: Haywood, J.D., ed. Proceedings of the Tenth biennial southern silvicultural reseach conference. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station: 185-189.

Ward, D.B. 1963. Southeastern limit of *Chamaecyparis thyoides*. Rhodora. 65: 359-363.

Ward, D.B.; Clewell, A.F. 1989. Atlantic white cedar (*Chamaecyparis thyoides*) in the southern states. Florida Scientist. 52: 8-47.

Wheeler, N.C.; Guries, R.P. 1982. Population structure, genic diversity, and morphological variation in *Pinus contorta* Dougl. Canadian Journal of Forest Research. 12: 595-606.

Wicker, M.; Hinesley, E. 1998. Restoring an Atlantic white cedar bog. Endangered Species Bulletin. 23: 18-19.

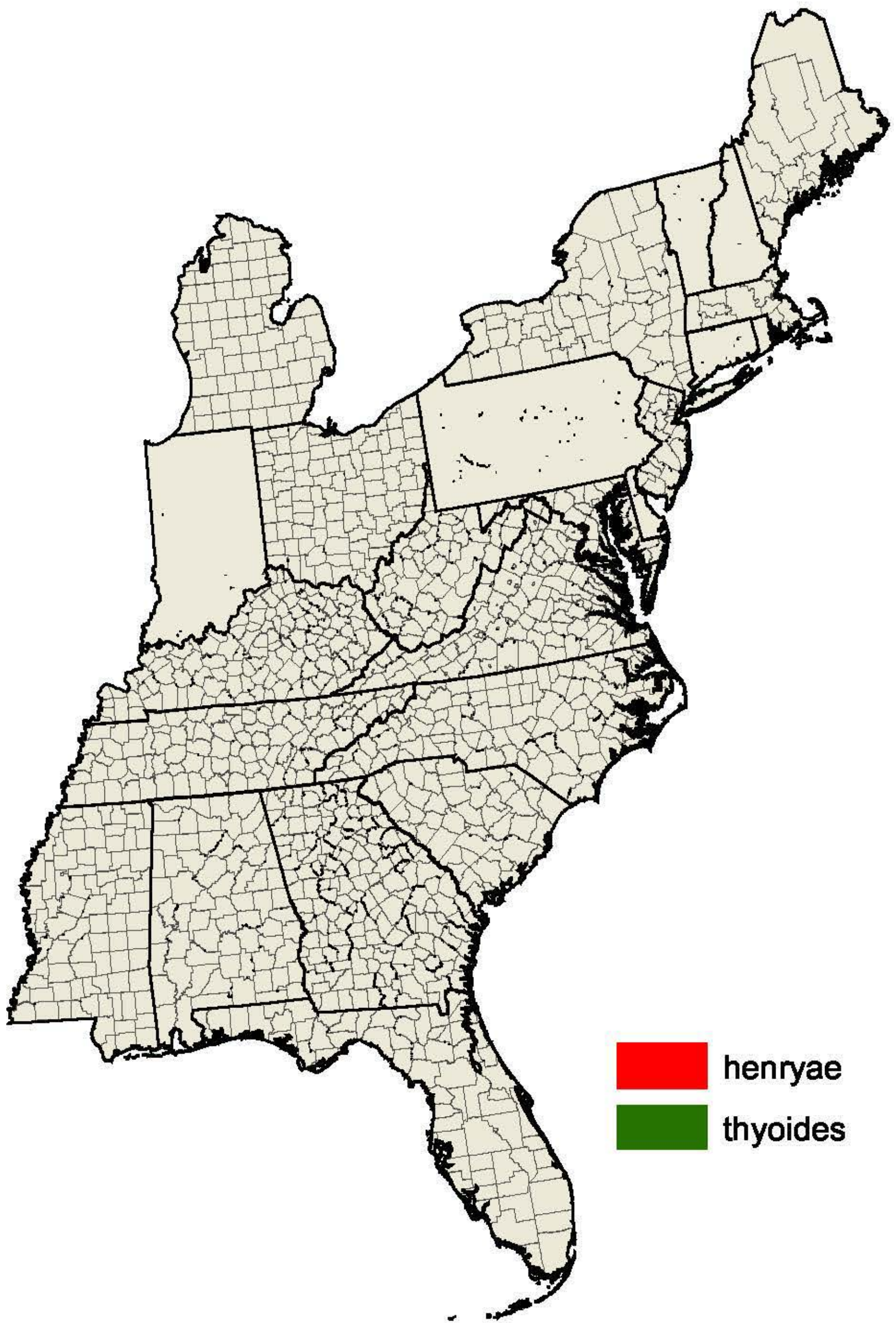
Wright, J.W. 1976. Introduction to Forest Genetics. New York, NY: Academic Press, Inc.

Zimmermann, G.L.; Mylecraine, K.A. 2004. Long-term data on effectiveness of treatments to regenerate Atlantic white-cedar on small sites (New Jersey). Ecological Restoration. 22: 47-48.

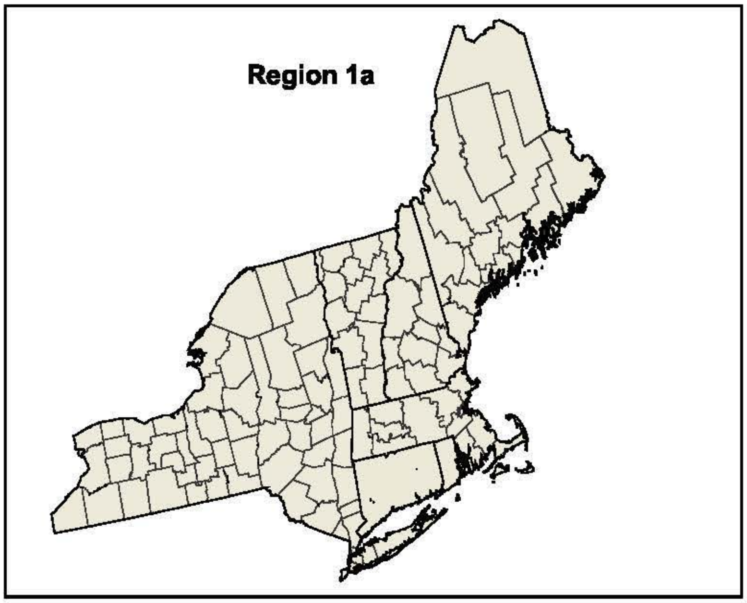
Zimmermann, G.L.; Mueller, R.; Brown, J.; Peer, K.; Shapiro, S.; Mylecraine, K.A.; Barber, C.; Cherpika, J.; Venafro, T. 1999. The Penn Swamp experiments: an overview. In: Shear, T.H.; Summerville, K.O, eds. Proceedings of the Atlantic white-cedar: ecology and management symposium. Gen. Tech. Rep. SRS-27. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station: 45-48.

Figure 1--Range of Atlantic white-cedar, *Chamaecyparis thyoides*, including all counties in which the species has been identified, based on published literature, herbarium specimens, and field observations. (a) Rangewide distribution of *C. t.* var. *thyoides* and *C. t.* var. *henryae*; (b) distribution in Region 1a, New England; (c) Distribution in Region 1b, mid-Atlantic coast; (d) distribution in Region 1c, southern Atlantic coast; and (e) distribution in Region 2, Florida peninsula, and Region 3, Gulf coast.

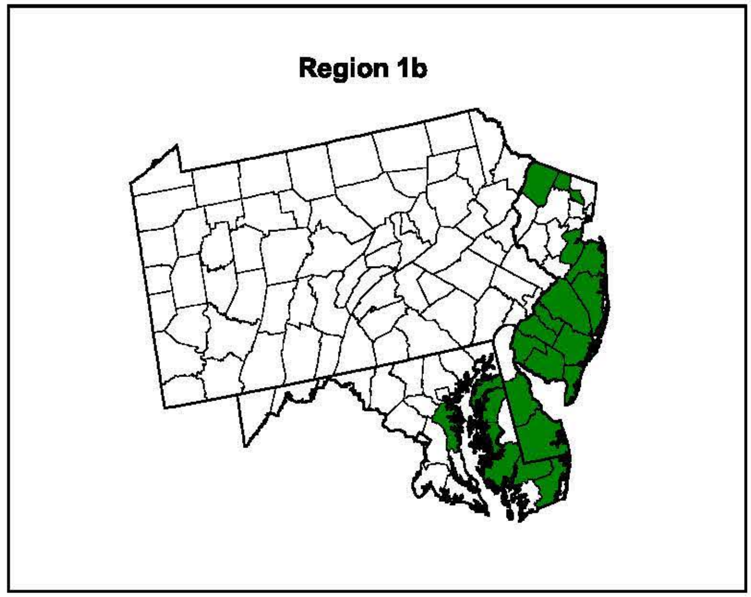
a.



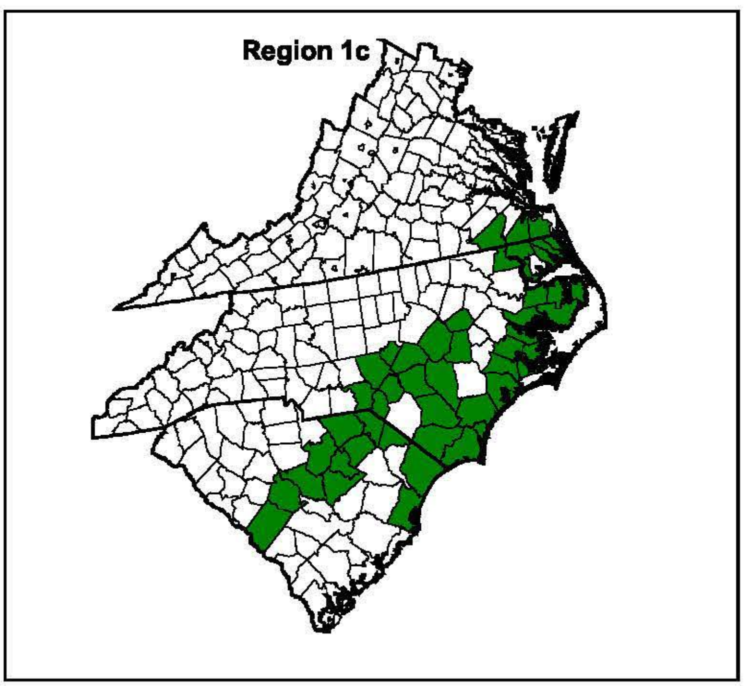
b



c.



d.



e.

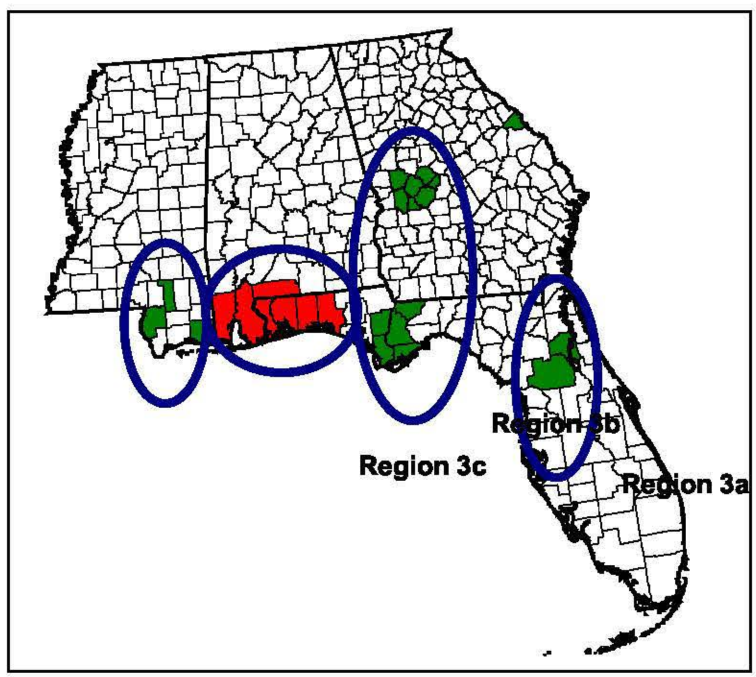


Figure 2--Morphological characteristics of *C. t.* var. *thyoides* and *C. t.* var. *henryae.* (a) Foliage characters; (b) foliage resin glands on *C. t.* var. *thyoides*: individuals of both varieties may have resin glands on the main axis, but only *C. t.* var. *thyoides* individuals have resin glands on all facial leaves; (c) typical seed cones of *C. t.* var. *thyoides*; and (d) typical seed cones of *C. t.* var. *henryae.*

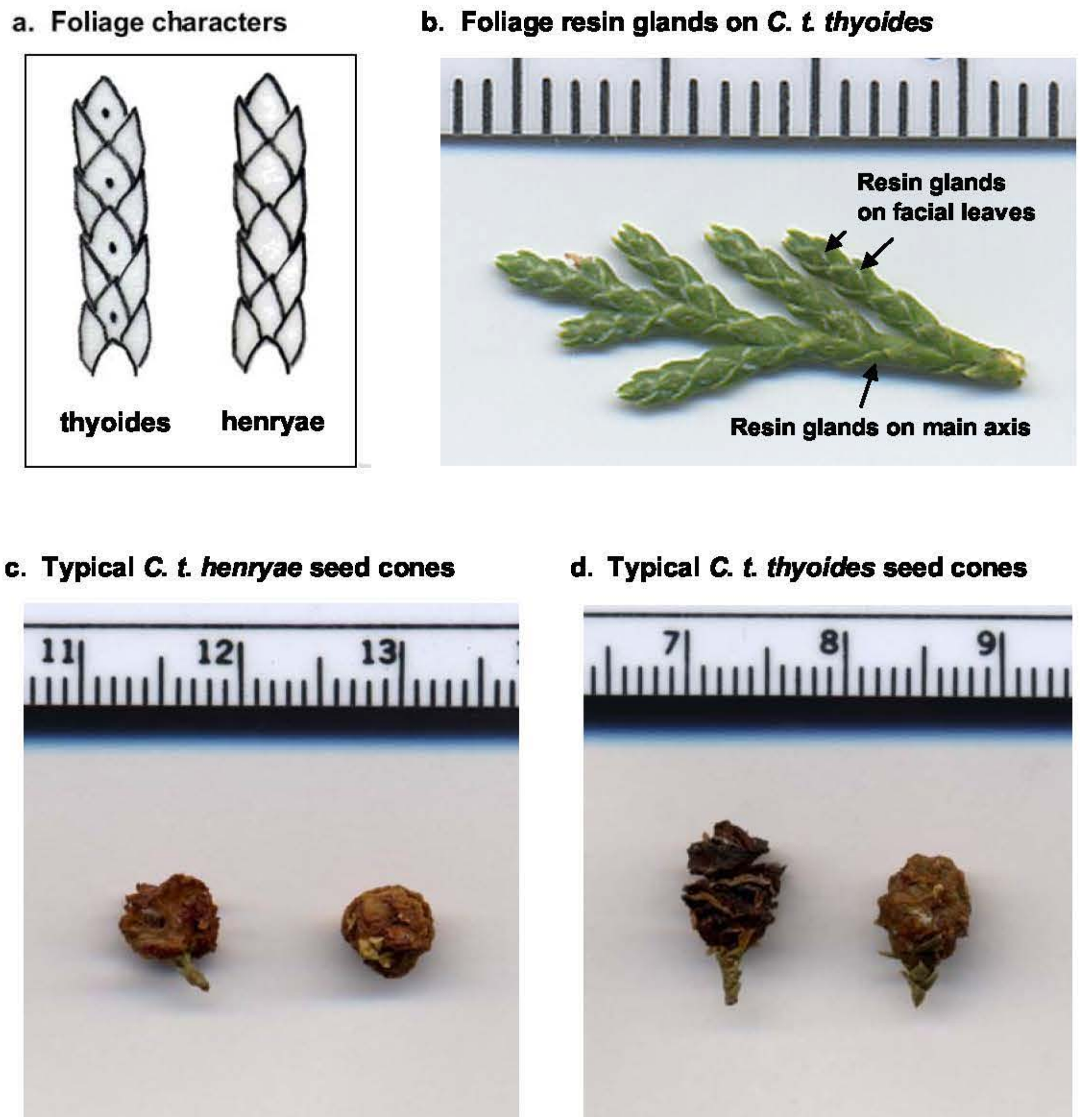


Figure 3 –Variation in Atlantic white-cedar habitats: (a) Saco Heath, Maine (Region 1b): AWC is found with a number of ericaceous shrubs and boreal species, such as black spruce; (b) dense, monospecific stand of AWC typical of many mid-Atlantic (Region 1b) populations; (c) Ocala National Forest, Florida (Region 2): AWC is found along clear, sand-bottomed, neutral to slightly alkaline streams, with a variety of southern species, including cabbage palmetto; (d) example of the large *C. t.* var. ***henryae*** individuals occurring in the western Florida panhandle (Region 3b); (e) typical stand of *C. t.* var. ***henryae***, occurring mixed with a number of species along streams that ultimately drain into the Gulf of Mexico.

a.

b.

c.

d.

e.