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Vegetation and disturbance history of a rare dwarf pitch pine community in western New England, USA

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Abstract

Aim This study documents the vegetation history and age-structure of a rare, ridgetop dwarf pine–oak community and compares the dynamics of this unusual vegetation with similar dwarf pine communities found elsewhere in the north-eastern United States (US).

Location The study area is located on the summit of Mt Everett in the Taconic Mountains of south-western Berkshire County, Massachusetts, USA (42°06′N 73°26′W).

Methods Vegetation composition, tree age-structure, physical site characteristics, and evidence of fire and other disturbances were determined for twelve 15 × 15 m plots in dwarf pine–oak vegetation and two plots in oak forests on the summit. Age-structure analyses, tree-ring patterns, and historical records of human and natural disturbance were used to investigate the long-term history and dynamics of the summit vegetation.

Results The summit of Mt Everett has been dominated by dwarf pines (1–3 m tall) and ericaceous shrubs similar to the modern vegetation throughout the historical period; there is no evidence that tall-stature forests occurred on the site at any point in the past few centuries. The summit supports uneven-aged stands; pitch pine (*Pinus rigida*) recruitment began in the 1830s and occurred in every decade since the 1860s. Average pitch pine age is seventy-eight with a range of 12–170 years. Red oak (*Quercus rubra*) and red maple (*Acer rubrum*) increased in importance in the twentieth century, with most stems establishing from 1940 to 1980. Pitch pine radial growth rates averaged <0.5 mm year^{-1} while red oak and red maple averaged 1.0 and 0.8 mm year^{-1}, respectively. In some areas, hardwoods have overtopped pitch pines, apparently resulting in pitch pine mortality. Whereas most dwarf pitch pine communities occur on sites that burn frequently and have a high degree of cone serotiny, we found no evidence of recent fires or cone serotiny. Small amounts of macroscopic charcoal that we documented may have resulted from fires in the pre-European or early historical periods.

Conclusions Harsh edaphic conditions and chronic low-level disturbances on the summit, including frequent winter storms, have apparently contributed to the establishment, long-term persistence, and slow radial growth of dwarf pitch pines on Mt Everett. The ability of dwarf pines to persist on a site in the absence of frequent fire is highly unusual among North-eastern barrens and has not been well-incorporated into previous conceptual ecological models of these communities. Our results suggest that even among North-eastern barrens, the summit of Mt Everett is characterized by highly unusual vegetation and dynamics. The site has long been recognized as regionally significant and should be afforded the strictest conservation protection. With no evident history of human disturbance or recent fire, there is no apparent need for immediate active management of the site.

Keywords
Disturbance, dwarf pitch pine, fire, land-use history, pine barrens, ridgetop.

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INTRODUCTION

Pitch pine (*Pinus rigida*) 'barrens' occur throughout the north-eastern United States (US) on xeric outwash and dune deposits, and on exposed ridgetops of acidic bedrock. Pine barrens are considered to be among the highest priorities for conservation in the North-east because they are uncommon, support numerous rare species, and are highly threatened by development and by altered disturbance regimes (Barbour *et al*., 1998). Although numerous studies have investigated the disturbance history and vegetation dynamics of pitch pine-scrub oak and related communities on sand plains throughout the region (e.g. Little, 1979; Olsvig, 1980; Patterson *et al*., 1984; Dunwiddie & Adams, 1995; Motzkin *et al*., 1996, 1999; Foster & Motzkin, 1999; Copenheaver *et al*., 2000; Eberhardt *et al*., 2003), the distribution, composition, and dynamics of ridgetop communities have been poorly documented. It is probable, however, that the history and dynamics of ridgetop communities differ substantially from those that occur on sand plains. For example, modern vegetation composition and stand dynamics on most outwash sites are strongly influenced by fire history and a wide range of historical land-use activities, including forest cutting and extensive clearing for agriculture (Seischab & Bernard, 1991; Motzkin *et al*., 1996, 1999; Copenheaver *et al*., 2000; Eberhardt *et al*., 2003; Parshall *et al*., 2003). In contrast, disturbance regimes on rocky ridgetops are likely to be characterized by relatively little historical clearing for agriculture, differing fuel and fire characteristics, and perhaps increased importance of damage from ice or other storms (Abrams & Orwig, 1995; Bernard & Seischab, 1995; Batcher *et al*., 1997; Orwig *et al*., 2001). In addition, ridgetop sites frequently have a unique history of disturbance associated with recreational and other human uses, including clearing of vegetation to improve views and construction of trails, roads, and fire and communication towers (Orwig *et al*., 2001). Thus, despite compositional similarities, it is unlikely that ecological models and conservation approaches developed for sand plain ecosystems are directly applicable to ridgetop communities.

We report here on our investigation of the age structure and dynamics of the pitch pine-oak communities on the summit of Mt Everett in the town of Mt Washington, Massachusetts. The site has long been recognized as supporting unusual 'dwarf' pitch pines which are rare throughout the eastern US, occurring primarily on sites where fires have been frequent such as the New Jersey and Long Island pine barrens and on scattered rocky ridgetops, including portions of the Shawangunk Ridge in New York, Panther Knob in West Virginia, and several summits of the Taconic Range (Fig. 1). Unlike krummholz vegetation, which is widespread in montane systems, the occurrence of 'dwarf' or 'pygmy' forests at elevations that are substantially below regional treeline is extremely rare across North America (Westman, 1975; Reich & Hinckley, 1980). Previous historical investigations of Mt Everett determined that while there is little documentary evidence of past fires, timber removal, or other clearing of vegetation on the summit,

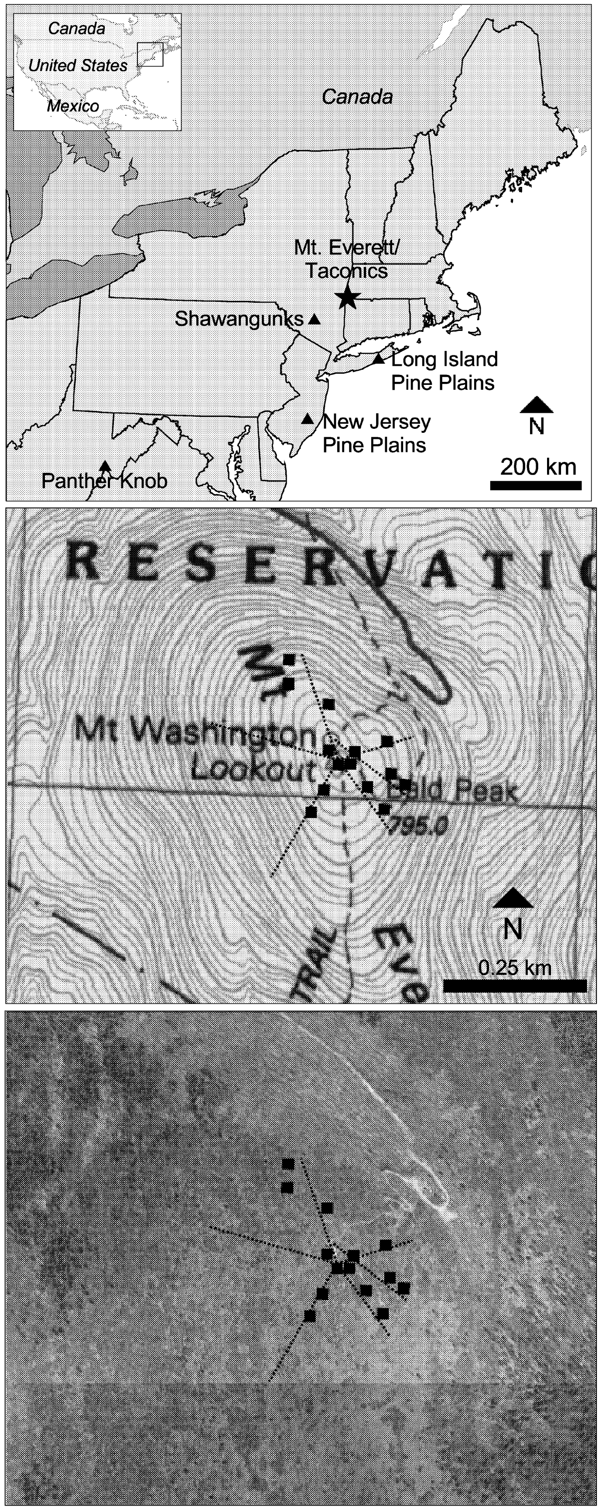

Figure 1 Study area, transect and plot locations on Mt Everett in south-western Massachusetts. Dwarf pitch pine communities elsewhere in the eastern US are indicated in the top panel. The topographic map (middle) has 3 m contour intervals and the aerial photo (bottom) is from 1997.

dwarf trees similar to the modern vegetation have long-dominated the site (Tillinghast, 1999). We selected this site for investigation in part because it provided the opportunity to compare the historical record with field evidence of disturbance, and in order to evaluate the age structure and dynamics of a ridgetop pine barren on a site where fire and land-use history may have had minimal importance. Specific objectives for the current study include: (1) to document the vegetation composition and age structure of the summit of Mt Everett, with particular emphasis on areas dominated by dwarf pitch pines, (2) to evaluate field or historical evidence of fire, cutting, or other disturbances on the summit, (3) to record observations on the growth form of the dwarf pitch pines, (4) to provide a perspective on the regional significance of the ridgetop dwarf pine barrens community that may aid in conservation planning.

STUDY SITE

Mt Everett is located in the town of Mt Washington, in south-western Berkshire County, Massachusetts (42°06′N 73°26′W), within the Taconic Mountains ecoregion (Griffith *et al.*, 1994; Fig. 1). The summit is located in the centre of the 445-ha Mt Everett State Reservation, managed by the Massachusetts Department of Environmental Management, at an elevation of 793 m a.s.l. The bedrock of Mt Everett and nearby portions of the Taconic Range is comprised of thrust sheets of phyllitic bedrock (Zen, 1983). Soils on the summit and upper slopes are very stony glacial tills of the Taconic–Macomber association, derived mainly from phyllite, slate and shale (Scanu, 1988). Soils are shallow, somewhat excessively drained gravelly loams, and bedrock outcrops are common. The regional vegetation is northern hardwoods, hemlock, and white pine (Westveld *et al.*, 1956).

Berkshire County has a continental climate with mean winter temperatures of −4.4 °C, mean summer temperatures of 18.9 °C, and mean annual precipitation of 109 cm, with *c.* 180 cm of snow (Scanu, 1988). Because of the high elevation of Mt Everett relative to the nearby region, mean temperatures are likely to be several degrees cooler than the surrounding lowlands, and snowfall amounts are likely to be much higher. Although no weather data are available from Mt Everett, numerous anecdotal accounts indicate that the summit is subject to more frequent ice storms than the surrounding lowlands (Leverett, 2000).

METHODS

Vegetation and age structure

Vegetation on the summit was sampled during the months of July–November, 2000 in a total of fourteen, 15 × 15 m plots (Fig. 1); nine plots were located along transects previously established for mycological studies by R. Van de Poll, and five additional plots were established in the north-western (two plots) and south-eastern (three plots) portions of the summit in areas not covered by the transects. Two of the fourteen plots only supported hardwood species.

At each plot, the basal diameter of all live and dead pitch pines >5 cm basal diameter, and the diameter-at-breast-height (d.b.h.: 1.37 m) of all other trees (>5 cm d.b.h) were measured using calipers, with the average of two measurements recorded for asymmetrical stems. The number of saplings (pitch pines 2.0–4.9 cm basal diameter and other trees <5 cm d.b.h) were tallied within the entire 15 × 15 m plot and seedlings of each species (pitch pines <2 cm basal diameter and other trees <1.37 m height) were counted within a 5 × 5-m subplot in the south-western portion of each plot.

In each plot, the per cent cover of each herb, shrub and overstory species was estimated in the following cover/abundance classes: 1 ≤ 1%; 2 = 1–2%; 3 = 3–5%; 4 = 6–15%; 5 = 16–25%; 6 = 26–50%; 7 = 51–75%; 8 ≥ 75%. A metal probe was used to determine the depth to bedrock in five random locations in the plot and slope, aspect and percent cover of exposed bedrock were estimated. As part of extensive reconnaissance, observations of tree growth-form and evidence of disturbance were recorded in each plot as well as across the summit. Average tree height per plot was estimated, and the heights of several of the tallest trees in each plot were recorded.

In order to determine the tree age-structure across the summit, increment cores were extracted from a minimum of eight stems per plot, representing the range of species and stem sizes characteristic of each plot. Increment cores also were extracted in some instances from nearby trees outside the sample plots. Cores were dried, mounted, and sanded using very fine sandpaper (600 grit) prior to ring counts with dissecting microscopes. The total age of stems was estimated for cores that did not include the pith. Despite great effort in preparing the cores, the extremely slow growth of many of the trees, coupled with the potential for false or missing rings, indicate that our estimates of tree ages are subject to several sources of potential error (Hager, 1995). However, in most cases we believe that they are accurate within several years.

Ring widths were measured to the nearest 0.01 mm with a Velmex (East Bloomfield, NY, USA) measuring system. Cores were examined to identify periods of suppression and release based on criteria established by Lorimer & Frelich (1989), who defined a 'major sustained release' as an average growth increase ≥100% lasting at least 15 years relative to the previous 15 years and a 'moderate temporary release' as an average growth increase ≥50% lasting from 10 to 15 years relative to the previous 10–15 years. In addition, 'abrupt growth decreases' of ≥50% sustained for at least ten consecutive years relative to the previous 10 years were tallied to indicate periods of canopy damage. These criteria, coupled with tree recruitment dates (age-cohorts), were used to differentiate disturbance events from short-lived responses attributed to climatic factors (Lorimer & Frelich, 1989; Nowacki & Abrams, 1997).

The history of Mt Everett

In order to evaluate the occurrence of fires on the summit, we searched each plot for fire scars, stem charring, and soil charcoal. Mineral soil grab samples were taken from 10 to 15 random locations within each plot and returned to the laboratory where they were sieved (5 mm mesh size) to determine the presence of macroscopic charcoal.

Historical maps and aerial photos were use to determine the disturbance and vegetation history of the summit. In addition, we relied heavily on Tillinghast's (1999) compilation of historical references to Mt Everett.

RESULTS

Vegetation and site characteristics

The summit of Mt Everett is dominated by pitch pine (*P. rigida*), which comprises more than 50% of the total tree density and basal area (Table 1). Red oak (*Quercus rubra*) represents *c*. 30% of the total relative importance value, whereas red maple (*Acer rubrum*) and birch (*Betula*) species contribute an additional 12%. Despite high stem densities of approximately 1500 ha^{-1}, total basal area (13.6 m^2 ha^{-1}) is quite low.

Pitch pine varies greatly in height and appearance, ranging from prostrate mats only 0.3 m tall (see Tree Growth Forms section) to upright, single stem trees 3 m tall. The average pitch pine height is 1.6 m, while the average height of the tallest pitch pine in each plot is 2.4 m. In contrast, the tallest hardwoods in each plot vary from 3.6 to 5.6 m with a few red oak and red maple individuals exceeding 7.5 m in height. Over 60% of all stems in this short-statured forest are <10 cm d.b.h and only a few red oak and pitch pine are larger than 20 cm in diameter (Fig. 2). Dead overstory stems occur in every plot, with the majority (85%) consisting of pitch pine <10 cm in diameter (Fig. 2).

Sapling densities are low, with only red maple, red oak and grey birch (*Betula populifolia*) exceeding 50 stems ha^{-1} (Table 2). The seedling layer is dominated by red oak with lesser amounts of red maple and mountain ash (*Sorbus americana*), which were found predominantly in the two hardwood plots. Low densities of pitch pine seedlings and saplings occur across the summit.

A prominent shrub layer occurs across the summit, consisting of dense patches of low bush blueberry (*Vaccinium angustifolium*), huckleberry (*Gaylussacia baccata*), chokeberry (*Aronia* spp.) and scrub oak (*Q. ilicifolia*). Common herbaceous species include hairgrass (*Deschampsia flexuosa*), wild sarsaparilla (*Aralia nudicaulis*), Canada mayflower (*Maianthemum canadense*), and starflower (*Trientalis borealis*; Table 3). Evidence of deer browse is common across the summit, especially on low shrubs and small hardwoods. The amount of exposed rock is variable among plots, averaging 16% and ranging from 2 to almost 50%. Soils are consistently shallow, averaging only 14.1 cm. Slopes average 11% and vary from flat to 24%.

Age-structure

The summit supports uneven-aged stands with pitch pine recruitment that began in the 1830s and occurred in every decade since the 1860s (Fig. 3). Pine recruitment was highest from 1910 to 1930 and lowest from 1950 to 1970. Average pitch pine age is 78 with a range of 12–170 years. Red oak recruitment began in the 1860s, increased in the early 1900s and then remained consistent from 1940 to 1980. Average red oak age is 56 years. Red maple establishment occurred sporadically at low densities from 1840 to the present and most stems became established between 1940 and 1980. Only six of a total of 119 trees cored were greater than 130 years old.

Tree ring dynamics

Tree diameter was not a reliable predictor of age, as red oak and pitch pine trees with similar diameters differed in age by more than 70–100 years (Fig. 4). Pitch pine growth rates vary substantially, with some individuals averaging as little as 0.08–0.2 mm $year^{-1}$ radial growth for periods of up to

Table 1 Overstory vegetation composition of live and dead stems on the summit of Mt Everett, south-western Massachusetts

Species	Density (No. ha^{-1})	Rel. Density (%)	Basal area (m^2 ha^{-1})	Rel. Basal area (%)	Rel. import. value* (%)
Live stems					
Acer rubrum	175	11.7	1.9	8.7	10.2
Betula species	35	2.4	0.2	1.4	1.9
Pinus rigida	826	55.4	7.3	53.3	54.4
Quercus rubra	422	28.4	4.7	34.7	31.5
Other species	32	2.1	0.3	1.9	2.0
Totals	1490		13.6		
Dead stems					
Acer rubrum	16	–	0.12	–	–
Betula species	6	–	0.01	–	–
Pinus rigida	295	–	1.58	–	–
Quercus rubra	19	–	0.18	–	–
Other species	10	–	0.03	–	–
Totals	346	–	1.92	–	–

*Importance value calculated as the average of relative density and relative basal area.

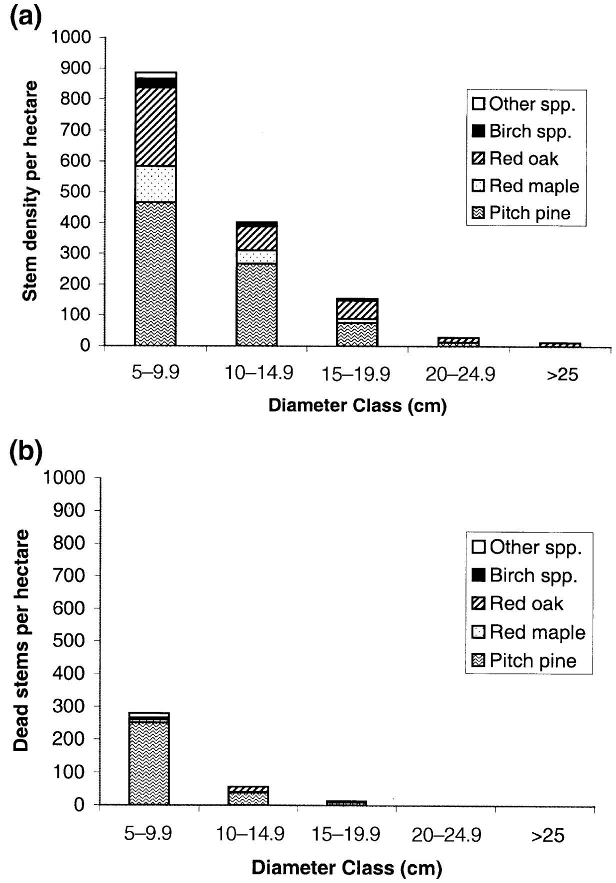

Figure 2 Diameter distribution of live (a) and dead (b) stems on the summit of Mt Everett, Massachusetts. Diameter is basal diameter for pitch pine and diameter at breast height for all other species. Other species include mountain ash, hemlock and striped maple.

50 years. Average pitch pine radial growth rate was 0.47 mm year^{-1} compared with 1.01 and 0.81 mm year^{-1}, respectively, for red oak and red maple (data not shown). Seventy percent of pitch pine stems had average radial growth rates less than 0.50 mm year^{-1} whereas only 7% of stems sampled from other species exhibited such low average growth rates.

Periods of release or suppression were detected in every 5-year interval since 1875 in pitch pine trees and since 1910 in hardwood trees (Fig. 5). Periods prior to 1900 for pitch pine and prior to 1930 for hardwood species contained sample sizes of less than twenty trees and should be interpreted with caution. Disturbance pulses estimated from tree-ring releases occurred during the early 1900s and from 1965 to 1985 in pitch pines and from 1955 to 1970 in hardwood trees. Periods of dramatic pitch pine ring-width reductions occurred from 1905 to 1910 and 1960–65. There were no intervals where >15% of hardwood trees exhibited sharp growth reductions.

Table 2 Density of tree saplings and seedlings on Mt Everett

Species	Saplings (no. ha^{-1})	Seedlings (no. ha^{-1})
Acer rubrum	51	1628
Acer pensylvanicum	3	0
Amelanchier sp.	0	343
Betula populifolia	57	286
Pinus rigida	13	143
Prunus pensylvanica	0	29
Quercus rubra	57	7143
Sorbus americana	0	1429
Total	181	10,999

Tree growth forms

The unusual growth forms of the pitch pine on the summit of Mt Everett have long been noted (Fig. 6; e.g. Warner, 1893; Manning, 1919). Several observations on these growth forms are warranted: (1) in addition to being short in stature, many pitch pines on the summit are highly contorted (Fig. 6b); as a result, the total extent of stem elongation is substantially greater than stem height, (2) prostrate pitch pine stems are common, often covering several to >10 m^2. In all occurrences that we investigated, these prostrate 'mats' are branches of upright stems that often extend several meters from the central stem, (3) although the lower branches of many pitch pine stems are buried by organic matter, we found no evidence of layering (e.g. root development) from these stems, (4) many pitch pines have broken branches in their crowns, presumably resulting from ice or other storm damage. Epicormic sprouting from the unbroken portions of these branches contributes to the contorted and 'bushy' appearance of these trees, (5) basal sprouting of pitch pines is quite common across the summit (Fig. 6c). We conservatively estimate that 46% of all pitch pine stems in our plots developed as basal sprouts, (6) cone production is common on upright as well as prostrate pitch pine stems, and we observed no evidence of cone serotiny on the summit of Mt Everett.

Although perhaps somewhat less unusual than the pitch pine growth forms, many hardwoods (especially oaks) on the summit have sustained repeated crown damage from ice or other storms (Fig. 6d). For example, in the winter of 2001, branch breakage was quite common on hardwood stems, whereas pitch pine stems were largely undamaged. Interestingly, in a number of instances, past crown damage to oaks apparently stimulated basal sprouting, even in the absence of cutting, fire, or mortality of the central stem. Approximately one-third of all hardwood stems sampled were of sprout origin.

The history of the summit

The Town of Mt Washington (formerly known as 'Taconic Mountain') was settled by Europeans by the mid-eighteenth century and was incorporated in 1779. From the mid-eighteenth century onward, travellers and naturalists recorded observations about Mt Everett that provide some insight into the vegetation and history of the summit. As early as 1781, Timothy Dwight (1821) described panoramic views from the summit, extending 40–70 miles (65–115 km) in all

Table 3 Frequency (%) of woody understory and herbaceous species in fourteen plots on the summit of Mt Everett

Woody understory	Freq. (%)	Herb layer	Freq. (%)
Acer rubrum	86	*Agrostis* spp.	7
Acer pensylvanicum	50	*Aralia nudicaulis*	93
Amelanchier spp.	79	*Aster acuminatus*	29
Aronia spp.	100	*Athyrium filix-femina*	7
Betula populifolia	79	*Carex pensylvanica*	36
Betula lenta	7	*Carex* spp.	64
Betula papyrifera	50	*Clintonia borealis*	50
Cornus canadensis	36	*Comandra umbellata*	7
Diervilla lonicera	14	*Coptis groenlandica*	7
Gaultheria procumbens	43	*Cypripedium acaule*	21
Gaylussacia baccata	100	*Danthonia spicata*	14
Hamamelis virginiana	29	*Dennstaedtia punctilobula*	7
Ilex verticillata	7	*Deschampsia flexuosa*	100
Kalmia angustifolia	7	*Dryopteris intermedia*	7
Kalmia latifolia	71	*Epigaea repens*	43
Nemopanthus mucronatus	43	*Juncus tenuis*	14
Pinus rigida	64	*Lycopodium obscurum*	29
Pinus strobus	14	*Lysimachia quadrifolia*	57
Prunus pensylvanica	36	*Maianthemum canadense*	93
Quercus ilicifolia	71	*Medeola virginiana*	7
Quercus rubra	100	*Monotropa uniflora*	50
Rhododendron prinophyllum	50	*Polypodium appalachianum*	36
Rubus sp.	7	*Potentilla tridentata*	50
Sorbus americana	86	*Pteridium aquilinum*	43
Tsuga canadensis	14	*Scirpus* sp.	7
Vaccinium angustifolium	100	*Smilax herbacea*	7
Viburnum cassinoides	71	*Solidago* spp.	14
		Thelypteris noveboracensis	7
		Trientalis borealis	71
		Uvularia sessilifolia	14

directions. Dwight's descriptions suggest that the summit did not support tall or dense forests during the late eighteenth century, for such stands would have obstructed the 'splendid prospect (that) spread around me.' Similar descriptions of unobstructed views were recorded throughout the nineteenth century (Tillinghast, 1999). In the 1820s, Dewey (1829a) noted the occurrence of scrub oak (*Q. ilicifolia*) and three-toothed cinquefoil (*Potentilla tridentata*) on 'Taconic Mountain', species that are shade intolerant and characteristic of open summits. Also in the 1820s, Hayden (1829) described the short stature of the vegetation on the rocky ridge around the town of Mt Washington, noting 'only soil enough intermingled with the rocks to support shrubs from one to two or three feet in height. The whortleberry bush abounds, and the inhabitants in the vicinity flock to it in the months of August and September to gather the fruit.' The first reference to dwarf pitch pines on the summit apparently comes from Hitchcock (1841), who observed that Mt Everett was an 'almost naked eminence; except that numerous yellow pines, two or three feet high, and whortleberry bushes, have fixed themselves wherever the crevices of rock afford sufficient soil.' In the late nineteenth century, the summit of Mt Everett continued to support extremely low stature vegetation, and numerous subsequent references confirm the occurrence of dwarf pines and open vegetation to the present (Tillinghast, 1999). We found no historical sources that suggest that the summit of Mt Everett was forested at any point during the historical period.

Several historical sources refer to the harsh nature of the summit, noting that little soil occurs on this 'wind-swept', rocky site (e.g. Adams, 1899; Manning, 1919; Eaton, 1930). We saw no evidence of tree windthrow on the summit. Numerous anecdotes document frequent ice storms on the summit (e.g. Bulkeley, 1964; M. Bulkeley pers. comm.).

Fire history

We have been unable to find any references to historical fires on the summit of Mt Everett. However, throughout the north-eastern US, documentary evidence for fires prior to the twentieth century is often lacking, even in areas that apparently burned in the early historical period (Lutz, 1934; Forman & Boerner, 1981; Motzkin *et al.*, 1996, 1999). After establishment of the Mt Everett State Reservation in 1908, the commissioners of the Reservation filed annual reports until at least 1955. Tillinghast (1999) reviewed each of the annual reports that was available (i.e. 1909, 1911, 1916–20, 1922–44, 1946–55) as well as the minutes from annual meetings of the commissioners of the Reservation for several years during the period from 1940 to 1964. None of these sources contains references to fires on the summit of Mt Everett, although they do include frequent references to

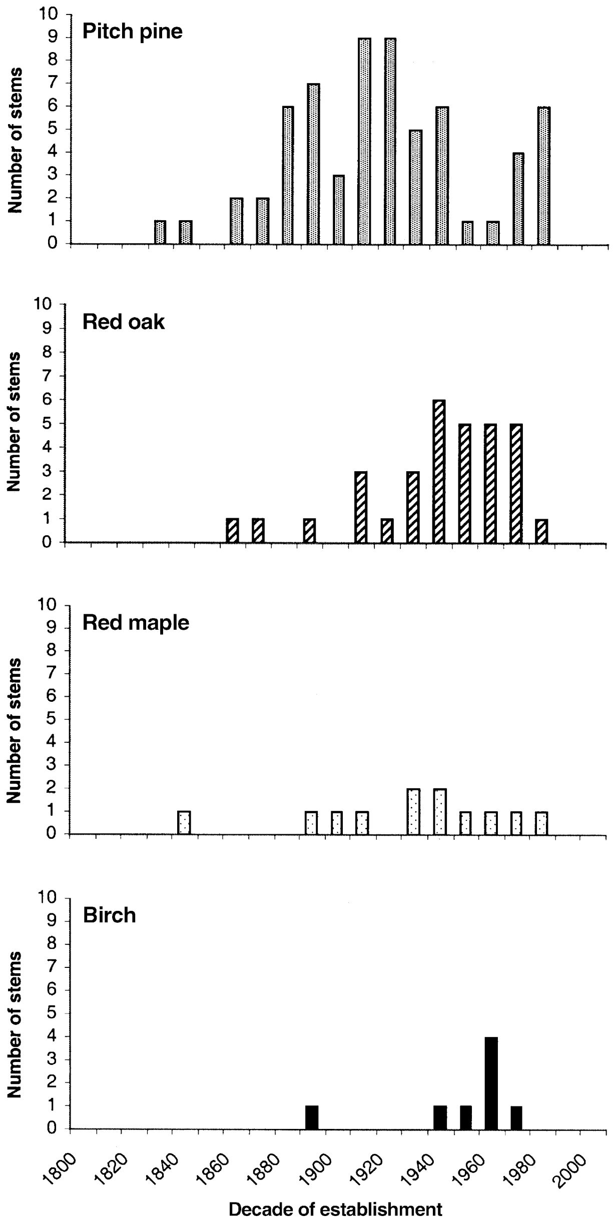

Figure 3 Recruitment dates by decade of major tree species sampled on the summit of Mt Everett, Massachusetts. Dates represent recruitment to 0.2 m for pitch pine and breast height (1.37 m) for hardwood species.

fire danger and fires on nearby summits outside the Reservation. Thus, it seems probable that no significant fires occurred on the summit of Mt Everett during the twentieth century.

We found no evidence of fire scars or stem charring in our plots or in extensive observations across the summit. Sieving of soil samples documented the occurrence of small amounts of charcoal in all but three plots. Two plots with abundant charcoal were located in close proximity to abandoned campfire sites. In general, soil charcoal was substantially less

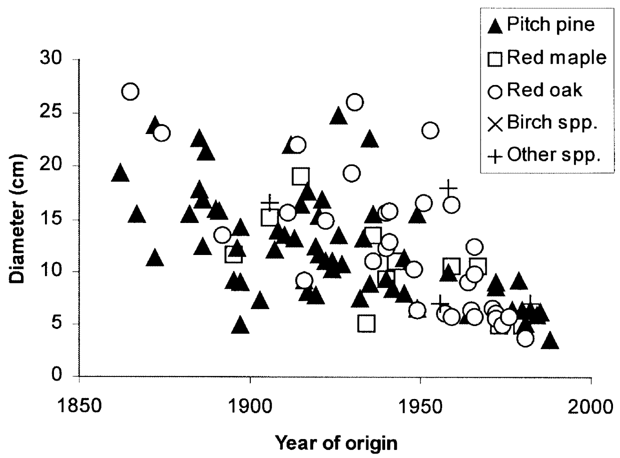

Figure 4 Age vs. diameter of cored trees ($n = 119$) on the summit of Mt Everett, Massachusetts. Diameter is basal diameter for pitch pine and diameter at breast height for all other species. Other species include mountain ash and hemlock.

abundant across this site than on many barrens sites that we have investigated.

DISCUSSION

Vegetation composition and age structure

The summit of Mt Everett supports approximately 8 ha of a dwarf pitch pine community that is highly uncommon across the north-eastern US, occurring only on few sites. Vegetation composition on the summit is characteristic of open, rocky ridges (Niering, 1953; Shaw, 1999), with no known rare vascular plant species (P. Weatherbee, unpublished data). However, rare lichens and insects do occur on the summit, including a few highly disjunct species (May, 1999; Wagner, 2000). Numerous historical sources indicate that the summit has been non-forested since at least the eighteenth century, with vegetation that was apparently quite similar to the modern vegetation (Dewey, 1829b; Hitchcock, 1841). Although Hitchcock (1841) provides the first specific reference to dwarf pines on the summit of Mt Everett, our results indicate that short stature pines on the summit may be quite old, with many stems that are 60 to more than 100 years old. If pitch pine grew at similar rates in the past, then Hitchcock's (1841) observation of 2–3 feet tall pines suggests that he was observing trees that had become established by the mid-eighteenth century. We suggest therefore that it is highly probable that pitch pines have occurred on the summit of Mt Everett throughout the entire historical period.

As a result of unusual site conditions and disturbance regimes, age structure and stand dynamics at Mt Everett differ substantially from many pine barrens in the eastern US. Our results indicate that pitch pines at Mt Everett are uneven-aged, with continuous recruitment since the 1860s and scattered older stems. Similarly, in one of the few previous studies to address long-term dynamics of ridgetop

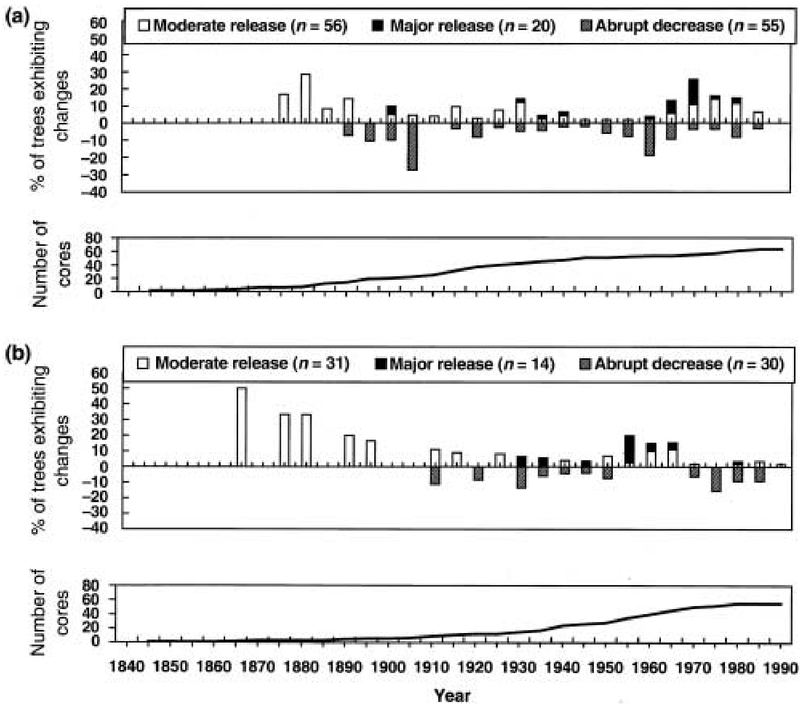

Figure 5 Frequency of growth releases (criteria from Lorimer & Frelich, 1989) and abrupt decreases (>50% growth declines sustained for at least ten consecutive years) measured in (a) pitch pines and (b) hardwoods including red oak, red maple, and birch species on Mt Everett. Frequencies are displayed by 5- year intervals. The bottom panel of each pair represents the sample size used to calculate the release frequencies. Sample size (*n*) refers to the number of abrupt, major, or moderate changes in ring width.

pitch pines, Abrams & Orwig (1995) determined that an old-growth (320 years old) pitch pine rock outcrop community in the Shawangunk Ridge of south-eastern New York was characterized by uneven-aged pitch pines, with continuous tree recruitment since the late 1600s. In contrast, on many sand plains throughout the region, pitch pine frequently occurs in relatively even-aged cohorts that established following fire, abandonment of agriculture, or other disturbance (Motzkin *et al*., 1999).

It is unclear why the average age and maximum longevity of pitch pines and hardwoods on the summit of Mt Everett are considerably less than on other harsh rocky summits, where trees exceeding 300 years have been documented (Abrams & Orwig, 1995; Orwig *et al*., 2001). Although rates of annual diameter growth of pitch pines on Mt Everett are among the slowest recorded for any tree species in the north-eastern US, they are comparable with those of old-growth pitch pines in the Shawangunk Mountains where trees exceeding 250 years old exhibited substantial growth releases in recent decades in response to favourable climatic conditions (Abrams & Orwig, 1995). In contrast, on Mt Everett standing dead pitch pine stems were observed in every plot, typically with no obvious cause of mortality and no evidence of damage from fire or windstorms. In some instances, the crowns of the dead stems are sufficiently intact to indicate that mortality was not directly associated with crown snapping or other severe physical damage from winter storms. It is probable that the harsh climatic and edaphic conditions on the summit contribute to the mortality and limited longevity of these trees; however, long-term studies are necessary to document the influence of ice storms and other disturbances on sprouting and mortality.

Although the modern vegetation composition and structure on the summit is broadly similar to that which has occupied the site for at least the past few centuries, questions remain about long-term vegetation trends and, in particular, the relative importance of hardwoods (especially oaks) vs. dwarf pines. A photograph of the summit from the 1890s indicates very short stature vegetation, with no emergent hardwoods visible. Because 5–7 m tall hardwoods are now common on some portions of the summit, this raises the possibility that over the past century, trees on the summit, and in particular hardwoods, may have increased in height and perhaps in relative importance. Age data suggest that oak recruitment has increased since the 1940s and most of the tall hardwood stems measured in each plot were only 30–70 years old. In addition, our data document substantially higher densities of oak seedlings and saplings than pitch pine, and in several locations on the summit we observed hardwoods that had over-topped pitch pines, apparently resulting in pitch pine mortality. Thus, although low densities of pitch pine seedlings and sprouts continue to establish on the summit, particularly on extremely open, rocky areas, there is evidence to suggest that the relative importance of hardwoods may have increased over the past century. These patterns suggest the possibility that undocumented past disturbance(s) (e.g. severe fire) prior to the twentieth century may have allowed widespread pitch pine establishment across the summit and that hardwoods may have increased recently with increasing time since disturbance. The extent to which such potential species replacement may be a relatively new phenomenon, resulting from altered disturbance regimes, climate change, or other causes, vs. a long-term dynamic

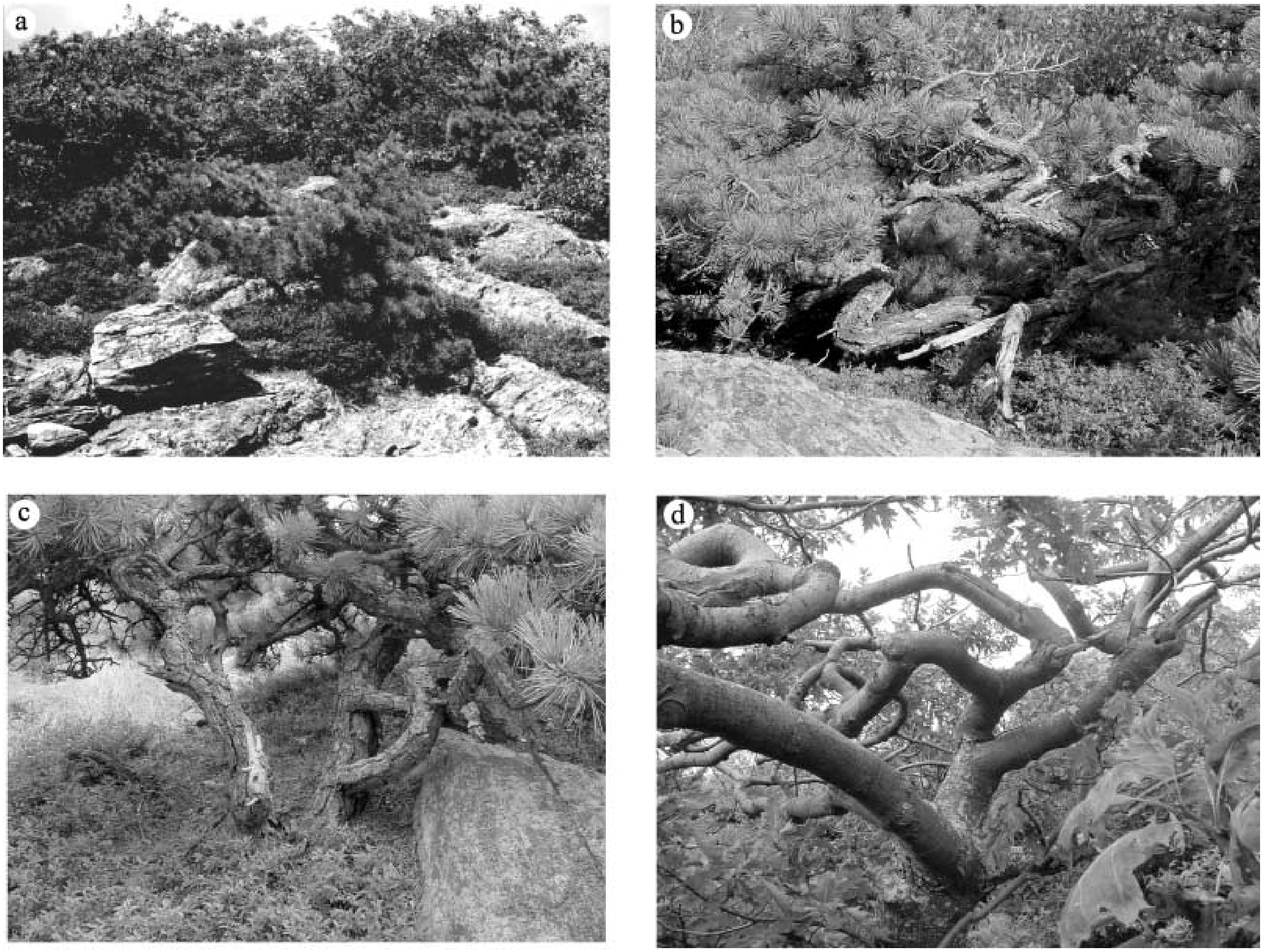

Figure 6 Photographs of the summit of Mt Everett showing (a) dwarf pitch pines (~1 m in height) with extensive bedrock outcrops (b) highly contorted growth form of pitch pines (c) multiple-stemmed pitch pine sprouts, and (d) contorted crown of red oak, with scars and broken branches.

that has resulted in shifts in abundance of pine vs. oak over time is unknown.

Disturbance history

No information is available about pre-European vegetation dynamics or disturbance history on Mt Everett. By the 1820s, Mt Everett was used by local residents for berry gathering (Hayden, 1829). Although we have found no references to historical fires on the summit, frequent burning to improve berry production was formerly common in many barren areas throughout the eastern US, including the Shawangunks of New York, Panther Knob in West Virginia, and the Waterboro Barrens in Maine (Batcher *et al*., 1997; Copenheaver *et al*., 2000), and it is possible that fire was similarly used on Mt Everett. Charcoal on exposed summits such as Mt Everett is frequently washed or blown from the site or concentrated in small topographic depressions or rock crevices (W. Patterson III, pers. comm.), perhaps contributing to our ability to find only small amounts of macroscopic charcoal. Similarly, despite the absence of historical references to cutting of vegetation, it is possible that woody vegetation that obstructed views or limited berry production was occasionally removed from the summit (e.g. 1936 in MESRC, 1909–1955). In addition, some clearing of vegetation presumably occurred in the twentieth century during construction of two fire towers and trails on the summit (Tillinghast, 1999).

The Shawangunk Mountains in New York support perhaps the best-studied rocky barrens in the north-eastern US (e.g. McIntosh, 1959; Olsvig, 1980; Laing, 1994; Abrams & Orwig, 1995; Seischab & Bernard, 1996; Batcher *et al*., 1997; Batcher, 2000), with little detailed information available for most other sites. Unlike Mt Everett, numerous documentary sources as well as Laing's (1994) palaeoecological reconstruction confirm the historical importance of fire in the Shawangunks, although substantial variation exists in fire regimes across the area (Batcher, 2000). In addition, cone serotiny, which is most common on pitch pines in North-eastern barrens thought to have very high fire frequencies (e.g. the dwarf pine plains of New Jersey and Long Island; Ledig & Fryer, 1972; Givnish, 1981), does not occur on Mt Everett but is common in the Shawangunks, further suggesting the long-term importance of fire in that area (Keeley & Zedler, 1998; Schwilk & Ackerly, 2001).

As a result of the intensive fire history in the Shawangunks, conceptual ecological models developed for that area emphasize fire effects on vegetation dynamics and composition and, to a lesser extent, edaphic, climatic, and pathogen driven dynamics (Batcher *et al*., 1997; Batcher, 2000). Similarly, the development and persistence of dwarf pitch pines in the pine plains of New Jersey and Long Island are strongly related to frequent fires (Lutz, 1934; Andresen, 1959; Givnish, 1981; Jordan, 1999). In contrast, we have been unable to document fires on the summit of Mt Everett during the historical period. Although we did find small amounts of macroscopic charcoal in our plots, we do not know whether such charcoal resulted from fire in the historical period or before European settlement. Despite this uncertainty, the historical record is sufficiently complete that we believe it to be highly unlikely that significant fires occurred during the twentieth century but were unrecorded. The fact that we did not find any charring or fire scars on live or dead stems further suggests that fires were absent or unimportant over at least the past century. Therefore, our data from the summit indicating that most stems are less than 100 years old provide strong evidence that current pitch pine and other species became established (or developed as sprouts) in the absence of fire. Such establishment is not well-incorporated into previous conceptual models of North-eastern barrens.

The summit of Mt Everett is substantially below the elevation at which treeline occurs in this region and the vegetation differs from typical krummholz growth-forms. However, numerous anecdotal accounts refer to frequent ice storms on the summit and it is probable that the dwarf growth forms of pitch pines on Mt Everett developed at least in part in response to such storms, as evidenced by the frequent branch breakage and epicormic sprouting of broken stems. Damage from such storms may also occasionally result in basal sprouting (Del Tredici, 2001). Results from our tree-ring analyses suggest that chronic small-scale disturbances have occurred throughout the twentieth century, perhaps reflecting the history of frequent ice storms. In addition, the period of peak pitch pine recruitment (1910–30) followed an abrupt decrease in pitch pine growth in 1905, suggesting that a disturbance event occurred that damaged existing stems and allowed for recruitment of new stems. Similarly, the main period of hardwood recruitment in the mid-twentieth century coincides with radial growth releases during the 1950s and 1960s, suggesting a response to disturbance or perhaps a period of favourable climatic conditions. Although we found no detailed historical records of major disturbance events, our results suggest that crown damage from storms or other disturbances may provide opportunities for new tree establishment on open rocky sites such as Mt Everett (Abrams & Orwig, 1995).

Several authors have suggested that stunted and highly contorted tree growth forms may also develop in response to extremely harsh soil nutrient conditions (e.g. Whittaker, 1954; Westman, 1975; Reich & Hinckley, 1980) and dwarf growth forms could potentially result from genetic variation (Andresen, 1959; Good & Good, 1975), although the extent to which these factors may be important on Mt Everett is unknown. We hypothesize that winter storms, in combination with harsh conditions resulting from limited soil development, wind and drought stress on this extremely rocky site, contribute to the structure, slow radial growth, and long-term persistence of the unusual vegetation on Mt Everett.

Perspectives on the conservation importance of Mt Everett

Mt Everett has long been recognized as a regionally significant conservation area (Siccama *et al*., 1982) and the greater Taconic Region that includes Mt Everett has recently been identified as among the highest priorities for conservation in the North-east by The Nature Conservancy and the Massachusetts Natural Heritage and Endangered Species Program, recognizing both the unfragmented nature of the region and its many unusual features, including the dwarf pitch pine communities of Mt Everett and nearby summits (MNHESP, 2001). Based on our experience with barrens throughout the north-eastern US, we consider Mt Everett to be an exemplary site worthy of the most stringent conservation measures. The summit supports several rare and/or highly disjunct species, and the dwarf pitch pines of Mt Everett and nearby summits in the Taconic Range are extremely uncommon, occurring elsewhere at very few sites in the North-east. Mt Everett and nearby summits also comprise critical components of the greater Taconic Region which represents one of the largest and most intact natural areas in southern New England and adjacent New York State.

The summit of Mt Everett is also significant regionally for its unusual history and dynamics. The persistence of the dwarf pitch pine community on Mt Everett and nearby summits in the southern Taconics in the absence of frequent fires (and the associated lack of cone serotiny) has not been previously documented and appears to be highly unusual among North-eastern barrens. In addition, few sites in the north-eastern US have experienced such limited disturbance by human activity over the past few centuries, with no documented history of cutting, grazing, or agriculture. This unusual history stems from the harsh and rocky conditions of the summit and has resulted in a relatively intact natural area with little evidence of alteration of vegetation or ecological process by historical land-use. In fact, the processes that have contributed to the persistence of unusual dwarf vegetation for at least several centuries, especially the extremely rocky, exposed conditions and frequent ice and other storms, continue to be operative and to allow for some establishment of dwarf pines and associated vegetation.

Although further investigation is warranted to determine the extent to which oaks are increasing on portions of the summit relative to pitch pine, there is no indication that this is occurring at a sufficiently rapid rate to warrant widespread active management in the immediate future (see Waldrop *et al.*, 2000). However, long-term monitoring and re-evaluation are warranted to insure the long-term persistence of the dwarf pitch pine community. The sprouting ability of pitch pines has been reported to decrease substantially with age (Lutz, 1934; Andresen, 1959; Little & Garrett, 1990), although multi-stemmed stools may retain their sprouting ability, and in some instances sprouting may be unrelated to stem age or size (Little & Garrett, 1990; F. Seischab, pers. comm.). Additional research is necessary to evaluate the response of dwarf pitch pines to a range of disturbances, and extreme caution is necessary in evaluating management activities that may negatively impact the existing dwarf pines. In summary, the summit of Mt Everett is a highly unusual site that is regionally significant and should be afforded the strictest of conservation protection.

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REFERENCES

Abrams, M.D. & Orwig, D.A. (1995) Structure, radial growth dynamics and recent climatic variations of a 320-year-old *Pinus rigida* rock outcrop community. *Oecologia*, **101**, 353–360.

Adams, J.C. (1899) *Nature studies in Berkshire*. G. P. Putnam's Sons, New York, NY.

Andresen, J.W. (1959) A study of pseudo-nanism in *Pinus rigida* Mill. *Ecological Monographs*, **29**, 309–332.

Massachusetts Natural Heritage and Endangered Species Program (MNHESP) (2001) *Biomap – guiding land conservation for biodiversity in Massachusetts*. Executive Office of Environmental Affairs, Boston, MA.

Barbour, H., Simmons, T., Swain, P. & Woolsey, H. (1998) *Our irreplaceable heritage – protecting biodiversity in Massachusetts*. Massachusetts Natural Heritage and Endangered Species Program and the Massachusetts Chapter of The Nature Conservancy, Boston, MA.

Batcher, M.S. (2000) *Ecological processes and natural communities of the northern Shawangunk Mountains*. Shawangunk Ridge Biodiversity Partnership, Buskirk, NY.

Batcher, M.S., Hall, T. & Bartgis, R. (1997) *Ecological processes in rock outcrop pine barrens and associated natural communities: comparative ecological models of the northern Shawangunks of New York and the Smoke Hole/North Fork Mountain ecosystem of West Virginia*. The Nature Conservancy, Arlington VA.

Bernard, J.M. & Seischab, F.K. (1995) Pitch pine (*Pinus rigida* Mill.) communities in northeastern New York State. *American Midland Naturalist*, **134**, 294–306.

Bulkeley, M. (1964) Ice storm. *The Berkshire Eagle*, 10 December 1964.

Copenheaver, C.A., White, A.S. & Patterson, W.A. III (2000) Vegetation development in a southern Maine pitch pine-scrub oak barren. *Journal of the Torrey Botanical Society*, **127**, 18–32.

Del Tredici, P. (2001) Sprouting in temperate trees: a morphological and ecological review. *Botanical Review*, **67**, 121–140.

Dewey, C. (1829a) Catalogue of plants found in the County of Berkshire, Massachusetts. *A history of the county of Berkshire, Massachusetts* (ed. D.D. Field), in two parts. Samuel W. Bush, Pittsfield, MA.

Dewey, C. (1829b) A general view of the county. *A history of the county of Berkshire, Massachusetts* (ed. D.D. Field), Samuel W. Bush, Pittsfield, MA.

Dunwiddie, P.W. & Adams, M.B. (1995) *Fire suppression and landscape change on outer Cape Cod, 1600–1994*. US Department of Interior Technical Report NPS/NESO-RNR/NRTR/96–08. US Department of Interior, Washington, DC.

Dwight, T. (1821) *Travels in New England and New York*. T. Dwight, New Haven, CT.

Eaton, W.P. (1930) *New England vista*. W. A. Wilde Company, Boston, MA.

Eberhardt, R.W., Foster, D.R., Motzkin, G. & Hall, B. (2003) Conservation in changing landscapes: vegetation and land-use history of Cape Cod National Seashore. *Ecological Applications* (in press).

Forman, R.T.T. & Boerner, R.E. (1981) Fire frequency and the Pine Barrens of New Jersey. *Bulletin of the Torrey Botanical Club*, **108**, 34–50.

Foster, D.R. & Motzkin, G. (1999) *Historical influences on the landscape of Martha's Vineyard: perspectives on the management of the Manuel F. Correllus State Forest*. Harvard Forest Paper No. 23. Harvard University, Petersham, MA.

Givnish, T.J. (1981) Serotiny, geography, and fire in the pine barrens of New Jersey. *Evolution*, **35**, 101–123.

Good, R.E. & Good, N.F. (1975) Growth characteristics of two populations of *Pinus rigida* Mill. from the pine barrens of New Jersey. *Ecology*, **56**, 1215–1220.

Griffith, G.E., Omernik, J.M., Pierson, S.M. & Kiilsgaard, C.W. (1994) *Massachusetts ecological regions project*. Publication No. 17587–74–70. US Environmental Protection Agency, Corvallis, OR.

Hager, A.E.S. (1995) *Interactions between climate and radial growth of pitch pine (Pinus Rigida Mill.) in the northern portion of its range*. MSc Thesis, University of Maine, Orono, ME.

Hayden, G. (1829) A history of the town of Mount Washington. *A history of the County of Berkshire, Massachusetts* (ed. D.D. Field), in two parts. Samuel W. Bush, Pittsfield, MA.

Hitchcock, E. (1841) *Final report on the geology of Massachusetts,* in four parts. J.H. Butler, Northampton, MA.

Jordan, M. (1999) *Conceptual ecological models for the Long Island Pine Barrens*. The Nature Conservancy, Long Island, NY.

Keeley, J.E. & Zedler, P.H. (1998) Evolution of life histories. *Pinus: ecology and biogeography of Pinus* (ed. D.M. Richardson), pp. 219–251. Cambridge University Press, Cambridge.

Laing, C. (1994) *Vegetation and fire history of the dwarf pine ridges, Shawangunk Mts., New York*. The Nature Conservancy, Eastern New York Regional Office, New York.

Ledig, F.T. & Fryer, J.H. (1972) A pocket of variability in *Pinus rigida*. *Evolution*, **26**, 259–266.

Leverett, R.E. (ed.) (2000) *Ecological significance of the Mount Everett summit – preliminary evaluations and recommendations for additional research and protection*. Unpublished report prepared for the Massachusetts Department of Environmental Management and the Town of Mount Washington, Massachusetts Department of Environmental Management, MA.

Little, S. (1979) Fire and plant succession in the New Jersey Pine Barrens. *Pine barrens: ecosystem and landscape* (ed. R.T.T. Forman), pp. 297–314. Academic Press, New York, NY.

Little, S. & Garrett, P.W. (1990) *Pinus rigida* Mill. *Silvics of North America*. (Technical coordinators R.M. Burns and B.H. Honkala), *Conifers*, 1, pp. 456–462. USDA Handbook 654. USDA, Washington, DC.

Lorimer, C.G. & Frelich, L.E. (1989) A methodology for estimating canopy disturbance, frequency, and intensity in dense temperate forests. *Canadian Journal of Forest Research*, **19**, 651–663.

Lutz, H.J. (1934) *Ecological relations in the pitch pine plains of southern New Jersey*. Yale University School of Forestry Bulletin no. 38. Yale University School of Forestry, New Haven, CT.

Manning, W.H. (1919) *Letter to members of the Mt Everett Committee: Boston Society of Landscape Architects, and the Appalachian Mt Club, 11 July 1919*. Collection of James Whitbeck. From Tillinghast (1999), E. Tillinghast, Mount Washington, MA.

May, P.F. (1999) Lichen survey of Mount Everett summit, southwest Berkshire County, Massachusetts 2000. *Ecological significance of the Mount Everett summit – preliminary evaluations and recommendations for additional research and protection* (ed. R.E. Leverett), pp. 31–37. Unpublished report prepared for the Massachusetts Department of Environmental Management and the Town of Mount Washington, Massachusetts Department of Environmental Management, MA.

McIntosh, R.P. (1959) Presence and cover in pitch pine-oak stands of the Shawangunk Mountains, New York. *Ecology*, **40**, 482–485.

Motzkin, G., Foster, D., Allen, A., Harrod, J. & Boone, R. (1996) Controlling site to evaluate history: vegetation patterns of a New England sand plain. *Ecological Monographs*, **66**, 345–365.

Motzkin, G., Patterson, W.A. III & Foster, D.R. (1999) A historical perspective on pitch pine-scrub oak communities in the Connecticut Valley of Massachusetts. *Ecosystems*, **2**, 255–273.

Mount Everett State Reservation Commissioners (MESRC) (1909–55) *County Commissioners' report upon the affairs of the County of Berkshire*. Note: Annual reports of the Mt. Everett State Reservation Commissioners were typically included in the County Commissioners reports. All available reports of the Reservation Commissioners (including those not printed in the County Commissioner's reports) are referenced here under 'MESRC'. See Tillinghast (1999). MSERC, Pittsfield, MA.

Niering, W.A. (1953) The past and present vegetation of High Point State Park, New Jersey. *Ecological Monographs*, **23**, 127–148.

Nowacki, G.J. & Abrams, M.D. (1997) Radial-growth averaging criteria for reconstructing disturbance histories from presettlement-origin oaks. *Ecological Monographs*, **67**, 225–249.

Olsvig, L.S. (1980) *A comparative study of Northeastern pine barrens vegetation*. PhD Dissertation. Cornell University, Ithaca, NY.

Orwig, D.A., Cogbill, C.V., Foster, D.R. & O'Keefe, J.F. (2001) Variations in old-growth structure and definitions: forest dynamics on Wachusett Mountain, Massachusetts. *Ecological Applications*, **11**, 437–452.

Parshall, T., Foster, D.R., Faison, E., MacDonald, D. & Hansen, B. (2003) Long-term vegetation and fire dynamics of pitch pine-oak forests on Cape Cod, Massachusetts. *Ecology* (in press).

Patterson, W.A. III, Saunders, K.E. & Horton, L.J. (1984) *Fire regimes of Cape Cod National Seashore*. USDI National Park Service Office of Scientific Programs, Report OSS 83–1. USDI National Park Service Office of Scientific Programs, Boston, MA.

Reich, P.B. & Hinckley, T.M. (1980) Water relations, soil fertility, and plant nutrient composition of a pygmy oak ecosystem. *Ecology*, **61**, 400–416.

Scanu, R.J. (1988) *Soil survey of Berkshire County, Massachusetts*. US Department of Agriculture, Soil Conservation Service, Amherst, MA.

Schwilk, D.W. & Ackerly, D.D. (2001) Flammability and serotiny as strategies: correlated evolution in pines. *Oikos*, **94**, 326–336.

Seischab, F.K. & Bernard, J.M. (1991) Pitch pine (*Pinus rigida* Mill.) communities in central and western New York. *Bulletin of Torrey Botanical Club*, **118**, 412–423.

Seischab, F.K. & Bernard, J.M. (1996) Pitch pine (*Pinus rigida* Mill.) communities in the Hudson Valley region of New York. *American Midland Naturalist*, **136**, 42–56.

Shaw, S. (1999) *Natural community inventory and classification of Mount Tekoa*. U.S. Fish and Wildlife Service, Silvio O. Conte National Fish and Wildlife Refuge, Turners Falls, MA. The Nature Conservancy, Boston, MA.

Siccama, T.G., Niering, W.A., Kalison, G., O'Dell, A.M.H. & Speer, E.B. (1982) *Potential ecological and geological landmarks of the New England-Adirondack region*. Unpublished Report, Submitted to the US Department of the Interior, Division of National Natural Landmarks. US Department of the Interior, Washington, DC.

Tillinghast, E. (1999) A brief history of the Mount Everett summit and comparison with other south Taconic summits. *Ecological significance of the Mount Everett summit – preliminary evaluations and recommendations for additional research and protection* (ed. R.E. Leverett), pp. 15–29. Unpublished report prepared for the Massachusetts Department of Environmental Management and the Town of Mount Washington, MA.

Wagner, D.L. (2000) The macrolepidopteran fauna of Mount Everett, Massachusetts. *Ecological significance of the Mount Everett summit – preliminary evaluations and recommendations for additional research and protection* (ed. R.E. Leverett), pp. 38–41. Unpublished report prepared for the. Massachusetts Department of Environmental Management and the Town of Mount Washington.
Waldrop, T.A., Welch, N.T., Brose, P.H., Elliott, K.J., Mohr, H.H., Gray, E.A., Tainter, F.H. & Ellis, L.E. (2000) Current research on restoring ridgetop pine communities with stand replacement fire. *Proceedings: workshop on fire, people, and the central hardwoods landscape* (Compiled by D.A. Yaussy), pp. 103–109. USDA GTE-NE-274, USDA, Richmond, KY.
Warner, C.F., (ed.) (1893) *Picturesque Berkshire: Part II – South*. Picturesque Publishing Co, Northampton, MA.
Westman, W.E. (1975) Edaphic climax pattern of the pygmy forest region of California. *Ecological Monographs*, **45**, 109–135.
Westveld, M., Ashman, R.I., Baldwin, H.I., Holdsworth, R.P., Johnson, R.S., Lambert, J.H., Lutz, J.J., Swain, L. & Standish, M. (1956) Natural forest vegetation zones of New England. *Journal of Forestry*, **54**, 332–338.
Whittaker, R.H. (1954) The ecology of serpentine soils. IV. The vegetational response to serpentine soils. *Ecology*, **35**, 275–288.
Zen, E. (ed.) (1983) *Bedrock geologic map of Massachusetts*. US Geological Survey, Reston, VA.

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