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Frost pockets on a level sand plain: Does variation in microclimate help maintain persistent vegetation patterns?[2]

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MOTZKIN, G., S. C. CICCARELLO AND D. R. FOSTER. (Harvard Forest, Harvard University, Petersham, MA 01366). Frost pockets on a level sand plain: Does variation in microclimate help maintain persistent vegetation patterns? J. Torrey Bot. Soc. 129:154–163. 2002.—Climatic variation is recognized as a major driver of vegetation patterns across broad geographic regions and areas of steep topography. However, few studies have evaluated the potential influences of local climatic variation on vegetation patterns or dynamics. We investigated the relationships between microclimatic variation, vegetation structure, and leaf phenology on a topographically level sand plain that is characterized by a forest mosaic with abrupt transitions to shrublands dominated by scrub oak (*Quercus ilicifolia*). The timing of bud break, leaf phenology, and height of scrub oak are strongly related to variation in temperature across the study site. Moderate maximum and minimum temperatures occur beneath forested canopies, whereas nearby shrublands experience frequent late-spring frosts and shorter frost-free growing seasons, resulting in chronic dieback of developing leaves, slow growth rates, and reduced stem height. Our results indicate that extreme radiational cooling in open areas on level, xeric sites may result in the development of 'frost pockets' similar to those that occur in topographical depressions and may contribute to slow establishment of a forest canopy after disturbance. Such frost-prone areas may have become more common as a result of historical cutting and burning and may contribute to the persistence of scrub oak stands that support several rare species and are high priorities for conservation.

Key words: frost pocket, phenology, pine barrens, pitch pine, scrub oak (*Q. ilicifolia*).

Plant community composition and structure are influenced by a wide range of factors, including variation in resource conditions, biotic interactions, and historical processes such as human and natural disturbance. Although local climatic conditions have the potential to influence vegetation patterns, few studies have evaluated the extent to which feedbacks between vegetation and local microclimate may control vegetation dynamics or the degree to which vegetation-microclimate relationships are affected by disturbance history. An understanding of the nature and strength of such relationships is critical when evaluating rates of vegetation change and determining the degree to which the vegetation itself may influence successional dynamics after disturbance.

In the current study, we investigated the relationships between vegetation structure, microclimate, and leaf phenology on a topographically level outwash plain that is characterized by a mosaic of forested stands with abrupt transitions to shrub-dominated areas. The site, which supports one of the largest remaining inland pitch pine-scrub oak communities in southern New England, has been the focus of several intensive investigations of the influence of historical factors on modern forest composition, species demography, and ecosystem function (Motzkin et al. 1996, 1999; Compton et al. 1998; Donohue et al. 2000). These studies determined that the structural and compositional transitions from shrub-thickets to surrounding forested stands developed primarily as a result of historical land-use practices; pitch pine (*Pinus rigida*) stands that largely surround the shrub thickets developed on former agricultural lands, whereas shrub thickets dominated by scrub oak (*Quercus ilicifolia*) occur on sites that were never used for agriculture and probably became increasingly shrub-dominated in the historical period as a result of repeated cutting and burning (Motzkin et al. 1996). The long-term dynamics and persistence of the scrub oak thickets is of particular conservation interest because these communities are uncommon throughout the northeastern U.S. and support several rare species (Goldstein

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1997). Although many scrub oak stands are thought to have developed or been maintained through repeated burning, little is known of the dynamics of these stands after disturbance or in the absence of repeated fire. Such an understanding is increasingly important because improved fire detection and suppression in recent decades has resulted in a widespread reduction of fire in these systems.

Preliminary observations in several scrub oak stands at the study site suggested that portions of the shrub thickets experienced frequent late-spring frosts as a result of local temperature variation related to structural patterns in the shrub thickets and the adjoining forested sites. Although 'frost pockets' are well-documented from topographical depressions (Aizen and Patterson 1995), we hypothesized that: 1) similar phenomena may occur on topographically level sites, 2) temperature and frost gradients are strongly related to variation in vegetation structure, and 3) microclimatic gradients initiated through historical disturbance events may exert persistent influence (positive feedbacks) on vegetation structure and composition. In order to address these hypotheses, we initiated a detailed study of one of the scrub oak stands that appeared to have a gradient of frost effects and the surrounding pitch pine woodland. Quantitative data from this intensive study site were augmented with observational data from several similar stands on the outwash plain. The specific objectives of the current study include: 1) to determine whether variation in temperature across the intensive study site is related to variation in vegetation structure; 2) to evaluate the relationships between variation in bud and leaf phenology and temperature and structural gradients; and 3) to evaluate the potential effects of microclimatic variation on vegetation change after disturbance.

Study Site. The 0.75 ha intensive study site is located in the northern portion of Montague Plain, a glacial outwash delta in central Massachusetts (42°34′N; 72°31′W). Soils on the Plain developed in water-sorted siliceous sand and gravel, with a surface layer of loamy sand. Geological studies as well as our own investigations suggest that the absence of restricting layers within the permeable sands and gravels renders the site highly drought-prone despite annual precipitation of approximately 110 cm that is well-distributed through the year (Mott and Fuller 1967; Motts 1971).

Montague Plain supports approximately 65 ha of scrub oak stands that are compositionally and structurally similar to the shrublands in our intensive study area, and which represent 93% of the scrub oak stands remaining in the Connecticut Valley (Motzkin et al. 1996; 1999). The intensive study site is characterized by a central stand of dense shrublands 0.5 to 3 m in height, bordered to the east, south, and west by pitch pine (*Pinus rigida*) stands that are approximately 15 m in height, and to the north by a dirt road. The shrublands are dominated by *Quercus ilicifolia* and *Q. prinoides*, with a few scattered tree saplings 3–5 m tall, and *Vaccinium angustifolium*, *V. pallidum*, *Comptonia peregrina*, and *Gaultheria procumbens* common throughout. With the exception of a small area (<0.1 ha) in the western portion, the entire intensive study site burned in an approximately 70 ha wildfire on May 3, 1986, apparently killing all above ground shrub and sapling stems. However, all of the dominant species are known to sprout prolifically after fire, and most of the current stems appear to be of sprout origin. Topographic survey indicates that elevation variation across the site is negligible (maximum: 38.7 cm). Additional information on the vegetation, disturbance history, and soils of the site is found in Motzkin et al. (1996, 1999), Compton et al. (1998), and Donohue et al. (2000). Nomenclature follows Gleason and Cronquist (1991).

Methods. In order to evaluate variation in temperature, vegetation structure, and phenology from the forested stands into the shrublands, three radiating transects (East, West, and South) were established from a point in the center of the scrub oak-dominated stand, extending into the adjacent forested stands 10 m beyond the boundary with the scrub thicket (Fig. 1). A series of temperature and phenological monitoring stations was located along each transect as follows: 'forest' stations (E3, S3, W3) were established beneath the forest canopy, 10 m from the border with the shrub thicket; 'scrub edge' stations (E2, S2, W2) were established in the shrub thicket, 10 m from the forested boundary; and 'scrub' stations (E1, S1, W1) were established halfway between the central station and the 'scrub edge' station along each transect. Thus, we established a total of 10 monitoring stations (i.e., 3 stations on each of the three transects plus one central station).

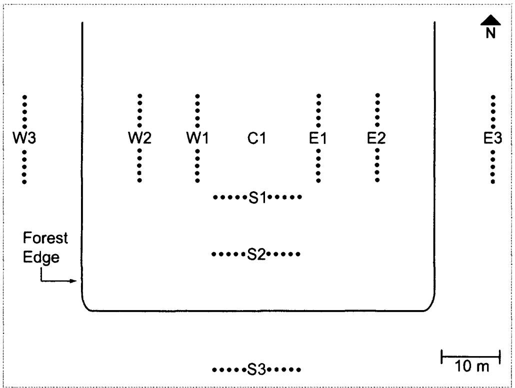

FIG. 1. Transect and plot line locations for temperature and phenological observations. See text for explanation.

TEMPERATURE AND PHENOLOGICAL MEASUREMENTS. At each station, maximum/minimum thermometers were mounted on posts at the local scrub oak canopy height (1–2 m). Thermometers were encased in open wooden housing to shield them from direct solar exposure, wind, and vandalism, with openings oriented north. Three thermometers were located at the central station, one each at ground level, 1 m (canopy height at that location) and 2 m. Weekly maximum and minimum temperatures were recorded from May 17–Aug. 30, 1996, and on Sept. 26 and Oct. 10, 1996.

At each station, weekly phenological observations were recorded along 10 m plot lines established perpendicular to each transect, centered on each observation station (Fig. 1). A total of 10 scrub oak stems at the top of the canopy were tagged at one meter intervals along each plot line. Bud break was recorded ('open' for buds that had expanded sufficiently that developing leaves were visible beneath the bud scales or 'closed' for tightly closed buds) and midrib leaf length was measured weekly from the base of the leaf blade to the tip of the bristle for the ten largest leaves on the tagged stem. Because of insect or other damage to individual leaves through the growing season, the ten leaves that were measured occasionally varied from week to week.

AGE STRUCTURE AND STEM HEIGHT. A 3 m × 3 m sample plot was established at each observation station, using the thermometer post as the northeast corner of the plot. Basal diameter and height of each scrub oak stem within the plot were recorded. To determine stand age, basal sections were cut from 5 scrub oak individuals per plot and from 10 individuals at the central station. Stems selected for aging were representative (i.e., within 0.5 m) of the local canopy height.

DATA ANALYSIS. In order to evaluate the relationship between leaf length, location within the study site, and temperature, length was treated as a dependent variable in the following multiple regression model: (leaf length = constant + location + date + minimum temperature + location*minimum temperature + date*minimum temperature). 'Location' represents the four station types within the study site (forest, scrub edge, scrub, and center). Analysis of covariance was used to test for significance of independent variables and interaction terms. Visual and quantitative regression diagnostics, including plotting of residuals and calculating the Kolmogrov-Smirnov/Lilliefors test (SYSTAT 1992), indicated no substantial departure from the assumptions of linear regression.

Results. TEMPERATURE GRADIENTS. Minimum temperatures throughout the growing season are strongly related to location within the study site, with the highest minimum temperatures recorded beneath the forest canopy and the lowest minimum temperatures in the scrub oak thicket at the 'center' and 'scrub' stations (Fig. 2). 'Scrub edge' stations typically have minimum temperatures that are intermediate between the forest and the center. With few exceptions, these trends are also consistent when each transect is considered separately (Ciccarello 1997). The weekly minimum temperatures at the central station average 2.8°C (5.0 °F) lower than the average forest minimum temperature, 2°C (3.6 °F) lower than the average scrub edge minimum, and 1.1°C (2.0 °F) lower than the average minimum at the scrub stations. However, there is some variability throughout the growing season. For instance, after mid-August, minimum temperatures at the East transect 'scrub station' (E1) were similar to the central station, and on a few dates minimum temperatures of the scrub edge stations along the west and south transects were lower than the central station.

In late Spring, the lowest temperatures were recorded during the week of May 17, prior to leaf out for many of the scrub oak stems, and again during the week of June 1, where temperatures as low as −7 to −2 °C (20–28 °F) were recorded in the center and several scrub and scrub edge stations, but not beneath forest can-

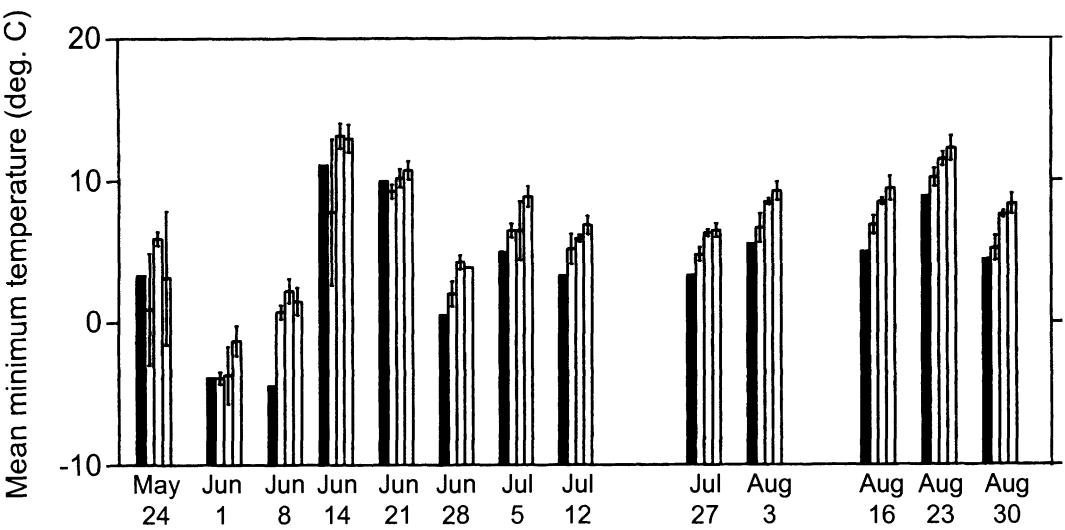

FIG. 2. Weekly mean minimum temperatures for May–August 1996. For each date, sampling stations are arranged from left to right as follows: 'center' (solid bar), 'scrub', 'scrub edge', and 'forest'.

opies. At the central station, minimum temperatures are typically lowest at 1 m, and minimum temperatures at ground level and 1 m are consistently lower than those recorded at 2 m above ground level (Fig. 3a). In contrast, weekly maximum temperatures are typically highest at 1m or ground level, with lower maximum temperatures at 2 m (Fig. 3b).

PHENOLOGY. The timing of bud break was significantly delayed in the center of the study site relative to the scrub, scrub edge, and forest areas. In week 1 (May 17, 1996), 94% of the buds at the central station remained closed, whereas >80% bud break had occurred at all other sample stations (Figs. 4 and 5). By weeks 2 and 3, all stations had 100% bud burst except for the central station and the scrub station of the South transect.

The overall multiple regression model relating leaf length to location (forest, scrub edge, scrub, and center), date, and minimum temperature (leaf length = constant + location + date + minimum temperature + location * minimum temperature + date * minimum temperature) was highly significant ($p < 0.0001$; multiple $r^2 = 0.705$). Analysis of co-variance indicated that location was a significant independent variable ($p < = 0.05$). The interaction of date and minimum temperature was also significant ($p < 0.001$), indicating that the effects of minimum temperature and time of season on leaf length are interdependent.

AGE STRUCTURE AND STEM HEIGHT. Basal sections of 55 scrub oak stems across the site indicate that, with the exception of the West scrub edge and forest area, the stand is even-aged, having regenerated after the 1986 fire. Eighty percent of stems sampled outside of the West scrub edge and forest areas had 9 or 10 growth rings (range = 7–11 years). In contrast, stems up to 19 (West scrub edge) and 16 (West forest) years occurred in the western portion of the study area, which was apparently the only area to have not burned in 1986.

The height of scrub oak stems varies by location within the study site. The average height of scrub oak stems near the central station is only 1.55 m, and the maximum height recorded from this area is 1.73 m (Fig. 6). In contrast, scrub oak canopies at the scrub, scrub edge, and forest stations are typically >2m in height, with a few stems approaching 3m.

Discussion. Variation in vegetation composition and structure at local and landscape scales is frequently related to edaphic factors (e.g., soil texture, drainage, or nutrients) or disturbance history. Although climatic variation is recognized as a major driver of vegetation pattern across broad regions or areas of steep topographic gradients, few studies have evaluated potential influences of local climatic variation on vegetation patterns or dynamics. In the uplands of the northeastern United States, factors such as maximum and minimum temperatures and

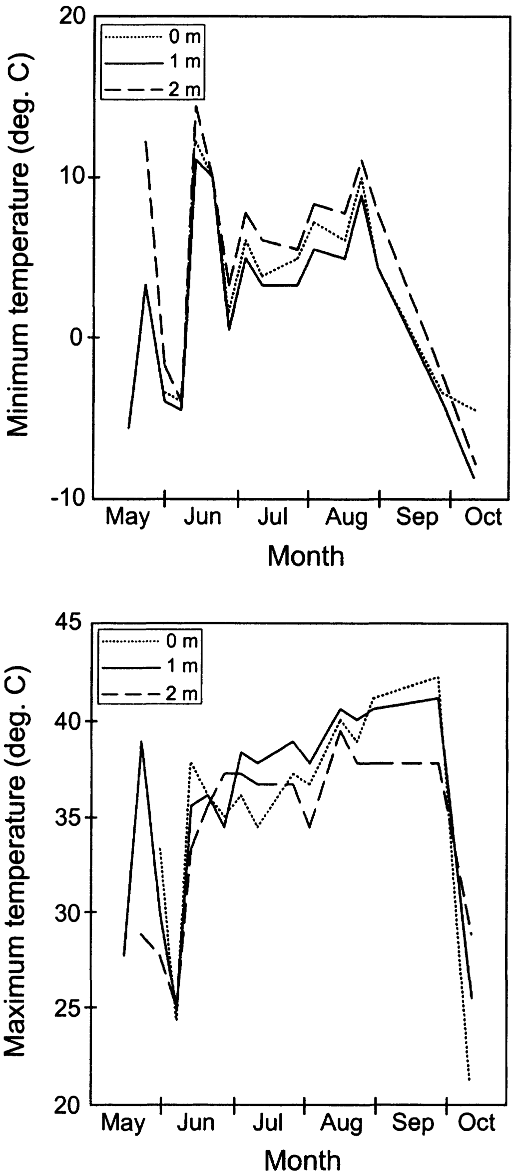

FIG. 3. Weekly minimum (top) and maximum (bottom) temperatures at ground level, 1m, and 2m height at the central station.

length of frost-free period vary substantially in relation to landscape position, suggesting that such variation may influence vegetation (Spurr 1957; Rasche 1958; Ross 1958). However, such climatic variation is frequently confounded with variation in soil moisture, depth to bedrock, and other edaphic factors, making it difficult to isolate the effects of climate on vegetation.

Local climatic variation is perhaps most pronounced in deep frost pockets, which experience unusual temperature extremes. The growing season, whether calculated as growing degree days or length of the frost-free period, may be substantially shorter in such sites than in immediately surrounding areas. For instance, in some dry ice-block depressions in eastern Massachusetts, frosts frequently occur in June and have been recorded in every month of the year, although the average length of the growing season in the region is 146–174 days (Upham 1969). Studies of such local differences in frost occurrence and variation in the length of the frost-free period are quite limited, however, and frequently restricted to documenting particularly severe events [e.g., '1816, the Year without a Summer' (Baron 1992; Baron and Smith 1996) or the spring frosts that affected much of the British Isles in 1935 (Forestry Commission 1946)]. A few studies have demonstrated that frequent late spring killing frosts in topographic depressions may significantly delay regeneration of frost sensitive tree species and re-establishment of a forest canopy after disturbance (Hough 1945; Barnes et al. 1989), and may have pronounced effects on flower and fruit production (Wolgast and Trout 1979; Aizen and Kenigsten 1990), leaf phenology, and herbivory (Aizen and Patterson 1995).

Our observations of temperature and phenological variation on a topographically level site offer insight into the mechanisms by which frost pockets may develop or persist. Whereas cold air drainage and trapping, in addition to radiational cooling, may contribute to the occurrence of frost pockets in topographic depressions, our results suggest that cold air drainage may not be necessary to generate such frost events. Rather, extreme radiational cooling appears to be the primary mechanism involved in generating such unseasonably low temperatures at our study site, and such cooling is expected to be greatest on cool, still, clear nights when atmospheric mixing is limited and cloud cover that may inhibit radiational heat loss is lacking (Geiger 1943). Under these circumstances, severe frosts are most likely on sites that lack forest canopies and have limited soil moisture, for dense canopies and abundant soil moisture may prevent sufficient loss of heat necessary to generate freezing temperatures. The frequency of late spring frosts and the magnitude of temperature gradients on the topographically level study site are in fact greater than those observed in nearby ice-block depressions (G. Motzkin *unpublished data*), apparently because the depressions have sufficient forest canopies to prevent radiational heat loss.

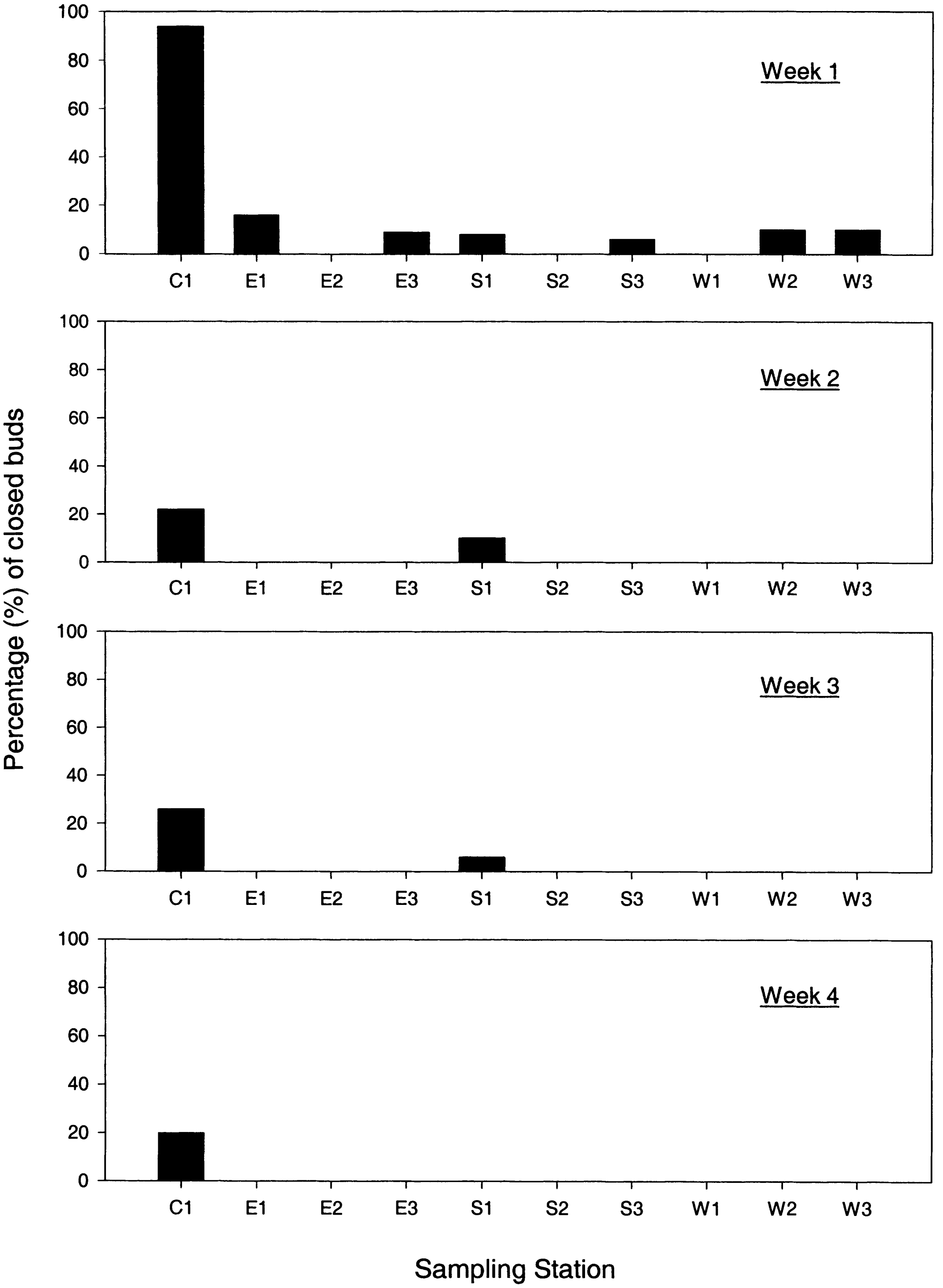

FIG. 4. Percentage of closed buds at each sampling station for weeks 1, 2, 3, and 4. Week 1 = week of May 17, 1996; Week 2 = week of May 24, 1996; Week 3 = week of June 1, 1996; Week 4 = week of June 8, 1996. At all stations, all buds had expanded by Week 5 (June 15, 1996).

We suggest, therefore, that on level sites similar to the one we investigated, radiational cooling rather than cold air drainage is most significant in generating the 'frost pocket' phenomenon (Hough 1945).

The development of several similar frost 'pockets' across the study site apparently resulted from similar histories of disturbance. Historical cutting and burning probably resulted in the development of dense shrublands dominated by *Quercus ilicifolia*, whereas the surrounding pitch pine woodlands largely developed on old fields after the abandonment of agriculture (Motzkin et al. 1996). Because only 15 years have passed since the last fire in our intensive study area, it is not possible to predict how long these patterns will persist. However, we observed similar variation in stand structure and frost damage in other scrub oak stands that last burned 30–60 years ago, suggesting that the frost phenomenon may have long-term effects on vegetation structure.

Despite the negligible topographic variation across the study site, the temperature gradient was apparently sufficient to result in delayed bud burst in the center of the shrub thicket and in the difference in height structure that we observed within several years after the stand-initiating fire in 1986. This is undoubtedly facilitated in part by the dominance of this site by *Quercus ilicifolia*, a highly frost-sensitive species that is close to the northern edge of it's geographic range at our study site. The short stature of scrub oak in the center of the site may result from chronically short growing seasons resulting, on average, in reduced annual shoot elongation. In addition, increased shoot or branch mortality may contribute to shorter stems in the center relative to the edges of the site. Increased

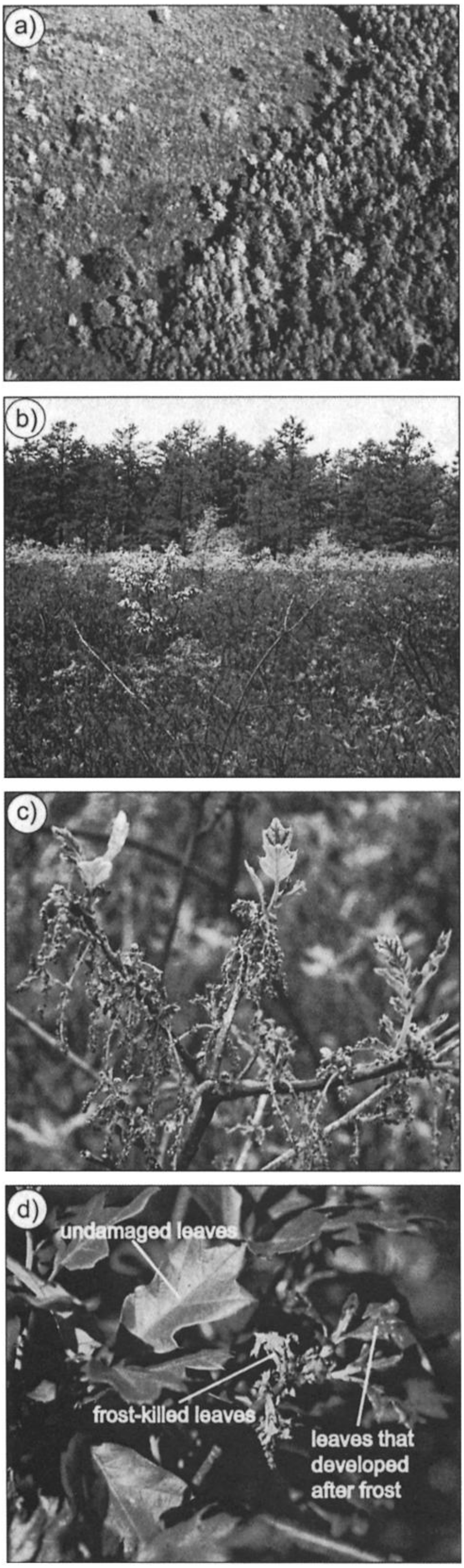

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FIG. 5. Variation in structure and phenology in scrub oak and pitch pine stands on Montague Plain: (a) aerial photograph of distinct boundaries between scrub oak and pitch pine stands, resulting from historical land-use; (b) phenological variation across the intensive study area in May 1997; (c) scrub oak stem with developing leaves and male flowers; (d) frost-killed, undamaged, and new scrub oak leaves that developed after a late spring frost. The photograph of the intensive study area (b) was taken from the central station looking towards the forest. The low scrub oak stems in the foreground had only recently broken bud (note small leaves), whereas the taller scrub oak stems adjacent to the forest had more fully developed leaves. Note also the presence of a few black cherry (*Prunus serotina*), a frost-tolerant species, emerging above the shrub thicket.

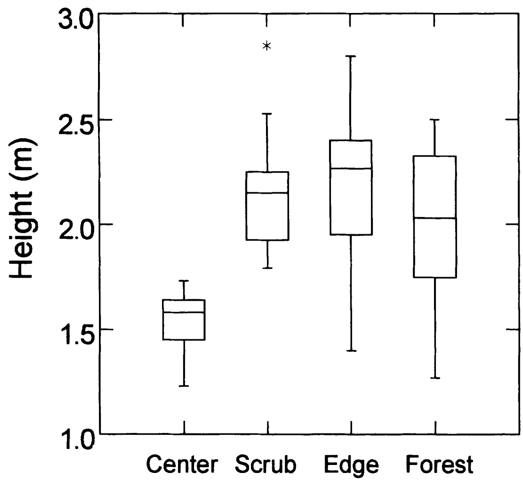

FIG. 6. Median height of scrub oak stems at the 'center', 'scrub', 'scrub edge', and 'forest' stations. Medians are indicated as the central line within each box, and boxes indicate the central 50% of the height data. Asterisks represent outliers.

drought stress associated with higher maximum temperatures in the center of the stand may also contribute to the structural variation. Thus, once established, a range of factors related to variation in microclimate, including short growing season, frequent late spring frosts, and perhaps drought stress, may contribute to the persistence of structural variation in these sites.

Because the frequency and severity of frosts decreases with increasing height above the low shrub canopies, an interesting feedback is established between the local microclimate and vegetation. The low stature of the scrub oak in the center of the site was maintained after the 1986 fire as a result of repeated frost damage or chronic short growing seasons, and, in turn, the low stature of the vegetation facilitates further frost effects by concentrating frost-sensitive foliage in the zone where it is most likely to be damaged. Repeated observations of the site since 1990 indicate that the short-term effect of frost events is strongly related to the timing of frosts relative to leaf-out in the spring. For instance, during the week of May 15, 2000, a severe frost occurred that killed all leaves on scrub oak at this site except for those on the tallest stems, above ~2.5 m. Because the scrub oak in the center of the stand had not broken bud at the time of this frost, leaves from these stems were not damaged. In the following week, the undamaged buds opened and the leaves on the short stature scrub oak were temporarily more mature than those of the taller stems that had been damaged and had not yet had time to re-sprout. By the following week, an additional, less severe frost occurred, with damage restricted to the central zone of short shrubs. Thus, after a brief period in which the shorter scrub stems had longer leaves than the taller stems, the leaves on taller stems once again were more fully developed. The central portion of the stand, with it's low vegetation, experiences the greatest number of growing season frosts (G. Motzkin pers. observ.) and, on average, experiences a shorter frost-free growing season than nearby portions of the stand that support taller stems.

HISTORY AND PERSISTENCE OF FROST POCKETS. Considerable uncertainty remains as to the long-term history and stability of frost-prone sites and scrub oak thickets on the landscape. In our extensive research on the history of sand plain vegetation across the Northeast (Motzkin et al. 1996, 1999; Foster and Motzkin 1999; Eberhardt et al. in press; Harvard Forest *unpublished data*), we have found no early historical references to frost-bottoms and few early references to scrub oak thickets, although early references to ' Shrubed plains' on Martha's Vineyard and 'barren, ragged plains' in several locations indicate that some areas dominated by frost-sensitive shrubs such as scrub oak did occur in the 17^{th} to early 19^{th} centuries (Foster and Motzkin 1999; Motzkin et al. 1999). It is therefore likely that some of these may have had compositional, structural, and functional similarities with modern 'frost pockets'. By the mid-to-late 19^{th} century, the frequency of references to extensive areas dominated by scrub oak or 'acorn bushes' increased (MA Archives 1830; Torrey and Allen 1962; Foster and Motzkin 1999; Motzkin et al. 1999), and numerous frost pockets were apparently created by cutting and fire in the historical period (Perry 1920; Hough 1945). For instance, in the mid 19^{th} century, Thoreau (Torrey and Allen 1962) observed numerous frost hollows in Concord, Massachusetts, frequently relating their development to the cutting and burning of forest trees:

> "It was a mistake for Britton to treat that Fox Hollow lot as he did. I remember a large old pine and chestnut wood there some twenty years ago. He came and cut it off and burned it over, and ever since it has been good for nothing. I mean that acre at the bottom of the hollow. It is now one of those frosty hollows so common in Walden Woods, where little grows, sheep's fescue

grass, sweet-fern, hazelnut bushes, and oak shrubs whose dead tops are two or three feet high, while the still living shoots are not more than half as high at their base. They have lingered so long and died down annually. At length I see a few birches and pines creeping into it, which at this rate in the course of a dozen years more will *suggest* a forest there. Was this wise?"

Similarly, frost pockets in the Allegheny Plateau of Pennsylvania apparently developed after logging and burning in the early historical period (Hough 1945). Large dead trees occur in some modern frost bottoms, further indicating that some of these sites were formerly forested (W. A. Patterson III, pers. comm.). The long-term persistence of such frost prone areas undoubtedly varies considerably, depending on the frequency and severity of frost events and other disturbances and the susceptibility of dominant species to frost damage. On our study site, in the absence of further disturbance, it is expected that structural variation within the site will lessen over time as: 1) the scrub oak in the central area becomes tall enough to avoid damage from all but the most extreme late spring frosts; and 2) scattered canopy trees emerge above the scrub oak and limit the amount of heat lost through radiational cooling (Geiger 1943; Schlegel and Butch 1980). Thus, the occurrence and ultimate disappearance of this phenomenon is largely controlled by the composition and height of the vegetation, with feedbacks between vegetation and frost damage delaying the development of a forest canopy that may eliminate this phenomenon. Petraitis and Latham (1999) have suggested that in some instances, feedbacks between vegetation and physical and biotic factors that develop as a result of disturbance may be sufficiently strong to allow for the persistence of alternate community states.

Although several studies indicate that plant species composition may vary according to degree of frost tolerance and local variation in frost frequency and severity (Cochran and Berntsen 1973), these relationships are poorly understood for many regions (Spurr 1957). In scrub oak stands, additional studies are necessary to determine the relationships between stand composition and structure and the distribution and abundance of a wide range of invertebrate taxa that are characteristic of scrub oak frost pockets. Observations from scrub oak-dominated frost depressions in coastal New England suggest that these sites may support an unusually high concentration of rare lepidopterans (Goldstein 1997). Thus, in some instances, cutting of overstory stems or use of prescribed fire may be warranted to create or perpetuate open, frost-prone scrub oak stands. However, caution is necessary, as some rare species are known to avoid frost pockets (Barnes et al. 1989). Interestingly, because many modern scrub oak stands developed as a result of historical cutting and burning of previously forested areas, some areas that currently are of great conservation interest support species assemblages and vegetation structure that have apparently been highly modified by human activity and are of relatively recent origin.

Our observations suggest that disturbance history and environmental variation may influence long-term vegetation patterns and dynamics not only through direct influences on composition, structure, and biotic interactions, but also through more subtle effects on relationships between the vegetation and the local environment. We have described such effects on local microclimate, and similar relationships are likely to effect a wide range of resources and environmental conditions.

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