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Reviewed work(s):

Source: *Bulletin of the Torrey Botanical Club*, Vol. 115, No. 1 (Jan. - Mar., 1988), pp. 32-44

Published by: [Torrey Botanical Society](#)

Stable URL: <http://www.jstor.org/stable/2996564>

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Character and distribution of American chestnut sprouts in southern New England woodlands

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ABSTRACT

PAILLET, F. L. (U.S. Geol. Survey, MS 403, Box 25046, Federal Center, Denver, CO 80225-0046). Character and distribution of American chestnut sprouts in southern New England woodlands. *Bull. Torrey Bot. Club* 115: 32-44, 1988.—American chestnut sprout populations were mapped on 14 sites of approximately 1 square kilometer in Connecticut and Massachusetts. Living sprouts were nearly continuous in distribution at 2 of the 14 sites, almost completely absent from 2 other sites, and sparsely distributed, with local concentrations of high density, on the remaining 10 sites. The highest densities of sprouts were found adjacent to old growth woodland that once contained chestnut seed sources. However, very few or no chestnut sprouts were found in the interior of old growth stands containing many chestnut snags and stumps. Differences in soil conditions and other natural factors do not fully account for the lack of chestnut reproduction on many of these sites. The absence of sprouts on suitable sites adjacent to former chestnut seed sources is attributed to the effects of former land use activities on chestnut seedling establishment in the years before chestnut blight, along with competitive exclusion of chestnut by more tolerant species on mesic sites. The present distribution of chestnut sprouts indicates that former forest edges, hedgerows, young stands of pioneer tree species in old fields, and shrub thickets on the margin of moist areas may have been especially suitable for chestnut seedling establishment. Some of these conjectures about the nature of chestnut seedling establishment are consistent with observations recorded by H. D. Thoreau in the mid-19th century.

Key words: chestnut, *Castanea dentata*, root sprouts, seedlings, mesic sites.

The ecology and growth form of American chestnut, *Castanea dentata* (Marsh.) Borkh., in New England has rarely been considered by modern scientists because it no longer is a major component of the eastern deciduous forest. American chestnut even has been cited as an excellent example of current extinction equivalent to other extinctions noted in the fossil record (Gleason 1964). Blight girdling of chestnut stems restricts sexual reproduction, and prevents chestnut stump sprouts from attaining a position in the forest canopy. The former niche occupied by chestnut trees seems likely to

be taken over by other forest tree species, unless an effective means of blight control is discovered in the near future (Braun 1950; Keever 1953; Mackey and Sivic 1973).

In spite of the damage caused by chestnut blight, *Castanea dentata* still is an abundant part of the deciduous forest more than 80 years after the original recognition of the disease (McCormick and Platt 1980; Adams and Stephenson 1983). Forest statistics maintained by the Connecticut Agricultural Experiment Station indicate that the small proportion of total stand basal area composed of chestnut stems has been increasing continuously since 1930 (Stephens and Waggoner 1980). The abundance of chestnut sprouting after canopy destruction by disease or clearcutting has been noted by several authors (Boring *et al.* 1981; Hebard *et al.* 1981). These observations indicate that American chestnut will be an important component of upland deciduous forests for many years to come.

In a recent study, Paillet (1984) investigated the growth form of chestnut sprout populations on test plots in Andover, Massachusetts, and concluded that destruction of individual sprout stems by blight rarely

¹ The author acknowledges the helpful comments and manuscript review provided by David Foster, William Patterson, Gordon Whitney, and Richard Phipps. Background data on the Connecticut Arboretum provided by William Niering, and on the Aton Forest by Frank Egler, were extremely helpful in defining the pattern of chestnut sprout distribution. The South Central Connecticut Regional Water Authority granted access to the Downs Road and West River sites. David Foster provided vital assistance in locating old records of forest conditions at Prospect Hill, and Sandra Anagnostakis added additional insight into chestnut distributions at the Cockaponsett site.

Received for publication on October 22, 1986 and in revised form October 1, 1987.

killed the whole sprout clone. Inspection of root crowns and the spacing of clones indicated that the majority of living chestnut sprouts had originated as seedlings, and not as sprouts from the roots or root crowns of former canopy trees. A similar conclusion was reached by Keever (1953). Early literature on chestnut sprouting supports the observation that sprouts originate from root crowns, and sprouting ability decreases with stem age after the first few decades (Zon 1904). American chestnut apparently does not propagate by sprouting from roots away from the root crown (Zon 1904). Therefore, vegetative reproduction was restricted to the slow expansion of root crown diameter. These conclusions indicated that the dense populations of chestnut sprouts in Andover were caused by the long term survival of an originally dense population of suppressed chestnut seedlings established before the appearance of blight in northeastern Massachusetts (about 1920).

The objective of the present study was to determine whether sprout clones were common in southern New England, and to explore the ecological character of the observed chestnut sprout populations. The occurrence of sprouts around mature tree stumps or trunks of former large chestnut trees also was examined. The sites selected for this study were chosen to consider differences in site character or stand history that could account for the observed differences in sprout population density.

Study Sites and Methods. Chestnut sprout populations and the distribution of the remains of former canopy chestnut trees were observed and described at 14 locations in southern New England (Fig. 1). Sites were selected to provide approximately 1 square kilometer areas where sprout distributions and the location of large chestnut logs and stumps could be mapped. Chestnut is known to avoid calcareous soil or soils developed on poorly drained alluvium (Hawley and Hawes 1925), but all of the study sites shown in Fig. 1 are located on well-drained upland sites with acidic or neutral soils developed on crystalline metamorphic or igneous rocks, or arkosic sediments. Most sites were found to consist of one or more cores of original (pre-1900) woodland, surrounded by larger areas of advanced stages of old field succes-

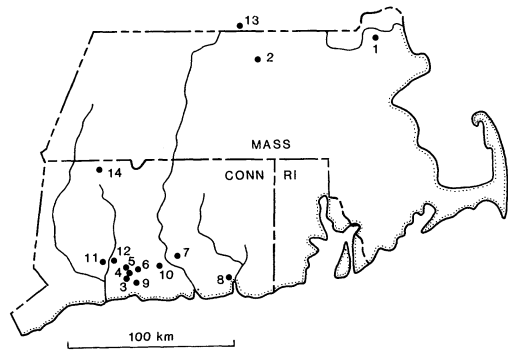


Fig. 1. Location of the 14 study sites in southern New England. 1) Wood Hill, Andover, Massachusetts; 2) Prospect Hill Tract, Harvard Forest, Petersham, Massachusetts; 3) West River Gorge, Bethany, Connecticut; 4) Unnamed ridge and adjacent valley, Downs Road, Bethany, Connecticut; 5) Mount Sanford, Bethany, Connecticut; 6) Brooksvale Park, Hamden, Connecticut; 7) Salmon River State Forest, Moodus, Connecticut; 8) Connecticut Arboretum, New London, Connecticut; 9) Sleeping Giant State Park, Hamden, Connecticut; 10) Cockaponset State Forest, Connecticut; 11) Spruce Brook Ravine, Naugatuck, Connecticut; 12) Beacon Hill, Naugatuck, Connecticut; 13) Pisgah Tract, New Hampshire; and 14) Aton Forest, Norfolk, Connecticut.

sion. Chestnut sprout and log locations were mapped by traversing sites in a grid by compass, and noting the approximate location of sprouts and logs on maps developed from U.S. Geological Survey 7½-minute quadrangle maps. More detailed maps of plots less than 1 hectare in area were made at locations of further interest. Chestnut wood is distinguished from the wood of other ring-porous angiosperms by the lack of rays, the characteristic red-brown color, and other properties (Panshin *et al.* 1964). In most cases, stand age and canopy history were inferred from growth rates and stem ages determined from increment borings made in selected trees. Ring counts were checked against counts made from recently cut trees when such fresh stumps were available. Most ring counts were made on site using a hand lens and cores from oaks and other tree species with readily identified rings.

The southern Connecticut sites (Mount Sanford, Sleeping Giant State Park, Brooksvale Park, and Downs Road) were described by Paillet (1982), and the Andover site by Paillet (1984). Vegetation changes over time at the Connecticut Arboretum have been documented by Hemond *et al.* (1983). The

Table 1. Chestnut sprout population density and pre-blight chestnut wood on the 14 study sites.

Forest type	Site type	Stand age (yr)	Approx. area surveyed (km)	Sprout density	Old wood density	Per cent hemlock
1. Wood Hill, Andover, Massachusetts						
Coppice oak	dry	40-50	1.0	A	C	0
Old field	med. moist	40-60	2.0	C	E	0
2. Prospect Hill Tract, Harvard Forest, Petersham, Massachusetts						
Old growth woodland	med. moist	70	0.5	E	B	50-90
Coppice oak	dry	50	0.25	A	C	10
Advanced old field	med. moist	50-60	1.0	B	E	10
Plantation	med. moist	50	0.25	C	E	0
3. West River Gorge, Bethany, Connecticut						
Old growth woodland	med. moist	100	0.5	E	A	70-100
Coppice oak	dry, med. moist	60-70	0.5	D	D	10
Advanced old field	dry, med. moist	80	0.5	E	D	20-30
4. Downs Road, Bethany, Connecticut						
Coppice oak	dry	40-60	1.0	E	C	10
Advanced old field	dry, med. moist	40-80	1.0	D	E	10-20
5. Mount Sanford, Hamden, Connecticut						
Coppice oak	dry	70-100	1.0	D	E	20-30
6. Brooksvale Park, Hamden, Connecticut						
Old growth woodland	med. moist	70-100	1.0	C	D	25
Advanced old field	med. moist	80	2.0	C	E	0
7. Salmon River State Forest, Moodus, Connecticut						
Old growth woodland	med. moist	100	1.0	D	D	50-100
Advanced old field	med. moist	100	0.5	D	D	30-50
8. Connecticut Arboretum, New London, Connecticut						
Old growth woodland	dry	100	0.25	D	B	50-100
Advanced old field	dry, med. moist	60	1.5	E	E	10
9. Sleeping Giant State Park, Hamden, Connecticut						
Old growth woodland	med. moist	100	0.25	E	B	50-100
Coppice oak	dry, med. moist	50-70	1.0	D	C	10
Advanced old field	med. moist	60-70	0.25	B	E	0
10. Cockaponset State Forest, Connecticut						
Coppice oak	dry	70-80	1.0	C	B	0
11. Spruce Brook Ravine, Naugatuck, Connecticut						
Old growth woodland	med. moist	100	0.75	E	A	80-100
Burned ridgetop	dry	50-60	0.50	D	E	10
12. Beacon Hill, Naugatuck, Connecticut						
Coppice oak	dry	50-60	0.05	B	C	20
Burned ridgetop	dry	0-50	0.05	D	E	0

Code for description of sprout and old wood abundance on mapped areas:

Sprout density	Old wood density
A. Living chestnut sprouts continuously distributed with densities averaging greater than 50 clones/ha	Chestnut logs or stumps found throughout the woodlot
B. Living sprouts scattered throughout the woodlot, averaging less than 50 clones/ha, but with local concentrations	Chestnut logs or stumps found at numerous locations, but absent from others
C. Living sprouts present in the woodlot at many locations, but absent from others, and never abundant	Chestnut wood found at a few isolated locations
D. Isolated sprouts found at a few locations; otherwise absent	Chestnut wood found only as remains of isolated trees in fencerows or pasture shade trees
E. Sprouts completely absent	Chestnut wood completely absent

Table 1. Continued.

Forest type	Site type	Stand age (yr)	Approx. area surveyed (km)	Sprout density	Old wood density	Per cent hemlock
13. Pisgah Tract, New Hampshire						
Old growth woodland	med. moist	100	1.0	D	B	50-90
Advanced old field	med. moist	100	0.25	E	C	10
14. Aton Forest, Norfolk, Connecticut						
Old growth woodland	med. moist	100	0.5	E	B	50-90
Advanced old fields	med. moist to dry	100	0.2	C	B	10-90

prehistory of the Pisgah tract is described by Henry and Swan (1974). Background for the Prospect Hill Tract is given by Hibbs (1983), Spurr and Barnes (1983), and numerous earlier references listed in those papers.

Woodlands on the study sites were classified under one of five broad categories: old-growth woodland, coppice woodland, advanced old fields, recent old fields, and periodically burned ridgetops. Old growth stands were probably stands of mature trees before 1900. Coppice woodlands had been continuously forested for many years before 1900; they probably were cut many times, and usually have been cut at least once since 1920. Oaks and other tree species probably were well established in advanced old fields, so such fields probably contained a significant population of chestnut seedlings and saplings.

Three of the 14 sites mapped in this study were selected for more detailed mapping. Two of these sites represented the extremes of chestnut sprout populations (West River, with almost no living sprouts, and Prospect Hill with a nearly continuous distribution). The third site (Downs Road) was selected as a typical example of the intermediate sprout densities. Transects and stand reconstructions are used to show the relation among sprout distribution, woodlot boundaries and the location of pre-blight chestnut trees. Transects were constructed by recording the number of chestnut sprouts present in each 10-m section of 2-m-wide strips along the transect. The remains of pre-blighted chestnut logs and stumps were counted in 10-m-wide strips centered on the transect, with percentage hemlock canopy estimated by recording the percentage of

dominant and codominant stems within the wider strip.

Results. The results of the survey of the 14 sites (Fig. 1) are summarized in Table 1, and sample transects through three of the sites are given in Figs. 2-4. The density and distribution of living chestnut sprouts and the remains of pre-blight chestnut trees varied greatly among the various sites listed in the table. The living sprout distributions at the first two sites listed, Wood Hill, Andover, and Prospect Hill, Harvard Forest (Fig. 2), represent examples of the highest densities and most uniform distributions found anywhere in southern New England. Even at these sites, there are some locations where chestnut sprouts are not very numerous. Low sprout densities (Table 1) did not correlate with any specific conditions within advanced old field stands at Wood Hill, but the lowest sprout densities at Prospect Hill were associated with the hemlock-dominated interiors of the oldest stands (Fig. 3).

The West River Gorge (Fig. 4), Downs Road (Fig. 5), Mount Sanford, and Brooksvale Park sites in southern Connecticut are located within the same general area. Living chestnut sprout densities were much lower on these sites than those at Wood Hill or Prospect Hill (Table 1). Sprouts were highly clustered in distribution, with a few isolated sprouts found away from the main distribution. Remains of pre-blight chestnut stems also were highly irregular in distribution, with little correlation between modern clusters of sprouts and locations of old chestnut logs or stumps.

The Salmon River, Connecticut Arboretum, and Sleeping Giant State Park sites

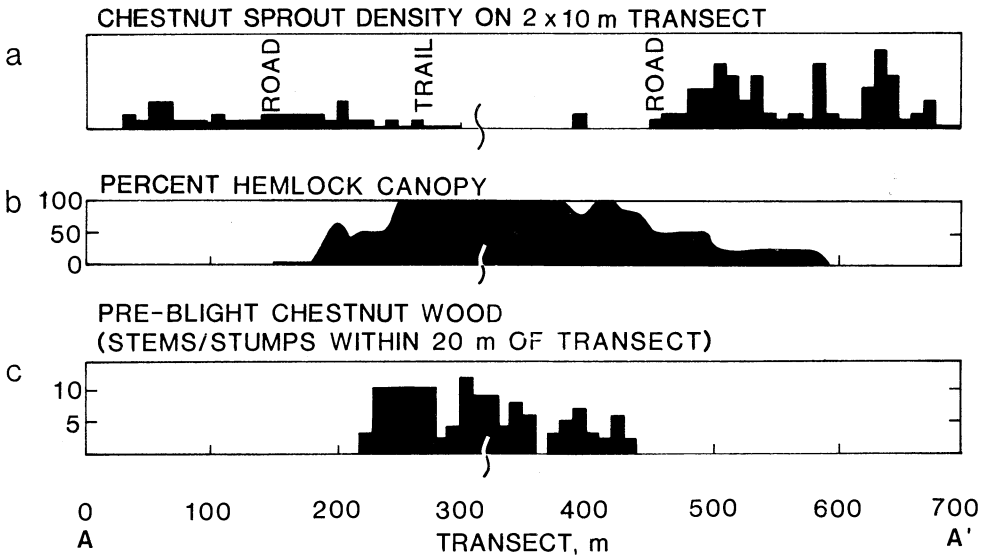
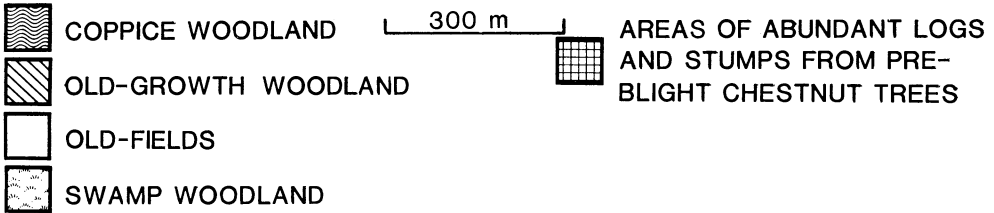
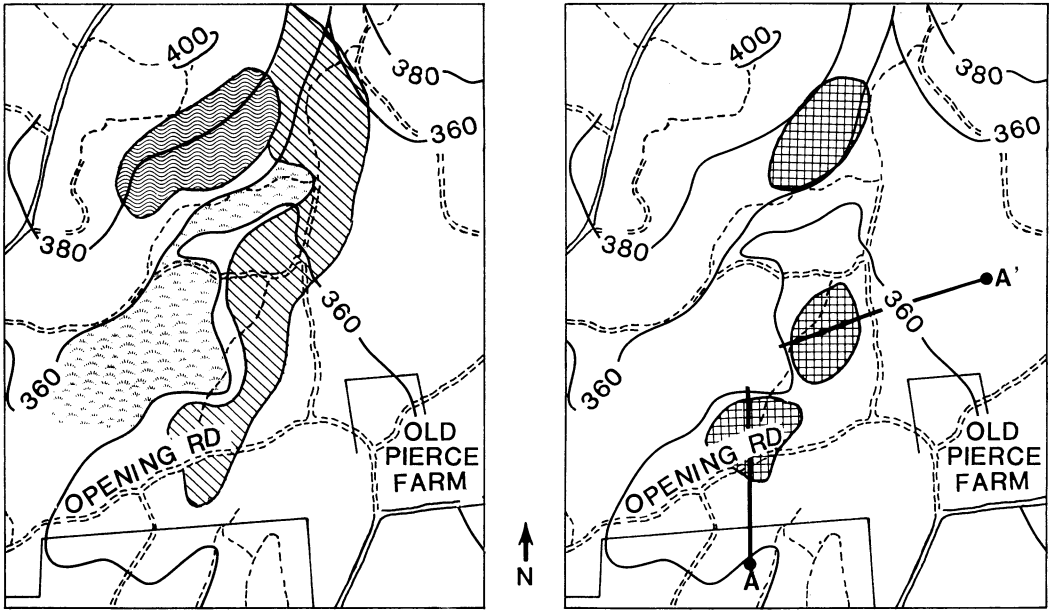


Fig. 2. Chestnut distribution at Prospect Hill: site map showing forest categories determined from Harvard Forest records, and transect showing a) chestnut sprout density; b) per cent hemlock canopy; and c) pre-blight chestnut wood.

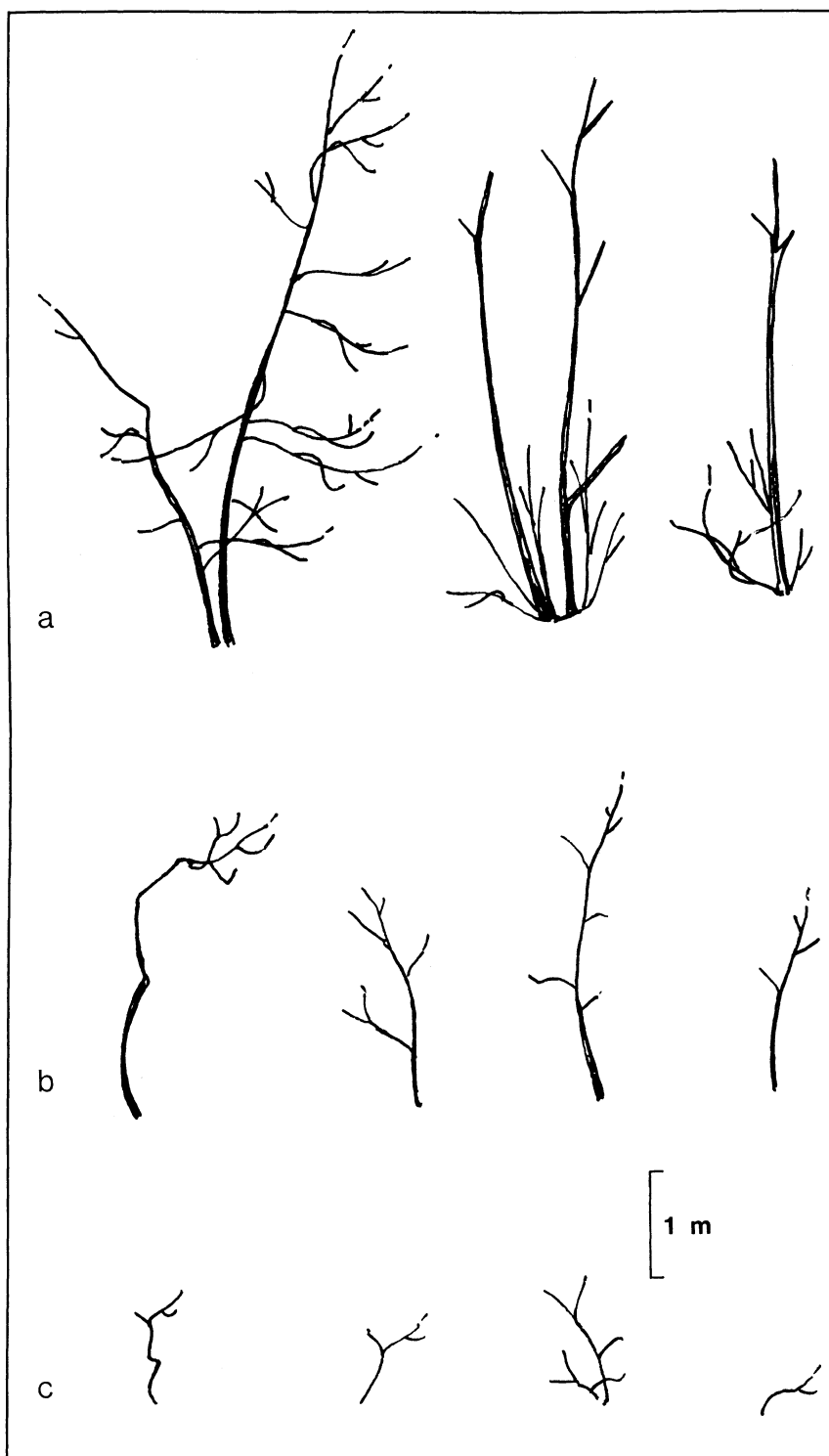


Fig. 3. Growth-form of chestnut sprouts along transect extending from white spruce plantation into old hemlock forest at Prospect Hill: a) sprouts under open spruce canopy; b) sprouts in mixed hemlock hardwoods; and c) sprouts under heavy hemlock shade.

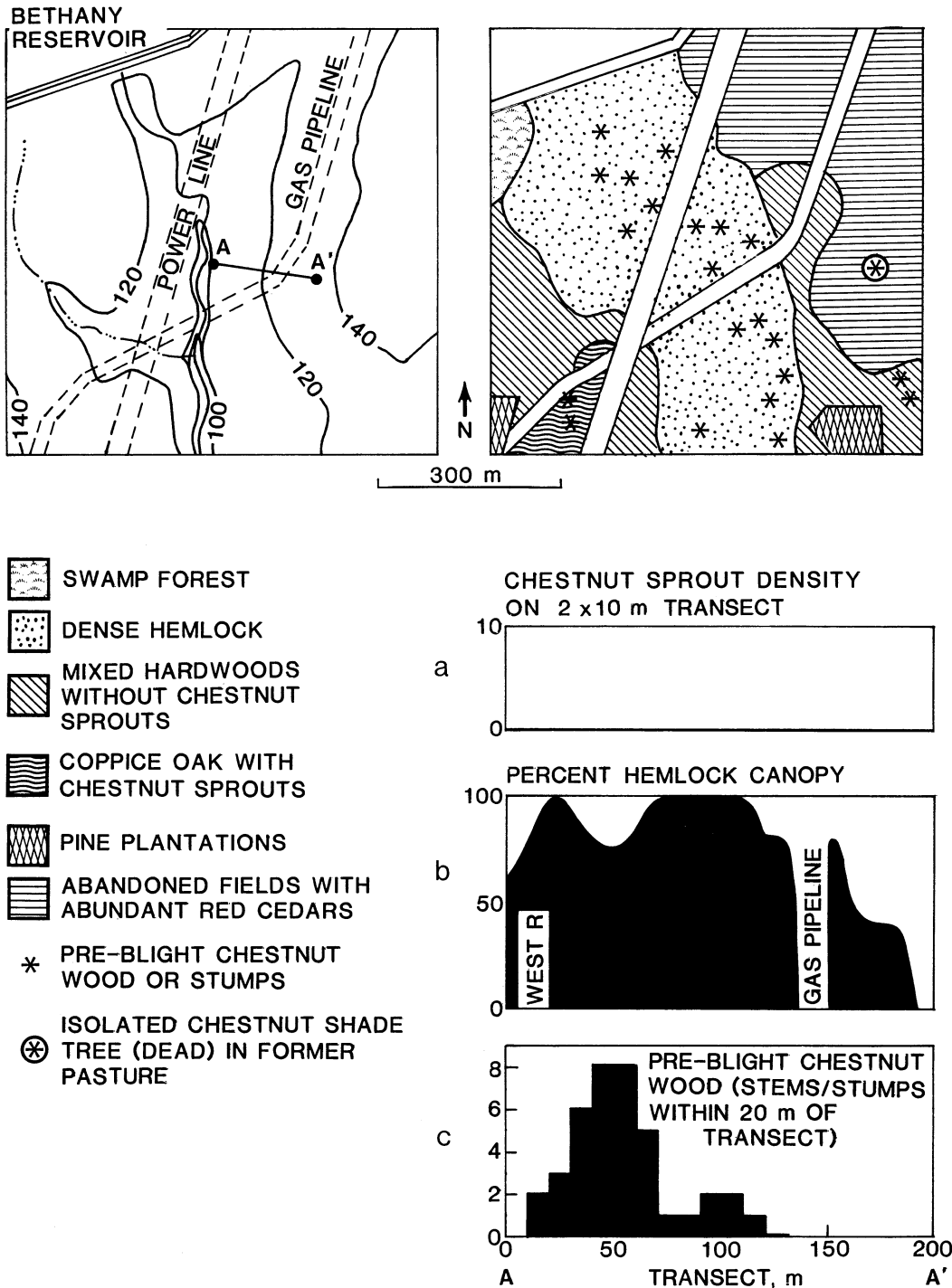


Fig. 4. Chestnut distribution at West River: site map showing distribution of forest types and living sprouts, and transect showing a) chestnut sprout density; b) per cent hemlock canopy; and c) pre-blight chestnut wood.

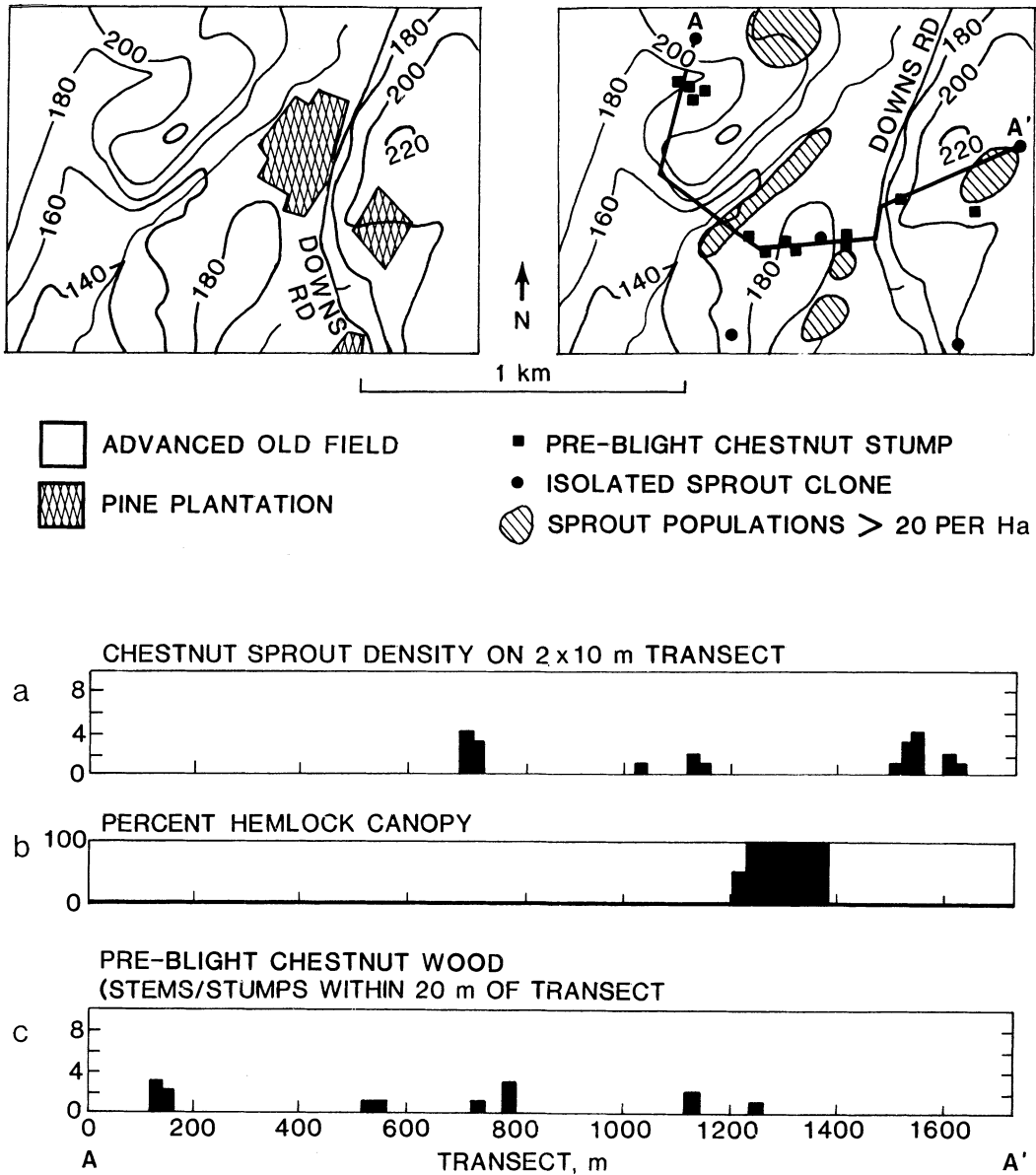


Fig. 5. Chestnut distribution at Downs Road: site map showing distribution of forest types and living sprouts: a) chestnut sprout density; b) per cent hemlock canopy; and c) pre-blight chestnut wood.

contained a somewhat higher percentage of old growth woodland than the other Connecticut sites. Remains of old chestnut trees were much more common at these sites, but living chestnut sprouts were not very numerous (Table 1). The only site with a small concentration of high sprout density was the Sleeping Giant State Park site. Even in that case, sprout densities were quite low over most of the area surveyed. Only a few living

sprouts were found at the Connecticut Arboretum in spite of the large number of pre-blight chestnut logs present under dense hemlocks on the northern part of the site. Isolated chestnut sprouts were distributed in an irregular manner in the hemlock-dominated woodland at the Salmon River site.

The Beacon Hill, Spruce Brook, and Cockaponset sites were selected as representative of typical exposed ridge sites (Ta-

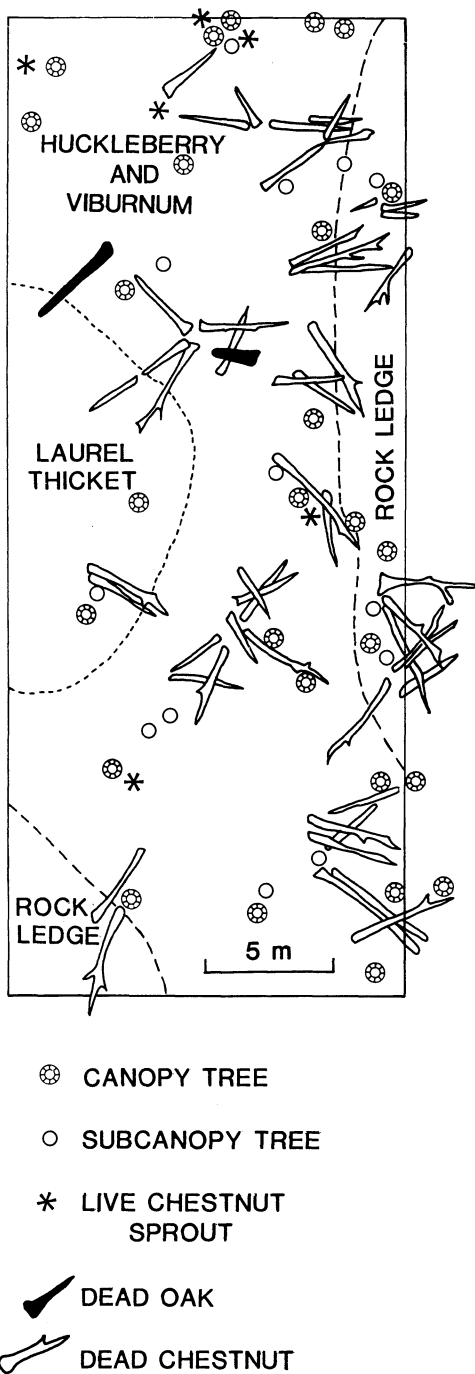


Fig. 6. Map of living chestnut sprouts and blight-killed chestnut stems on a typical gneiss ledge at the Cockaponset site.

ble 1). Living chestnut sprouts were moderately abundant in mid-slope woodlands, but were nearly absent from xeric ridgetops and mesic ravines. A nearly continuous dis-

tribution of chestnut stumps was found under a dense hemlock stand in the bottom of Spruce Brook Ravine, but no living sprouts were found in that location. Numerous remains of pre-blight chestnut trees were found on rocky ridges at Beacon Hill and the Cockaponset site (Fig. 6), but living sprouts were more numerous at more mesic locations downslope from these concentrations of chestnut wood.

The Pisgah Tract is located just north of the Massachusetts border in southern New Hampshire near the northern limit of the natural distribution of chestnut (Table 1). The surveyed portion of the site consists of a ridge dominated by oaks and other deciduous species, and adjacent hemlock-dominated woodland greatly disturbed by windthrow during the 1938 hurricane. Several concentrations of large pre-blight chestnut stumps were found on the ridge, and numerous chestnut logs and stumps in the hemlock-dominated woodland. No living sprouts were found on the ridge, with only a few, isolated chestnut sprouts found in more open portions of the hemlock stand. Sample cores taken from hemlocks adjacent to large chestnut stumps indicated that release associated with chestnut blight approximately 65 years ago resembled similar release events in earlier years, and after the 1938 hurricane.

The relatively small numbers of living chestnut sprouts found at the Aton Forest site were all associated with stone walls or old roadsides. Sprouts were found as isolated individuals along the old town road, and in small clusters extending along stone walls or former split rail fences. Moderate numbers of pre-blight chestnut logs and stumps were also found. Many of these former trees had originated in or adjacent to stone walls and roadsides. Moderate numbers of pre-blight logs were found in the one small stand of old growth forest, but no chestnut sprouts were found on that portion of the site.

Discussion. The distribution of living chestnut sprouts on the 14 sites mapped in this study indicates two general patterns: 1) the absence or scarcity of sprouts in the understory of mature woodlands that once contained many large chestnut trees; and 2) the highly variable densities of sprout pop-

ulations in formerly abandoned fields surrounding those old growth woodlands. The limited distribution of old growth woodland and the inverse correlation between chestnut sprout densities and pre-blight chestnut tree remains at the Prospect Hill site are indicated in Fig. 2. The chestnut sprout densities on the transect portrayed in Fig. 2 represent the upper limit of chestnut sprout densities measured on the 14 sites. The opposite extreme is illustrated by the West River site (Fig. 4). Chestnut sprouts were absent from the interior of old growth woodland at West River, but there also were no sprouts in the adjacent abandoned fields, or in the vicinity of a large blight-killed chestnut located beyond the eastern end of the transect. Living chestnut stems mapped at the West River site were limited to a few sprouts located in coppice oak woodland on the southwestern edge of the mapped area.

The difference between the chestnut sprout densities at Prospect Hill and West River typifies the variation in chestnut sprout density found among the 14 sites. In some cases, such variations in sprout density were evident within the area mapped at a single site (Fig. 5). The over-all density of chestnut sprouts on the Downs Road site was quite low, but several small locations within the area mapped in Fig. 5 contained sprout densities approaching those found at Prospect Hill. The transect in Fig. 5 was constructed to pass through two such concentrations, and along the edge of a third. This was the only site not containing a clearly-defined central core of old growth woodland, but pre-blight chestnut trees were present in fencerows, and as isolated groves in former pasture. The great variation in chestnut sprout abundance between the Prospect Hill and West River sites, and within different portions of the Downs Road site, appears to be one of the most significant characteristics of the modern distribution of chestnut sprouts in New England.

Evaluation of the known ecological requirements of chestnut indicates that soil conditions, site topography, and forest succession might influence chestnut abundance. Early forestry literature indicates that the natural distribution of chestnut avoided poorly drained or calcareous soils, and that chestnut was especially prone to frost damage by cold air drainage into topographic

lows (Frothingham 1912; Hawley and Hawes 1925; Russell 1987). Chestnut also is classed as a relatively intolerant species which could be excluded by competition with more shade tolerant species in old growth woodlands (Hawley and Hawes 1925). The first two factors, soil and topography, do not appear to be important in determining the irregularity of chestnut sprout distribution on the 14 sites. All sites were selected to contain abundant remains of pre-blight chestnut, so these sites appear to have once been suitable for that species. Modern forests on the sites are dominated by oak and other species typically associated with chestnut in pre-blight forests. Although there are some small parts of poorly-drained soils in some of the mapped areas, all sites are primarily composed of medium-moist to dry uplands with well-leached, acidic soils developed on glacial till overlying igneous or metamorphic basement rocks. Differences in soil type or topography do not appear to explain the great difference in modern sprout density between the Prospect Hill and West River sites, especially when one considers the large amount of pre-blight chestnut wood found at both sites.

The relative intolerance of chestnut does appear to be an important factor in limiting chestnut sprout densities on at least some of the 14 sites. For example, the transect shown in Fig. 2 indicates a strong negative correlation between hemlock canopy and chestnut sprout density. A definite pattern in the vigor of chestnut sprouts also was apparent, with the size and growth rates of chestnut sprouts decreasing towards the interior of hemlock-dominated stands (Fig. 3). The inverse correlation between hemlock canopy and chestnut sprout density is not as clearly indicated at West River and Downs Road because of the more irregular distribution of sprouts at those sites. However, chestnut sprouts were either absent or very rare underneath hemlocks at all 14 sites. Those few entries in Table 1 in which low chestnut sprout densities are associated with hemlock-dominated woodlands represent limited numbers of sprouts located in small, hardwood-dominated openings. The consistent association of hemlock-dominated canopies with abundant pre-blight chestnut wood at many of the study sites appears to indicate the process of forest succession and

land abandonment following intense agricultural activity in the early 19th century (Cronon 1983). The release of suppressed hemlock saplings by blight destruction of a chestnut-dominated canopy may have been an important factor in the origin of modern hemlock-dominated stands at some of the sites as reported for southeastern Massachusetts by Jacobsen and Bradshaw (1981).

Although exclusion of intolerant chestnut by hemlock appears to have influenced chestnut sprout abundance in the interior of some old growth stands, the lack of chestnut sprouts on other sites appears related to other factors. For example, Fig. 6 indicates the distribution of chestnut sprouts on a former chestnut-dominated ridgetop on the Cockaponest site. The modern density of chestnut sprouts is much lower than the density of pre-blight chestnut stems. In addition, the modern forest is relatively open, and free of competition from shade tolerant species. This site appears similar to many other upland sites with much more abundant chestnut sprout populations. An extreme example of chestnut sprout absence under a completely hardwood-dominated canopy is given by a ridge adjacent to the hemlock-dominated forest on the Pisgah site. No chestnut sprouts were found on this ridge even though there were numerous stumps from large, pre-blight chestnut trees. The absence of chestnut sprouts from such upland sites apparently cannot be attributed to soil conditions, topography, intolerance, or lack of seed source.

The inability of natural site conditions to fully explain the irregularity of chestnut sprout distribution indicates that land use conditions and the disturbance regime imposed by a declining agricultural economy may have had an important effect on chestnut reproduction. This hypothesis is supported by the character of the chestnut sprout distribution on many of the study sites. The association of local concentrations of chestnut sprouts with former woodland edges was noted at the Sleeping Giant and Connecticut Arboretum sites. Chestnut sprouts were absent from the xeric ridgetop and old growth woodland at Spruce Brook, but were relatively common in the intervening younger, mixed woodland. Chestnut sprouts were completely absent from stands containing numerous pre-blight chestnut stems at the

Aton Forest site. However, some living sprouts were found distributed along existing stone walls, former wooden fencerows, and the edge of the old town road. Such a distribution corresponds to the distribution of seedlings and saplings around an introduced plantation of Chinese chestnut (*C. mollissima* L.) reported by Jaynes (1967). In that case, the increased density of seedlings along stone walls was attributed to the pattern of seed dispersal by rodents. The chestnut sprout distribution at the Downs Road site (Fig. 5) indicates an association between the edges of relatively moist areas and chestnut sprout abundance. Three of the five locations with dense chestnut sprout populations occur along small streams, while the other two are located in small depressions forming the sources of first order drainage channels. Although it is now difficult to infer conditions in these locations at the time before the appearance of chestnut blight, the edges of such moist areas may have offered cover for rodents in a much more open agricultural environment. Land use conditions otherwise appear to at least partially explain local differences in chestnut sprout densities because records show that fields at Prospect Hill were abandoned long before the appearance of chestnut blight, while at least part of the West River site was being grazed until transformed into public watershed after 1920.

Some additional insight into chestnut seedling establishment and sprout growth can be obtained from reports written before the appearance of chestnut blight. Zon (1904) and Matoon (1908) indicate that the ability of chestnut root crowns to sprout declines with age, becoming very low after a century. Chestnut trees originating from seed apparently retained the ability to resprout from root crowns longer than trees starting as sprouts from large stems. These observations support the hypothesis of Paillet (1984) that most modern chestnut sprouts in New England originated from seedlings and not canopy trees. The modern distribution of sprouts may, therefore, reflect the distribution of seedlings at the time when chestnut blight destroyed large chestnut trees, and greatly diminished the source of chestnut seed.

The journals of Thoreau (1906) contain numerous references to chestnut trees, seed-

Table 2. Summary of observations on chestnut contained in the field notes of H. D. Thoreau for the years 1860–1862.

Generalized observation	Page, Vol. XIV
Large chestnut trees uncommon; agricultural and forestry practices likely to inhibit establishment of such slowly-reproducing trees as chestnut and hickory	133, 134, 137
Chestnut outgrows oak as both seedling and stump sprout	136, 137, 184, 252
Seedlings or apparent seedlings more common under cover of pioneer tree species (pitch pine) than in established oak forests	135, 136, 140, 144, 148, 168, 188
Chestnut seedlings have a much finer root structure than oak seedlings	128, 129, 158
Chestnut seedlings and saplings surprisingly common at a distance from known seed sources	137, 188
Stump sprouting in both oak and chestnut is erratic; some do and some don't under identical conditions	121, 165, 167, 168, 177, 184, 188
Large chestnut trees in possible remnants of original forest have large, nearly horizontal side branches close to ground level	216, 244

lings, and sprouts in the middle 19th century when the process of land abandonment in New England had just begun (Cronon 1983; Whitney and Davis 1986). A summary of Thoreau's observations is given in Table 2. These references confirm that the chestnut seedling distribution was correlated with forest conditions and land use activities. One important observation is that chestnut seedlings were much more abundant under pines and other pioneer tree species in abandoned fields than under established oak and chestnut canopies. Thoreau's observations otherwise support the conclusion that the distribution of chestnut seedlings did not correlate with the distribution of established chestnut trees, and that land use conditions had an important influence on seedling establishment.

All of these observations provide useful insight into the reproductive strategy for *Castanea dentata*. Emplacement of mature chestnut trees in the forest canopy apparently depended upon the slow establishment of a population of hardy, suppressed stems. Poorly formed, but living chestnut sprouts were present under dense hemlock canopies at Prospect Hill, demonstrating a surprising degree of tolerance for this species. Seedling establishment was apparently the critical stage in chestnut reproduction. Local concentrations of sprouts in some areas with low chestnut sprout densities apparently indicate sites that offered protection for newly established chestnut seedlings. The character of chestnut sprout concentrations identified on the study sites described here indicates that such protection may have been provided by concentrations of brush and

dense thickets of saplings at former woodlot edges, along fence rows and roadsides, or along the perimeter of wet areas.

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