

## Growth-form and ecology of American chestnut sprout clones in northeastern Massachusetts<sup>1</sup>

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PAILLET, F. L. (U.S. Geological Survey, Denver, CO 80225). Growth-form and ecology of American chestnut sprout clones in northeastern Massachusetts. *Bull. Torrey Bot. Club* 111: 316-328. 1984.—The present distribution of chestnut sprout clones in Andover, Massachusetts, includes areas with abundant stumps from canopy trees killed by blight before 1922, and former abandoned pastures adjacent to woodlots that once contained mature chestnut trees. Sprout densities range from less than 1 to more than 200 living clones per hectare. Greatest densities occur in areas with abundant logs and stumps from preblight chestnut trees, but some areas with abundant chestnut wood have very few living sprouts. Limited numbers of chestnut sprouts were found with living stems growing from small knobs of cambium on the root collars of otherwise completely dead stumps of former canopy trees. More than 95 per cent of all observed chestnut sprouts show no connection with remains of preblight trees, and almost all appear to have been through several cycles of blight infection. The distribution pattern of these sprouts indicates that they originated as suppressed seedlings established before 1922 and not as sprouts from the roots of canopy dominants. No signs of recent seedling establishment or vegetative reproduction by sprouting from roots away from the root collar on either small live sprouts or long dead chestnut stumps were found. Vegetative reproduction is now occurring by relatively rare instances of layering, and by slow expansion and division of root crowns at a rate which probably more than offsets the low mortality of entire clones. Chestnut sprouts that have escaped blight for many years indicate that the natural growth condition of suppressed chestnut seedlings is a single stem with controlled release of individual basal buds. This process involves a complex mechanism for apical control of the entire clone that appears to be part of a definite reproductive strategy.

Key words: American chestnut, *Castanea dentata*, seedling sprouts, reproductive strategy

On the basis of the classical theory of competing forest tree species (Gleason 1964), the American chestnut (*Castanea dentata* (Marsh.) Bork.) has been dealt a severe blow by the introduction of the chestnut blight (*Endothia parasitica* (Murr.) And.). This introduced fungal parasite effectively girdles chestnut stems before they become more than a few centimeters in diameter. The disease was introduced by infected foreign wood in New York sometime after 1900, reaching the northern limit of chestnut in Maine by 1930, and the southern limit of chestnut in Alabama sometime after 1950 (Hepting 1974). The ecological

effect of chestnut blight in former oak-chestnut forests is the complete elimination of chestnut from the forest canopy, and the severe limitations of sexual reproduction by those chestnut sprout systems that are able to persist (Shelford 1963; Mackey and Sivic 1973). The classic theory of competition indicates that these effects should eventually remove *Castanea* from any significant role in eastern deciduous forests. It has been noted consistently, however, that chestnut sprouts remain an important component of vegetation throughout many locations within the former range of the oak-chestnut association (Adams and Stephenson 1983; McCormick and Platt 1980; Keever 1953). In one instance where all canopy and subcanopy stems have been monitored over time, chestnut sprouts have been increasing continuously in size and number (Stephens and Waggoner 1980). Chestnut sprouts also are one of the dominant woody components in the early revegetation of clear-cuts in the southern Appalachians (Boring *et al.* 1981).

Many tree species in New England pro-

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duce sprouts when injured or cut. For at least one species, the American beech (*Fagus grandifolia* Ehrh.), root sprouting is a major form of reproduction (Fowells 1965). For most of the common species in the oak-chestnut forests of southern New England, sprouting from root crowns is an adaptation to such injuries as stem breakage and fire (Braun 1950). It is assumed that the resources available in the root systems of such injured stems provide an advantage in situations where surface fires do not severely damage underground parts of plants, and where soil conditions inhibit the initial growth of seedlings. If modern chestnut sprouts persist largely because of the previous abundance of chestnut root systems, one would expect chestnut biomass to exhibit the exponential decline characteristic of reservoir depletion. The data given by Stephens and Waggoner (1980) indicate that living chestnut stems had begun to depart from such a decline before 1940, or within two decades after the appearance of blight in the New Haven area. The subsequent increases in chestnut stem density and chestnut basal area indicate that living chestnut sprouts have been capable of producing more than enough photosynthetic reserves to offset regular losses of stem biomass to blight destruction, while accounting for the observed increase in living stems.

Previous work in southern New England has shown that chestnut sprouts are especially effective competitors in filling canopy gaps created by the defoliation-induced mortality of canopy oaks (Paillet 1982). This observation led to the hypothesis that the modern abundance of chestnut sprout clones results from the existence of a shrub stage as a natural part of the chestnut life cycle. According to this theory, chestnut stems are preadapted for competition with shrubs as part of a strategy for canopy emplacement similar to that described for other forest trees by Oliver and Stephens (1977). This adaptation for suppressed survival has permitted the species to survive in a "shrub" stage in spite of the severe biomass depletions imposed by blight. This study was undertaken in an effort to identify the modes of vegetative reproduction employed by chestnut sprouts in the modern forests of New England. Cook

(1983) and Legere and Payette (1981) discuss some of the important ecological advantages inherent in vegetative reproduction. The study of chestnut growth form and possible clone propagation may help explain the conditions in prehistoric oak-chestnut forests that resulted in the relative abundance of chestnut stems reported by Braun (1950) and Whittaker (1956). An understanding of the conditions under which the reproductive strategy described by Paillet (1982) becomes especially effective may also provide important insight into the late Holocene climatic transition recorded by the abrupt increase in chestnut pollen in New England sediments (Deevey 1939, 1943; Davis 1969; Watts 1980).

**Study Site and Methods.** The study area is located in Andover and North Tewksbury in Essex County, Massachusetts. The study focuses on approximately 20 square kilometers of rolling upland south of the Merrimack River in the central portion of the region that is shown by the U.S. Geological Survey 7-1/2 minute Lawrence quadrangle map. The parts of this area mapped in detail are located on the Harold Rafton Reserve owned by the Andover Village Improvement Society, and adjacent lands owned and managed by the Andover Conservation Commission. The central portion of this site is dominated by Wood Hill, which was apparently named after the small coppice woodlot that once dominated an otherwise open agricultural landscape.

The woodlands in the study area consist of mixed oaks of sprout origin or former old fields now dominated by more diverse mixtures of pine, oak, aspen, birch, hickory, and ash. Many of the old-field forests contain numerous dead red cedars (*Juniperus virginiana* L.), large mats of common juniper (*J. communis* L.), and senescent pitch pines (*Pinus rigida* Mill.); all of these species are indicators of once heavily grazed fields. There are extensive adjacent lowlands dominated by maple-elm forests that contain no chestnut, and therefore were not surveyed in detail. The core area of forest on Wood Hill has apparently remained as woodland for an extensive period, although the oaks have been repeatedly cut. These coppice woodlands contain a very

large percentage of the sprouting oaks (northern red oak, *Quercus rubra*; black oak, *Q. velutina* Muench.; and scarlet oak, *Q. coccinea* Lam.) with relatively smaller proportions of other oaks, hickory, and pine. The coppice woodlands contain a well-developed shrub layer composed of sheep laurel (*Kalmia angustifolia* L.) and huckleberry (*Gaylussacia baccata* Wang.), with a discontinuous stratum of such higher shrubs as mountain laurel (*Kalmia latifolia* L.) and various *Viburnum* spp.

The Wood Hill area has been protected from disturbance for at least 20 years. Firewood cutting has been prohibited on these public lands, and there have been no signs of deer browsing in recent times. Old-field stands were selectively cut for the largest white pines (*Pinus strobus* L.) at various times in the 1940's and 1950's. Ground fires have occurred during earlier decades, but no recent fires have occurred except in one small location. This one exception was the study site for the effects of an intense ground fire on chestnut sprouting. Gypsy moth defoliation was extensive in the study area during 1982 on the basis of local reports and the extremely narrow growth ring produced by canopy trees during that growing season. Wood Hill apparently escaped extensive defoliation prior to 1982. The defoliation-related mortality of canopy oaks described by Ehrenfeld (1980) and Dunbar and Stephens (1975) has not occurred here.

The soils in the study area are developed on thin basal till overlying the granitic rocks of a Paleozoic intrusive body. These soils are classified as very stony loams of the Paxton and Canton series by Fuller and Hotz (1981). Both soil types are listed as extremely acidic and unsuitable for agriculture.

The distribution of chestnut within the study area was determined by surveying all woodlots indicated on the U.S. Geological Survey Lawrence quadrangle map (1952 edition) that appear to have been in at least the early stages of succession from old fields at the time of original appearance of chestnut blight in the area. In most cases, stand ages were verified by ring counts on increment borings made on canopy dominants. Surveys were made by walking compass lines across woodlots. The character of woodlots

(swamp forest, old fields, and coppice stands) usually could be determined from the aerial photographs included with the Essex County Soil Survey (Fuller and Hotz 1981). These tentative classifications were field-checked during surveys of chestnut distribution. Most increment cores from canopy trees were examined in the field for determination of stand age, periods of release, and age of fire scars. Cores selected for detailed chronologies were submitted to the U.S. Geological Survey Dendrochronology Laboratory for measurement of annual ring widths to the nearest hundredth of a millimeter according to the techniques described by Fritts (1976). Chestnut wood persisting from canopy chestnut trees killed shortly after the first appearance of blight in the study area was identified according to the criteria given by Panshin *et al.* (1964). Several old chestnut logs that remained in relatively good condition also were sectioned and submitted for increment measurements.

Five test plots from .3 to 1.0 hectare in size were selected for detailed study. All stems within these plots were marked and mapped. Chestnut sprouts within the mapped areas were sketched on graph paper using a specially constructed framework installed around the sprout clone in the field. Two-dimensional orientations were selected to display the maximum lateral displacement of leaning stems and major branches. The root crowns of all chestnut stems within mapped areas were exposed by the removal of leaf litter and the excavation of soil needed to determine the orientation of major roots. In almost all cases this could be accomplished with minimal disturbance to living sprouts. Several groups of closely-spaced sprouts were selected for more detailed excavation in an attempt to determine the existence of possible underground connections. Three large, pre-blight chestnut stumps were also excavated in cross-section in order to map possible connections with modern chestnut clones. Detailed growth histories of chestnut stems in the burned area were reconstructed by identifying the terminal bud scars on stems initiated after the fire that occurred before the 1979 growing season. Such growth histories could be determined unambiguously

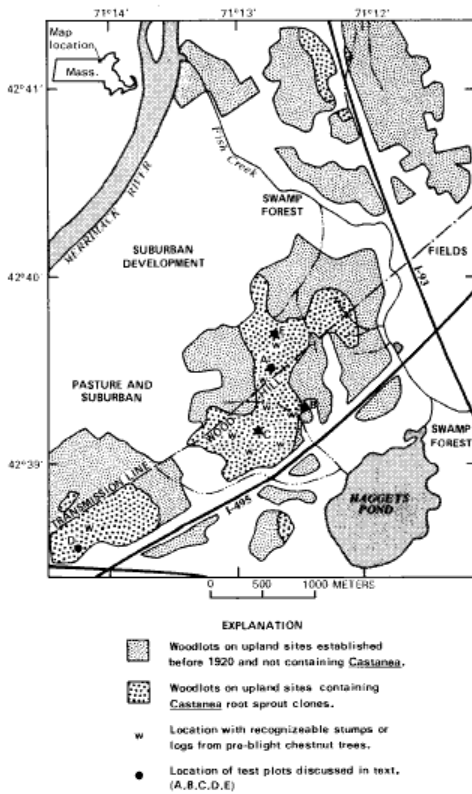


Fig. 1. Distribution of relatively undisturbed woodlands containing chestnut sprouts in the study area.

for all stems in the 14 separate sprout clones that were identified in the burned area.

**Results and Discussion.** CHESTNUT SPROUT DISTRIBUTION. The occurrence of chestnut sprouts within the study area is illustrated in Fig. 1. The figure shows the location of modern woodlots containing trees that are at least 60 years old, or that have been wooded for more than a century although cut at least once since 1920. Lowland maple-elm woodlands are not shown. The present occurrence of chestnut sprouts in western Andover effectively coincides with the distribution of coppice woodlands, with irregular extensions into former pastureland surrounding those woodlands. Increment borings and abundance of pitch and white pines indicate that a large proportion of the woodlands indicated in Fig. 1 were dominated by open stands of

the typical old-field invaders [pines, red cedar, and gray birch (*Betula populifolia* Marsh.)] during 1900. At that time, oaks and chestnut were just becoming established, probably with the aid of rodent dispersal from seed sources provided by large trees in fence rows.

The areas containing abundant wood from pre-blight chestnut trees are indicated in Fig. 1. The amount of this wood that still can be identified indicates that the chestnut comprised approximately 20 percent of canopy stems in established coppice woodlots and a smaller proportion of long-lived trees invading abandoned fields. Ring widths and diameters of old chestnut logs show, however, that chestnut may have been more important than indicated by the former proportion of chestnut stems in the canopy. Old chestnut logs consistently show larger growth rates and diameters than those observed in the cores taken from large oaks in the same woodlots. Large living oaks ad-

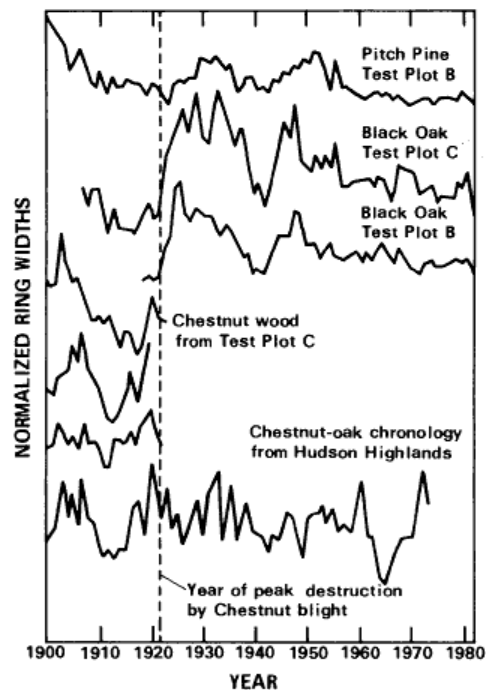


Fig. 2. Sample ring chronologies from test plots B and C showing release of suppressed oaks by death of chestnut trees during 1922; chestnut oak chronology from Dewitt and Ames (1978).

adjacent to the remains of dead chestnut consistently show large increases in growth rates at the time when chestnut blight first appeared in western Andover, indicating that many oaks were once suppressed by larger chestnut trees. Sample ring chronologies for large oaks in the study area are compared to the ring width trend in a representative pitch pine and a standardized chronology for chestnut oak in southeastern New York (Fig. 2). All increments have been normalized with respect to the largest measured increment for each tree. The two oaks indicate strong release starting in the 1922 growing season. The undated chronologies for the three preblight chestnut logs shown in Fig. 2 appear to match the 1914 drought in the chestnut-oak record from the Hudson Highlands of southern New York (Cook and Jacoby, 1978). These results confirm the maps of chestnut blight spread given by Hepting (1974) in that blight first appeared in the study area around 1920, and that most large chestnut trees on Wood Hill were dead or dying by 1922.

Observations on Wood Hill indicate that the small proportion of living chestnut sprouts that actually are derived from mature chestnut trees killed by blight before 1922 still are closely associated with the original stumps. In some locations, there are dense populations of chestnut sprouts dispersed among preblight chestnut logs and stumps. No instances of clustering of living sprouts around individual stumps was observed, with the exception of those few sprouts still directly attached to the stumps. In the instance of isolated chestnut stumps located in former pastures, the lack of correlation between old chestnut stumps and living sprouts is especially evident (Fig. 3). The six sprout clones located at this site (test plot B in Fig. 1) are all more than 30 meters from either of the two large, multiple-stemmed chestnut trees present in 1922. The sprouts are even further from other sprouts and old chestnut logs located beyond the limits of the area shown in the figure. All six of the sprouts shown in Fig. 3 consist of either a single stem more than 20 years old, or smaller stems arising from the base of a previously blight-killed stem.

The excavation of three preblight chestnut stumps provided definite indications that sprouting has been confined to

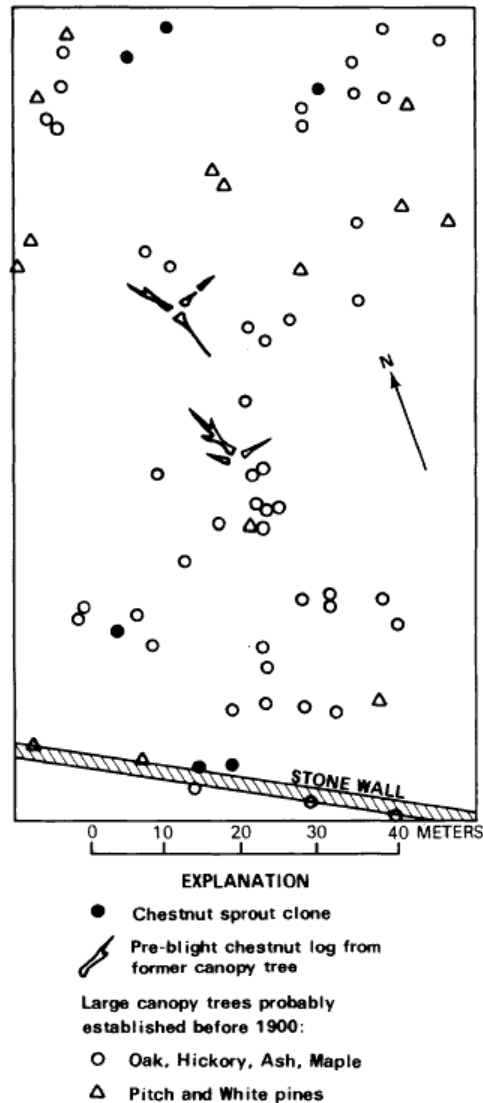


Fig. 3. Relationship between surviving chestnut sprouts, old canopy trees and pre-blight chestnut logs on test plot B.

the root collar of the original stump. A typical example is illustrated in Fig. 4. A multiple-stemmed stump with living and recently blight-killed sprouts attached to woody knobs located on the side of the old root collar is shown in the figure. Although the top of the stump appears rather sound, excavation indicated that most of the stump wood in close contact with moist soil was in

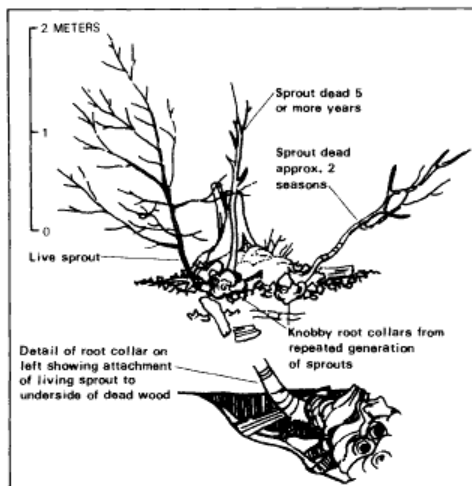


Fig. 4. Typical chestnut sprout attached to remains of preblight chestnut cut during salvage of standing dead timber around 1930.

an advanced state of decay. The two points on the stump from which repeated sprouting has occurred consist of multiple knobs of woody tissue, most of which also are now dead. The one living sprout attached to the stump arises from beneath a mass of such dead knobs, and appears to have developed its own independent root system after being initiated from the base of a previous sprout. The size of the knobby growths and the number of knotholes representing former stem attachment sites indicate that there have been five or more previous incidents of blight reinfection of this clone since 1922.

All sites in the study area with many fallen chestnut logs contain very few living sprouts attached to the roots of preblight trees. In the majority of cases, the spoke-shaped pattern of collapsed logs from multi-stemmed canopy chestnut indicates that these stems fell under their own weight after root-system decay. This pattern contrasts with the uniform northwest orientation and pronounced windthrow mounds of pines and oaks blown over by the 1938 hurricane. On some parts of Wood Hill, however, approximately half of the recognizable preblight chestnut stumps have living attached sprouts. In all instances of such high proportions of stump survival, living sprouts are associated with chestnut trees salvaged after 1922. The appearance of the living

sprout illustrated in Fig. 4 indicates why the salvage of chestnut wood should have had such an effect on stump survival. If the surviving sprouts arise from only the small knobs attached to the sides of root crowns, the toppling of long-dead chestnut snags can pull the sprouts out of the ground. In the few instances where living sprouts were associated with the base of a toppled chestnut snag, the sprout was attached to a large piece of root or portion of the stump left behind. In the majority of cases, the more rapid decay of roots in contact with moist soil enables the falling trunk to severely disrupt the original root crown.

**VEGETATIVE REPRODUCTION.** One of the most important questions about the modern distribution of chestnut sprout clones is the extent to which this distribution has resulted from vegetative reproduction since 1922. Although many larger chestnut sprout stems were cored during this study, the oldest documented stem had approximately 40 annual rings, whereas most larger sprout stems had from 15 to 25 rings. It is, therefore, clear that all living clones have stems which originated one or more decades after the destruction of the original canopy trees by blight in the 1920's. After studying the distribution of sprout clones on sites A, B, D, and E (Fig. 1), a larger area (site C) was selected for further study because of the high sprout density and unusually good preservation of the remains of preblight trees. The distribution of individual clones within this one-hectare area is illustrated in Fig. 5. Almost all of the individual clones mapped in the figure consist of either a single stem more than 20 years old and several centimeters in diameter, or 1 or more smaller stems arising from the base of an older, blight-killed stem.

Although the distribution of individual chestnut sprout clones in Fig. 5 shows some clustering, there is no pattern of clustering around the stumps and logs of preblight chestnut. Several closely spaced sprout clones were excavated with a hand trowel, but definite instances of root sprouting at a distance of more than 10 centimeters from an established sprout clone could not be found. There also are no indications from the patterns of sprout distribution anywhere within the study area that sprouts are reproducing by root suckering as de-

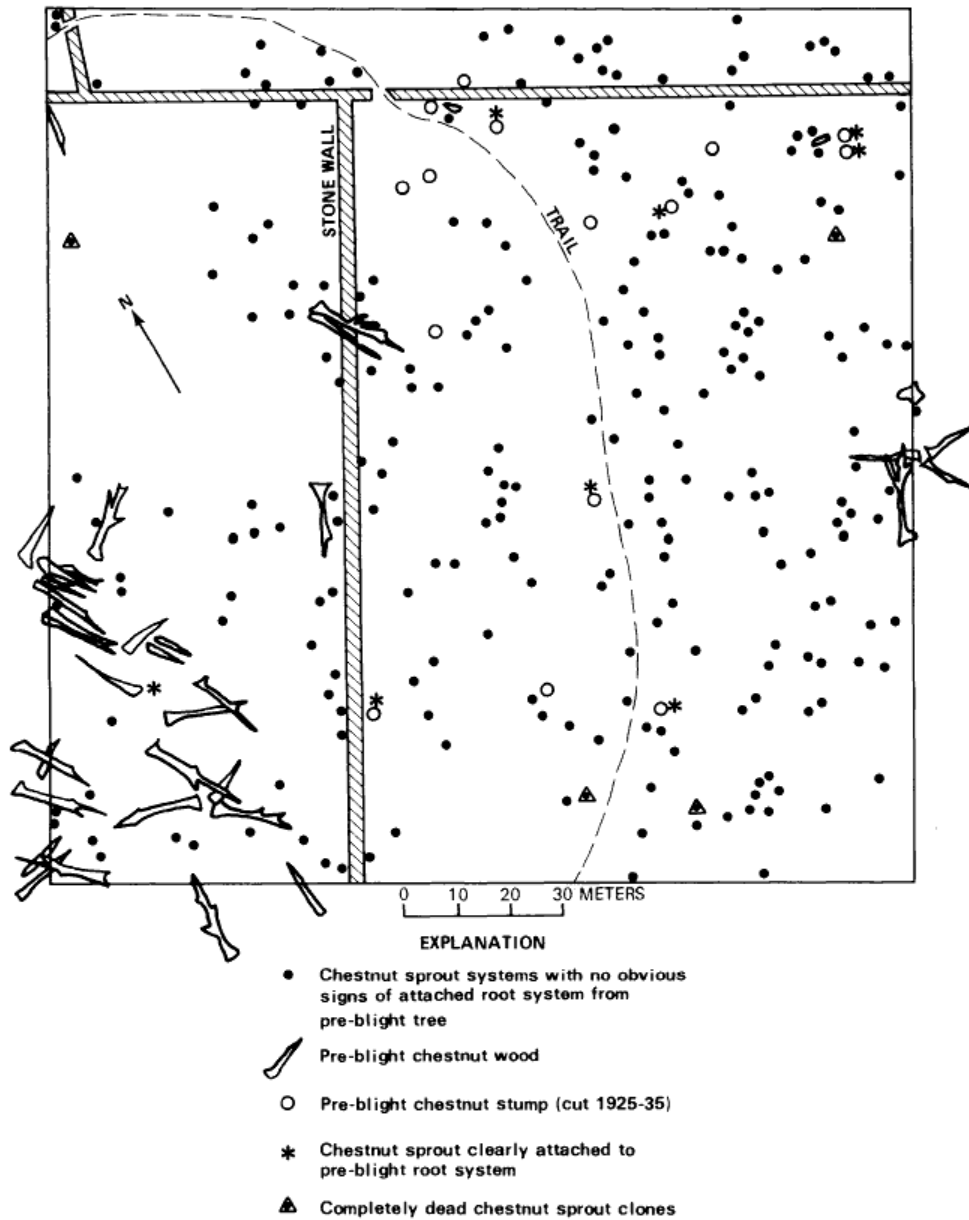


Fig. 5. Chestnut sprout clone distribution on test plot C.

scribed for some regional varieties of beech by Fowells (1965), Held (1983), and Vankat *et al.* (1975). Mapping of the area that burned during early 1979 (test plot D, Fig. 1) indicated that all sprouts have arisen from the root crowns of standing dead chestnut sprouts killed by the fire. Size and vigor of

living sprouts appear to correlate with the size of the prefire stems, and no signs of sprouting away from the root crowns could be detected. One unusually large sprout clone located in the transmission line right-of-way (Fig. 1) has been repeatedly treated with herbicide. This vigorous, open-grown

clone has responded to the repeated effects of herbicide injury and blight reinfection by resprouting from all points on the circumference of the enlarged root crown, but shows no indications of root sprouting. The only forms of vegetative reproduction observed during this study were the direct expansion of root collars through repeated response to blight infection, and stem layering when leaning chestnut stems were pinned to the ground by falling branches. Chestnut stems do not appear to root readily even when buried in moist debris, but one instance of layering was observed on test plot C, and two others were noted in the general study area. In several other cases, two or more closely spaced chestnut clones appeared to have arisen by the division of a single root crown. The large diameter of many of the preblight chestnut stumps has resulted in several independent clones spaced around the circumference of the original tree. A few rings of autonomous sprout clones appear to have separated through this mechanism by up to 2 meters in the case of old stumps, and by up to 50 cm through the similar division of clones not associated with old stumps.

All of the information presented here indicates that individual chestnut sprout clones have not arisen by division or large-scale root suckering from root systems of preblight trees. However, the density of existing sprouts in areas such as test plot C appears to greatly exceed the density of the original canopy trees. It is possible that some of the closely spaced clones in Fig. 5 have arisen by root crown division, but the process seems too slow to account for the high density of sprouts. The best explanation for the numbers and distribution of modern chestnut sprouts is that they represent seedlings established on the forest floor prior to 1922. This hypothesis can explain the general association of modern chestnut sprout populations with preblight trees which would have provided seed sources in the years prior to 1920. The loose grouping of sprouts in Fig. 3, or the clustering of some of the sprouts in Fig. 5, may represent the location of rodent cover or sites otherwise favorable for chestnut seedling establishment (Jaynes 1967). The old seedling hypothesis is consistent with the observation by Keever (1953) that most

American chestnut sprouts on a Virginia site appeared to have originated as seedlings and not root sprouts. The lack of root sprouting observed in a limited number of root excavations cannot be considered conclusive. But the inability to find living sprout distribution patterns or recent root sprouts indicative of vegetative reproduction at a distance of more than a few centimeters indicates that large-scale vegetative reproduction has not been occurring on Wood Hill. The increase in chestnut stem densities reported by Stephens and Waggoner (1980) probably can be explained by expansion of established root crowns, stimulation of multiple stems by blight injury, and limited reproduction by layering.

**NATURAL GROWTH FORM OF CHESTNUT SPROUTS.** The long-term survival of chestnut sprouts in the understory of mature woodlands indicates that chestnut clones have specific adaptations for competition with shrubs. The growth form of chestnut sprout clones on Wood Hill may be compared to the character of shrub species known to expand aggressively into upland woodlands. A typical example of such shrubs is illustrated by beaked hazel (*Corylus cornuta* Marsh.) in the open pine woods of Minnesota (Tappeiner 1971). Observations on the growth form of chestnut sprout clones on Wood Hill indicate that the resemblance between some chestnut clones and common shrubs is produced by the effects of repeated blight girdling of stems.

The varieties of stem shapes observed in the study area are shown in Fig. 6. A relatively large percentage of chestnut clones consist of a single stem with several major horizontal layers formed by large lateral branches. The general open growth form of these stems exhibits many of the adaptations for low light conditions described by Horn (1971). The relatively upright form of the primary stem on many of these clones indicates that they have repeatedly overcome the formation of "bayonet" joints described by Tomlinson (1983). The plasticity of growth form exhibited by suppressed chestnut stems does not appear to fit any of the standardized forms of tree architecture described in the literature, but rather appears to represent a continuum of forms such as that described for North American *Tsuga* spp. (Hibbs 1981). Clones dominated



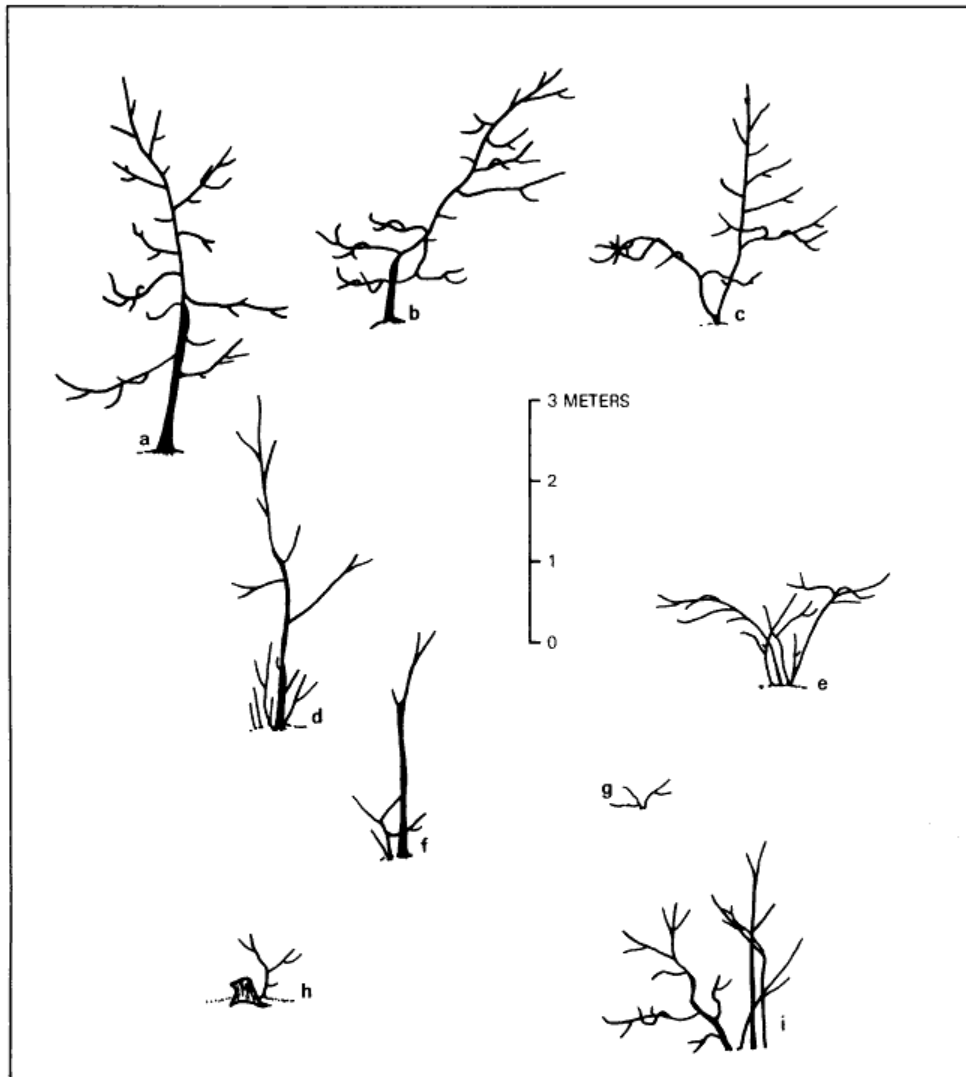


Fig. 6. Chestnut sprout clones on test plot C illustrating variations in number, size and shape of stems present.

by single stems can be relatively straight (Fig. 6a), or sharply leaning (Fig. 6b); or may have smaller, secondary stems originating at the root collar (Fig. 6c). Destruction of the primary stem by blight infection produces many new shoots from the perimeter of the root collar (Fig. 6d), which can develop into multistemmed shrubs after several rounds of blight infection (Fig. 6e). Repeated blight infection can sometimes deplete the resources of sprout clones, pro-

ducing clones with a few small, slowly growing stems (Fig. 6f). This process may explain the relative abundance of small sprouts in test plot C (Fig. 6g). The dwarfed condition of the few living sprouts still attached to preblight chestnut stumps (Fig. 6h) may result from the xeric conditions caused by their location on the side of a stump being further exposed by soil erosion. In several instances, blight appears to have infected only the largest, most vigorously growing

stems of clones, leaving clones with a few poorly formed stems (Fig. 6i).

The proportions of chestnut sprouts exhibiting the various growth forms illustrated in Fig. 6 were determined by classifying the shapes of the stems mapped in Fig. 5 (Table 1). Because the frequency and severity of blight infection may depend on the density of sprout populations (Hebard *et al.* 1981), a similar classification was performed on sprout clones encountered while walking compass lines through areas with relatively low chestnut-sprout densities (Table 2). Both of these surveys indicate that approximately two-thirds of all clones not infected by blight in the two years prior to the 1983 growing season were dominated by a single primary stem. There appears to be no great difference in the recent incidence of blight between the high and low density areas, but the greater percentage of small, multistemmed sprouts in Table 1 may indicate that blight has been more frequent in the high density areas in the past. In both surveys, less than 5 percent of all living sprout clones appeared to be associated with the remains of preblight canopy trees.

Four completely dead sprout clones were found on test plot C (Fig. 5). Three of these clones had apparently been dead for many years, while the fourth had died during the

1982 growing season after being released by the death of a small canopy oak. The large primary stem of this clone had been girdled by blight several years after release, and all subsequent stem and root collar sprouts had been reinfected by blight. This round of reinfection apparently coincided with canopy reclosure by the expansion of adjacent oak and maple crowns. The expenditure of resources during the recent release superimposed on the stresses of blight infection and canopy closure may have fatally weakened the entire clone.

The observations of chestnut growth form described here indicate that multistemmed clones result from repeated blight infection or other injury, whereas undisturbed clones tend to evolve towards a single-stemmed form. The appearance of a typical chestnut stem after decades of suppressed growth is illustrated in Fig. 7. The figure shows the base of a single large stem with many suppressed, scaly buds located on the perimeter of an enlarged root collar. Single buds are released periodically but do not continue to expand after the first year unless the main stem has been injured or otherwise begun to fail. The root collar usually appears to have developed around the base of the living stem, while the adjacent root collar of the previous stem soon decays due to contact with moist soil. These

Table 1. Characteristics of 236 discrete chestnut-sprout clones in the densely populated test plot C.

	Recent <sup>a</sup> blight	No recent blight	Total
Total	50	186	236
Single major stem, > 1 cm diameter	12	124	136
Single major stem, alone	0	76	76
Multiple stems, all <1 cm diameter	14	42	56
Single weak stem, <1.5 m tall	1	31	32
Old sprout wood <sup>b</sup> present	13	22	35
Attached to original <sup>c</sup> stump (all definite)	0	8	8
Completely dead sprout clones	1	3	4

<sup>a</sup>Recent blight: stem death due to blight during 1981–82 seasons.

<sup>b</sup>Old sprout wood: bleached chestnut wood without trace of bark that clearly represents previous cycle of sprouts dead by 1980.

<sup>c</sup>Original stump: mound of decayed wood or persistent snag indicating preblight chestnut wood.

Table 2. Survey of entire tract excluding areas of greatest sprout density (117 clones).

	Moderate <sup>a</sup> density	Low <sup>b</sup> density	Recent blight	No recent blight	Total
Total	50	67	19	97	117
Single major stem >1 cm	32	44	0	76	76
Single major stem alone	20	29	0	49	49
Double major stems >1 cm	8	13	0	21	21
Multiple stems all <1 cm	6	2	1	7	8
Very old sprout wood present	10	10	12	8	20
Possibly attached to original stump	8	4	—	—	12 (4 definite)
Recent blight	10	9	—	—	19

<sup>a</sup>Moderate density: more than 20 but less than 50 clones per hectare.

<sup>b</sup>Low density: less than 20 clones per hectare.

repeatedly abandoned root collars are preserved only in cases where they are exposed to the atmosphere as in the case of erosion around preblight stumps (Fig. 4). The primary mechanism for clone reproduction in modern woodlands, therefore, is the expansion of root crowns produced by blight infection or other injury. With the exception of those upland sites subject to frequent ground fires, the suppressed chestnut seedlings located in preblight woodlands probably resembled small, single-stemmed trees rather than multi-stemmed shrubs.

**SPROUTING AND LIGHT.** The character of chestnut sprout populations on Wood Hill indicate that chestnut sprouts are adapted for survival under low light conditions, but not necessarily for rapid clone propagation. Observations indicate that the natural growth form for chestnut involves a combination of adaptations for competition with shrubs, and adaptations needed to insure that chestnut stems will be able to dominate canopy openings when they become available. The clone apparently does not expend resources in repeated attempts at vegetative reproduction such as those described for hazel by Tappeiner (1971). The survival of chestnut clones depends upon the efficiency of chestnut stems in the subcanopy. The oak forests on Wood Hill are relatively open, so that subcanopy light levels are never extremely low. Successful

competition with shrubs on well-drained, infertile uplands appears to be the single most important requirement for survival under these conditions. The plasticity of chestnut stems in lateral growth towards light sources coupled with a controlled husbanding of resources, appears to explain the survival of chestnut clones in the study area. The key to this growth form appears to be the hormonal regulation of the entire clone system. Apical dominance by the main stem (Zimmermann and Brown 1969) may control the development of the enlarged root crown, keeping the many basal buds

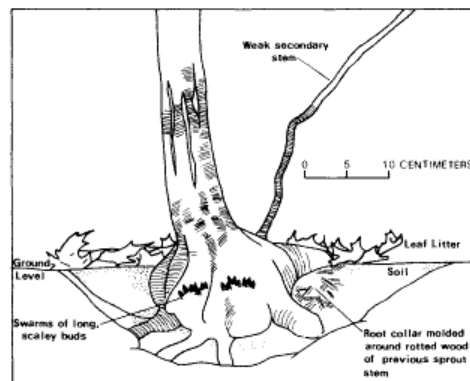


Fig. 7. Typical structure of root collar at base of chestnut stem held in suppression and free of blight infection for more than 2 decades.

in a suppressed state. The eventual senescence of the main stem under low light conditions may allow the systematic release of individual buds until one of these secondary stems becomes strong enough to assume control. Such a sequence of events allows several generations of stems to develop without greatly depleting clone resources, while maintaining a stem suitable for rapid upward growth when canopy openings become available.

**Conclusions.** The present distribution of chestnut sprouts in Andover, Massachusetts mirrors the distribution of forests likely to have contained chestnut at the time of initial blight incidence. This expected result is augmented by the presence of locally abundant chestnut sprouts in abandoned fields adjacent to woodlands that contained chestnut in 1922. The detailed distribution of chestnut sprouts shows no close spatial correspondence with stumps and logs of preblight chestnut trees. At the same time, almost all existing chestnut sprout stems are associated with the decayed remains of previous blight-killed sprouts, indicating that they have existed as separate root systems for some time. No definite instances of vegetative reproduction by root suckering or recent seedling establishment could be found. Vegetative reproduction by layering and lateral expansion of root crowns, in addition to increases in stem numbers induced by blight infection and other injury, appear adequate to explain the increases in numbers and size of chestnut stems recorded by Stephens and Waggoner (1980).

All of the observations cited here indicate that the majority of modern chestnut sprout clones originated as seedlings already established on the forest floor prior to 1922, or in recently abandoned pastures adjacent to such stands. A relatively large number of preblight chestnut stumps still have living sprouts attached after more than 60 years of repeated blight infection. These weak stump sprouts appear to be the only living vestige of the original canopy trees. The remaining majority of modern chestnut sprouts, therefore, appear to have been seedlings in storage on the first floor, supporting the theory that a subcanopy stage is part of a definite reproductive strategy for chestnut (Paillet, 1982). The adaptation

of chestnut seedlings for survival over extended periods in a small, suppressed stage appears similar to reproductive strategies described for hemlock and oak by Oliver and Stephens (1977), for beech by Vankat *et al.* (1975), and for many climax species in the equatorial rain forests by Richards (1952). The effectiveness of a seedling sprout stage in forest succession in New England is documented by evolution in species composition in the Harvard Forest in northcentral Massachusetts following canopy destruction by the 1938 hurricane. Hibbs (1983) reports that a significant proportion of the present oak-dominated canopy originated as seedling sprouts rather than sprouts from large injured stems or seedlings established after the 1938 disturbance.

Observations of the growth form of chestnut sprouts indicate that sprout clone systems are subject to strong hormonal regulation controlling the switching from growth patterns necessary for survival as a suppressed shrub to strong apical dominance and rapid upward growth. Sprouts unaffected by blight for many years appear to evolve into a single, laterally-layered stem capable of existing for decades, and having many of the adaptations for survival under low light conditions described by Horn (1971). Eventual senescence of this stem results in the orderly release of one or two from among many suppressed buds located on a large root collar. Once chestnut root systems become established, this process probably can be prolonged indefinitely until a canopy opening becomes available.

Many of the characteristics of chestnut sprouts described here appear to be adaptations included in a reproductive strategy based on the long-term storage of seedlings awaiting the occurrence of a canopy opening. The repeated incidence of blight alters the form of chestnut sprout systems by allowing release of multiple competing shoots after the abrupt girdling of the main stem. Multi-stemmed chestnut sprouts bearing a superficial resemblance to shrubs are probably much more abundant in modern woodlots than they were in relatively undisturbed prehistoric forests. The effects of repeated blight infection normally do not kill the entire sprout clone, but blight infection may be lethal in cases where blight

is superimposed on the resource depletion induced by rapid stem release and other environmental stresses.

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