

Chestnut: history and ecology of a transformed species

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Abstract

Aim The character and distribution of American chestnut (*Castanea dentata*) populations in New England are analysed to identify the extent to which the introduced chestnut blight and historic land use practices have affected chestnut distribution and life history.

Location The study focuses on chestnut in Connecticut and Massachusetts but includes analysis of data related to other *Castanea* species in North America and Europe.

Methods The ecology and palaeoecology of chestnut is investigated using a range of techniques, including examination of the growth form of chestnut trees in plantations located away from blight, mapping of chestnut sprouts and blight-killed trees at various locations, anatomical examination of chestnut stems, analysis of early forestry practices, identification of changes in the relative abundance of chestnut pollen in Holocene lake sediments and comparison of American chestnut with other *Castanea* species.

Results Examination of chestnut sprouts surviving in the former range of that species shows that most sprouts originated from suppressed seedlings and that environmental factors severely limited the survival of sprouts from large blight-killed trees. Palynological data show that chestnut was either present in very low populations or entirely absent from New England and only became abundant after about 2500 years ago. All factors suggest that chestnut abundance is related to the natural disturbance cycle, while human-induced transformations of the landscape and the introduction of chestnut blight have further transformed the character of chestnut in New England.

Main conclusions Most surviving chestnut sprouts in New England forests represent old seedlings that have continued to re-sprout since establishment before the introduction of blight nearly 100 years ago. The growth form of these sprouts ensures a minimal substrate of bark tissue for blight establishment so that blight has a relatively minor effect on seedling–sprout survival. The identification of modern chestnut sprouts as old seedlings indicates that the observed distribution of sprouts in New England woodlands is strongly influenced by land use conditions and especially field abandonment at the time when chestnut blight arrived from its point of introduction.

Keywords

American chestnut, *Castanea dentata*, seedling sprouts, natural disturbance.

INTRODUCTION

The American chestnut (*Castanea dentata*) was and still is an important part of the forest ecosystem in southern New England. Chestnut has an unusual – but unfortunately not unique – history in that it has been completely transformed

in the modern forests of eastern North America as a result of an introduced disease (*Cryphonectria parasitica*). Although this transformation is of interest in its own right, the latest change in the character of chestnut tree populations in New England is only the most recent of several significant changes in the past distribution of chestnut inferred from sediment cores. The only other *Castanea* species in North America that could possibly be confused with chestnut in palynological investigations is chinquapin (*C. pumila*), with a

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northern range limit far to the south of New England (Fig. 1; Saucier, 1973; Paillet, 1993). Thus, past changes in climate, disturbance regime, or patterns of land use can potentially be related to the ecological tolerances of a tree species that can be unambiguously identified as American chestnut in the fossil record. The fact that several such changes can be recognized suggests that chestnut may be a useful indicator of past environmental change. The historic and prehistoric records of chestnut in New England demonstrate that the transformed chestnut populations we see today represent the cumulative effect of more than just the disease-induced pruning of a former forest tree.

Possible changes in the role of chestnut in the forests of New England can be understood in the context of the known sequence of events associated with the re-establishment of forest cover at the end of the Wisconsin glacial period. The boreal forest arrived in Connecticut about 12,000 years ago (pollen zone A, as defined by Deevey, 1939; Davis, 1969) and yielded to a pine-dominated forest over a period from 10,000 to 8000 yr BP (Deevey's pollen zone B). These relatively dry forests were then replaced by mixed deciduous forest in the

south and by northern hardwood-hemlock-white pine forest in the north under a presumably less continental climate regime (Deevey's pollen zone C). Within this general context, chestnut pollen data show three distinct 'events' that are not reflected by pollen records from other tree species: (1) A late Holocene increase in the abundance of chestnut pollen everywhere within the range of that species in New England, from trace amounts that could be indicative of long-distance transport to values representing local populations of chestnut (Davis, 1969); (2) A near doubling of chestnut pollen as a percentage of total arboreal pollen associated with the onset of European agricultural practices in southern Connecticut in the seventeenth century (Brugham, 1978); and (3) An abrupt disappearance of chestnut pollen after the destruction of mature chestnut trees by the arrival of chestnut blight in the 1900–25 year period (Anderson, 1974). Only the last of these three changes can be evaluated by direct, first-hand investigation of *Castanea* in modern forests. Even in that case, the lack of naturally reproducing chestnut populations complicates the study of chestnut ecology and the environmental calibration of chestnut pollen data.

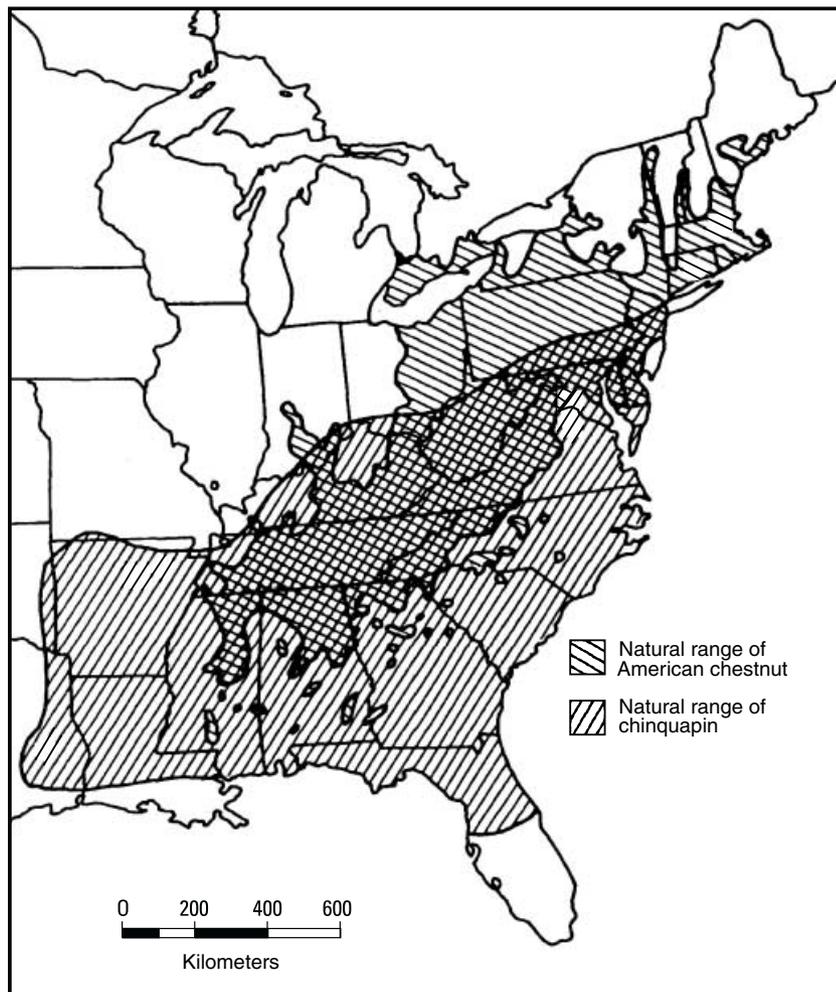


Figure 1 Range of *Castanea dentata* and *C. pumila* in North America (based on data from Saucier, 1973).

CHESTNUT PERCEPTIONS IN EARLY FORESTRY

The elimination of American chestnut from eastern forests occurred decades before modern principles of forest ecology were established. Chestnut survives today in the form of sprouts originating from trees or seedlings established before the arrival of blight. These stems rarely if ever, survive long enough to produce a seed crop, so that the propagation of chestnut cannot be studied in modern forests. However, chestnut was of such economic importance that considerable information on chestnut silviculture can be found in the early forest science literature. Frothingham (1912) describes chestnut in southern New England (Connecticut) and two other reports describe chestnut in the Appalachians (Buttrick, 1913, North Carolina; and Zon, 1904; Maryland). Matoon (1909) describes the characteristics of chestnut regeneration by sprouting as they apply to current forestry practices. All four of these authors indicate that chestnut comprised over 50% of timber by volume on well-drained slopes developed on non-calcareous substrates within their study areas. The principle associates of chestnut on these locations were oaks (northern red, black and chestnut) and hickory (pignut and shagbark). Chestnut was not as abundant on dry ridge tops and in mesic coves and was mostly absent from frequently burned forests of pitch pine and scrub oak.

Because of the economic importance of chestnut as compared with other timber types, the early forest literature concentrates almost exclusively on topics related to the establishment and maintenance of chestnut stands as a renewable resource. In fact, chestnut is cited by Buttrick (1913) as the only useful tree species in the region with a growth rate fast enough to allow for effective resource management. Early chestnut references repeatedly discuss concerns about the future of chestnut because many existing chestnut stands did not appear to be reproducing, and because chestnut appeared to be in the process of replacement by other, less valuable tree species. Buttrick (1913), in particular, cites the rarity of chestnut reproduction by seed. Thoreau (1906) reported a similar lack of seedling establishment in chestnut stands in north-eastern Massachusetts. Essentially, all silvicultural references recommended that timber harvest operations be designed to encourage chestnut sprouting by such mechanisms as: (1) cutting stumps close to the ground to favour root collar sprouting; (2) avoiding mid-summer timber harvest where tender sprouts can be damaged by browsing or might fail to harden before the first frost; and (3) cutting poorly formed and heavily suppressed chestnut stems to force regeneration of straight and defect-free trunks (Matoon, 1909; Buttrick, 1913; Smith, 2000). The early literature concluded that chestnut seed predation was so extensive and chestnuts so susceptible to damage by frost or desiccation that propagation of chestnut by seed was just not feasible under prevailing conditions in commercial woodlots.

The one disturbance most frequently cited in the early forest literature as affecting chestnut reproduction is fire.

Buttrick (1913) concludes that human-caused fire in Appalachian oak–chestnut stands was one of the primary factors limiting the replacement of chestnut. He cites the relatively thin bark and shallow root system of chestnut as compared with trees such as oak and hickory. Early forest scientists recognized that chestnut sprouts originated from pre-formed buds located on the root collar of mature chestnut trees (Matoon, 1909; Zon, 1904). These buds are not well protected by forest litter and can be damaged by even light ground fires. When chestnut root collars are not damaged in a disturbance that kills or injures a chestnut stem, the very thin bark of the sprouts that originate after a timber harvest or fire would make these sprouts very susceptible to damage from any subsequent fire. Thus, the early literature suggests that chestnut is not favoured by fire and this is corroborated by the absence of chestnut from fire-prone landscapes such as the pitch pine barrens of Cape Cod and Long Island. Modern studies and palynological data from forest soils suggest that the relation between chestnut and fire may not be so simple. The author's personal observations indicate that light surface fires in Massachusetts served to suppress competition from shrubs and favoured chestnut sprouts. Although most subcanopy stems were injured or killed by such fires, new chestnut root sprouts were able to grow faster than other sprouts in the years after the fire. Studies of chestnut pollen in sediments adjacent to Black Gum Swamp clearly demonstrate the presence of charcoal indicative of fire preceding a sharp increase in the proportion of chestnut pollen in the sediment (Foster & Zebryk, 1991). It is possible that early foresters were incorrectly blaming a lack of chestnut stand reproduction on frequent burning of the understory, or that the relationship between chestnut reproduction and fire is a complex function of site conditions, fire intensity, fire frequency and time of year in which the fire occurs.

Overall, the early forest literature provides a rather consistent picture of the status of chestnut in Appalachian forests around the turn of the century. Chestnut was the dominant timber species over much of its range. Most of the standing chestnut timber was assumed to have originated from root collar sprouts. Chestnut was observed to be disappearing from some sites where it was formerly dominant and there was little evidence that chestnut was propagating by seed. These facts confirm that chestnut stands in New England a century ago were mostly governed by disturbance history and were probably very different from chestnut-dominated stands that existed before the arrival of the Europeans. On the basis of known land use conditions in nineteenth century New England, most chestnut trees were either clumps of coppice sprouts in woodlots regularly harvested at about 20-year intervals (Fig. 2a; Gleason, 1975), or open-grown pasture trees subject to wind and lightning damage (Fig. 2b; author's photograph). Neither of these chestnut images is likely to represent chestnut in the forests of New England before settlement. In contrast, compare these images with a photograph (Fig. 2c; Paillet & Rutter, 1989) of a chestnut tree that became naturalized in a relatively undisturbed oak–hickory woodlot adjacent to a



Figure 2 Chestnut photographs: (a) Chestnut coppice forest in Concord, Massachusetts (from Gleason, 1975); (b) Open grown chestnut in Lundy, Wisconsin (author's photograph); and (c) Naturalized American chestnut established in oak-hickory forest in Wisconsin (from Paillet & Rutter, 1989).

chestnut plantation in western Wisconsin. There is no guarantee that this naturalized tree is any more like chestnut trees in prehistoric New England forests than those in Fig. 2a or b. Even so, the contrast in appearance and general proportions of the tree in Fig. 2c with the trees in the other two photographs strongly suggests that the character of prehistoric chestnut trees may have been different from that noted by nineteenth century naturalists such as Thoreau.

CHESTNUT IN THE HOLOCENE FOSSIL RECORD

Although most native deciduous tree species became established in New England by about 8000 years ago, chestnut may not have reached Connecticut until after about 2500 yr BP (Davis, 1969; Brugham, 1978). In one of the earliest pollen studies, Deevey (1939) defined an uppermost pollen zone on the basis of an increase in the proportion of chestnut pollen consistent throughout Connecticut. Because chestnut pollen is released in early July, when the forest canopy is filled with leaves, chestnut pollen is not as abundantly dispersed as that of many other wind pollinated tree species such as oak and hemlock. Chestnut pollen typically comprises 15–20% of total arboreal pollen near the top of sediment cores from lakes that were historically surrounded by chestnut-dominated forests (Nichols, 1913; Paillet *et al.*, 1991). However, chestnut pollen grains are relatively small, so that the fraction of chestnut pollen entrained above the forest canopy can be transported across long distances. As a result, the few grains of chestnut pollen found in deposits from the early and mid-Holocene could be attributed to either long distance transport, or to a sparse population of chestnut trees in New England forests. Deevey and subsequent authors divided the late-Holocene pollen zone C in southern New England into three subzones: oak–hemlock (C1), oak–hickory (C2), and oak–chestnut (C3). Only after about 2500 years ago, at the bottom of pollen zone C3, does chestnut pollen increase to levels that are clearly consistent with local populations of chestnut such as those described by early settlers.

The relatively late appearance of chestnut in New England has most often been attributed to the slow northward migration of that species in the Holocene (Davis, 1969). Paillet (1982) points out two problems with that explanation: (1) other large-seeded tree species such as hickory did not lag appreciably behind associated deciduous species in Holocene migration in response to climate warming; and (2) pollen data show that chestnut reached as far north as south-eastern Pennsylvania at *c.* the same time as other deciduous tree species (Watts, 1979). Furthermore, the late Holocene increase in chestnut in New England coincides with a region-wide increase in spruce pollen. The latter varies from a minor increase in southern Connecticut that probably represents long distance transport to more significant increases in Massachusetts and New Hampshire indicative of increasing populations and lowering elevations for spruce. The coincidence of the increase in both spruce and chestnut pollen is especially evident at sites where the

northern range of chestnut and the southern range of red spruce overlap (Whitehead, 1979; Foster & Zebryk, 1991). Most authors attribute this late-Holocene increase in spruce to a general cooling of climate after the mid-Holocene thermal maximum (Davis *et al.*, 1980). However, pollen data suggest that the explanation may not be that simple. The mechanism whereby a deciduous species at the northward limit of its range should increase in response to cooling is not obvious. The cause may involve competitive interaction with other species or changes in the prevailing disturbance regime rather than simple response to climatic cooling.

Most of the earliest pollen studies in New England were concentrated on sites in southern Connecticut and were based on sediment cores from lakes and bogs that provide a regional sample of the pollen production. These early cores repeatedly showed that an increase in regional chestnut pollen defined the base of pollen zone C3 and that a further increase in chestnut pollen coincided with European settlement. Cores from soils and small catchments beneath closed forest canopy give a more local indication of chestnut tree populations. Paillet *et al.* (1991) demonstrate that the entrapment of chestnut pollen by the fully leaved forest canopy causes chestnut to be over-represented in the pollen percentages from soil beneath chestnut forests. Thus, forest soils and forest hollow sediments are much more effective at indicating the presence of chestnut than are lake sediments. Compare pollen data from an open bog (Fig. 3a) with pollen data from a small forest hollow in the adjacent forests (Fig. 3b). The bog profile shows the increase in chestnut pollen defining the base of zone C3. In contrast, the hollow profile shows much larger proportions of chestnut pollen and major fluctuations in the relative abundance of chestnut pollen. A comparison of the chestnut fluctuations with pollen for other species makes it clear that chestnut is responding to cycles of disturbance on this site. Thus, the pair of pollen profiles in Fig. 3 indicates a regional population of chestnut that is relatively stable, while clusters of chestnut trees formed a continuously variable mosaic within that regional forest.

The distribution of chestnut in New England is illustrated by the relative abundance of chestnut in witness tree records (Fig. 4). Although these data indicate that chestnut was common throughout central Massachusetts, the proportion of chestnut in the early forests decreased northwards from the vicinity of Rogers Lake and Lindsley Pond. The relatively simple, stepwise increases in chestnut identified in southern Connecticut at the bottom of Deevey's Zone C3 and at the time of European settlement are not very well produced in pollen profiles from more northerly sites such as those in Fig. 3. The age when chestnut pollen percentages rise to significant levels varies among these sites and there is no clear association of increases in chestnut with settlement. The latter may be attributed to the later and more irregular settlement of these lands, especially in times when outlying settlements were subject to attacks by British or French forces and their native allies. These pollen data are probably consistent, on the average, with a late Holocene increase in

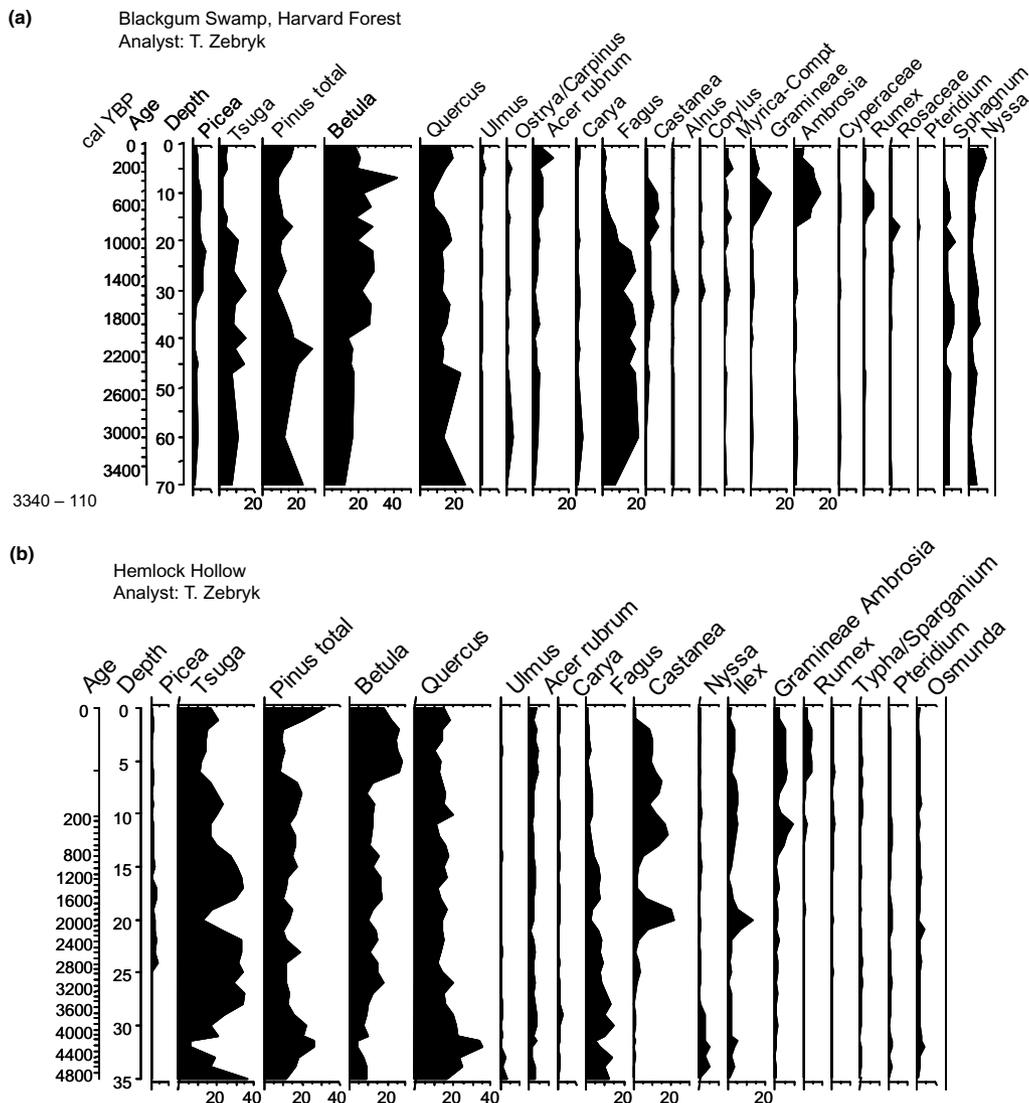


Figure 3 Comparison of pollen profiles from (a) an open bog and (b) a forest hollow in north-central Massachusetts (reproduced from Foster & Zebryk, 1991).

chestnut and a further settlement induced increase, but only on the regional average. The local trends in chestnut pollen seem to indicate responses to disturbances where chestnut displaced the most tolerant species such as maple and beech, along with other less-tolerant species normally associated with disturbance such as birch and oak.

MODERN CHESTNUT SPROUT POPULATIONS

The arrival of chestnut blight in North America effectively removed the possibility of sexual reproduction for the species. The effects of such a limit on reproduction seemed so severe that Gleason & Cronquist (1964) proposed American chestnut as an example of ongoing extinction. That chestnut is far from extinction nearly a century after

chestnut blight arrived in New England is indicated by the great number of chestnut sprouts surviving in New England today. For example, periodic surveys of sample plots in Connecticut showed chestnut slowly increasing as a percentage of total stem basal area (Stephens & Waggoner, 1980). Paillet (1982) noted that chestnut consistently began to fill canopy gaps in the oak forests of southern Connecticut during episodes of gypsy moth defoliation in the 1970s. Studies in the southern Appalachian region show that chestnut sprouts are abundant in forests almost everywhere within its range (Adams & Stephenson, 1983; Stephenson *et al.*, 1991) and that *Castanea* comprised the leading component of woody biomass on experimental clear-cuts in the first 5 years after cutting (Boring *et al.*, 1981). Although Allegheny chinquapin has ecological tolerances somewhat different from chestnut, the author

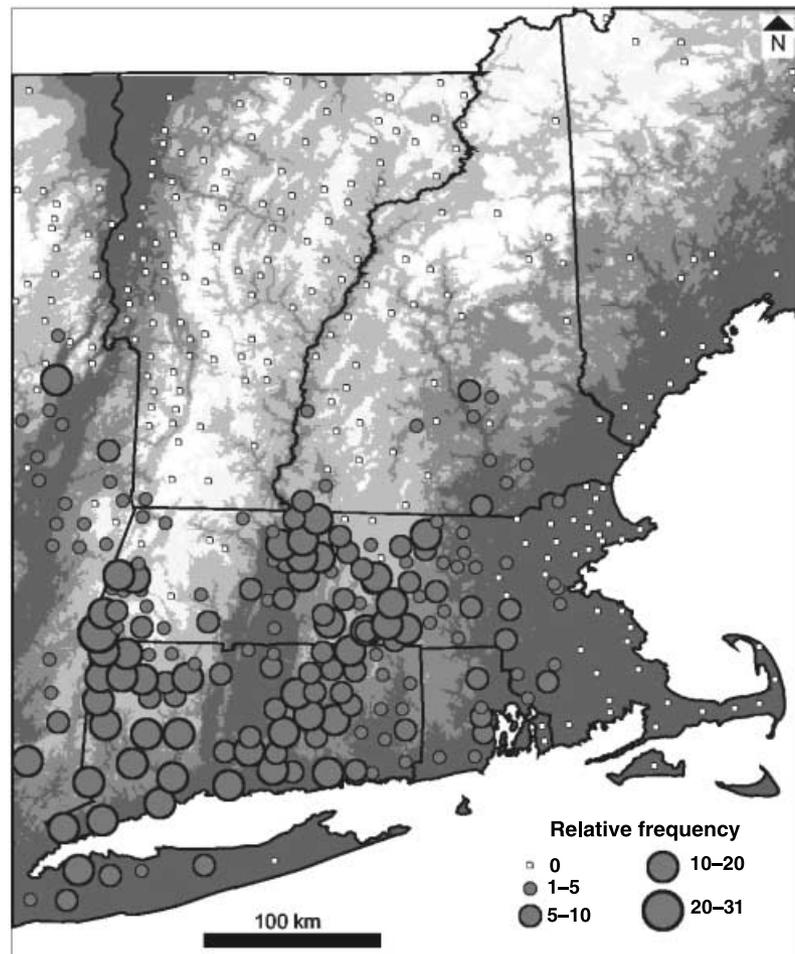


Figure 4 Chestnut witness trees in early historic surveys in New England and adjacent states.

has observed chinquapin sprouts dominating the biomass of recent clear-cuts in the Ozark Mountains of northern Arkansas. All of these results indicate that chestnut is surviving and perhaps even thriving in spite of blight and that this survival is related to the ability of *Castanea* to regenerate stems by sprouting.

Chestnut blight effectively prevents chestnut stems from reaching the canopy long enough to flower and produce seed. When an isolated sprout is released in a location where blight spores are few, the small tree can produce female flowers. However, chestnut is not self-fertile and cross-pollination is needed to produce nuts. Blight eventually finds and kills these isolated trees after they have attained a height of 15 m and a diameter of at most 20 cm. When a number of sprouts are released by forest cutting or natural disturbance, the emerging chestnut crowns are capable of cross-pollination, but the density of substrate for blight colonization is sharply increased. This results in epidemic-like episodes of blight infection that quickly kill the growing trees (Hebard *et al.*, 1981). These observations demonstrate that any chestnut seed production by wild American chestnut sprouts in New England is a very rare and unusual event. Essentially, all of the living chestnut sprouts found today must represent

chestnut clones that originated before the appearance of blight. The only exceptions apply to isolated chestnut stands originating from introduced trees beyond the range of chestnut, or existing as widely separated islands near the recorded range limit. The author has identified chestnut reproduction from seed adjacent to chestnut plantations in Wisconsin and northern Illinois and in isolated natural outliers of chestnut in central Maine.

A careful inspection of chestnut sprouts in the understory of New England forests shows a range of growth forms that reflects the combined effects of suppression and repeated blight infection (Fig. 5). Suppressed chestnut stems that have escaped blight for several decades develop a form with a single stem (Fig. 5a or b), or a single dominant stem and one or more weak secondary stems (Fig. 5b). A close inspection of the base of these little trees shows an enlarged root collar with clusters of small pointed buds that are continuously 'growing' by release of bud scales so that they form small 'spurs' up to a centimetre in length (Fig. 6). Occasionally, one of these buds will be released to produce a weak secondary stem that is generally shaded by the main stem. It is often possible to identify the 'mould' where the root collar of the current stem conforms

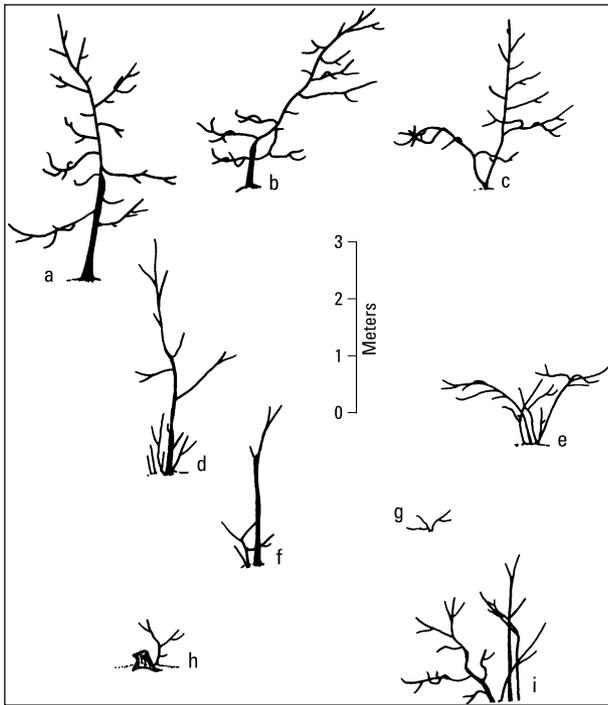


Figure 5 Examples of growth forms of chestnut sprouts in modern forests (from Paillet, 1984).

to the shape of a previous root collar that has since rotted away. As a result, suppressed chestnut stems often appear to be much younger than their true age based on the time

since origin from seed. These stems survive for as many as four decades before they are killed by blight, resulting in release of many vigorous basal sprouts from the formerly suppressed buds at the root collar (Fig. 5d). The new stems eventually become heavily suppressed to form bush-like clusters of stems (Fig. 5f–i). After decades, a single stem often dominates, returning to the small tree form of Fig. 5a–c. In general, it is very rare to find a suppressed chestnut sprout associated with the stump from a former canopy tree, as in Fig. 5h.

The abundance of living chestnut sprouts and the highly irregular distribution of these sprouts are described in detail by Paillet (1984, 1988). Chestnut sprout densities were found to vary from a very few (Fig. 7) to hundreds per hectare (Fig. 8) in woodlots containing the remains of former chestnut trees killed by the original blight infection. A careful mapping of sprouts demonstrated that more than 95% of sprouts were not associated with the remains of former canopy trees. Paillet (1988) showed that <5% of all chestnut trees killed by blight and allowed to topple over under their own weight had surviving sprouts. A much greater number (sometimes more than 10% depending upon site conditions) of chestnut trees cut before they could fall had surviving sprouts. In either case, more than 95% of all living chestnut sprouts at sites in Connecticut and Massachusetts were found to be ‘old seedlings’. These sprouts were so far removed from any chestnut stump that they could not have originated as root collar sprouts from former trees. Therefore, they are assumed to represent former seedlings that have been through several cycles of blight infection and re-sprouting. Thus, the biological characteristics of chestnut sprouting strongly influence the survival of root collar

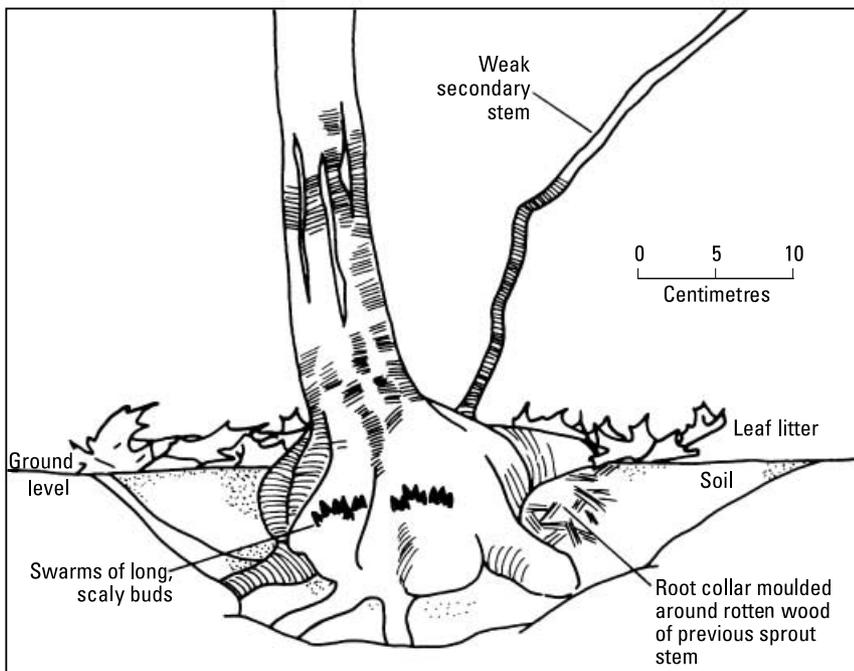


Figure 6 Base of mature chestnut sprout illustrating enlarged root collar and numbers of slowly growing buds embedded in root collar tissue (from Paillet, 1984).

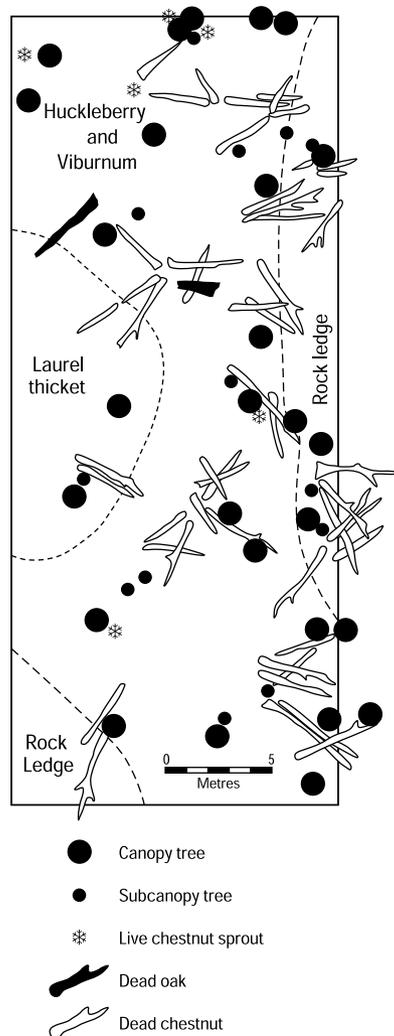


Figure 7 Old chestnut wood and living chestnut sprouts on a rocky ridge in Connecticut for comparison with Fig. 2a (from Paillet, 1988).

sprouts. New sprouts with new root systems readily develop from the pre-formed buds located on the root collars of established seedlings when they are girdled by blight. Chestnut logs that fell under their own weight almost always pulled any root collar sprouts out of the ground when they fell over. Even when wood of standing blight-killed trees was salvaged before the dead trees fell, erosion of soil and litter from around the upright stump often undermined living root collar sprouts (Fig. 9a). In the few cases where sprouts survive in such exposed and inhospitable locations, they now show living root systems draped over and running through fissures in the dead wood of the parent stump (Fig. 9b). The structure of the root system on these sprouts shows absolutely no indication that the stem did not arise as a separate seedling, except for the stem's point of origin on the remains of the root collar bud tissue of the former tree and the

improbability of a nut lodging on the hard, convex surface of the root collar.

The primary conclusion derived from sampling of chestnut sprouts is that today's chestnut population represents the advanced regeneration of the former chestnut forest. Paillet (1984) hypothesized that chestnut reproduction involved an extended period of subcanopy suppression before natural disturbance provided access to the forest canopy. The ability of chestnut seedlings to survive in the understory is demonstrated by the number of old seedling sprouts present today, nearly a century after the seed source was removed from the forest. Not only does this reproductive strategy allow chestnut to survive indefinitely without sexual reproduction, but it also confers other advantages. For example, the incidence of active blight in the 226 sprout clones shown in Fig. 8 indicated that blight was only a minor influence on stem survival. Many more incidents of stem destruction were related to mechanical damage from falling branches than to blight girdling. The natural habit of slow, suppressed growth in the understory of deciduous oak forests confers an advantage in the presence of blight by minimizing the amount of bark surface available for blight infection. Other oak and hickory species share this ability to establish advanced reproduction in the forest understory (Hibbs, 1983). The demonstrated ability of large numbers of chestnut seedling sprouts to remain alive for nearly a century shows that chestnut is very efficient in establishing and maintaining such advanced reproduction, while the ability of chestnut seedling sprouts to remain small confers a coincidental protection against blight.

One result of the observation that most chestnut sprouts represent old seedlings is that the distribution of sprouts can be used to identify the pattern of chestnut reproduction in the decade or so before the appearance of blight. Paillet (1988) suggested that the relationship between chestnut seedling establishment and site conditions explained the irregular distribution of chestnut sprouts in otherwise similar woods. For example, the distribution of chestnut sprouts along a transect through a former chestnut-dominated woodlot on the Prospect Hill Tract at the Harvard Forest showed a 'halo' of chestnut reproduction in the abandoned fields around that woodlot (Fig. 10). A careful investigation of the remains of chestnut at this site showed that the original chestnut-dominated woodlot was cut in 1899, about 12 years before blight arrived in central Massachusetts (David Foster, personal communication). The stumps of the multiple-stemmed chestnut trees harvested in 1899 could still be recognized in 1985 and showed no signs of having sustained sprouts larger than a few centimetres in diameter. In contrast, numerous dead chestnut 'poles' up to 15 cm in diameter still (as of 2001) lean into the crowns of hemlock trees, showing where seedling sprouts had been released by the cutting and then killed by blight. These 'poles' clearly did not originate from the stumps of large trees and their root collar sprouts failed to survive under the combined stress of their location on the root collar of a modest-sized tree and the shade from the competing hemlock-dominated stand.

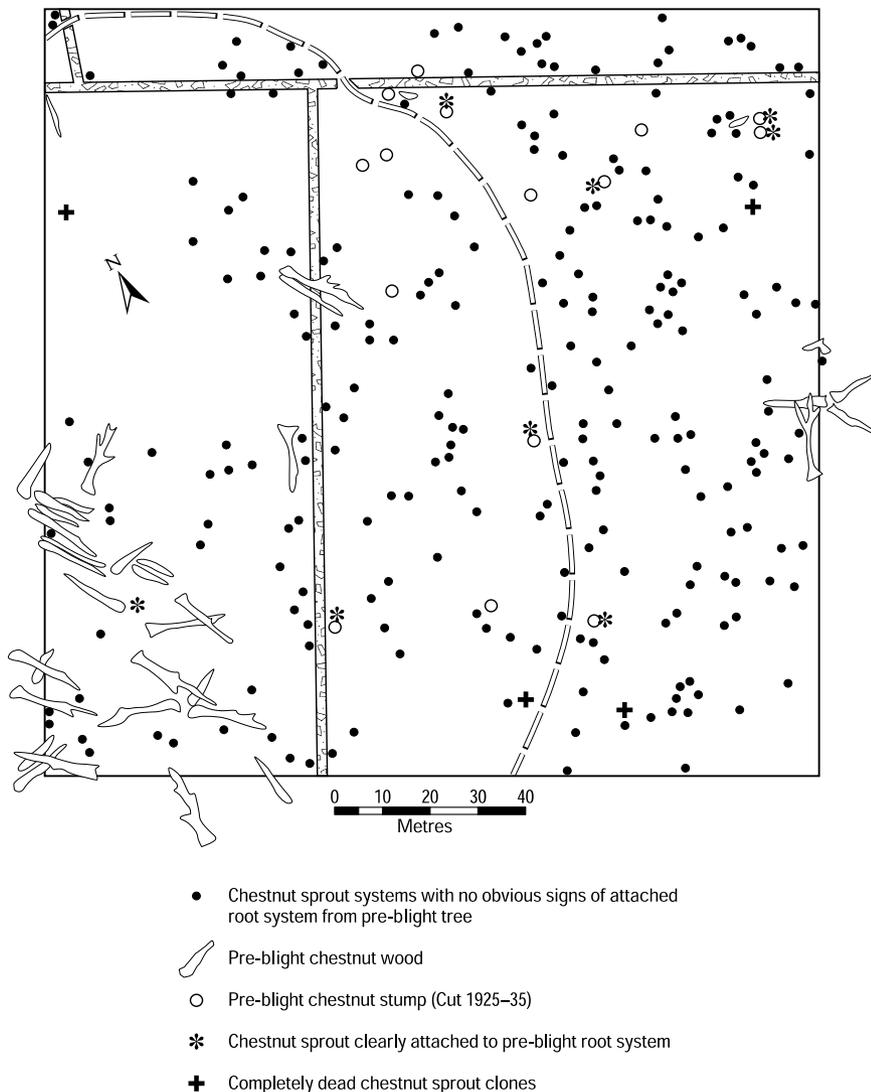


Figure 8 Old chestnut wood, chestnut stumps and chestnut sprouts in a woodlot in Andover, Massachusetts (from Paillet, 1984).

In contrast to the abundance of chestnut sprouts on the Prospect Hill Tract, 'Chestnut Ridge' on the Pisgah Tract in southern New Hampshire contains the stumps of many blight-killed chestnut trees within old-growth forest, but less than one living chestnut sprout per hectare (Paillet, 1988). Such conditions imply that chestnut was not reproducing in the old-growth forest on Chestnut Ridge in the years before blight arrived in southern New Hampshire. Irregular clusters of chestnut sprouts on other New England sites of a few hectares or less may represent places where exclusion of livestock or protection for rodents may have offered conditions suitable for chestnut seedling establishment. Following this line of reasoning, the dense distribution of chestnut sprouts at many southern New England locations may be an artifact of land use history. When blight appeared in New England over the period 1910–25, much former agricultural land had been abandoned for several decades. These abandoned fields were filling in with red cedar, pine and oak and

may have formed ideal locations for chestnut seedlings. Thoreau (1906) reported that he could hardly find a single chestnut seedling underneath chestnut groves in Concord in 1870, but that there were abundant chestnut seedlings in pitch pine woods nearby. Thus, the locally dense populations of chestnut sprouts in New England woodlands have been transformed by a unique combination of ecological adaptations, chestnut blight and land use history, rather than blight alone.

ADAPTATIONS OF CHESTNUT SPROUTS FOR UNDERSTORY SURVIVAL

Much of the available chestnut research indicates that the populations of chestnut sprouts found in modern New England forest survive because chestnut was adapted for survival in the understory for extended periods. Although the presence of chestnut blight represents a major

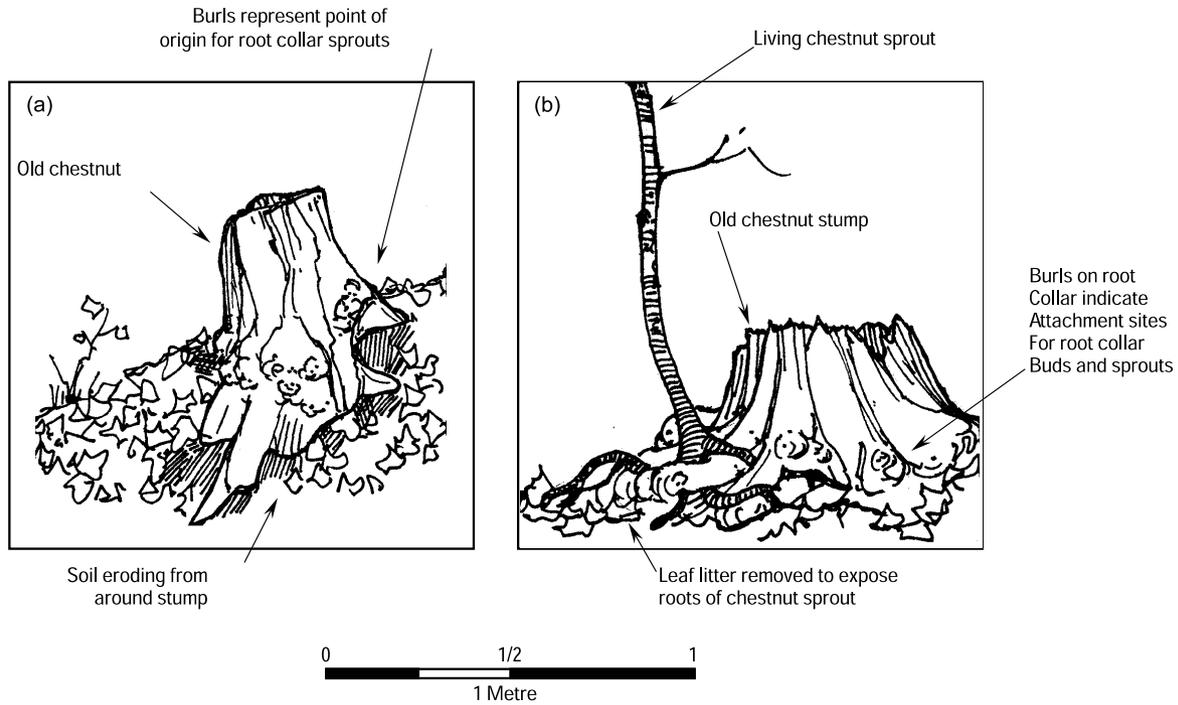


Figure 9 Examples from southern Connecticut where mature chestnut trees were killed by blight about 1910 showing the effect of site conditions on stump sprout survival: (a) Erosion from around stump prevented root collar sprouts from developing a new root system; and (b) Collection of organic debris along uphill side of stump allowed root collar sprouts to develop roots and survive.

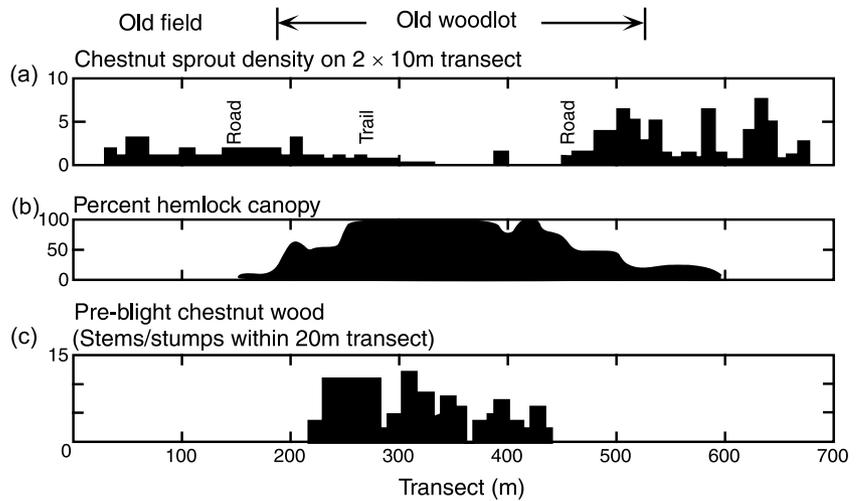


Figure 10 Distribution of (a) chestnut spouts (b) chestnut wood and stumps and (c) hemlock along a transect through a former chestnut woodlot surrounded by old fields on the Prospect Hill Tract at the Harvard Forest (from Paillet, 1988).

perturbation to conditions in former chestnut-dominated woodlands, the demonstrated ability of seedling sprouts to survive in suppression for almost a century suggests that the seedlings are physiologically equipped to do so. The coincidental result that suppressed seedling sprouts remain a small target for blight is completely fortuitous. Hibbs (1983) shows that the suppressed seedlings of several New England tree species are capable of sprouting and that sprouts from seedlings established before tree harvest were more success-

ful in regenerating forests in Massachusetts than were either stump sprouts or new seedlings. Some interesting insights into the ecology of chestnut sprouts can be obtained by comparing the growth form of chestnut sprouts with the growth form of chinquapin. The latter is clearly a shrub or small tree that almost never attains a position in the forest canopy and is evidently adapted for life in the understory. Comparisons of chestnut and chinquapin populations as affected by blight in modern forests show very little differ-

ence in growth forms. Paillet (1993) showed that chinquapin sprout clones tended to be slightly shorter in height and to contain more stems than chestnut clones growing on the same site, but the overlap in size and shape was considerable. In Arkansas, where chinquapin grows without competition from chestnut, chinquapin clones were found to be virtually identical to chestnut clones in Virginia and New England. The comparison suggests that the growth form of chestnut of suppressed chestnut seedling sprouts is essentially identical to that of a related and highly successful subcanopy species.

Although chestnut and chinquapin are similar in many ways, there is an important difference: chinquapin sprouts from an extended region along the lower stem and these sprouts do not have to originate from pre-formed buds. The region of the stem where chinquapin sprouts originate is an enlarged zone of tissue often described as a 'woody lignotuber' (Del Tredici, 2001) and exhibited by a wide variety of shrubby species. This is obviously an adaptation for the expansion of shrub clones. The other significant difference between chestnut and chinquapin is that chinquapin clones do not respond in the same way to release. Although Ozark chinquapin stems subject to release in clear-cutting are almost identical to released chestnut clones in New England, Paillet (1993) found that chinquapin growth does not continue rapidly upward for more than a few years after release. Instead, chinquapin crowns begin to broaden and bear large mast crops. These observations suggest that chestnut and chinquapin possess similar growth forms but different reproductive strategies (Fig. 11). Chestnut is a long-lived and canopy-dominant tree that uses a period of suppression and subsequent release to gain a position in the forest canopy. In contrast, chinquapin is a forest shrub adapted for growth in the understory, but relies on periods of release to produce nut crops. Both species have adaptations for survival in competition with other shrubs and both are adapted to respond to release, but their careers sharply diverge in the period after release.

Once the advantages of chestnut sprout adaptations are assessed, one has to wonder about some of the details. Why does chestnut sprout from pre-formed buds, why do the new sprouts so quickly abandon the root systems of their parents and why do the root collar sprouts persist on canopy-dominant trunks? The first two questions are answered together in Fig. 12, showing the hollow base developed on a northern red oak that apparently originated as a stump sprout. Many species of oak, hickory, maple, linden and birch reproduce by spouting and sprouts originating from the vicinity of the root collar on these trees often develop into well-formed trees. Such sprouts remain attached to the living root system of the original tree and benefit from the resources provided by that root system for an extended period. Chestnut appears unusual in being equipped to generate sprouts from pre-formed buds located on the root collar and the generation of a completely new root system soon after re-sprouting. Although this seems an inefficient use of resources, the development of a mechanically sound base probably has great adaptive advantage for a long-lived canopy tree in an environment where windthrow is an important cause of tree

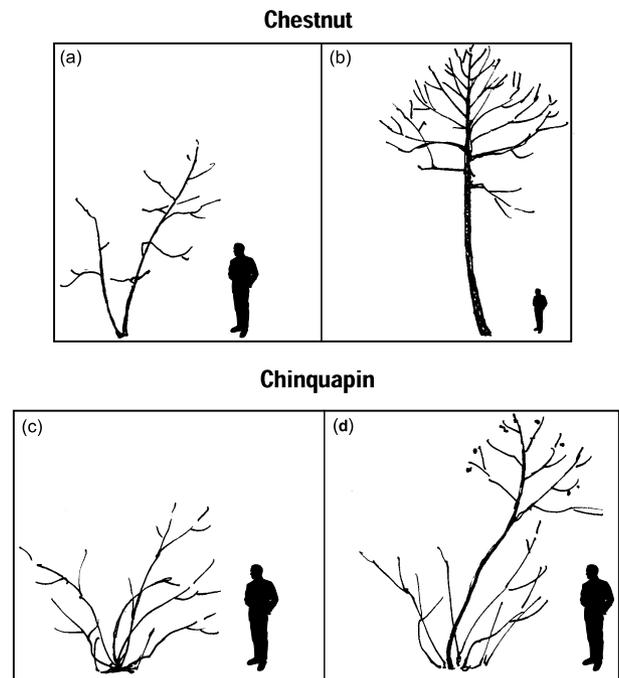


Figure 11 Comparison of chestnut and chinquapin response to release: Chestnut can exist through many cycles of stem recycling as a suppressed seedling sprout (a), becoming a large canopy-dominant forest tree upon eventual release during a disturbance (b); Chinquapin grows as a large shrub in the subcanopy where it expands laterally through the development of woody lignotubers (c), producing periodical nut crops when canopy opening occurs as a result of disease or disturbance.

mortality. The persistence of basal sprouts into maturity might simply be a case of basal sprouts persisting past their period of use. However, chestnut observations in old-growth forest in the Caucasus region suggest that basal sprouting may have advantages for naturalized trees. Pridnya *et al.* (1996) report that landslides are the primary disturbance on steep slopes in these humid forests. The author examined several such landslide disturbances in 1995 and found all of them were being colonized by rapidly growing chestnut saplings. In every case, these saplings originated from the root plates of overturned chestnut trees. Each of the new saplings originated from pre-formed buds on the root collars of the former canopy-dominant trees, showing that the persistence of these root collar sprouts on mature canopy-dominant trees may have real advantages in landslide-prone landscapes.

SUMMARY

Dense thickets of chestnut sprouts can be found today in the regenerating woodlands of southern New England. Numerous studies show that these small and suppressed trees are slowly increasing in size at locations where the basal area of stems is monitored and that released chestnut sprouts quickly dominate canopy openings created by natural tree mortality or timber cutting. This modern image of



Figure 12 Base of northern red oak in Connecticut that originated as a stump sprout and where the remains of the old stump weakened the otherwise sound trunk.

chestnut contrasts sharply with the historic role of chestnut as a canopy-dominant tree in the sprout hardwood forests of Connecticut and Massachusetts. There are also important ecological questions about how a tree species can persist and even expand as a subcanopy shrub without benefit of sexual reproduction. Chestnut blight is perceived as the primary agent of this transformation through the effects of blight cankers in repeatedly pruning the stems of chestnut trees. A careful study of chestnut ecology suggests that there is much more to the story than that. First of all, chestnut appears to be adapted for survival in the understory of forests as part of the natural process of gaining a position in the canopy. A comparison of American chestnut with a closely related shrub species, Allegheny chinquapin, indicates that both species display the same adaptations for success in competition with other shrubs and both show an ability to respond to release. Chinquapin uses the release response to produce a mast crop, while chestnut uses the release to generate a long-lived canopy-dominant tree. Thus, blight has not necessarily transformed chestnut. Instead, blight has destroyed all large chestnut trees, while an existing population of chestnut shrubs happens to display adaptations that allow these shrubs to evade the effects of blight for an extended period. The observed abundance of chestnut sprouts probably results from past land use conditions where a cycle of land abandonment produced abundant old fields adjacent to woodlots containing chestnut seed sources that were suitable for colonization by chestnut seedlings.

Placing the modern persistence of chestnut in the context of Holocene forest development shows that the historic record of land use practices and blight introduction are superimposed on earlier changes in the distribution of chestnut in New England. Pollen in sediment cores shows that the abundance of chestnut has been changing for at least three millennia. Early pollen studies identified two step-like

changes in chestnut abundance, one starting about 2500 years ago and another associated with early European settlement. The most recent pollen data from other New England locations suggest that the late Holocene increase in chestnut is more complex than that simple picture. Thus, the latest transformation of chestnut in New England that most ecologists attribute to chestnut blight alone may represent the combined effects of changes in disturbance regime, climate and land use history that extend over almost the entire post-glacial history of the region.

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BIOSKETCH

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