

CHESTNUT AND WILDLIFE

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Abstract: The interaction of chestnut with wildlife can be separated into two issues: 1) Chestnuts as a resource for wildlife consumption; and 2) Wildlife as a dispersal agent for chestnut seed. The chestnut mast resource was probably not qualitatively different from that of other large-fruited mast species. Chestnut mast may have been quantitatively better because chestnut crops were probably more reliable from season to season, and because chestnut has been partly replaced by tree species such as tulip poplar that do not produce nuts. These factors may result in a 20 to 50% increase in total mast production if chestnut is re-established as a canopy-dominant tree in American forests. Dispersal of chestnut seed and seed burial by wildlife were important because chestnuts have little resistance to frost or desiccation. However, chestnuts as seed exhibit few of the mechanisms usually associated with a trade-off between dispersal and predation. Various field studies and old forestry data confirm that chestnut reproduction occurred most often by coppice sprouting, and that chestnut seedlings were rare or absent in many chestnut stands. I propose that there is no selective pressure on chestnut for the deterrence of predators because chestnut reproduction is based on a combination of wildlife dispersal of nuts and long term survival of the few seeds that do manage to germinate. My studies show that many chestnut seedlings have survived for at least a century and possess root collar sprouting characteristics designed to insure that “old seedlings” remain juvenile essentially forever. Thus, chestnut reproduction by seed is heavily biased in favor of mechanisms to promote long-distance transport. The near immortality of established chestnut root stocks probably offsets any selective value in deterring seed predation within chestnut-dominated stands.

INTRODUCTION

American chestnut, *Castanea dentata*, was once one of the leading tree species in the forests of the Appalachians, Allegheny Plateau, and southern New England (Smith, 2000; figure 1). Mature chestnut trees were removed from these forest ecosystems after the introduction of chestnut blight in the New York City area sometime around 1900 (Anderson, 1974). Chestnut mast was completely removed from eastern forests, although numerous chestnut sprouts continue to exist and even flourish in the forest understory (Paillet, 2003). A related species, Allegheny chinquapin (*Castanea pumila*), was also affected by blight, but chinquapin grows as a shrub or small tree, so that some fruiting probably continued to occur even after the appearance of blight within the range of that species (Paillet, 1993). I therefore conclude that blight effectively eliminated seed reproduction by chestnut, and drastically limited seed reproduction on the part of chinquapin.

The elimination of a significant chestnut mast crop from American forests had two important effects: loss of an important food source for wildlife, and loss of the mechanism for seed dispersal on the part of the two native *Castanea* species. This report addresses the relationship between wildlife and chestnut by considering these distinct issues. The analysis begins by assessing what is known about chestnut ecology and the character of the chestnut mast crop in the years before blight arrived in America. These facts are the used to project how a restoration of that resource might affect wildlife in future forests. The projection is made possible by the general similarity of chestnuts to large acorns in terms of size, seed packaging, and nutrition (grams of carbohydrate, fat, and protein per kilogram, Krockmal and Krochmal, 1982). The analysis then considers how wildlife predation on chestnut seed might affect chestnut dissemination and reproduction. This, in turn, requires consideration of both the physiology of chestnut production and the ecological factors related to chestnut seedling establishment in the wild.

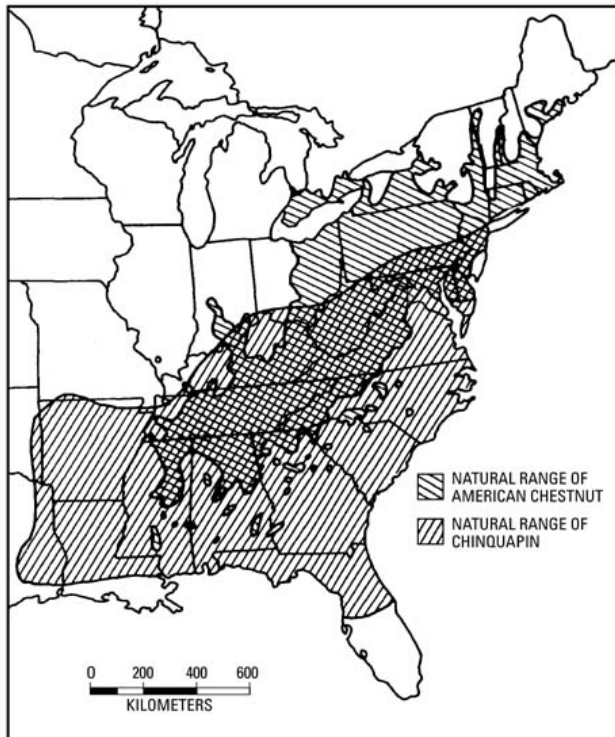


Figure 1. The natural range of chestnut and chinquapin in North America (from Paillet, 2003)

THE FACTS WE HAVE TO WORK WITH

Although there are no natural American chestnut forests to study using the techniques of modern ecology, several different avenues of investigation provide some information about the role of chestnut in pre-blight American forests. These methods include: 1) Analysis of early forestry literature; 2) Pollen analysis from bogs and ponds that were once surrounded by chestnut forests; 3) Study of naturalized stands of American chestnut established beyond the range of blight and natural forests of related chestnut species in Russia and China; and 4) Reconstruction of conditions in former chestnut forests by examination of stumps and surviving sprouts. The known facts can be summarized as follows:

Chestnut was a leading species in eastern North America, often approaching 50% of total stand basal area in upland forests from North Carolina to Connecticut (Nichols, 1913; Frothingham, 1912; Zon, 1904; Buttrick and Holmes, 1913). Chestnut was successfully propagating in natural forests both before and after the arrival of Europeans.

Pollen studies demonstrate that chestnut was one of the last deciduous tree species to arrive within its natural range in the Holocene from a glacial refuge probably located on the southern coastal plain (Davis, 1969; Whitehead, 1979). The best estimate of the glacial habitat of chestnut includes the well-drained bluffs along rivers draining western Florida and Georgia (Watts, 1979).

Chestnut was only found growing on non calcareous soils, and was rare on soils developed on clay-rich glacial till (Russell, 1987). The survival of isolated chestnut trees on till soils in the Midwest

demonstrates that the aversion to heavy soils is probably not the result of toxicity, but is caused by a combination of inability to compete and microsite conditions (Paillet and Rutter, 1989)

Pollen studies show an abrupt expansion of chestnut at about 3000 years ago in New England (Brugham, 1978; Whitehead, 1979; Foster and Zybyrk, 1991). Pollen ratios shift from less than a few percent to 20% or more. Chestnut pollen is under-represented in pollen profiles by a factor of 3 (Paillet et al, 1991) and yet relatively small chestnut pollen particles can be transported long distances. Thus it is unclear whether chestnut was present in low numbers in New England and upstate New York before 3000 years ago, or the small amount of chestnut pollen present before then resulted from long-distance transport. The 3000 year old shift in chestnut pollen corresponds almost exactly with an increase in spruce pollen in the same catchments, suggesting a climate change may be involved (Davis et al, 1980).

The introduction of European land use practices apparently affected chestnut because many pollen profiles show a near doubling of the proportion of chestnut coinciding with the arrival of European settlers (Brugham, 1980). This is almost certainly a result of the conversion of bottomland soils to fields or pasture, and the changes in disturbance regime on remaining upland woodlots.

Chestnut was destroyed as a forest tree by blight over the period 1900-1950 throughout its natural range (Anderson, 1974). All evidence suggests that the chestnut seed crop was completely removed from the forest as a source of food for wildlife and as a source of seed propagation for the forest (Paillet, 2003).

Even though chestnut trees were destroyed, chestnut sprouts are abundant in modern forests. In fact, chestnut sprouts are so pervasive that they consistently show up a significant contribution to shrub cover (Adams and Stephenson, 1983; Boring et al, 1981).

Chestnut sprouts grow as fast as or faster than the sprouts from other competing species when released by disturbance (Adams and Stephenson, 1983; Stephens and Waggoner, 1980). Chestnut sprouts are recognized as the leading component of biomass in the years immediately after clear cutting in some Appalachian forests (Boring et al, 1981). This ability represents a strong adaptive advantage in “sprout hardwood” forests where canopy regeneration is dominated by coppice sprouts (Hibbs, 1983)

Early historic forestry practices were based on coppice sprout regeneration (Buttrick and Holmes, 1913; Matoon, 1909; Smith, 2000). Older references clearly and repeatedly indicate that chestnut propagation from seed was not effective and that woodlots should be managed so as to encourage regeneration of chestnuts by stump sprouting.

Chestnut has a significant range overlap with chinquapin. Both species reproduce by sprouting as well as by seed. The one major difference is that chestnut (a large forest tree) sprouts only from pre-formed buds on the root collar, whereas chinquapin (a large shrub or subcanopy tree) sprouts from an extend region of the lower stem and upper root system (Paillet, 1993).

THE CURIOUS CASE OF THE ANCIENT SEEDLINGS

Although much of the early forest literature and folklore refers to “chestnut trees smoldering at the roots”, careful study of surviving chestnut sprouts shows that almost all of these sprouts are old seedlings. The old forestry literature indicates that chestnut sprouts only from the root collar and not from roots at a distance from the stump as in the case of aspen and beech (Matoon, 1909; Zon, 1904). Chestnut wood is resistant to decay so that the remains of blight-killed trees can be recognized in the field (Saucier, 1973). Thus, it is possible to determine whether surviving chestnut sprouts originated from former trees. Such analysis shows that almost all living sprouts never were attached to a canopy-dominant tree (Paillet,

1984). Most sprouts survive for an extended period as small upright trees 2-4 m in height, with an enlarged root collar covered with suppressed buds (figure 2). Maps of dense sprout population show that only a small number originated from the base of former trees (figure 3).

These results indicate that the many living chestnut sprouts in modern forests are old seedlings that have survived for many years without ever becoming a large tree. The remains of large chestnut trees on the site illustrated in figure 3 were killed in 1922 according to the cross-correlation of ring widths with standard chronologies (Paillet, 1984). In addition to simply surviving, the many chestnut sprouts retained their small tree form through several cycles of stem destruction by blight or mechanical damage. Paillet (1993) suggests that this is not coincidence, and indicates this is an adaptation to insure that established chestnut seedlings remain “perpetually juvenile” (figure 4). This cycle of stem regeneration and root system abandonment appears designed to maintain seedling form indefinitely as a method of advanced regeneration. As a result of this sprouting mechanism, an established chestnut seedling might be able to assume its place in the canopy a century or more after germinating from a chestnut deposited in the forest litter. Although other American trees species are capable of producing coppice sprouts, the controlled release of stems and systematic replacement of the roots system in the chestnut seedling sprout cycle is unique to *Castanea dentata*.

CHESTNUT AS A RESOURCE FOR WILDLIFE

Chestnuts must have been a nearly ideal food for mast-consuming wildlife. Ripe chestnuts are not protected by a predator-resistant husk or shell, or by chemicals such as tannins. The general food “package” presented by chestnut was probably similar to that of the northern red oak or swamp chestnut oak (oak species producing relatively large fruit) in terms of fruit size and quantity of seed produced by an individual tree. The nutritional value of chestnuts (grams of carbohydrates, proteins, and fat per kilogram of nuts; Krochmal and Krochmal, 1982) is comparable to that of various oak species. Chestnut canopy crowns in naturalized stands of American chestnut are qualitatively similar to large oaks, and probably produce about the same number of nuts per branch tip as a northern red oak when the tree is producing at full capacity. These arguments suggest that a chestnut-dominated woodlot produced a nut crop that was qualitatively similar to the crop produced by an analogous stand of northern red oak trees.

Restoration of chestnut to American forests might still have an effect on wildlife by making a quantitative difference in total mast crop. An increase in total mast could be produced by two mechanisms: 1) chestnut seed crops would be more regular than those of other nut producing trees; and 2) chestnut might displace some tree species that do not produce nuts. Chestnut seed crops would exhibit relatively few years of low production because chestnut flowers in early summer when there is no possibility of frost damage to ovaries and catkins, and because the nuts mature quickly so as to minimize exposure to insects or other damage to the immature fruit. This would produce a net increase in mast crop when averaged over several years, and could have a beneficial effect for wildlife in those years when a late frost diminishes other nuts. Chestnut is adapted for relative well-drained sites, and would displace mostly other nut producing trees like oak and hickory on the drier end of the spectrum. However, chestnut can also grow on more mesic sites where it mixes with beech, tulip poplar, maple, basswood, and hemlock. Of these trees, only beech produces a significant mast crop. Together, these mechanisms suggest that reintroduction of chestnut might increase total nut production for wildlife by something like 20 to 50%.



Figure 2. Typical chestnut sprout living in the understory of former oak-chestnut woodland in New England; the log leaning against the stone wall represents the typical appearance in 1983 of a chestnut tree killed by blight in 1922.

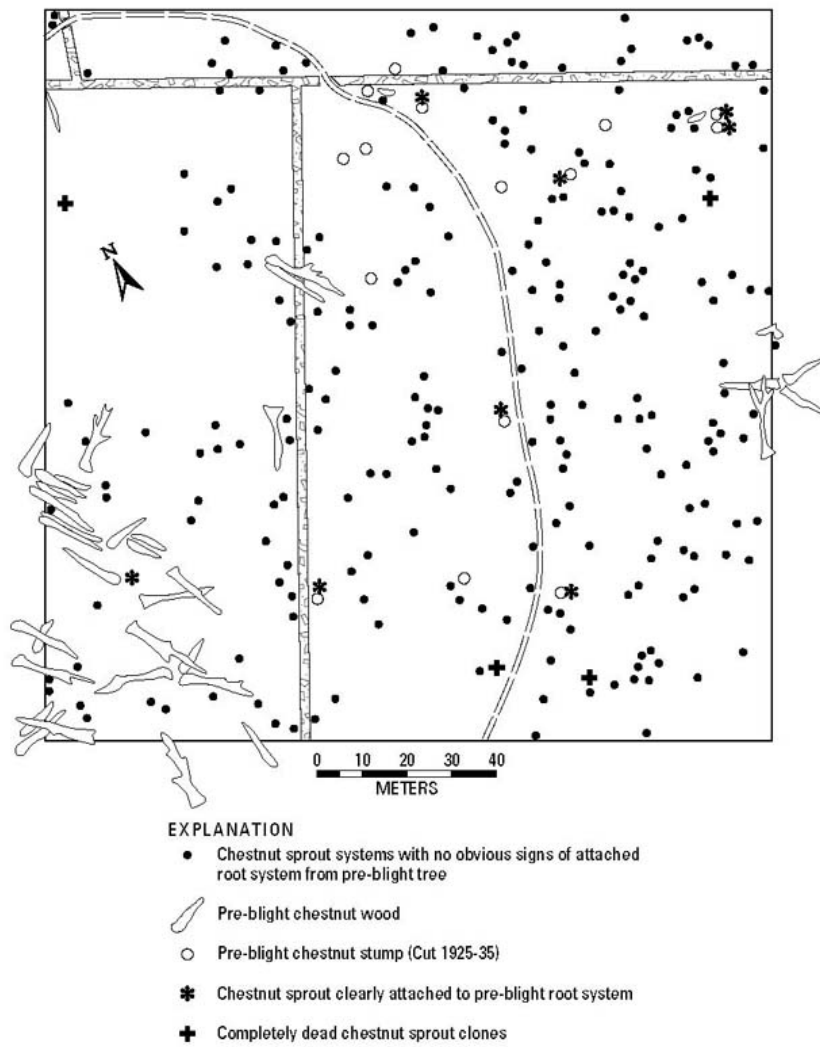


Figure 3. Remains of chestnut trees killed by blight in 1922 and living chestnut sprouts present in 1983 on a one-hectare plot in Andover, Massachusetts (from Paillet, 1984)

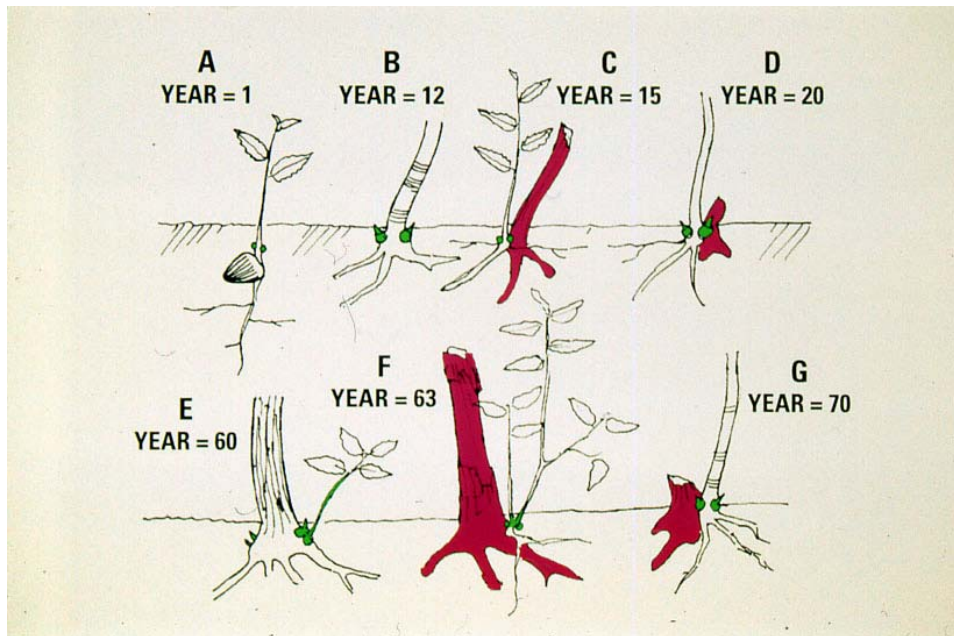


Figure 4. Schematic illustration of the chestnut seedling growth cycle where seedlings develop root collar buds that replace injured or senescent stems, generate a new root system and root collar buds, and retain juvenile growth form and defect-free stem base throughout an indefinite number of such stem replacement cycles.

WILDLIFE AS A DISPERSAL AGENT FOR CHESTNUT

Ecological literature assumes that mast crops are “designed” to be attractive to wildlife to provide effective dispersal of seed. Seed predators and trees interact in complex ways to insure that predators are “rewarded” for their role in planting nuts, while seed protection mechanisms insure that at least some nuts survive to germinate and grow. The seasonality of nut crops naturally results in seed caching by some predators to make the mast crop last the entire year. But this also allows other predators to develop rooting behavior to “harvest” these caches. Thus it is beneficial for nut-producing trees to develop features that deter seed predators. The most often cited mechanism is the irregularity of seed crops from year to year. Most nut-producing trees (oak, hickory, walnut, beech) flower in the early spring. This allows wind to transport pollen through the bare canopy, and causes late frost and spring storms to damage seed crops in certain years. Ecologists suggest that the natural cycling of the seed crop serves to keep predator populations under control. Nuts are also protected by thick, hard seed coats and/or chemicals such as tannins.

Chestnut is unique among nut producing trees in North America in having essentially no deterrence for seed predators. The seed itself is protected by a thin shell and contains no tannins or other chemicals to reduce palatability. Young chestnuts are protected by a formidable burr during development, but the burr opens wide when the seed is ripe. The maturing fruit is exposed to possible damage for a relatively short period and is protected from predation by its burr during that period. Chestnut flowers in late June or July when there is no possibility of frost. All of these factors show that chestnut fruit is produced with regular seed crops that are designed to be as attractive to predators as possible. This presents a paradox in that chestnut seems to defy the logic of predator/prey cycles.

Various studies suggest that seed predation is a real problem in chestnut reproduction. All of the early forestry literature cites a lack of chestnut reproduction by seed. Buttrick and Holmes (1913) suggest that lack of seedling establishment may be the cause of the loss of chestnut from some North Carolina piedmont sites where it was formerly abundant. Thoreau (1906) likewise describes a nearly complete lack of chestnut seedlings in chestnut woodlots in Massachusetts. Paillet (1988) noted that there were some New England sites where logs and stumps showed that chestnut was once dominant in the canopy, but where the low density or lack of living sprouts shows that chestnut seedlings were not being established. He also noted that maps of living chestnut sprouts indicated microsites such as fences, rights of way and brush thickets influenced seedling establishment. Pridnya et al (1996) note a similar condition in old-growth European chestnut forests in southern Russia. Since it is unlikely that these forests were not producing chestnuts and since there is no obvious reason why some seedlings would not germinate, seed predation by livestock or wildlife is assumed to have caused the lack of surviving seedlings. Such observations leave no doubt that seed predation can be a significant problem for chestnut reproduction. The nearly complete lack of any deterrence with regard to seed predation and the apparent effects on seed predation for at least the short term in many historic woodlands presents an ecological paradox that may have implications in attempts to restore naturally-reproducing chestnut trees to American forest.

A POSSIBLE EXPLANATION

My hypothesis addresses this paradox under the assumption that chestnut is a successful forest tree and recognizable as a distinct genus in the fossil record for at least 50 million years (Graham, 1990). If chestnut is a successful species, why has competitive interaction with other forest trees not selected seed traits for factors that deter seed predation? The simplest answer is that such adaptations have not arisen because there is no significant adaptive advantage to them. I suggest that the unique seedling re-sprouting capability of chestnut produces “immortal” seedlings that can survive for centuries. I propose that the longevity of viable seedlings (viable in the sense that they can be released to form a cleanly-formed, canopy-dominant stem) completely compensates for seed predation. At the same time, the extended life cycle of chestnut as a tree (centuries in the understory and then several centuries in the canopy) implies that chestnut “invasion” of new territory is a slow process. This, in turn, places added significance on mechanisms for seed dispersal. I conclude that seed predation is not important for chestnut because the longevity of a few established seedlings compensates for predation. At the same time, the inherent slowness in forest turnover associated with this process places a premium on seed dispersal. Chestnut is “designed” to encourage seed transport in every way, and is largely unaffected by seed predation in the long term.

This explanation is largely a “default option” that suggests chestnut does not deter seed predation because such deterrence has a metabolic cost but has no selective advantage. Is there any positive support for this idea? One line of evidence comes from the comparison of chestnut pollen on two adjacent sites in Massachusetts (Foster and Zybruk, 1991). The data give profiles for a bog catchment receiving pollen for many square km around the site, and a forest hollow catchment underneath the forest canopy receiving mostly local pollen from directly above. The bog pollen shows a rather consistent regional proportion of 10% chestnut pollen over the past 3000 years. In contrast, the forest hollow pollen shows fluctuations from near zero to 60% or more that follow discrete disturbance events (fire and windstorm). This suggests that the regional proportion of chestnut was constant, but that the local abundance of chestnut was highly variable. I interpret this as a situation where seed predation concentrated on the areas immediate around and beneath mature trees, while chestnut seedlings could escape predation in other parts of the forest. This is exactly the same situation as reported by Thoreau (1906), where he could not find chestnut seedlings in chestnut woodlots, but found them abundant in adjacent old-field pine stands. Russian ecologists identify a similar “bottleneck” in chestnut reproduction related to the need to establish chestnut seedlings in the understory (Pridnya et al, 1996; figure 5)

Does any of this have a bearing on the introduction of blight resistant chestnut into national park forests? This hypothesis explains why chestnut is such a slowly migrating species under the influence of climate change. Introduction of blight-resistant chestnut would also be a lengthy process. Several approaches could be used to hasten the process. First, one could use special seed-predator exclusion techniques to produce microsites suitable for chestnut seedling establishment. One could also transplant seedlings to generate established old seedlings to bypass the reproductive “bottleneck” related to seedling establishment. Then one could also rely on the artificial generation of disturbance to promote the release of suppressed seedlings. Although such manipulation may seem ill suited for wilderness areas in national parks, the alternative is a period of 1000 years or more before restored chestnut reaches a natural equilibrium with the surrounding forest.

SUMMARY

The interaction of chestnut with wildlife can be separated into two issues: 1) Chestnuts as a resource for wildlife consumption; and 2) Wildlife as a dispersal agent for chestnut seed. Making an analogy between the growth form and nut crop of northern red oak and chestnut, the former chestnut mast resource is estimated to be qualitatively similar to that of other large-fruited mast species. Chestnut mast may have been quantitatively better because chestnut crops were probably more reliable from season to season, and because chestnut has been partly replaced by tree species such as tulip poplar that do not produce nuts. These factors may result in a 20 to 50% increase in total mast production if chestnut is re-established as a canopy-dominant tree in American forests. The availability of chestnuts in years of frost or insect damage to acorns may make chestnut an especially valuable addition to the forest. Dispersal of chestnut seed and seed burial by wildlife was important because chestnuts are relatively fragile and have little resistance to frost or desiccation. However, chestnuts as seed exhibit none of the mechanisms usually associated with a trade-off between dispersal and predation. Chestnut reproduction occurred most often by coppice sprouting, and chestnut seedlings were reportedly rare or absent in many chestnut stands. One explanation for this apparent paradox is that there is no selective pressure on chestnut for the deterrence of predators. This happens because chestnut reproduction is based on a combination of wildlife dispersal of nuts and long-term survival of the few seedlings that do manage to germinate. Many living chestnut seedlings have survived for at least a century as small suppressed stems and possess root collar sprouting characteristics designed to insure that “old seedlings” remain juvenile essentially forever. Thus, chestnut reproduction by seed is heavily biased in favor of mechanisms to promote long-distance transport. The near immortality of established chestnut rootstocks could offset any selective value in deterring seed predation within chestnut-dominated stands.



Figure 5. Many European chestnut (*Castanea sativa*) trees in old growth forests of southern Russia show multiple stems indicative of origin as sprouts derived from suppressed seedlings (from Pridnya et al, 1996).

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