Bulletin of the Torrey Botanical Club 123(3), 1996, pp. 213–222

Ecology and pathology of European chestnut (*Castanea sativa*) in the deciduous forests of the Caucasus Mountains in southern Russia[1]

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PRIDNYA, M. V. AND V. V. CHERPAKOV (Caucasus State Biosphere Preserve, Sochi, Russia) AND F. L. PAILLET (U.S. Geological Survey, MS 403, Box 25046, Federal Center, Denver, CO 80225). Ecology and pathology of European chestnut (*Castanea sativa*) in the deciduous forests of the Caucasus Mountains in southern Russia. Bull. Torrey Bot. Club 123: 213–222. 1996.—Chestnut-dominated forests of the Caucasus Mountain area of Russia are very similar to former chestnut-dominated forests in eastern North America. The distribution, pathology, and reproductive status of European chestnut (*Castanea sativa*) in the Caucasus are described and compared to that of American chestnut (*C. dentata*). Chestnut forests are distributed continuously along the southern slope of the Caucasus mountains near the Black Sea, and are found in isolated populations on the north side of the Caucasus, at elevations ranging from 200 to 1300 meters. Chestnut blight was apparently introduced into the region after 1880 and continues to destroy chestnut forests today. Chestnut in the Caucasus is also infected by several other fungal and bacterial parasites and the joint infection of blight and bacteria may be especially dangerous for chestnut trees. Chestnut-dominated forests comprise only a few percent of total forest cover in the Caucasus Biosphere Preserve, and usually occur in mountain valleys or coves with deep brown soil. The age structure and reproductive status of chestnut in the Caucasus was investigated on six study plots in the Caucasus Biosphere Forest Preserve near the upper altitudinal limit of chestnut. Although chestnut is at least 70 percent of the overstory on these sites, there are very few trees less than 50 years old, and very few recent seedlings on any of the plots. Most large chestnut trees appear to have originated as basal spouts from previously established stems. Although chestnut seed production appears adequate, we suspect that competition with shrubs and other tree seedlings, and predation by herbivores and rodents, now prevent the establishment and survival of chestnut seedlings in the Biosphere Preserve.

Key words: chestnut blight, *Castanea, Caucasus,* deciduous forests.

American chestnut was one of the dominant trees in the forests of eastern North America before chestnut blight reduced the importance of that species (Anagnostakis 1987). Recent plans to introduce blight-resistant forms of chestnut into eastern U.S. forests, and efforts to reconstruct the ecological role of chestnut in prehistoric forests has generated intense interest in the ecology of *Castanea,* and especially the interaction between chestnut trees and pathogens in the forest (Burnham et al. 1986). Paleoecological studies have raised questions about the reproductive characteristics of chestnut in natural forests, and under the disturbance regime imposed by aboriginal and European settlers (Foster and Zebryk 1993; Russell 1980). The observations recorded by the nineteenth century North American naturalist Thoreau further indicate that chestnut reproduction was strongly influenced by agricultural and silvacultural practices in New England (Paillet 1988). One way of discerning the ecological characteristics of chestnut and the interaction between *Castanea* and other forest species is to examine the characteristics of related species in a similar but independently evolving forest ecosystem. In this paper we review the ecology and pathology of European chestnut (*C. sativa*) in the deciduous forests of the Caucasus region of Russia where chestnut grows in competition with other deciduous species such as beech, oak, hornbeam, and maple, and where chestnut has been interacting with chestnut blight and other pathogens. We review the distribution of chestnut in the region, and discuss ongoing efforts to evaluate the reproductive status of chestnut in the Caucasus Biosphere Forest Preserve. We also attempt to highlight similarities and differences in the ecology of American and European chestnut species that may be relevant to investigations of chestnut paleoecology, and the study of the interaction between American chestnut and blight.

[1] English translation of the original Russian manuscripts used to prepare this manuscript was provided by Dorothy Vitaliano. Sandra Anagnostakis, Wayne Martin, and an anonymous reviewer provided helpful reviews of earlier versions of this manuscript.

Received for publication March 5, 1995, and in revised form December 17, 1995.

DISTRIBUTION OF CHESTNUT IN THE CAUCASUS REGION OF RUSSIA. In 1956, the total area of forests containing chestnut (*C. sativa*) in the Caucasus was estimated to range from 70,000 to 80,000 hectares (Issinskiy 1968; Scientific Technical Conference of the Sochi NILSS 1956). Most of these chestnut forests (about 50,000 ha in 1956) were distributed along the Black Sea coast. The 1956 estimates indicate about 17,000 ha of chestnut forest in Krasnodor Krai, 23,000 ha in Abkazia, and 20,000 in western Georgia. The designation of forest as chestnut-dominated is somewhat arbitrary, because chestnut usually grows in mixed associations with beech, hornbeam, various oaks, aspen and fir. At the present time we estimate that the total area of chestnut forest in the western Caucasus has decreased to about two thirds of the 1956 estimated area (about 50,000 ha) as a result of disease and cutting.

More than 90 percent of all chestnut stands in the Caucasus region occur on the southern slope of the Caucasus Mountains, in the vicinity of the Black Sea. However, a few natural stands of chestnut have persisted away from the southern part of the range in the form of isolated stands on the northern side of the Caucasus Mountains. The discontinuous distribution of chestnut in the Caucasus today is attributed to the great antiquity of the species in this region. We can explain the origin of these northern outliers in the distribution of chestnut in two ways: 1) as local penetration of forests where chestnut is not otherwise present; and 2) as preservation of refuges suitable for survival of the diverse flora of mesic Black Sea coastal forests [the Colchis flora of Sokolov (1931)] from the previous interglacial period.

CHESTNUT IN THE CAUCASUS FOREST PRESERVE. The Causasus Biosphere Forest Preserve (Fig. 1) was established to preserve economically valuable chestnut stands and other broad-leaved forest communities, at a time when there was widespread destruction of forests in the western Caucasus region (Dolukhanov 1953; Issinskiy 1968). The presence and local predominance of European chestnut (*C. sativa*) in the Preserve is worth special attention because of the tertiary-relict nature of chestnut in the Caucasus, and because the natural populations of chestnut exist at their upper altitudinal limit at this location. Previous studies of chestnut in the Black Sea region have concentrated on adjacent, lower elevation forests (Sokolov 1931; Sinskaya 1933; Khar'yuzova 1936; Kats 1936; Sosin 1939; Grosgeym 1952; Krasil'nikov 1953; Budyanskiy 1956; Kalgin 1958; Tugushi 1971). In this paper we describe the natural chestnut forests of the Preserve, and the natural regeneration of chestnut within old-growth chestnut stands at various elevations in the Preserve.

The area of forests containing a significant proportion of chestnut within the Preserve is small compared to that dominated by other forest tree species. Chestnut occurs on only about 1.8 percent of the total 2200 forested hectares within the Preserve boundaries. This figure compares with an estimated 2.4 percent of the total forest in Krasnodor Krai as a whole (Skripko 1969). Chestnut in the Preserve is most common on slopes with northerly exposures, but is also found on all other exposures. Forests where chestnut is the dominant tree, or where chestnut shares dominance with one or more deciduous tree species, are located in a belt ranging from 200 to 1000 meters in elevation (Fig. 2), where annual rainfall varies from about 100 to more than 150 centimeters per year. Isolated stands of chestnut also occur at higher locations, ranging from 1000 to 1300 m in elevation, where the forest contains substantial amounts of Nordmann fir. Chestnut-dominated forests are generally established on the thick brown forest soils which usually occur in the lower slopes of mountain valleys rather than on the steep upper slopes and ridge crests. However, chestnut is at least a minor constituent of most deciduous forests south of the Caucasian divide in the Preserve.

Chestnut is generally found in association with other hardwoods in the Preserve, rather than as pure stands (Fig. 2A and C). The common associates of chestnut in the Preserve are: Oriental beech (*Fagus orientalis*), hornbeam (*Carpinus betulus*), and durmast oak (*Quercus petraea*). Less common associates of chestnut include European ash (*Fraxinus excelsior*), planetree maple (*Acer pseudoplanatus*), Norway maple (*A. platanoides*), hedge maple (*A. campestre*), pear (*Pirus communis*), linden (*Tilia caucasia*), and fir (*Abies nordmannii*). Aspen (*Populus tremula*) and bird cherry (*Prunus avium*) are locally present where windstorms and landslides have produced openings in the forest. Although the shrub stratum in chestnut-dominated forests is sometimes lacking, the most common shrub species associated with *Castanea* are hazel (*Corylus avellana*), high-bush blueberry (*Vaccinium* sp.), and rhododendron and de-

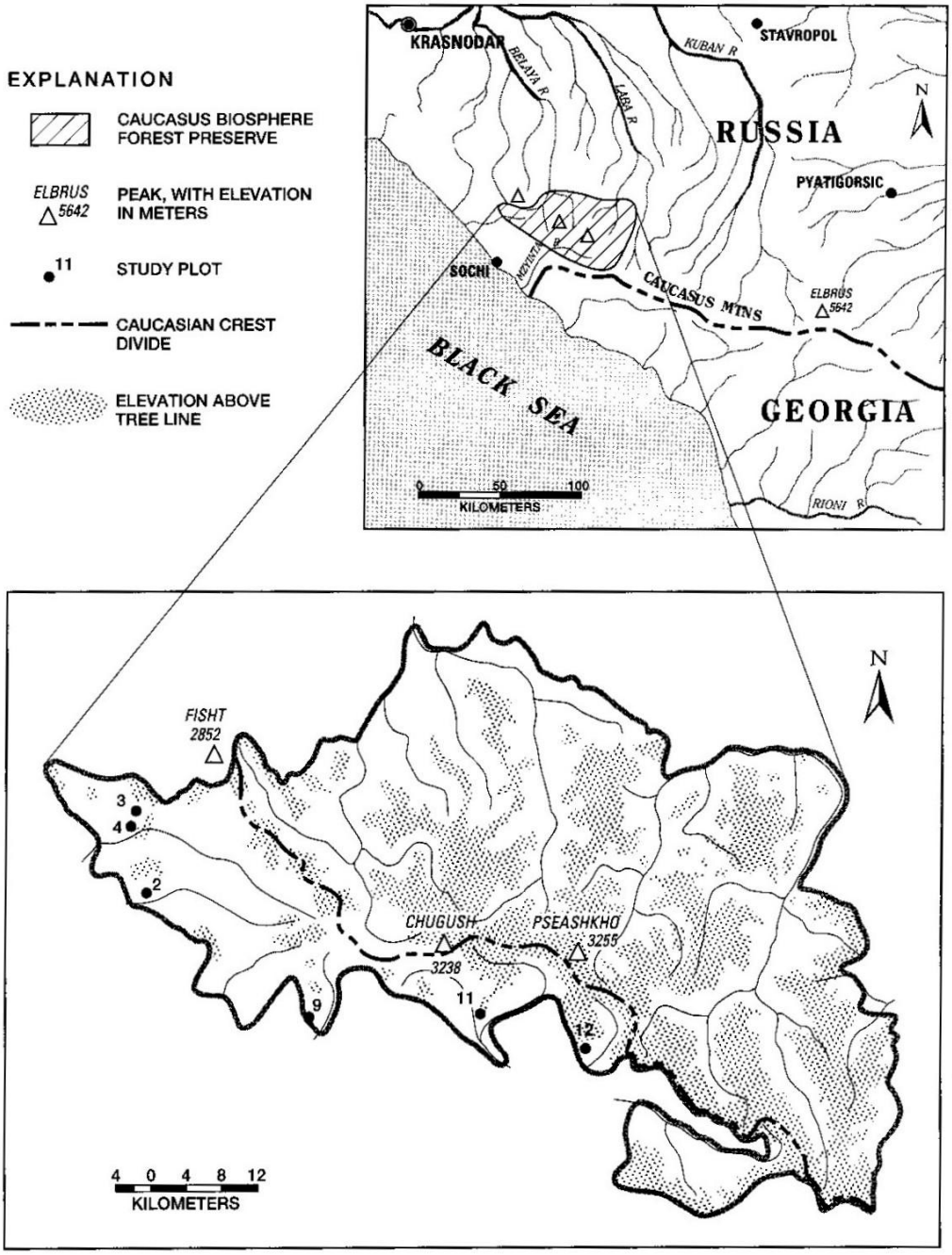

Fig. 1. Location of the Caucasus State Biosphere Preserve in the Caucasus Mountains of southern Russia.

ciduous azalea (*Rhododendron* sp.). The two tree species most commonly found in association with chestnut are hornbeam and beech, and the average proportion of chestnut in such mixed forests is about 70 percent. Chestnut forests show a broad distribution of ages, with an average tree age of about 130 years, many trees in the 100–120 year age group, and a few trees

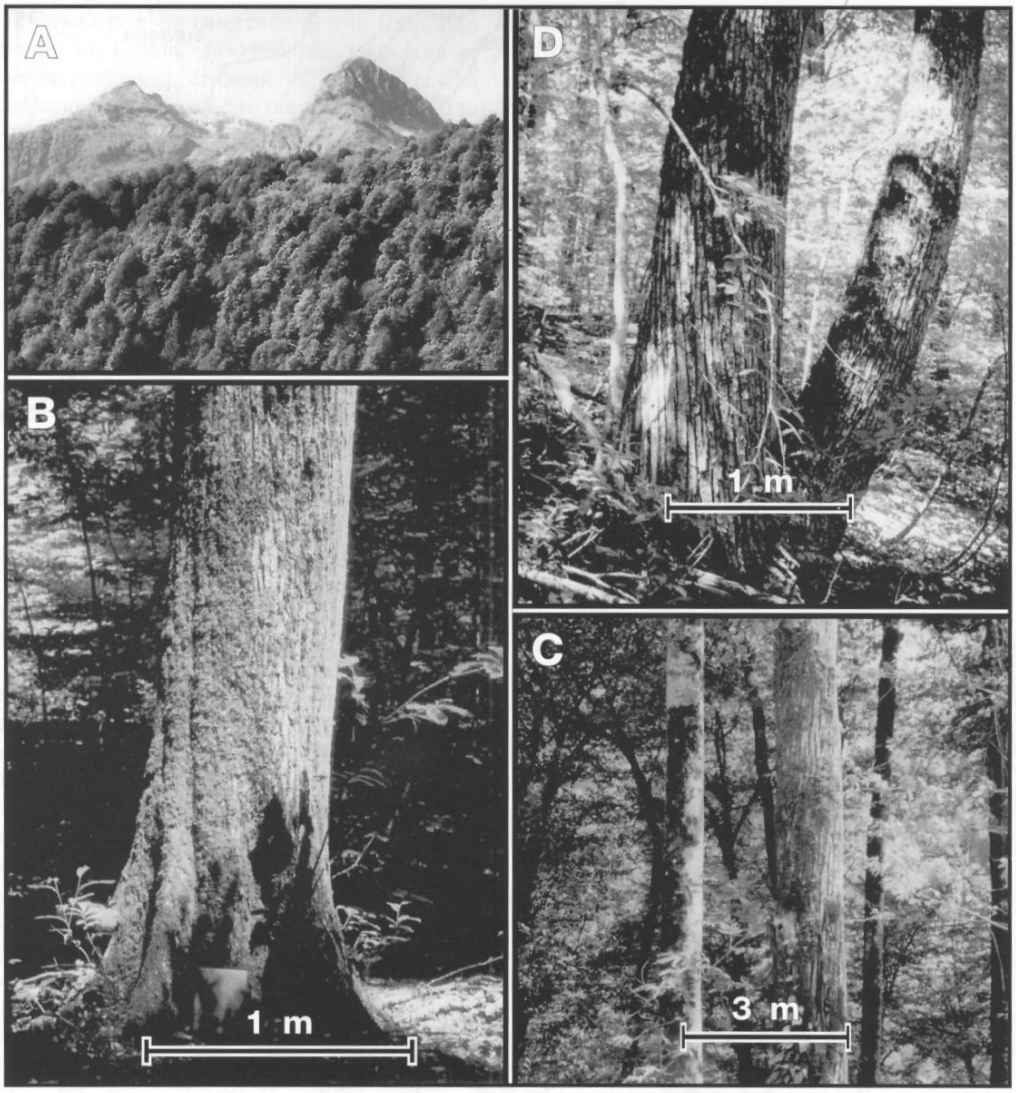

Fig. 2. Chestnut in the Caucasus State Biosphere Preserve: A) Chestnut, beech, hornbeam and oak slope forest at about 700 m in elevation; B) typical size of old-growth chestnut in the Caucasus; C) chestnut and beech with hornbeam in the background; and D) many chestnut trees have more than one stem, indicating origin as root collar sprouts.

over 200 years old (Fig. 3). The area of young stands of chestnut is very small. The fact that the age distribution is so skewed towards older trees indicates that there has been little recent reproduction. The relative proportion of chestnut in the stand appears to decrease with age as hornbeam and beech increase in the percentage of total stand composition.

PATHOLOGY OF CHESTNUT IN THE CAUCASUS. Disease in chestnut stands, denoted as "drying" or "desiccation" of chestnut in the Russian literature, was first noted in the 1880's. Since the beginning of the present century such desiccation has encompassed considerable areas in the present Sochi Forestry Farm. The first systematic investigations of the cause of the disappearance of chestnut on the Black Sea Coast was made by A. P. Shcherbin-Parfenenko (1950, 1939), who noted large-scale disappearance in the once excellent natural chestnut stands along

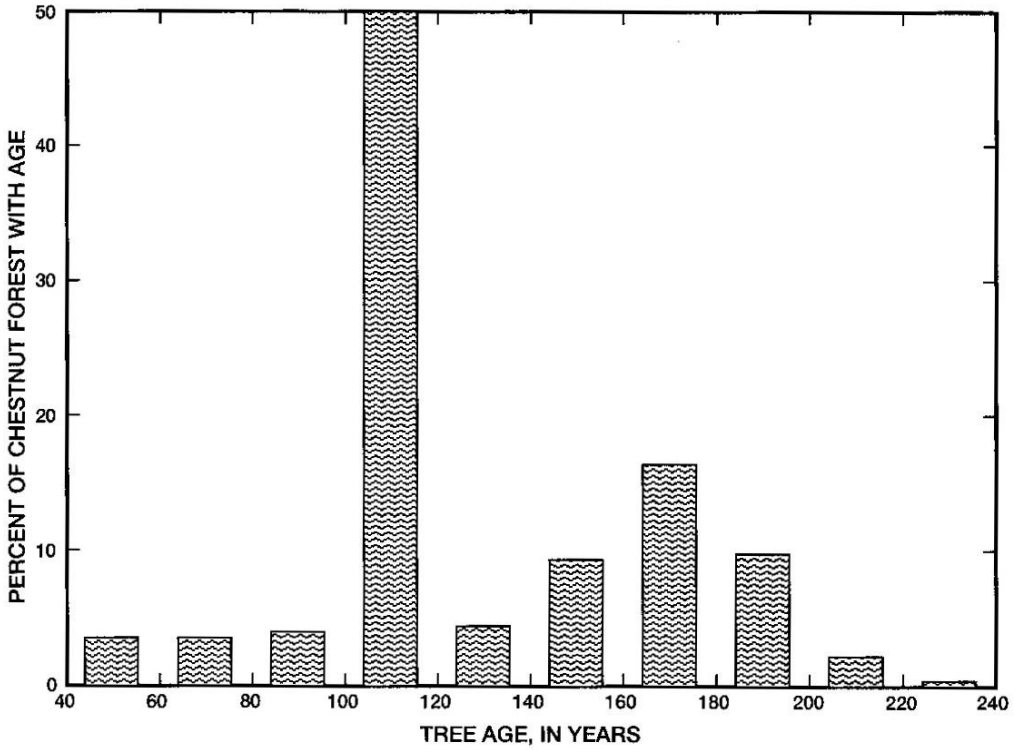

Fig. 3. Age distribution of chestnut trees in the Caucasus Biosphere Preserve.

the upper course of the Matsesta River in the vicinity of Sochi where about half of the stands were affected, and in the Lazarevskoye area. In 1937–1938, chestnut (but not other species) was observed to disappear from natural indigenous stands, from cultivated stands, and from nurseries in the Loo forest sector. Since that time, desiccation has involved practically the whole range of chestnut in the Caucasus region (Issinskiy 1968; Shcherbin-Parfenenko 1950).

Desiccation of chestnut stands in the Black Sea region may be due to many different disturbances and pathogens, including the damage by fire, bark beetles and long-horned beetles, and various kinds of microorganisms. A leading Russian scientist, Academician N. I. Vavilov, hypothesized that the centers of diversity of specialized parasites in a host-parasite system coincide with the centers of diversity of the host species (Cherpakov 1987). Because of this, we questioned whether the desiccation observed was due to a new pathogen imported into the Caucasus region, or whether it was due to a local mutation of a native, saprophytic species.

The investigations of Shcherbin-Parfenenko (1950) identified fungi of the genus *Cryphonectria* (formerly *Endothia*), including the pathogen *C. parasitica* and the saprophyte *C. radicalis* (*fluens*). Attempts by Shcherbin-Parfenenko to inoculate chestnut trees with a pure culture of *C. parasitica* yielded no positive results, but tests in the United States of chestnut trees from the Caucasus Mountains indicated that they are highly susceptible to chestnut blight, caused by *C. parasitica,* as were most other *C. sativa* from different countries growing in the United States (Gravatt 1952). Shcherbin-Parfenenko was able to initiate cankers on chestnut trees by inoculating with pieces of diseased bark tissue from infected trees.

Cultivated trees in isolated areas on the northern slope of the Caucasus Mountains (20 to 50 km from the main range of chestnut) were found to have desiccation, and Shcherbin-Parfenenko (1958) isolated *Amphiporthe* (*Cytodiplospora*) *castanea* and *Xenotypa* (*Radalum*) sp. from these cankers.

A number of bacteria are also implicated in diseases of the *C. sativa* in the Caucasus (Cherpakov 1979, 1987). In the late 1970's, we found

evidence of a bacterial blight on otherwise-healthy chestnut trees in the Lazarevsk Forest Farm and the Caucasus Forest Preserve. We isolated and identified *Erwinia ligniphila,* a bacterium in the *Amylovora* group. In the same canker we found another bacterium identified as *E. multivora,* which was able to cause symptoms resembling those of ink disease of chestnut (caused by *Phytophthora cambivora,* Gravatt 1952). These two bacteria, separately or together, can kill chestnut trees. There are often both bacterial and fungal infections in the same tree.

One important feature of the bacterial infections is the lack of external symptoms, and our inability to recover bacteria when isolations are made onto acidified fungal media. One possible explanation for the infection failures of Shcherbin-Parfenenko is that bacteria were contained in the pieces of infected bark tissue used in his infection experiments, but not in his pure cultures of fungi. We suspect that dual infections may play an important part in the observed desiccation of chestnut in the Caucasus. The dual infection of chestnut tissue by fungi and bacteria may be an important subject in future studies of the effects of these pathogens on chestnut.

Desiccation of chestnut in the Caucasus continues, and the investigation of pathology in chestnut plantings indicates that bacteria are involved in the disappearance of chestnut trees from the forest. Recent forest pathology surveys show that either partial ("shelterwood") cutting or clear cutting of diseased chestnut stands aggravates the situation. Coppice stands of chestnut, resulting from clear cutting of chestnut forests, seem to be no more resistant to disease than the former canopy trees. In our investigations of such second-growth stands, we find about 20% of the chestnut stems dead and fallen, 50% clearly infected and suffering desiccation, and the remaining 30% probably suffering from latent infection. The typical time period between cycles of cutting in these forests is 40–50 years.

In the future, the preservation of the Caucasian chestnut trees may depend on the identification of reliably resistant individuals, or on the hybridization of susceptible trees with other species, if they are found to be resistant to desiccation.

CHESTNUT REGENERATION ON TEST PLOTS IN THE CAUCASUS FOREST PRESERVE. Information on the natural regeneration of chestnut forests in the preserve was obtained by surveying the stands in the basins draining into the Shakha and Mzymty Rivers. These chestnut forests are listed as the Colchis type according to the classification of Sokolov (1931). We sampled vegetation along transects crossing these basins, and established permanent test plots at locations along the sampling routes. The test plots were situated in similar topographic positions: the floor of relatively broad valleys of various steepness and exposure, surrounded by the very steep slopes forming the sides of these U-shaped valleys. All of these sites have deep brown soils developed on metamorphosed Jurassic shales. During the survey we recorded the presence, condition, and relative abundance of chestnut reproduction under various conditions. All woody plants were identified and mapped on each of the test plots; tree species were divided into canopy and reproduction classes. In tabulating the data for the study plots, canopy and subcanopy trees were defined in a single class as stems greater than 8 cm in diameter measured 1.5 meters above ground level. The diameter and height of all canopy and subcanopy trees were measured, and the ages of these stems were determined from increment borings. All smaller diameter stems of tree species were considered to be saplings or seedlings forming the reproductive class. True seedlings were defined as seedlings clearly having originated within the previous year.

The relative abundance of chestnut and associated tree species on the test plots are given in Table 1 and Fig. 3. Most of the chestnut stems on these plots are clustered in groups (Fig. 2D). The lack of identifiable remains of "parent" trees in association with these clusters of stems suggests that they arose from seedlings and not as sprouts from the base of former trees. This observation is similar to the observations that most understory chestnut sprouts in New England are "old" seedlings and not basal sprouts from former trees (Paillet 1984). We suspect that these clusters of stems arose from the base of former seedlings damaged by animals. An alternative explanation for these clusters of stems is the origin of multiple stems from a single seed as described by Kalgin (1958). None of the chestnut trees on these test areas showed any sign of disease or "desiccation," except for the indirect evidence given by the observed lack of stems identified in relatively young age groups.

In examining the extent of chestnut reproduction on our test plots, we found a very small number of older chestnut seedlings and saplings in comparison to the generally abundant reproductive class of other tree species and shrubs

Table 1. Composition of chestnut stands in the Caucasus Forest Preserve.

Study plot number	2	3	4	9	11	12
Site elevation (in meters)	770	740	690	540	730	1210
Site area (in hectares)	0.16	0.26	0.40	0.20	0.26	0.40
Slope steepness (in degrees)	20	25	10	7	33	22
Exposure	SE	E	N	S	S	S
Canopy composition (in percent)						
Castanea sativa	90	80	30	80	50	70
Carpinus betula	10	20	30	20	30	10
Pyrus communis	—	—	10	—	—	—
Abies nordmannii	—	—	10	—	—	10
Fagus orientalis	—	—	—	—	20	10
Stand density (percent fully stocked)	90	80	90	90	90	90
Study Plot Averages for Castanea:						
Stems per ha	1180	1280	400	1005	668	475
Age in yrs	54	55	100	55	140	140
Diameter in cm	24.0	19.7	30.0	23.0	47.8	44.0
Height in m	23.6	19.9	26.9	26.2	29.0	24.0

(Table 2). Chestnut does not exceed 10 percent of the smaller stems of tree species on the test plots, and is a much smaller percent if both shrubs and trees are considered. These smaller chestnut stems are also generally shorter and of smaller diameter than those of other tree species growing in the understory. All of the data in Table 2 indicate that hornbeam, beech, maple, or fir (on area 4) will replace chestnut on the test plots when the present chestnut-dominated overstory is eliminated by age, disease, or disturbance. Our data generally show that chestnut seedlings established beneath the canopy of chestnut-dominated stands do not survive into their tenth year and rarely reach 1 meter in height. We conclude that there is very poor seed regeneration of chestnut beneath canopies dominated by trees of various species composition, and with various age structures and densities. These results agree with those given by Budyanskiy (1956) for the Krasnopolyanskoye forest area which is adjacent to the Preserve, but at lower elevations (300–500 m). Our results differ from those of Sokolov (1931) who concluded that regeneration of chestnut forests of the Colchis type was adequate in the lower portion of its range in the Shaka River basin.

In our study we find that there is a striking absence of chestnut stems in the 10–40 year age group in all parts of the Preserve, in contrast with the abundant reproduction of other tree species. We also find chestnut reproduction absent

Table 2. Natural regeneration of chestnut in chestnut-dominated forests.

Study plot number	2	3	4	9	11	12
Understory tree composition (percent)						
Castanea sativa	10	<1	10	<1	10	—
Carpinus betula	90	90	—	100	70	30
Acer campestre	—	10	—	—	—	—
Abies nordmannii	—	—	90	—	—	20
Fagus orientalis	—	—	—	—	20	20
Acer pseudoplanatus	—	—	—	—	—	30
Average Height (cm)						
All tree species	50	200	400	450	250	800
Castanea	10	100	200	100	50	—
Average Diameter (cm)						
All tree species	0.5	1.0	2.5	3.0	1.6	7.5
Castanea	0.3	0.3	1.5	0.3	0.2	—
Number of Species Present						
Trees and shrubs	10	21	10	11	10	16
All plant species	19	68	21	14	19	23

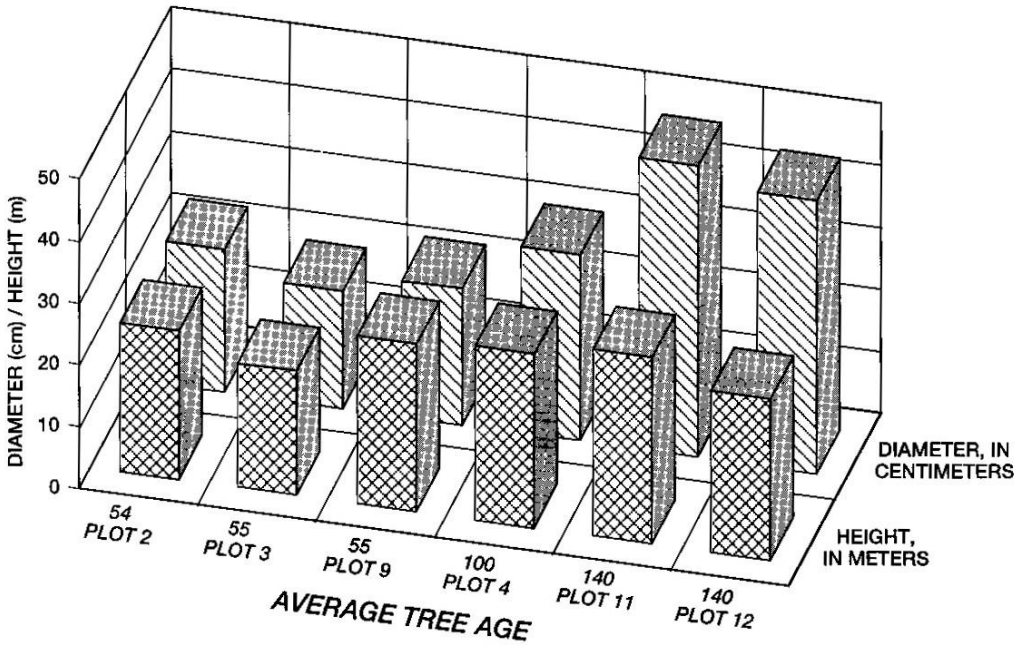

Fig. 4. Average chestnut stem age, height, and diameter on six test plots in the Caucasus Biosphere Preserve.

from open areas. These results cannot be attributed to a lack of seed production, because we observe that chestnut produces sufficient seed crops in most years. We infer that chestnut is able to colonize open areas because we find broad and high crowned trees (indicating that they developed in the open) scattered in stands of younger, more densely crowned trees. We conclude that these older trees first inhabited the so-called "Circassian Meadows," and that the dense stand of younger trees represent their descendants. Because there is no apparent lack of chestnut seed production, and because we infer that chestnut has been able to colonize forests and open areas in the past, we believe that specific ecological and environmental conditions of the Preserve account for the lack of chestnut reproduction. Competition between species is probably important. The number of different tree and shrub species present on our test plots varies from 10 to 21 (Table 2). The plot with the most species (area 12) had no small chestnut saplings even though chestnut comprised 70% of the canopy, and the stand density was no higher than in the other stands. There is a high population of ungulates and rodents within the Preserve and we suspect that their predation on seeds and young plants is important.

The relationship between disturbance regime, seed predation, and regeneration in chestnut forests was investigated by surveying the chestnut-dominated forests around study site 11 during July, 1995. The two main forms of disturbance identified were windstorm and landslide. Numerous openings in the forest were created where one to several large trees were blown over by windstorm. Several areas of ongoing landslides were identified, and a "stairstep" contour to steep slopes indicated the location of many more inactive landslides. Large cherry and aspen trees were growing on these stabilized slopes, and aspen seedlings were found on areas of exposed soil in active landslides.

Very few instances of chestnut sapling release were identified in areas in recently created canopy openings. In almost all instances where new chestnut stems were regenerating, these stems originated from the root collar of former canopy trees overturned by windstorm or landslides. However, chestnut saplings were very rare in this watershed in comparison to beech saplings, which were consistently present, and which were being released in recently created canopy gaps. Twelve small beech saplings were excavated and all were found to have root systems with no indication of connection to root systems of larger trees. We conclude that beech does not reproduce by root sprouting in the Preserve, and

that beech seedlings have been able to become established in the understory in the past. In contrast, the rarity of chestnut saplings in the understory indicates that chestnut seedlings have not been surviving in past years.

Although we speculate that seed predation has caused the absence of chestnut saplings in the Preserve, inspection in the vicinity of study site 11 in July, 1995 indicated an abundance of year-old chestnut seedlings. Our local sampling indicated an average of about 1500 chestnut seedlings per hectare, which was more than twice the number of beech seedlings counted in the same areas. In contrast, we sampled only a few chestnut saplings greater than 0.5 meter tall. This observation indicates a recent change in conditions that have allowed the establishment of chestnut seedlings. Earlier observations in this and adjacent areas in the Preserve indicated extensive disruption to leaf litter by the foraging of wild pigs (*Sus scrofa*) (Wayne Martin, pers. comm. 1995). Almost no indication of leaf litter disruption was found in 1995. Very little rodent activity was noted, and the only active seed predator identified were European jays (*Garrulus glandarius*) actively feeding on immature beechnuts. We conclude that the large numbers of recently-established chestnut seedlings result from a recent decrease in the level of seed predation related to a temporary reduction in the number of seed and seedling predators.

COMMENTS ON FUTURE CHESTNUT RESEARCH IN THE CAUCASUS FOREST PRESERVE. The chestnut forests of the Caucasus Biosphere Forest Preserve consist of high-density, vigorous trees producing sufficient crops of seed at reliable intervals. In spite of the vigor of the older chestnut trees, regeneration of chestnut in the understory of Preserve forests seems to be exceptionally poor. This observed lack of chestnut reproduction appears similar to reports of limited chestnut reproduction on certain North American sites given by Paillet (1988), and appears to be related to factors such as seed production and land use practices described by that author. Our data indicate that there has been no regeneration of chestnut stands in the past 10–40 years, while there were a very large number of chestnut trees established about 100 years ago. These results naturally raise the fear that chestnut forests will not retain their relative position in the forests of the Caucasus area. These high-altitude outlying chestnut forests could be especially important as the source of germplasm of chestnut. We recommend that a combination of ecological studies be continued to identify the underlying causes of the lack of regeneration of this valuable forest tree species in the Caucasus Biosphere Forest Preserve.

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