Incidence of Chestnut Blight and Survival of American Chestnut in Forest Clearcut and Neighboring Understory Sites

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ABSTRACT

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In 1985 and 1987, chestnut blight incidence and survival of American chestnut sprout clusters (groups of stems sprouting from a single stump) were assessed in Virginia and West Virginia forest clearcut sites, 13–19 yr after clearcutting, and in understory sites. Overall, sprout cluster blight incidence averaged 96.3% in 17 clearcuts and 37.1% in 13 understory sites; chestnut sprout cluster survival averaged 55.7 and 94.2% in clearcut and understory sites, respectively. In the 1987 survey, mean chestnut survival (49.8%) in 12 clearcut sites was significantly less than mean survival (93.7%) in 12 adjacent understory sites. Chestnut survival was 0% in three 13- to 19-yr-old clearcut sites, but 100% chestnut survival was found in one 13-yr-old clearcut site. Among clearcuts, chestnut survival greater than 0% was associated with a relatively open canopy. Superficial cankers, assayed by canker dissection, were found in 15 of 30 clearcut and understory sites, and had a greater frequency on sprout clusters with canopy or subcanopy stems than on clusters with small stems.

Additional keywords: *Cryphonectria parasitica*, *Endothia parasitica*, hypovirulence

Clearcutting of hardwood forests in the southern Appalachians is a common practice. American chestnut (*Castanea dentata* (Marsh.) Borkh.) sprouts vigorously in forest clearcuts, and grows as fast or faster than other competing hardwood stems (10,13) until killed by the blight fungus, *Endothia parasitica* (Murr.) P. J. And. & H. W. And. Hebard (8) showed that blight incidence in Virginia forest clearcuts was low initially but reached very high levels 9–10 yr after clearcutting. The fate of American chestnut sprout clusters (group of stems sprouting from a single stump) in clearcuts, after blight reaches a high level, has not been documented. Field observations and clearcut management and biocontrol studies by Griffin and Smith (*unpublished*) have indicated that some sprout clusters or clones may not survive blight. This study was undertaken to determine the survival level of American chestnut sprout clusters in old forest clearcuts (13–19 yr after clearcutting) and to compare survival in clearcuts to survival in neighboring understory sites. The frequency of superficial cankers in both types of sites also was determined because dsRNA-containing, hypovirulent *E. parasitica* strains have been found in clearcuts (3,6,7,16), and hypovirulent strains are frequently associated with superficial cankers (5). Information on American chestnut survival may be critical to evaluations of the impact of clearcutting on the surviving population of American chestnut sprouts in the eastern United States, and to studies on the biocontrol of blight in forest clearcuts.

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MATERIALS AND METHODS

Twelve study sites were located in the Jefferson National Forest in Montgomery, Giles, and Craig counties in Virginia, and one (SCM-1A) was located in the Monongahela National Forest in Greenbrier County, West Virginia. Based on species present, most appeared to be former oak-chestnut forests (2). Stephenson and others (1,9,11,15,16) have shown that oak species mainly have replaced chestnut following the chestnut blight pandemic. The stands were located on a bench or intermediate slope, which is where American chestnut was most important as a forest tree in the southern Appalachians (4). Age of clearcuts was obtained from forest district ranger station records. Clearcut sites were selected based on age (>13 yr), representative elevations, and aspects (directions slopes faced) for the general forested area of Virginia and West Virginia sampled.

In the 1985 survey, two to four transects, about 55 m long and 7 m wide each, were walked along the contour of the slope in five clearcuts (CC-1A, JC-OB, SCM-1A, CC-OA, and CC-3A). The number of chestnut sprout clusters sampled for blight incidence and survival varied from 27 to 39 per site. In the 1987 survey, transects in 12 clearcut sites were walked in a similar manner until two subplots of 25 chestnut sprout clusters per subplot had been surveyed for blight incidence and survival. Five clearcuts, indicated above for 1985, were studied in both 1985 and 1987 and were surveyed in similar but not identical areas of the clearcuts. In 1987, understory sites that were surveyed similarly were located as closely as possible to clearcut sites, and, in most instances, were within 50–100 m of the neighboring clearcuts. Neighboring understory and clearcut sites were labeled with the same code letters and numbers, except that a "U" was inserted for the understory site codes. Only one understory site, near clearcut site CC-OA, was examined in 1985, whereas 12 were examined in 1987.

American chestnut was identified by bud, leaf, and bark characters. In a few instances, old, standing, dead stems were identified by examining with a hand lens the characteristic xylem structure (12) of sawed and smoothed transverse sections of the stem. Blight was determined by the presence of cankers, stroma, or mycelial fans within dissected bark. A sprout cluster was classified as blighted if one or more stems in the cluster had blight. All suspected superficial cankers were dissected with a knife to the xylem. Cankers were termed superficial if 1) at least one-third of the circumference of the stem or canker width did not have necrotic tissue extending to the xylem, and 2) the presence of this healthy tissue below the canker surface extended the entire length of the canker. Usually this layer of healthy tissue was readily apparent upon canker dissection.

Survival of chestnut sprout clusters was assessed by determining if one or more living stems or shoots were present in a cluster. In 1985, diameter measurements were made on the largest living and dead stems in each cluster. For large stems, this measurement was made at a height of 1.4 m, but for small shoots (< 1.4 m), it was made below this level. In 1987, the number of clusters with canopy and subcanopy stems was determined. Canopy stems were defined as those extending to the upper portion of the canopy and exposed to direct sunlight, whereas subcanopy stems extended to the lower portion of the canopy. Mountain laurel (*Kalmia latifolia* L.) abundance in the shrub layer was estimated on a scale of 0 (none) to 3 (dense). Observations were made in each plot on browse damage of young shoots, but quantitative data were not obtained due to the small size, deteriorated condition, and large number of such shoots on some sprout clusters. Dieback of stems was classified as competition-induced (14) if no signs or symptoms of other agents were observed. Student's *t* test and linear regression analysis were used in the statistical analysis of data.

RESULTS

The 1985 survey in five clearcuts, 15 or 17 yr old, indicated that the percentage of sprout clusters with one or more blighted stems was 100%, and that only a portion (44–86%) of the sprout clusters had survived (Table 1). In contrast, blight incidence was low in the understory site and sprout cluster survival was 100%. In the five clearcut sites, a mean of 22% of the largest live stems in the sprout clusters had blight, even though all clusters were blighted. Largest chestnut stems in clearcuts, grown after clear-

Table 1. American chestnut sprout cluster survival, blight incidence, and superficial canker incidence in forest clearcut and understory sites in Virginia and West Virginia in 1985

Plot code	Stand type	Clearcut age (yr)	Elevation (m)	Aspect (degrees)[a]	Chestnut sprout cluster blight incidence[b] (%)	Chestnut sprout cluster survival[c] (%)	Superficial cankers (no.)[d]	Largest live stem diameter (cm)[e]	Largest live stem blight incidence[f] (%)	Largest dead stem diameter (cm)[e]
CC-1A	Clearcut	15	670	120	100	44(39)	0	0.5	12	4.8
JC-OB	Clearcut	17	760	330	100	70(27)	0	0.6	35	4.6
SCM-1A	Clearcut	15	790	210/320	100	74(31)	0	0.9	13	4.4
CC-OA	Clearcut	17	670	320	100	75(28)	0	1.6	14	4.7
CC-3A	Clearcut	17	670	170	100	86(29)	6	2.0	36	5.4
CC-UA	Understory	···	730	150	29	100(42)	1	2.3	5	3.1

[a] Indicates predominant direction stand faced; if point of land, aspects of both sides are indicated.
[b] Based on the frequency of sprout clusters that had one or more stems with blight.
[c] Based on the frequency of sprout clusters that had one or more living stems. Plots are ranked by percent survival. Number in parentheses is the number of sprout clusters examined.
[d] Indicates the total number of superficial cankers found per plot by canker dissection.
[e] Based on the largest live and dead stems in each cluster examined.
[f] Based on the frequency of blight on the largest live stem in each cluster examined.

Table 2. American chestnut sprout cluster survival, blight incidence, and superficial canker incidence in forest clearcut and neighboring understory sites in Virginia and West Virginia in 1987

Plot code	Stand type	Clearcut age (yr)	Elevation (m)	Aspect (degrees)[a]	Chestnut sprout cluster blight incidence[b] (%)	Chestnut sprout cluster survival[c] (%)	Superficial cankers (no.)[d]	Chestnut trees canopy/subcanopy (no.)[e]	Mountain laurel abundance index[f]
HR-2A	Clearcut	13	910	130	100*[g]	0	0	0/0	0.0
BSC-1A	Clearcut	19	940	330	100*	0	0	0/0	0.0
BSC-3A	Clearcut	18	1,010	340	100*	0	0	0/0	0.0
JC-OA	Clearcut	19	760	320	94*	34	1	0/0	1.0
CC-1A	Clearcut	17	670	120	92*	44	1	0/1	0.5
BSC-1B	Clearcut	19	940	330	100*	44	0	1/1	2.0
CC-3A	Clearcut	19	670	160	98	58	6	0/7	2.0
CC-OA	Clearcut	19	670	330	80*	76	1	1/7	2.0
JC-OB	Clearcut	19	760	320	100*	80	3	0/1	2.0
SCM-1A	Clearcut	17	790	210/320	98*	80	2	1/1	2.0
HR-2B	Clearcut	13	880	130	92*	82	4	6/7	3.0
CC-OUA	Understory	···	670	20/300	44	82	0	0/2	1.5
HR-2UA	Understory	···	910	130	48	90*	2	0/1	0.0
CC-1UA	Understory	···	670	120	50	90*	2	0/2	0.5
HR-1UA	Understory	···	730	190	56	90	3	1/5	2.0
CC-3UA	Understory	···	700	130/160	80	92*	5	0/4	1.5
HR-2UB	Understory	···	880	130	34	92	1	1/9	3.0
JC-OUA	Understory	···	730	340	46	94*	0	0/0	1.0
JC-OUB	Understory	···	730	0/340	34	96	0	0/0	1.5
BSC-3UA	Understory	···	1,010	340	4	98*	0	0/0	0.0
HR-1A	Clearcut	13	730	180	82*	100	6	7/15	2.0
BSC-1UA	Understory	···	940	330	0	100*	0	0/0	0.0
SCM-1UA	Understory	···	790	230/320	42	100	0	0/0	2.0
BSC-1UB	Understory	···	940	330	16	100*	0	0/0	1.5
Overall	Clearcut	16.9			94.7*	49.8	2.0	1.3/3.3	1.4
Overall	Understory	···			37.8	93.7*	1.1	0.2/1.9	1.2

[a] Indicates predominant direction stand faced; if point of land, aspects of both sides are indicated.
[b] Based on the frequency of sprout clusters that had one or more stems with blight.
[c] Based on the frequency of sprout clusters that had one or more living stems. Plots are ranked by percent survival.
[d] Indicates the total number of superficial cankers found per plot (50 sprout clusters) by canker dissection.
[e] Indicates the total number of clusters per plot that had one or more canopy or subcanopy stems.
[f] Indicates average relative abundance of mountain laurel in the understory of two subplots: 0 = none, 1 = light, 2 = moderate, and 3 = dense.
[g] Indicates values for clearcut and understory sites are significantly different ($P < 0.05$) in orthogonal comparisons. Neighboring clearcut and understory sites were labeled with the same code letters and numbers, except that a "U" was inserted for the understory sites.

cutting, reached a diameter of 4.4–5.4 cm before they died (Table 1). Surviving stems in sprout clusters of clearcuts were much smaller than dead stems (Table 1). Survival of sprout clusters was related to stem growth. Among all plots, diameter of the largest live stem per sprout cluster was significantly ($P < 0.02$) correlated with percentage sprout cluster survival ($r = 0.87$) in regression analysis. One to 10 stems that were at least 1.4 m tall were generally found in each sprout cluster, but occasionally larger numbers were present. They were commonly associated with an old stump rotten to the ground level, or occasionally with an intact stump.

The incidence of chestnut blight among sprout clusters in clearcut sites was about the same in 1987 (mean of 12 sites = 94.7%) as in the 1985 survey, but in 1987, mean sprout cluster survival for 12 sites (49.8%) was lower than in 1985 for five sites (69.8%) (Table 2). However, for the five clearcuts examined in both 1985 and 1987, sprout cluster survival was about the same (69.8 and 67.6%, respectively). The difference in mean survival between the 12 sites surveyed in 1987 and the five sites surveyed in 1985 was due in large part to four clearcut sites that had low (0–34%) sprout cluster survival in the 1987 survey (Table 2). In contrast, one clearcut site examined in 1987 (HR-1A) had 100% sprout cluster survival, even though sprout cluster blight incidence was high. The highest frequencies of canopy and subcanopy chestnut clusters and superficial cankers were found at this site (Table 2). This clearcut site had a due-south exposure, was located at moderate elevation, had moderate abundance of mountain laurel in the understory (Table 2), and had a very open canopy. Clearcut sites with 0% sprout cluster survival (HR-2A, BSC-1A, and BSC-3A) were located at higher elevations, supported dense stands of hardwoods (Fig. 1), had no mountain laurel in the understory (Table 2), and had relatively closed canopies. They were located either on a north-facing slope or on a flat, benchlike shelf of a south-facing slope that retained moisture.

Understory sites surveyed in 1987 generally had low sprout cluster blight incidence and high sprout cluster survival, with one (site CC-3UA) exception (Table 2). Over all 12 locations, mean sprout cluster blight incidence (37.8%) in understory sites was significantly ($P < 0.05$) lower than in neighboring clearcut sites (94.7%). Mean chestnut sprout cluster survival over 12 locations was 93.7% in understory sites, significantly greater ($P < 0.05$) than in neighboring clearcut sites (49.8%). Among companion clearcut and understory sites surveyed in 1987, sprout cluster blight incidence was significantly greater ($P < 0.05$) in 11 clearcut sites than in neighboring understory sites (Table 2). Sprout cluster survival was significantly greater ($P < 0.05$) in seven understory sites than in neighboring clearcut sites. Understory site CC-3UA had 80% cluster blight incidence, but 92% survival. This site also had the greatest number of superficial cankers of all understory sites examined (Table 2). Understory sites situated near clearcut sites with 0% sprout cluster survival had 90–100% sprout cluster survival, but live shoots were usually small (Fig. 2). Almost twice as many superficial cankers were found in clearcut sites, where blight incidence was high, than in understory sites, where blight incidence was low. Only one clearcut site with surviving stems did not have superficial cankers, whereas seven understory sites did not have superficial cankers. Superficial cankers had a significantly ($P < 0.05$) and much greater frequency on clusters with one or more canopy or subcanopy stems than on clusters with smaller stems, for sites with either a higher or lower frequency of superficial cankers (Table 3). Canopy or subcanopy clusters generally had one or two large stems.

Fig. 1. Blighted and dead, large, single stem of American chestnut, with sloughing bark, in clearcut site BSC-1A. Small chestnut shoots (arrow) at the stem base are all dead from browse damage and blight. Note the absence of a mountain laurel shrub layer in the understory. Sprout cluster survival was 0% at this site. Scale intervals on pole are 30.5 cm long.

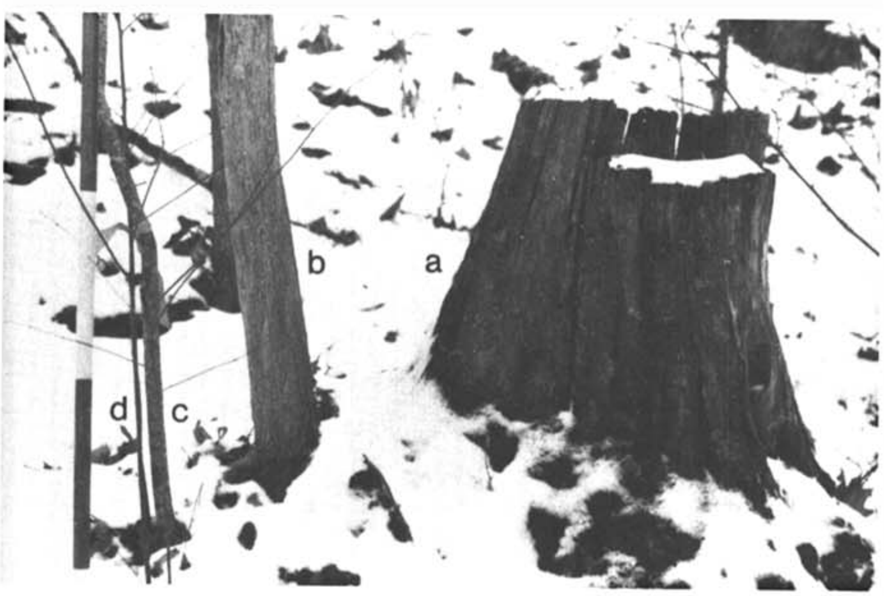

Fig. 2. Four cycles of American chestnut stems in understory site BSC-1UA, about 100 m from clearcut site BSC-1A. Sprout cluster survival was 100% at this site. **(A)** The prominent stump, an uncommon occurrence, and **(B)** larger stem have no bark and are highly weathered; **(C)** the third largest stem, with intact bark, recently died, most likely from competition. **(D)** Three live shoots (one clearly visible) are located near the base of the dead stem. Scale intervals on pole are 30.5 cm.

Sprout clusters with probable competition-killed stems, at least 1.4 m tall, were common in understory sites (Fig. 2) but not in clearcut sites. The dead stems often had intact bark on the stem with no symptoms or signs of blight. In almost all instances, however, these dead stems in understory sites had one or more smaller, living shoots at their base (Fig. 2). For example, in understory site BSC-1UA, 10 of 50 sprout clusters had probable competition-killed stems, but all 10 had live, young shoots at the stem base. Browse damage of young chestnut shoots was uncommon in understory sites, but was common at the base of blight-killed stems in clearcut sites (Fig. 1). Blight of small shoots also was common in clearcut sites. Ten to 20 dead, small shoots were sometimes found at the base of blight-killed stems in clearcut sites.

DISCUSSION

The results of the study indicate that chestnut sprout cluster blight incidence was high in 13- to 19-yr-old forest clearcuts, as found by Hebard (8) for 9- to 10-yr-old clearcuts. Many sprout clusters did not survive after the large stems were killed by blight. Thus, American chestnut clones may be lost as parts of the southern Appalachian forests are clearcut in the future, unless practical biocontrol measures are developed for blight. In neighboring understory sites, however, sprout cluster survival was high, and blight incidence was generally much lower than in clearcut sites. It is possible that some sprout clusters in clearcuts with no live shoots in 1987 will produce new shoots in 1988. However, the 1985–1987 survival data for the same five clearcuts suggests this would be of little significance.

No single indicator of chestnut sprout cluster survival in clearcut sites was found, although some degree of openness in the forest canopy was most commonly associated with sprout cluster survival. To a certain extent, the presence of mountain laurel in the understory was associated with chestnut survival. Braun (2) indicated the oak-chestnut forest is generally characterized by an abundance of ericaceous shrubs, such as mountain laurel, in the understory. The ericaceous layer is absent only on mesic sites or where the oak-chestnut forest contains some of the species of the mixed mesophytic forest of the coves. In a nearby study area in Craig County in Virginia, McEvoy et al (11) found the cove hardwood vegetational type to be mostly devoid of an ericaceous understory. The absence of mountain laurel, together with a relatively closed canopy, was observed at all three clearcut sites where 0% sprout cluster survival was found. These locations appeared to be the better locations for chestnut and hardwood growth among the locations studied. Thus, a relatively closed canopy (high competition) or more mesic hardwood growth site, in combination with browse damage and blight of small shoots, appeared to be important factors in the lack of chestnut sprout cluster survival in clearcut sites. In the neighboring understory sites, where sprout cluster survival was high, a relatively closed canopy also was present, but browse damage and blight of young shoots were generally not important. This relative absence of browse damage and blight of young shoots may be important in the high survival of young chestnut shoots in understories on mesic sites. Probable competition-induced death of chestnut stems was observed in understory sites, but was generally not observed for small (< 1 m tall) chestnut shoots. Competition-induced stem dieback, followed by resprouting, is commonly observed for hardwood species in the understory, and is believed to be due to low light irradiance and reduced root system size due to low light (14). Further research is required to determine the relative importance of browse damage and blight of young shoots, as well as chemical and physical environmental factors, in chestnut sprout survival in old clearcuts. The amount of *E. parasitica* inoculum produced in low-survival clearcuts may be important, but most chestnut bark and stromata are in a deteriorated condition in old clearcuts. Also, further research is required to determine what factors may be important to chestnut survival as clearcut sites become older and undergo a transition to an understory site.

Superficial cankers were found in both clearcut and understory sites. Cluster blight incidence was 56% or greater (mean = 83.3%) in the six sites with a higher frequency of superficial cankers (> 3 per site) in 1987 (Table 2). Griffin (5) recently hypothesized that an ecological succession of chestnut growth, blight incidence increase, and superficial canker development, due to hypovirulence, occurs in forest clearcuts and relatively open areas. If competing hardwoods and/or other factors severely restrict chestnut growth, the ecological succession leading to superficial cankers is not completed. In the six sites indicated above with three or more cankers per site, superficial cankers occurred 5.8 times more frequently in sprout clusters with canopy or subcanopy stems than in sprout clusters with relatively smaller stems (Table 3). Almost always the superficial cankers were found on the largest stems in a cluster. Calculations for the seven sites with one or two superficial cankers per site yielded the same value. Clearcut site HR-1A (along with clearcut site CC-3A) had the highest number of superficial cankers and the greatest number of canopy and subcanopy trees; dsRNA-containing, hypovirulent strains of *E. parasitica* were recovered from this clearcut by Wendt (5,6,17). Overall, however, the number of superficial cankers found in clearcut sites was small.

Wendt (17) found that three of 27 (11.1%) *E. parasitica* isolates recovered from Virginia forest clearcuts were hypovirulent in pathogenicity trials, using superficial canker development as one criterion for hypovirulence; all contained dsRNA (6). In contrast, only five of 171 (2.9%) isolates recovered from American chestnut in Virginia, West Virginia, and Pennsylvania understory forest areas were hypovirulent in pathogenicity trials. Double et al (3) reported that dsRNA-containing *E. parasitica* isolates were commonly found in West Virginia. Nine of 21 abnormal-colony-morphology isolates tested contained dsRNA, and many isolates with abnormal morphology were found among more than 1,000 *E. parasitica* isolates examined. If dsRNA is common in *E. parasitica* strains in West Virginia and Virginia clearcuts or forests, expression of this factor in terms of superficial cankers appears to be low. Possibly, more superficial cankers would be found in forest clearcuts and other relatively open canopy forest sites if conditions were made optimal for survival of chestnut sprouts during and following blight epidemics.

Table 3. Frequency of superficial cankers on American chestnut clusters with canopy and/or subcanopy stems and on clusters with small stems in 13 clearcut and understory sites surveyed in 1987

Superficial cankers per site	Sites (no.)[a]	Frequency of superficial cankers[b]: Canopy/subcanopy clusters	Small clusters	Ratio[c]
3 to 6	6	0.2830	0.0486	5.8
1 or 2	7	0.1250	0.0215	5.8

[a]Thirteen of 24 clearcut and understory sites assayed in 1987 contained superficial cankers.
[b]Based on the number of superficial cankers on the population of canopy and/or subcanopy clusters or the number of superficial cankers on the population of small clusters. Frequency of superficial cankers on canopy or subcanopy clusters was significantly different than on small clusters by Student's *t* test ($P < 0.05$).
[c]Ratio of canopy/subcanopy clusters to small clusters.

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