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American chestnut as an allelopath in the southern Appalachians

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Abstract

Prior to the chestnut blight (*Cryphonectria parasitica*), American chestnut (*Castanea dentata* (Marsh.) Borkh.) was the most common overstory tree in eastern deciduous forests. Chestnut's dominance has often been attributed to its resistance to fire and subsequent propensity to sprout vigorously and grow rapidly. Its role as an allelopath has rarely been studied.

Allelopathic qualities of chestnut leaves were tested with five native co-occurring tree species: red maple (*Acer rubrum*), sugar maple (*A. saccharum*), eastern white pine (*Pinus strobus*), eastern hemlock (*Tsuga canadensis*), yellow-poplar (*Liriodendron tulipifera*), a native shrub rosebay rhododendron (*Rhododendron maximum*), and a bioassay species lettuce (*Lactuca sativa* var. "black seeded Simpson"). For each species, six replicates of 100 seeds each were stratified for 90 days in distilled water or chestnut leaf extract, then germinated for 21 days. Six additional replicates of red maple, eastern hemlock, yellow-poplar, and rhododendron were germinated without stratification. Lettuce seed was not stratified. When germination percentage peaked, seeds were removed from the experiment and radicle length was measured. Chestnut leaf extract lowered germination rates of extract-treated lettuce, stratified and unstratified eastern hemlock, and unstratified rhododendron seeds. Radicles of extract-treated lettuce and unstratified rhododendron were significantly shorter than radicles of water-treated seeds. In general, radicles of extract-treated seeds were thinner, broke more easily, and were less likely to have developed secondary roots than radicles of water-treated seeds. This study suggests leachate from American chestnut leaf litter could have suppressed germination and growth of competing shrub and tree species and that allelopathy was a mechanism whereby American chestnut may have controlled vegetative composition and dominated eastern forests. Current vegetative composition in southern Appalachian forests may be attributable, in part, to the disappearance of American chestnut as an allelopathic influence. © 2002 Elsevier Science B.V. All rights reserved.

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1. Introduction

American chestnut (*Castanea dentata* (Marsh.) Borkh.) was often listed as the most common canopy

tree from southern New England to northern Alabama and Mississippi (Russell, 1987). In the southern Appalachians, it reached its greatest size and stand density (Ayres and Ashe, 1902), where it usually grew in association with other trees (Zon, 1904). Chestnut is thought to have represented roughly 40–45% of canopy trees in some pre-blight southern Appalachian forests (Keever, 1953). Chestnut's abundance throughout the

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eastern deciduous forest has been attributed to its ability to sprout from the root crown (Zon, 1904), rapid growth rate (Graves, 1905), overall growth in height (Zon, 1904), longevity (Zon, 1904), resistance to rot (Scheffer and Cowling, 1966), tolerance to shade when young (Paillet, 1982), ability to grow on poor soils (Zon, 1904), mast production (Zon, 1904), and resistance to fire (Reed, 1905).

Chestnut **allelopathy** has been little studied. In New Jersey, Good (1968) found the strongest chestnut leaf extracts significantly reduced shoot length in black birch (*Betula lenta*), yellow birch (*B. allegheniensis*), tomato (*Lycopersicon esculentum*), and eastern hemlock (*Tsuga canadensis*). Good (1968) also found evidence that chestnut leaf extract reduced the germination rate of eastern hemlock.

Chestnut relatives such as oaks affect germination of herbs and grasses through the production of coumarins and other phenolics (Fisher, 1980). As a long-lived dominant species (Zon, 1904), allelopathic qualities of chestnut leaves could have affected large areas of eastern forests. Chestnut foliage was dense, the leaf litter abundant and the leaves slow to decay (Zon, 1904). Other studies indicate rain throughfall, dripping off live foliage, can contain concentrations of phytotoxic chemicals sufficient to inhibit germination of co-occurring species (Al-Naib and Rice, 1971; Lodhi and Rice, 1971; Nilsen et al., 1999). With the abundance of competitive tree and shrub species in the southern Appalachians, it is possible allelopathy had an influence on maintaining chestnut's dominance in the region.

Our review of the literature found at least 17 studies documenting changes in forest composition and structure since the demise of the American chestnut. These studies have focused on replacement of chestnut by other canopy tree species with findings split between evidence for succession to an oak-hickory forest or an oak association forest. Woods and Shanks (1959) found eastern hemlock to be an important regenerative element in post-blight chestnut-associated forests. Effects of chestnut demise on the shrub and herb synusia have not been studied, although the blight has been implicated in the expansion of rosebay rhododendron thickets in the southern Appalachians (McGee and Smith, 1967).

We hypothesize that chestnut leaf leachates have an allelopathic effect on associated tree and shrub

species in the southern Appalachians. Our objective was to determine the effects of chestnut leaf extract on germination rates and radicle growth of co-occurring tree and shrub species in a germination-chamber environment.

2. Methods

2.1. Plant materials

American chestnut leaves were collected in the fall of 1998 from young chestnut sprouts in the Andrew Pickens Ranger District of Sumter National Forest in northern Oconee County; SC, after natural abscission. After collection, they were dried in an oven at 50 °C for 24 h and stored in a paper bag at room temperature (roughly 30 °C).

Seeds of six species were used to test for reduced germination and radicle growth. Seeds of common forest tree species, red maple (dewinged), sugar maple (dewinged), eastern white pine (dewinged), eastern hemlock, and yellow-poplar (dewinged) and the ericaceous shrub rosebay rhododendron were acquired from F.W. Schumacher, Sandwich, MA. Seeds of lettuce, the bioassay species, were acquired locally.

2.2. Preparation of extract

Chestnut leaf extract was prepared by grinding dried leaves in a Wiley mill with 20 mesh screen. Ground leaf matter was mixed with distilled water in a 1 g per 20 ml concentration and stirred for 30 min. The mixture was then poured through cheesecloth and squeezed to extract as much liquid and remove as much leaf matter as possible. The remaining liquid was vacuum-filtered through Whatman #4 filter paper.

2.3. Experimental design

A randomized complete block design was used to test for differences in germination between water- and extract-treated seeds. Six replications of 50 seeds each for water and extract treatments were used for each species. Seeds of tree species and rhododendron were stratified by placing them on Whatman #1 filter paper

in a sterile petri-dish, adding 3 ml of extract or distilled water, and placing them in a refrigerator at 3 °C for 90 days. After stratification, seeds were immediately placed in a Cenviron germination chamber maintained at 25 °C, 60% relative humidity, and a 12/12 h day. Additionally, six replicates of red maple, sugar maple, eastern hemlock, yellow-poplar and lettuce were germinated without stratification.

2.4. Biological measurements and analysis

On the 17th day of the study, humidity and temperature setting were changed to 25 °C day temperature with 60% relative humidity, and a 15 °C night temperature with 70% relative humidity. These changes were made to enhance germination rates. At the same time, seeds of stratified **rosebay** rhododendron and stratified eastern hemlock were moistened with distilled water (control seeds) or chestnut leaf extract (experiment seeds), so a moisture deficit would not negatively influence germination.

Germination (defined as emergence of the radicle from the seed coat) was monitored daily for 21 days. Length of the radicles of germinated seeds was measured when germination peaked and those seeds were permanently removed from the experiment. Germination percentage and radicle length of extract-treated seeds were compared to those of water-treated seeds using the Mann-Whitney U-test (SAS, 1987).

3. Results

3.1. Delayed germination

American chestnut leaf extract significantly ($\alpha = 0.01$) inhibited germination of lettuce, unstratified rhododendron, and stratified/unstratified eastern hemlock seeds. Germination rates of stratified red maple, sugar maple, and white pine were not affected. Germination of unstratified red maple and stratified/unstratified yellow-poplar seeds was poor (less than 30 seeds in each treatment) precluding meaningful analysis for these species.

From 24 to 53% of stratified red and sugar maple seeds germinated during stratification. For these species germination tallies began once they were removed from the refrigerator (Table 1). Mean germination

percentages for stratified red maple and sugar maple water and extract treatments peaked, and had begun to wane by the sixth day of the study. In addition, an odor of decay was noticeable, so these seeds were removed from the germination chamber and their radicles measured. Germination of water-treated maple seeds was higher than that of extract-treated seeds, although differences were not significant. Despite their reputation as poor germinators, nearly 50% of red maple and 63% of sugar maple seeds germinated by the end of the study.

Seeds of white pine were relatively slow to germinate, i.e. only 11% of 600 seeds had germinated after 5 days. As germination continued, extract-treated white pine seed began to germinate at a higher rate than water-treated seed. This difference became greater with time and by the time *P. strobus* was removed from the experiment on day 15, significantly more extract-treated seeds had germinated. Radicle growth of extract-treated white pine was also greater than the control (Table 2).

The allelopathic qualities of chestnut leaf extract were most dramatic for lettuce (Fig. 1). After 2 days, only 3% of treated seeds had germinated, whereas over 90% of control seeds had germinated. As the germination test continued, the differential between control and treated seeds became less, indicating that the chemicals causing the allelopathy were losing their effectiveness. Under field conditions, frequent rains would continually bathe seeds of competing species with allelopathic chemicals.

Extract-treated **rosebay** rhododendron in the stratified set germinated at a higher rate than water-treated seed until day 17, when 3 ml of fresh leaf extract and water were added to their respective treatments, because it appeared the filter paper was dry. Immediately after the addition of fresh extract, germination in the extract treatment stopped and did not increase for the next 4 days (Fig. 2). Water-treated seeds continued to germinate at the pre-moistened rate.

Unstratified **rosebay** rhododendron was treated with fresh water and extract at the beginning of germination. Germination of extract-treated seed in the unstratified set was significantly inhibited throughout the experiment (Fig. 3).

Germination of both stratified and unstratified eastern hemlock seeds were suppressed by chestnut leaf extract (Table 1). Unstratified seeds, treated with

Table 1

Germination percentages for control (distilled water) and experimental (chestnut leaf extract) treatments for six co-occurring southern Appalachian tree species^a

Day	Redmaple		Sugarmaple		Lettuce		White pine		Rosebayrhododendron				Eastern hemlock			
	stratified		Stratified		Stratified		Stratified		Stratified		Unstratified		Stratified		unstratified	
	Control	Experimental	Control	Experimental	Control	Experimental	Control	Experimental	Control	Experimental	Control	Experimental	Control	Experimental	Control	Experimental
0	33.3 a ^b	24.3 a	52.7 a	51.7 a	-	-	-	-	-	-	-	-	-	-	-	-
4	50.7 a	42.3 a	63.1 a	63.7 a	93.7 a	51.7 b	5.3 a	2.7 a	-	-	-	-	-	-	-	-
8	-	-	-	-	91.0 a	71.0 b	47.3 a	46.0 a	-	-	-	-	21.0 a	5.0 b	8.7 a	1.3 b
12	-	-	-	-	-	-	72.1 a	83.0 a	-	-	-	-	44.3 a	21.0 b	34.7 a	12.3 b
16	-	-	-	-	-	-	-	-	4.1 a	7.3 a	13.3 a	1.0 b	51.7 a	26.3 b	45.0 a	15.0 b
20	-	-	-	-	-	-	-	-	11.0 a	9.0 a	20.7 a	3.3 b	73.1 a	62.3 a	67.3 a	44.1 b
22	-	-	-	-	-	-	-	-	13.7 a	9.7 a	25.0 a	5.3 b	78.0 a	65.3 a	12.3 a	51.7 b

^a Data include stratified seed only for red maple, sugar maple, and white pine; for rosebay rhododendron and eastern hemlock, both stratified and unstratified seed results are shown.

^b For a given species, means followed by the same letter within a mw are not significantly different at the $\alpha = 0.01$ level.

Table 2
Radicle length (mm) of eight germinated seed species in control (distilled water) and experimental (chestnut leaf extract) treatments

Species	Radicle length (mm)		P-value
	Control	Experimental	
Red maple (stratified)	18.19 a	23.75 a	0.1898
Sugar maple	24.23 a	21.04 a	0.4983
Lettuce	49.65 a	40.70 b	0.003 1
White pine	18.92 a	31.69 a	0.1909
Rhododendron (stratified)	1.67 a	3.26 a	0.0894
Rhododendron (unstratified)	2.93 a	1.15 b	0.0003
Eastern hemlock (stratified)	0.95 a	0.70 a	0.4455
Eastern hemlock (unstratified)	0.50 a	0.50 a	1.0000

^a For a given species, means followed by the same letter within a row are not significantly different at $\alpha = 0.01$.

fresh extract on day 0, showed the greatest inhibition. Germination rates of extract-treated seed for the unstratified set were significantly lower throughout the study. Extract-treated seeds in the stratified set were suppressed at a significant level until the last few days of the study (Table 1), but still exhibited reduced germination rates.

3.2. Reduced radicle growth

Chestnut leaf extract also affected radicle growth of test species, but results were mixed (Table 2). The extract-treated radicles of four species (sugar maple, white pine, and stratified red maple and rosebay rhododendron) were longer than radicles from seeds treated with water, but the differences were not significant. Radicles of extract-treated lettuce and unstratified rosebay rhododendron were significantly shorter than the control. In general, radicles growing in the chestnut leaf extract were thinner, more fragile and less likely to have developed secondary roots at the time of measurement. For lettuce, roughly 45% of water-treated radicles had developed secondary roots, whereas none had done so in the extract-treated group.

Radicle growth of unstratified eastern hemlock was poor, with few radicles extending more than a few millimeters from the seed coat. Even though stratified extract-treated seeds were 16% shorter than the control, high rates of post-emergence mortality of both water- and extract-treated seed resulted in no significant difference in radicle length for treated and control seeds of this species.

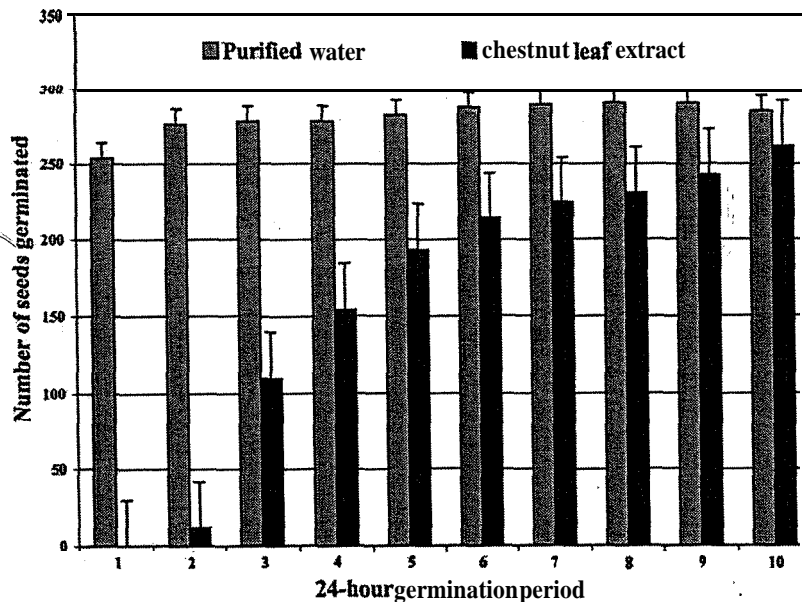


Fig. 1. Number of lettuce seeds germinated. All differences between control (distilled water) and chestnut leaf extract treatments are significant at $\alpha = 0.01$ until day 10. Error bars represent the standard error of the mean.

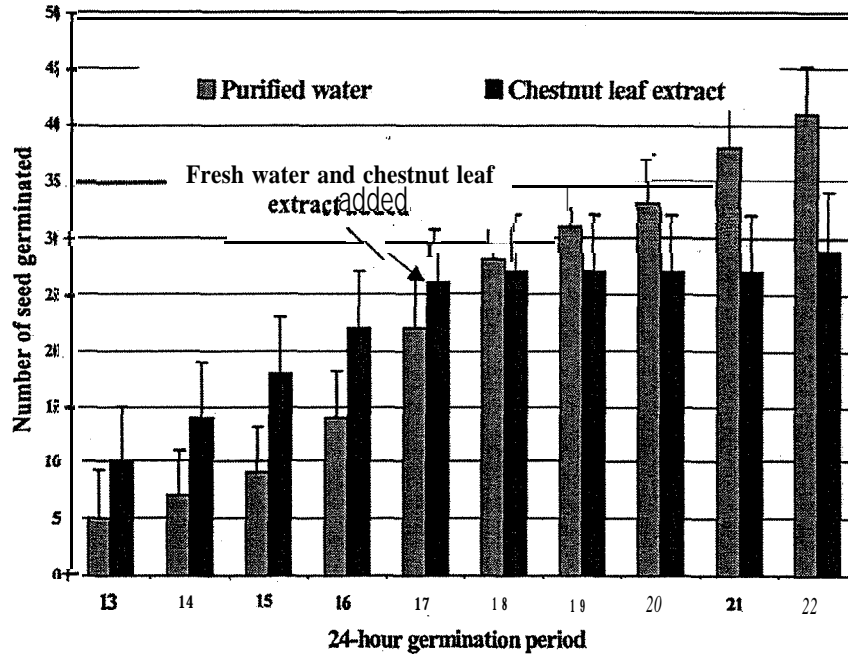


Fig. 2. Number of stratified *rosebay* rhododendron seeds germinated before and after the 17th day of the study when fresh distilled water and chestnut leaf extract were added to their respective treatments. Error bars represent the standard error of the mean.

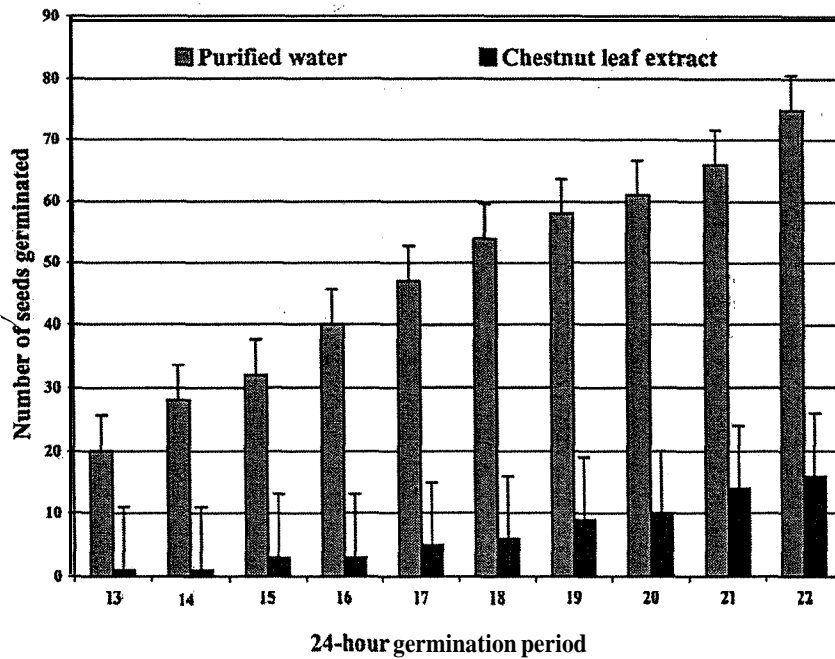


Fig. 3. Number of germinated *unstratified rosebay* rhododendron seeds. Fresh distilled water and chestnut leaf extract were added at the beginning of germination. All differences between control (distilled water) and chestnut leaf extract treatments are **significant** at $\alpha = 0.01$. Error bars represent the standard error of the mean.

4. Discussion

Extracts of American chestnut leaves inhibited germination of eastern hemlock, a major riparian tree species in the southern Appalachians, and **rosebay** rhododendron, a dominant ericaceous shrub on moist sites. In addition, germination rates and radicle growth of lettuce, a common bioassay species, were inhibited.

While germination chamber studies cannot replace in situ experiments, results of this study suggest continual influxes of chestnut leaf **leachate** into soil during rainfall could have been capable of influencing vegetative composition of forests once dominated by chestnut. Chestnuts were dominant, long-lived trees whose leaves, which were slow to decay, covered the ground after abscission (Zon, 1904). Abundant, **well**-distributed rainfall in the southern Appalachians would cause **dormant** seeds in the forest floor and soil to be bathed frequently by chestnut leaf leachate, potentially limiting germination year-round. Production of **phytotoxic** chemicals that affect germination and growth of competitor species is not unusual in trees, e.g. black walnut (*Juglans nigra*) (Cook, 1921), sycamore (*Platanus occidentalis*) (Al-Naib and Rice, 1971), sugarberry (*Celtis laevigata*) (Grant and Clebsch, 1975), and **sassafras** (*Sassafras albidum*) (Lodhi, 1978) are known to have allelopathic qualities.

Germination studies using phytochemical extracts are the most widely used methods of measuring allelopathic potential in vegetation. Allelopathic chemicals in organic material can inhibit or, sometimes, facilitate seed germination (Leather and Einhellig, 1986), and may inhibit radicle growth (Chaves and Escudero, 1997). Foliage and fruits usually have the highest **concentration** of phytotoxic compounds. It is not known what allelopathic chemicals chestnut leaves may contain but oaks, another fagaceous species, produce coumarins and other phenolics known to inhibit germination of herbs and grasses (Fisher, 1980).

Post-blight loss of allelopathic chestnut leaf litter could have contributed to changes in vegetative composition of eastern forests. When fresh chestnut leaf extract was added to stratified **rosebay** rhododendron seeds, cumulative germination rates immediately stabilized and did not increase again for 4 days. Prior to adding fresh extract, germination of extract-treated seed increased steadily and exceeded the control group. These results suggest chestnut may have had a

controlling influence on rhododendron germination and growth. Expansion of rhododendron thickets throughout the 20th century may be due as much to the cessation of chestnut's allelopathic influence as the more commonly cited factors of invasion of canopy openings following the blight (Clinton et al., 1994), heavy logging (McGee and Smith, 1967), and fire exclusion (Van Lear, and Waldrop, 1989). Dense rhododendron thickets adversely affect regeneration of overstory species and threaten the diversity of southern Appalachian cove forests (Hedman and Van Lear, 1995; Baker and Van Lear, 1998).

Germination rates of seeds of red **maple**, sugar maple, and white pine were little affected by chestnut leaf extract, perhaps because it had lost its toxicity during stratification. If no imbibition of extract-tainted liquid occurred during stratification, seeds probably began germinating in a non-toxic organic broth, possibly explaining the excellent germination rate of white pine in the experimental treatment. Chemicals washed from or exuded through the seed coats of red maple, sugar maple and yellow-poplar stained filter papers a dark brown color. Organic compounds in this stain may **counteract** effects of allelopathogens in the soil. More testing is needed to confirm this hypothesis.

The ability of chestnut leaf extract to suppress germination of eastern hemlock in this experiment agrees with the results of Good (1968) and is one of the most interesting findings of this study. Eastern hemlock, a common cove mesophytic species, may have been able to migrate into former chestnut-dominated forests because of the loss of a continual input of allelopathic substances from chestnut leaves. Eastern hemlock is one of the **most** important species invading former chestnut-associated forests after the blight (Woods and Shanks, 1959). Older accounts mention chestnut and eastern hemlock rarely associated with one another (Reed, 1905). Eastern hemlock also has allelopathic qualities that reduce understory plant growth (**Daubenmire**, 1930) and affect soil properties (**Beatty**, 1984). In the northeast, **Paillet** (1982) noted a lack of chestnut sprouts in a mature hemlock forest despite the presence of pre-blight chestnut logs. Chestnut's ability to suppress germination of eastern hemlock and anecdotal evidence of hemlock's ability to exclude chestnut suggests a dynamic competitive relationship between two important southern Appalachian tree species.

Due to its allelopathic effects on lettuce, eastern hemlock and rosebay rhododendron, American chestnut should be added to the list of trees known to contain phytotoxic compounds in their leaves. Williamson et al. (1992) proposed that allelopathy could be an evolutionary response to fire, where plants with phytotoxic leaves effectively formed a fire break around themselves by controlling competing vegetation. Fire was an important historical disturbance event in the southern Appalachians (Van Lear and Waldrop, 1989), and has been implicated in the increased abundance of chestnut in the region (Delcourt and Delcourt, 1998). It is possible that fire and allelopathy interacted to create a situation where chestnut, with its superior growth habits, was the species most able to take advantage of environmental conditions in eastern forests.

5. Conclusions

American chestnut leaves produce allelopathic chemicals that inhibited the germination of lettuce, rosebay rhododendron, and eastern hemlock seeds and the radicle growth of lettuce and rosebay rhododendron in a germination chamber study. These results suggest that allelopathy could have been a mechanism whereby American chestnut was able to control competition from both tree and shrub species in pre-blight southern Appalachian forests. The fact that both American chestnut and eastern hemlock exhibit allelopathic properties may explain their rare association in pre-blight forests. The rapid expansion of rosebay rhododendron during much of the 20th century may be attributed, at least in part, to the loss of the allelopathic properties of American chestnut leaves.

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