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# EVIDENCE THAT *CASTANEA DENTATA* PERSISTS ON XERIC, MID-ELEVATION SITES IN THE SOUTHERN APPALACHIANS

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# EVIDENCE THAT *CASTANEA DENTATA* PERSISTS ON XERIC, MID-ELEVATION SITES IN THE SOUTHERN APPALACHIANS

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*Abstract:* *Castanea dentata* (American chestnut) persists today in the southern Appalachian forests of North Carolina as sparsely occurring sprouting root systems. The introduction of two exotic fungal diseases into North America, root rot (*Phytophthora cinnamomi*) in the early 1800s and chestnut blight (*Cryphonectria parasitica*) in the early 1900s, eliminated *C. dentata* as a dominant canopy species. Identifying and understanding the characteristics of sites where *C. dentata* persists could offer insights for management and restoration. Using a regional forest inventory and analysis (FIA) database, I studied the ecology of *C. dentata* on 831 forested sample plots in 21 mountainous counties of western North Carolina. The purpose of my study was to determine if the presence of *C. dentata* was associated with common topographic variables and the co-occurrence of other tree species that could be used in a regression model for evaluation of sites for potential management activities. I found that *C. dentata* occurred on only 3.5% of the sample plots. Its presence was directly associated with elevation >900 m, positively related to the co-occurring species *Quercus prinus* (chestnut oak) and *Q. rubra* (northern red oak), and negatively related to *Liriodendron tulipifera* (yellow-poplar). Logistic regression revealed poor performance of formulations with multiple significant biological variables (i.e., tree species) because of multicollinearity effects with elevation. Good model performance was achieved with a two-variable formulation using elevation and a weighted averages score derived from direct gradient analysis and ordination of moisture affinities of the 30 tree species in the study plots. An explanation for the effect of elevation on occurrence of *C. dentata* on sites >900 m is unknown, but the arborescent species scores suggest probable xeric to subxeric plot moisture regimes. Limitations of the FIA data for my study were many including few plots with *C. dentata*, lack of plot soil characteristics and history of disturbance from fire. Results from my study may have application to rank forest sites for investigation of biological control of *C. parasitica* through hypovirulence and for identifying stands for application of silvicultural practices to reduce environmental stress and increase survival of existing root systems.

*Key Words:* *Castanea dentata*; *Cryphonectria parasitica*; elevation; habitat model; hypovirulence; logistic regression; *Phytophthora cinnamomi*; species moisture affinities; weighted averages.

## INTRODUCTION

*Castanea dentata* was a highly desirable and valuable canopy species throughout eastern upland hardwood forests from Mississippi to Maine until its distribution and dominance was reduced by two exotic pathogens, first by *P. cinnamomi* in the early 1800s (Crandall et al. 1945) and followed by *C. parasitica* in the early 1900s (Anagnostakis 2001). *Phytophthora cinnamomi*, a lethal soil borne pathogen, which produces zoospores that can move readily in saturated soils, is likely the cause for loss of *C. dentata* in the Appalachian Piedmont region in general (Russell 1987) and specifically in South Carolina (Hilgard 1884, p. 37). *Cryphonectria parasitica* is a nonlethal pathogen that produces airborne spores that infect stems of *C. dentata*, resulting in cankers that cause death by girdling, but allows survival of root systems by a periodic cycle of top dieback and sprouting (Anagnostakis 2001). Restoring *C. dentata* as a forest canopy species has become the goal of many organizations, particularly The American Chestnut Foundation (Hebard 2004) and state and federal governments (Steiner and Carlson 2006; Thompson 2012). Research has focused primarily on four approaches to restoration: hybridization with blight-resistant non-native *Castanea* species, genetic modification, stand management, and biological control through hypovirulence (Griffin 2000). Hypovirulence refers to the weakened virulence of *C. parasitica* fungus when infected by certain fungal viruses, which results in nonlethal stem cankers. Site selection is an important consideration for all restoration approaches, but particularly for the latter two methods, which depend on the presence of naturally occurring sprouting root systems. Hypovirulence has been widespread on *C. sativa* in Europe (Zamora et al. 2014), however successful biological control has been highly variable for *C. dentata* and appears to be associated with a complex of factors, particularly environment (Milgroom and Cortesi 2004). In managed stands, Griffin et al. (1991) found that survival and growth of *C. dentata* root systems varied by site conditions and competition. Information from sites where *C. dentata* has persisted offers insight on environmental and stand conditions potentially favorable for survival of existing root systems (Griffin 2000). Such information could be useful to identify and rank potential sites for restoration activities (Fei et al. 2007) and to develop management practices for reducing future environmental stress on surviving sprouts and thereby maintain genetic diversity, which is important for breeding programs (Kubisiak and Roberds 2003).

A number of studies have investigated the persistence of *C. dentata* throughout its natural range. Studies in New England (Paillet 1988), Kentucky (Fei et al. 2007), Ohio (Schwadron 1995), Kentucky and Tennessee (Schibig et al. 2005; Schibig et al. 2006), Virginia (Parker et al. 1993), and the Ridge and Valley Province (Griscom and Griscom 2012) have associated sprouting root systems of *C. dentata* with soil and topographic variables. These studies reported surviving *C. dentata* were typically on sites with elevations >900 m, with moisture regimes characterized as intermediate to xeric, and where canopy gaps and competition resulted in light regimes adequate for periodic root system sprouting.

Historical occurrence of *C. dentata* in relation to environment has been determined from canopy inventories in forests following the onset of blight-related canopy mortality in the southern Appalachian Mountains of North Carolina and Tennessee. Keever (1953) found that the density and frequency of occurrence of canopy *C. dentata* were much greater on north-facing compared to south-facing slopes of undisturbed stands >900 m elevation, but reported lesser influence of aspect for saplings and sprouts. In the western part of the Great Smoky Mountains National Park (GSMNP), Whittaker (1956) reported that dead *C. dentata* trees increased as a stand component with elevations >750 m on open slopes of all aspects and seldom occurred on mesic sites. Woods and Shanks (1959) inventoried *C. dentata* in the GSMNP and reported it was most often found in coves and on mesic slopes, but occasionally occupied drier sites. Golden (1974), working in the central part of GSMNP, reported that evidence of *C. dentata* was present in 34% of stands sampled and occurred most often above 800 m elevation on sites with landform and vegetation suggesting subxeric to xeric moisture regimes.

Observations on the occurrence of *C. dentata* in North Carolina based on snags and stumps (Keever 1953; Golden 1974) generally agree with results from studies of persistent sprouting root systems elsewhere. Higher elevation is a consistent positive significant factor in most studies of *C. dentata* occurrence in the southern part of its range. Although the biological effects of elevation on *C. dentata* survival have not been explained, elevation is a surrogate for air and soil temperature regimes (Clinton 2003). Elevation, however, also affects site moisture relations through orographic precipitation and evapotranspiration (Shanks 1954). Persisting *C. dentata* sprouts have been reported on slopes facing all directions (Whittaker 1956), but are typically associated with southerly aspects and xerophytic vegetation. My study sought to quantify the current landscape-scale ecology of *C. dentata* throughout the mountainous region of North Carolina to better understand its occurrence in relation to environmental site characteristics that may be associated with temperature and moisture regimes. I hypothesized that the current occurrence of *C. dentata* could be explained by a combination of (1) physical site characteristics associated with common topographic variables, and (2) biological indicators of site moisture regimes evidenced by co-occurring indicator tree species. Based on results of other studies, I anticipated that topographic variables would account for much of the variation of *C. dentata* occurrence and that several co-occurring tree species would refine the relationship. The purpose of my study was to identify variables associated with the occurrence of *C. dentata* and develop a model that quantifies their interrelationships. Such a model could have potential value to identify and rank sites for management, conservation and restoration of the species.

## STUDY AREA

I conducted the study throughout the southern Appalachian Mountains of North Carolina, centered on Asheville, NC (35.58°N, 82.56°W) (Fig. 1), where elevation ranges from 600 to >2,000 m. The climate of this region is classified as temperate humid with mean annual air temperature of 13°C. Precipitation is distributed uniformly throughout the year and ranges from about 950 to >1,500 mm, varying primarily with elevation. Geologic formations are Precambrian metaigneous and metasedimentary gneisses and schists that have weathered to form highly dissected landscapes of low to moderate relief (Pittillo et al. 1998). Soils are generally deep (>100 cm), acidic (pH < 5.5), and infertile. Forests are dominated by deciduous hardwoods consisting of various species of *Quercus* and *Carya* on dry middle slopes and ridges, and mixtures of mesophytic species on moist lower slopes and valleys. Before being eliminated as a canopy species by *C. parasitica*, *C. dentata* was a component of about half of the forests in western North Carolina at elevations between 760–1,370 m (Pinchot and Ashe 1897), codominant with *Q. prinus* on ridges and dry slopes, *Q. rubra* on moist slopes and *L. tulipifera* in coves (Holmes 1911).

## METHODS

*Study area and sample plots.*—Using data from the Forest Inventory and Analysis (FIA) program of the Forest Service, U.S. Department of Agriculture (Scrivani 2011), I sampled the occurrence of *C. dentata* on approximately 2

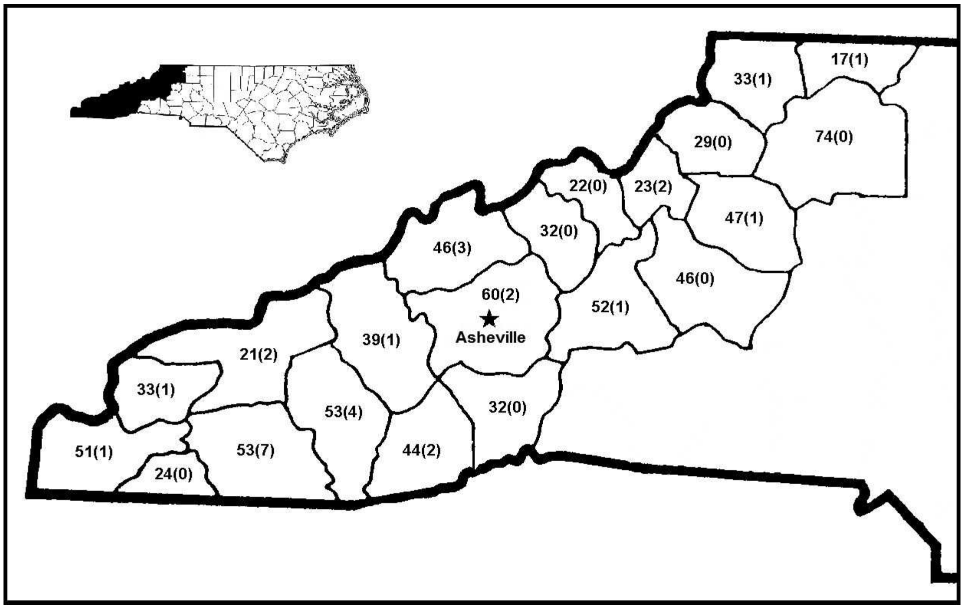

Fig. 1. Distribution of 831 Forest Inventory and Analysis sample plots in 21 counties of the southern Appalachian Mountains of North Carolina. Displayed in each county are the total plots and (in parentheses) plots with occurrence of *Castanea dentata*.

million ha of forested land in 21 mountainous counties of western North Carolina (Fig. 1). Data were available from 831 FIA permanent field plots. Each plot represented approximately 2,430 ha of forest land. Timber stand data for each plot included ownership, age, *Quercus* site index (50-yr base), and basal area. Physical plot data included elevation, slope gradient and slope aspect; aspect was recorded in eight categories of 45 degrees each. Biological data included the binary inventory (presence or absence) by tree species of all woody stems >2.54 cm diameter at breast height (d.b.h., 1.37 m). I inferred the site moisture regime (i.e., mesic, xeric) of sample plots from their species composition using categories reported by Whittaker (1956).

*Statistical analyses.*—I subdivided the sample plots into two groups: those with and without *C. dentata*. I assumed non-normal distributions of variables for the two groups and used nonparametric tests to evaluate differences. I tested categorical variables for differences between the two groups using chi-square and continuous variables using Wilcoxon rank sum with continuity correction for tied ranks. Spearman's rank-order correlation was used to measure the direction and strength of association between pairs of variables. I used chi-square tests with 2 × 2 contingency tables to determine if the presence of *C. dentata* was independent of commonly co-occurring tree species. I subjectively defined "common species" as those co-occurring with *C. dentata* on >5 plots, which was the minimum number judged adequate to reduce the possibility of illogical relationships resulting from the influence of uncommon species (e.g., *Juglans nigra*). Gauch (1982, p. 214) suggests uncommon species are those present in fewer than 5 to 20 of the sample plots. I used multivariate logistic regression to evaluate the individual and collective effects of significant timber stand, topographic factors, and tree species (determined from the univariate analyses) on the probability of occurrence of *C. dentata*. Akaike Information Criterion (AIC) was used to evaluate the best model with differing formulations. McFadden's pseudo R-squared ($R^2_{MCF}$) was used as a measure of variation explained by various logistic model formulations. I used version 3.2.2 of the R statistical package (R Core Team 2015) for data analysis and tested for significance at the $p \leq 0.05$ level.

*Post-hoc analysis.*—My planned analysis revealed that a suitable logistic model including significant topographic and biological variables could not be developed to estimate the probability of occurrence of *C. dentata*. In an unplanned analysis, I determined that many tree species in assemblages occurring on the study plots were highly correlated with elevation (Spearman's $r_s$ range 0.04–0.35, results not shown). The occurrence of those species among plots were also correlated with one another (results not shown), which suggested undesirable effects of multicollinearity in the logistic models (Graham 2003). To circumvent multicollinearity I used direct gradient analysis and weighted averages ordination to derive an index of plot moisture regime based on species occurrence. Direct gradient analysis arranges species in relation to their response to a presumed primary environmental influence (e.g., moisture). Site moisture is a complex phenomenon that is a function of slope, aspect, landform and soil texture. The

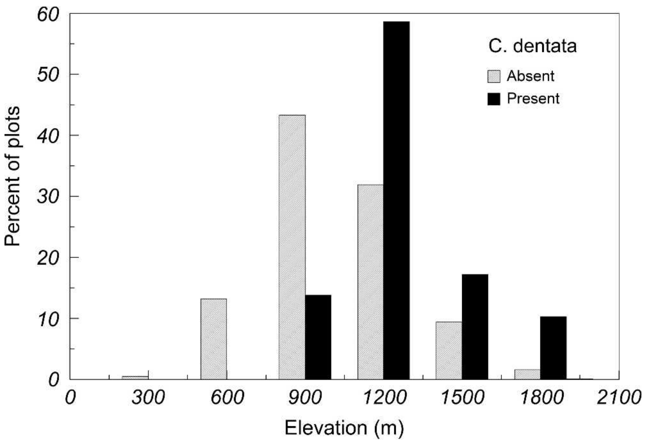

FIG. 2. Relative distribution of Forest Inventory and Analysis sample plots in relation to elevation where *Castanea dentata* was present (n = 29) or absent (n = 802) in the southern Appalachian Mountains of North Carolina.

assemblage of tree species, each with their own moisture affinities, provides an integrated assessment of moisture availability. I used the four categories of species-moisture relationships reported by Whittaker (1956) to assign an integer weight value to each tree species according to its perceived moisture affinity. Weighted averages ordination was used to calculate a sample score (S) for each plot to express its position on a moisture gradient using the algorithm:

$$Sj = \sum (Aij\ Wi) / \sum Aij$$

where $A_{ij}$ is the abundance (binary presence = 1 or absence = 0) of species $i$ on plot $j$ and $Wi$ is the moisture weight for species $i$ reported by Whittaker (1956), which ranged from 0 for those classified as mesic to 3 for xeric.

## RESULTS

The study sampled 831 plots in the 21-county study area (Fig. 1). Land ownership at sample plot locations was primarily nonindustrial-private (47.5%), national forest (25.8%) and farmer (11.7%). *Castanea dentata* was an uncommon species in the study area, occurring on 29 (3.5%) of the sample plots. It occurred more frequently ($p < 0.01$) on plots located in national forests (6.5%) compared to other ownerships (2.4%). I found a weak relationship ($p < 0.10$) of *C. dentata* among the 25 forest types present in the study area. However, the relationship was strong ($p < 0.01$) among the 10 forest types where *C. dentata* was present, with greater relative frequency in stands classified as either *Quercus*/*Carya* or *Q. prinus*.

*Stand and topographic variables.*—Timber stands ranged in age from 1 yr to 200 yr, site index ranged from 9.1 m to 30.2 m, and basal area ranged from 0 (for newly regenerated stands) to 56.9 $m^2$/ha. Stands with *C. dentata* were older than stands where *C. dentata* was absent ($p < 0.01$) (Table 1). Site index and basal area were similar for plots with and without *C. dentata*.

Table 1. Mean (SD) timber stand and topographic habitat variables associated with the presence or absence of *Castanea dentata* saplings (d.b.h. ≥ 2.5 cm) on 831 Forest Inventory and Analysis plots in the southern Appalachian Mountains of North Carolina.

| | *Castanea dentata* | | |
|---|---|---|---|
| Variables | Present (n = 29) | Absent (n = 802) | p[a] |
| Stand | | | |
| Age (years) | 71.2 (29.1) | 57.1 (27.2) | <0.01 |
| Site index (m) | 21.3 (4.6) | 22.9 (4.6) | <0.10 |
| Basal area ($m^2$/ha) | 20.6 (8.8) | 21.2 (9.9) | <0.10 |
| Topographic | | | |
| Elevation (m) | 1091.1 (262.6) | 871.6 (272.2) | <0.01 |
| Slope aspect (°) | 170.7 (81.0) | 181.3 (82.4) | >0.10 |
| Slope gradient (%) | 44.6 (17.2) | 40.8 (18.3) | >0.10 |

[a] Wilcoxon rank-sum test used to evaluate probability of different populations between plots where *C. dentata* was present or absent.

The study plots ranged in elevation from 274 m to 1860 m, ranged in slope gradient from 1% to 95%, and included all aspect quadrants. Mean elevation of plots was higher where *C. dentata* was present compared to sites where it was absent ($p < 0.01$) (Table 1). Most plots where *C. dentata* was present (86%) were >900 m elevation compared to 44% of plots where the species was absent (Fig. 2). Mean aspects and gradients were similar for plots where *C. dentata* was present or absent (Table 1).

The lack of importance of aspect on occurrence of *C. dentata* was surprising. Accordingly, I examined in greater detail sample plots where *C. dentata* was present to determine if their distribution within an elevation group was related to aspect (Table 2). In a test of homogeneity, the distribution of plots among aspects (expressed as octants of azimuth) was similar for plots <900 m and ≥900 m elevation. Presence of *C. dentata* was not correlated with aspect or slope gradient.

*Biological variables.*—Thirty tree species (including *C. dentata*) were inventoried on the 831 FIA plots (Table 3). The number of species occurring ranged from 1 to 15 across all plots and from 4 to 12 on plots

Table 2. Frequency of occurrence of 29 sample plots with *Castanea dentata* in relation to elevation and octant of azimuth in the southern Appalachian Mountains of North Carolina.

| | Elevation (m) | | |
|---|---|---|---|
| Octant (degrees) | <900 | ≥900 | All (%) |
| | | number | |
| 1–45 | 0 | 0 | 0 (0.0) |
| 46–90 | 0 | 2 | 2 (6.9) |
| 91–135 | 1 | 5 | 6 (20.7) |
| 136–180 | 0 | 6 | 6 (20.7) |
| 181–225 | 3 | 4 | 7 (24.1) |
| 226–270 | 0 | 1 | 1 (3.5) |
| 271–315 | 0 | 4 | 4 (13.8) |
| 316–360 | 0 | 3 | 3 (10.3) |

Table 3. Tree species commonly co-occurring with *Castanea dentata* on 831 Forest Inventory and Analysis sample plots in the southern Appalachian Mountains of North Carolina and their association with elevation.

| | *Castanea dentata* | | | |
|---|---|---|---|---|
| Common Tree Species[a] [b] | Present (n = 29) | Absent (n = 802) | p[c] | Association With Elevation (type)[d] [e] |
| *Quercus prinus* (X)[f] | 72.4 | 44.3 | <0.01 | <0.01 (+) |
| *Acer rubrum* (M) | 65.5 | 68.3 | >0.10 | <0.05 (–) |
| *Quercus rubra* (M) | 62.1 | 35.8 | <0.01 | <0.01 (+) |
| *Carya* spp. (X) | 44.8 | 39.5 | >0.10 | >0.10 (0) |
| *Nyssa sylvatica* (X) | 44.8 | 29.7 | <0.10 | <0.01 (–) |
| *Oxydendrum arboreum* (X) | 41.4 | 46.5 | >0.10 | <0.01 (–) |
| *Quercus alba* (X) | 41.4 | 36.5 | >0.10 | <0.05 (–) |
| *Quercus coccinea* (X) | 34.5 | 34.5 | >0.10 | >0.10 (0) |
| *Cornus florida* (M) | 31.0 | 41.1 | >0.10 | <0.01 (–) |
| *Quercus velutina* (X) | 24.1 | 27.1 | >0.10 | <0.05 (–) |
| *Liriodendron tulipifera* (M) | 24.1 | 48.5 | <0.05 | <0.01 (–) |

[a] Common tree species occurring with *Castanea dentata* on >5 sample plots.

[b] Uncommon tree species occurred with *C. dentata* on ≤5 plots: *Acer pensylvanicum*, *A. saccharinum*, *Fagus grandifolia*, *Fraxinus americana*, *Halesia carolina*, *Magnolia acuminata*, *M. grandiflora*, *Pinus strobus*, *P. echinata*, *P. pungens*, *P. rigida*, *P. virginiana*, *Prunus serotina*, *Quercus stellata*, *Robinia pseudoacacia*, *Sassafras albidum*, *Tilia americana*, *Tsuga canadensis.*

[c] Chi-square test of independence for 2 × 2 contingency tables.

[d] Wilcoxon rank-sum test.

[e] Type (in parenthesis) of association with elevation is designated as positive (+), negative (–), or none (0).

[f] Moisture affinity (Whittaker 1956): M = mesic or submesic; X = xeric or subxeric.

where *C. dentata* was present. Eleven of the total 29 species inventoried co-occurred with *C. dentata* on >5 plots and were subjected to contingency table analysis. Three of the 11 commonly co-occurring species were significantly associated with the presence of *C. dentata*: *Q. prinus* and *Q. rubra*, which had a positive relationship, and *L. tulipifera*, which had a negative relationship. A fourth species, *Nyssa sylvatica* (blackgum), was marginally ($p < 0.10$) associated with *C. dentata*. Two of the four significant species were classified as mesophytic (*Q. rubra* and *L. tulipifera*); the other two were xerophytic.

*Probability of* C. dentata *occurrence.*—The multivariate logistic regression analysis identified elevation as the variable of primary importance affecting the probability of occurrence of *C. dentata*. A model including the highly significant variable elevation (AIC = 240.00, df = 828) indicated that the probability of *C. dentata* occurrence increased rapidly between approximately 750 m and 1,500 m (Fig. 3), but accounted for little variation ($R^2_{MCF} = 0.06$). Various model formulations that included elevation and co-occurring species explained little additional variation of *C. dentata* occurrence. The strong association of many common species with elevation (Table 3) may explain the insignificant effect of species in combination with elevation in various model formulations. The unexpected small improvement of model performance that resulted from including two xerophytic species (*Q. prinus* and *N. sylvatica*) of opposite correlations with elevation (i.e., positive and negative respectively, Table 3) also suggested a likely complex relationship among other species. I hypothesized that multicollinearity was the probable cause of the unexpected poor model behavior when multiple species were included with elevation (Graham 2003), which resulted in modification of my planned analysis.

In a post hoc unplanned analysis, I addressed multicollinearity by developing a plot moisture score by direct gradient analysis using the relationships reported by Whittaker (1956). The resulting weighted average ordination scores, ranging from 0 to 3, suggested a moisture gradient of tree communities ranging from entirely mesophytic species to xerophytic species, respectively. The mean score was lower on plots without *C. dentata* ($\bar{x} = 1.51$, $p < 0.01$) compared to plots with *C. dentata* ($\bar{x} = 2.28$). A logistic model including elevation and moisture score was clearly superior (AIC = 115.97, $R^2_{MCF} = 0.56$) compared to models utilizing individual species. Including stand age resulted in a small improvement of model performance (AIC = 111.37, $R^2_{MCF} = 0.59$). Solving the highly significant two-variable model produced realistic

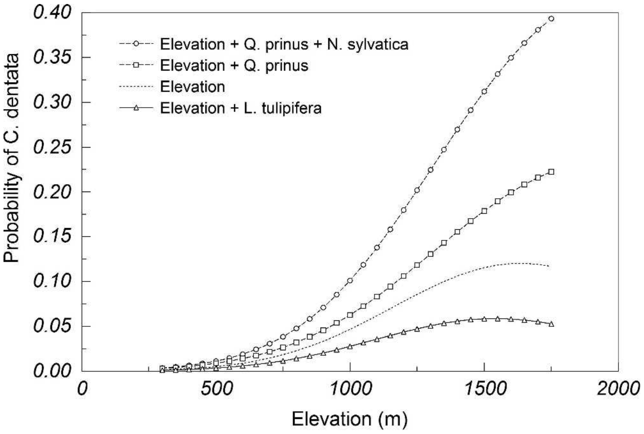

FIG. 3. Probability of occurrence of *Castanea dentata* in relation to elevation and the presence of three relatively abundant co-occurring tree species on 831 Forest Inventory and Analysis sample plots in the southern Appalachian Mountains of North Carolina.

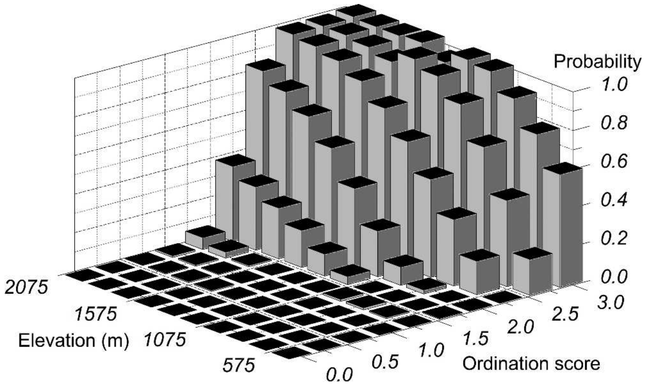

FIG. 4. The probability of occurrence of *Castanea dentata* increases on sites at middle to high elevation and supporting xerophytic tree communities (i.e., indicated by moisture ordination scores > 1.5) in the southern Appalachian Mountains of North Carolina.

estimated probabilities of occurrence of *C. dentata* in relation to elevation and moisture score (Fig. 4). Based on the elevation and ordination score model, the probability of occurrence of *C. dentata* was predicted as near zero for elevations <900 m and moisture scores <1.5, but increased rapidly with larger values of those two variables.

## DISCUSSION

Occurrence of *C. dentata* saplings >2.5 cm d.b.h. was uncommon in the Appalachian Mountains of North Carolina, occurring on 3.5% of the 831 sample plots. McWilliams et al. (2005) conducted a similar survey and reported similar findings of *C. dentata* on 0.42% of all FIA plots throughout its natural range. Composition of forests where *C. dentata* occurred in my study area, mainly in *Quercus/Carya* stands, was similar to composition of forests where it occurred in *Quercus*-dominated stands of northeastern Ohio (Schwadron 1995) and Virginia (Parker et al. 1993). The reduced occurrence of *C. dentata* in timber stands of non-Federal ownership, younger ages and lower elevations suggest that historical land use could have been a factor influencing my results. In the Appalachian Mountains of North Carolina, Nesbitt and Netboy (1946) reported that a hundred years of historical land use had resulted in extensive clearing of forests for agricultural fields, particularly at lower elevations, followed by abandonment and reversion of old fields to forests. Fei et al. (2007) reported nearly complete absence of *C. dentata* on former agricultural lands.

The current distribution of *C. dentata* in my study area was most strongly associated with elevation, which is a strong driver of daily and annual temperature regimes (Fridley 2009). I found that *C. dentata* was uncommon below 900 m, but its occurrence increased rapidly between 900 m to 1,200 m. My findings agree with Burke (2011), who reported that the presence of *C. dentata* sprouts in Virginia was more likely on sites with elevations >857 m. An explanation for the rare occurrence of *C. dentata* at low elevations in my study area is unknown, but a possible explanation could be from the detrimental effects of logging (Burke 2011) and also from lethal effects of the exotic root disease *P. cinnamomi* on species of the genus *Castanea* (Crandall et al. 1945). This disease is associated with warm and wet soil conditions (Nesbitt et al. 1979), such as provided by heavy clay and highly eroded soils common at low elevations, where chestnut mortality was reported before arrival of *C. parasitica* (Holmes and Bradfield 1907, in Rhoades et al. 2003). Balci et al. (2007) reported common occurrence of *P. cinnamomi* in soils of *Quercus* dominated forests, but found no correlation with site factors. Clark et al. (2010) reported mortality from *Phytophthora cinnamomi* of planted American chestnut. Although explanations for the strong association of *C. dentata* with higher elevations have not been well established, lethal effects of soil temperature on *P. cinnamomi* could be a contributing factor (Balci et al. 2007).

I found *C. dentata* was not associated with topographic variables of either slope aspect or slope gradient, both of which are typically important factors affecting site moisture regimes and the distribution of vegetation in the southern Appalachians (Pittillo et al. 1998). The lack of importance of aspect in my study was surprising and could have resulted from insensitive tests associated with the small number of plots where *C. dentata* occurred. In contrast to my findings, Keever (1953) reported a strong association of canopy *C. dentata* with aspect in her study of six stands, although the relationship was weaker for saplings and sprouts. Schibig et al. (2005) sampled four widely separated areas in the Highland Rim section of Tennessee and found *C. dentata* sprouts were primarily found for aspects associated with dry sites. In a similar study in the Cumberland Plateau, however, Schibig et al. (2006) found that *C. dentata* occurred more often on north and east-facing slopes (61%) compared to south and west-facing slopes (22%). Fei et al. (2007), working in karst topography of central Kentucky, did not examine effects of aspect but found a strong affinity of *C. dentata* with steeper slope gradients and several non-topographic variables (e.g., geologic formation, soil series) that were possibly associated with site moisture regimes. These inconsistent findings among studies and results from my study suggest that the effects of aspect on occurrence of *C. dentata* are poorly understood and could be confounded with a complex of other environmental variables, which collectively influence moisture gradients.

Unlike many studies of *C. dentata* where a large sample of occurrences is correlated with site factors, my database of random locations provided a small sample size that, except for elevation, was probably inadequate to detect a significant relationship with other topographic variables. Another limitation of my FIA database was lack of other environmental variables associated with moisture regimes, such as landform, soil depth and texture (Helvey et al. 1972). Also, the lack of sprouting root systems may be a poor indicator of favorable sites for *C. dentata* as reported by Golden (1974, p. 168) who found evidence of past presence of the species on 98% of his plots (n = 46) in *Q. prinus* forests, but living sprouts on only 19%.

A moisture gradient based on tree species assemblages provided substantial explanatory power in modeling *C. dentata* occurrence. Although weighted averages of vegetation has long been used for direct ordination (Wentworth et al. 1988), no studies were found where Whittaker moisture affinity scores had been used for gradient analysis of tree species occurrence in forests. Because of the correlation of the distribution of many southern Appalachian tree species with elevation (Steele 2007), collinearity effects restricted entering multiple species into regression models, which reduced the indicator effects of the total vegetative assemblage on the FIA plots. Excluding selected species to reduce collinearity was unsatisfactory because relationships expressed by a final model would have been limited to the FIA data set and the possible importance of other species would be unknown. My serendipitous discovery that a model based on Whittaker's weighted averages ordination score was clearly superior to using individual indicator species could have other ecological applications where a particular biological response by a vegetative community, such as productivity, is believed to be associated with moisture gradients.

I found occurrence of subxeric *C. dentata* was positively correlated with *Q. rubra*, a species typically classified as mesophytic (Whittaker 1956; Burns and Honkala 1990), although it is occasionally classified as xerophytic (Kubisiak and Abrams 1992; Nowacki and Abrams 1992). However, Whittaker (1956) reported that *C. dentata* and *Q. rubra* were usually codominants at elevations above about 1050 m. Blackman and Ware (1982) reported occurrence of *Q. rubra* stands on dry sites in the southern Appalachians of Virginia. Abrams (1994) suggests that genotypic variation within species may account for their occurrence on different habitats in small areas. Kubisiak and Abrams (1992) studied side by side stands of *Q. rubra* in Pennsylvania and found ridge populations were more drought tolerant than valley populations, suggesting ecotypic variation of the species. Although not as ubiquitous as *Acer rubrum* (red maple) in relation to moisture affinity, *Q. rubra* apparently has tolerance for a range of moisture regimes, from mesic to xeric.

Competition could account for the negative relationship of *C. dentata* with elevation and mesic sites, particularly resulting from *L. tulipifera*, a mesophytic species that typically dominates moist sites <1,000 m. However, *C. dentata* was a common canopy component of hardwood stands on mesic sites, which included *L. tulipifera* before onset of the blight (Keever 1953; Whittaker 1956). Griffin (1992), working in mature stands mostly >900 m in West Virginia, found abundant sprouting root systems of *C. dentata* on mesic sites (e.g., coves, north aspects) that did not include *L. tulipifera*. Burke (2011) found a direct relationship of *C. dentata* sprout abundance with overstory basal area in mixed-species stands not recently harvested. The current lower canopy position of *C. dentata* as an understory species could reduce its vigor, particularly following disturbance, when regeneration of *L. tulipifera* and other mesophytic trees and shrubs form a multi-layered canopy that can densely shade much of the forest floor (Griffin 1989). In young clearcut stands Griffin et al. (1991) reported increased mortality of *C. dentata* root systems with increasing basal area of hardwood saplings in the regenerating stand. A satisfactory understanding of *C. dentata* survival in relation to environment and types of disturbance, such as timber harvest and fire, is not available.

The FIA database did not include information on site disturbance from fire, which is a factor related to control of competing vegetation (Jacobs et al. 2013) and increased survival and growth of *C. dentata* (McCamment and McCarthy 2004). Fire exclusion in eastern upland hardwood forests has been suggested as a factor resulting in increased competition by mesophytic species on dry sites (Abrams 1992; Nowacki and Abrams 2008), which could have influenced occurrence of *C. dentata* on plots in the FIA database. However, prescribed fire had no effect on incidence of *P. cinnamomi* in soil (Meadows et al. 2011). The effects of fire on *C. dentata*, its pathogens and competitors are emerging from ongoing studies, but relationships are currently unclear.

Results of this study could have application for investigation of biological control of *C. parasitica* on *C. dentata* such as ranking stands for successful hypovirulence (MacDonald and Fulbright 1991). Hypovirulence has been successful for control of *C. parasitica* in *Castanea sativa* plantations in Europe (Zamora et al. 2014) and in the United States under experimental (Anagnostakis 1982) and natural conditions (Fulbright et al. 1983; Griffin 1992). Overall, however, hypovirulence in natural conditions has been unsuccessful on *C. dentata* (Nuss 2005), largely because of genetic differences of the pathogen (Milgroom and Cortesi 2004). A related issue is lack of knowledge on vectors of transmission of the virus between cankers (e.g., via ants, aphids) among trees on sites where hypovirulence could be established. Milgroom and Cortesi (2004) suggested that detailed study of environment conditions is needed for the few stands where hypovirulence has been successful. Reduction of competition and other cultural actions to increase longevity of sprouting *C. dentata* root systems could be important in allowing hypovirulence to become established (Griffin 1992) and for maintaining genetic diversity of the species (Namkoong 1991).

In summary, the purpose of this study was to investigate the association of surviving *C. dentata* root systems with co-occurring tree species. *C. dentata* rarely occurred in upland hardwood forest communities in the southern Appalachian forests of North Carolina. It occured primarily as understory saplings originating from repeated sprouting of root systems and occurs primarily in stands at elevations >900 m. Based on the presence of co-occurring xerophytic vegetative species, *C. dentata* occurs most frequently on sites characterized as dry. *C. dentata* sprouting root systems occur frequently with *Q. prinus*, but seldom with the mesophytic *L. tulipifera*. Results from this study may have application to rank forest sites for investigation of biological control of *C. parasitica* through hypovirulence and for identifying stands for application of silvicultural practices to reduce environmental stress and increase survival of existing root systems. Based on these results, it is recommended that the scope of future research on this subject be expanded to include forms of vegetation not included in this study, such as ericaceous shrubs usually present on dry sites, for example *Kalmia latifolia* (mountain laurel).

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