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Distribution of American Chestnut (*Castanea dentata*) in National Park Service Units of the National Capital Region

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ABSTRACT

Once a dominant tree species of eastern U.S. forests, American chestnut (*Castanea dentata*) populations were devastated in the early 1900s by the introduction of an exotic fungal pathogen. The chestnut blight fungus (*Chryphonectria parasitica*) effectively eliminated the American chestnut as a canopy species throughout its native range, although it persists today as an understory species. Due to its ecological, economic, and cultural importance, various research approaches have been used to develop a blight-resistant chestnut, and after many decades of work, blight resistant trees may soon be available for restoration. Most of the National Park Service (NPS) units of the National Capital Region (NCR) fall within the native range of the American chestnut and may play a role in restoration efforts through research, interpretation, or demonstration plantings. Understanding the current distribution of American chestnuts in the NCR is the foundation for any of these actions. To this end, we inventoried trees in eleven park units in the summer of 2014 and described their frequency with respect to size, presence of blight, reproduction, and associated vegetation types. Most American chestnut trees in the NCR are small (mean dbh = 7.3 cm and mean height = 6.8 m) understory trees, and only a few exhibited signs of reproduction. Approximately 11% of the inventoried trees showed visual symptoms of blight. Chestnuts in the NCR were most frequently associated with U.S. National Vegetation Classification associations that are dominated by oaks (*Quercus* spp.) and ericaceous shrubs. We anticipate that these results will inform future inventory efforts and may provide guidance for the selection of reintroduction sites.

Key words: American chestnut, exotic species, forest vegetation, mid-Atlantic vegetation, restoration.

INTRODUCTION

Prior to the introduction of an exotic pathogen in the early twentieth century, the American chestnut (*Castanea dentata* (Marshall) Borkh.) was a dominant tree species of eastern U.S. forests (Russell, 1987; Ellison et al., 2005). Its range extended from Mississippi to Maine (Little, 1977), and it comprised over 50% of the total basal area in some forest stands (Braun, 1950; Keever, 1953). Due to leaf tissue with allelopathic compounds and a relatively low C:N ratio, American chestnuts likely had a strong impact on forest composition and ecosystem functions, including decomposition, nutrient cycling, and productivity (Keever, 1953; Vandermast et al., 2002; Ellison et al., 2005; Rhoades, 2007; Elliott & Swank, 2008). Its seeds were a valuable food resource for wildlife, domestic livestock, and humans (Anagnostakis, 1987; Paillet, 2002; Lutts, 2008), and the trees were an important economic resource for Southern Appalachian communities due to the high value of their lumber and seeds (Russell, 1987; Paillet, 2002).

In 1904, the chestnut blight fungus (*Chryphonectria parasitica*) was documented at the Bronx Zoological Park in New York (Anagnostakis, 1987; Jacobs, 2007). The pathogen was probably introduced on *Castanea* spp. seedlings imported from Asia, and it spread through eastern forests rapidly (~37 km/year). By 1950, trees within the entire native range of *C. dentata* were dead or dying (Anagnostakis, 1987). Symptoms of the chestnut blight include bark cankers, wilted foliage, epicormic sprouting below the cankers, and orange

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fungal stromata that appear on the bark (Anagnostakis, 1987). The fungus eventually girdles the infected tree, killing the cambium above the fungal mass, but it does not directly infect and kill the roots of the tree (Burke, 2011). Consequently, American chestnut persists today as re-sprouts originating from roots of trees or seedlings that established before the introduction of the blight (Stephenson et al., 1991; Paillet, 2002; Burke, 2011). These re-sprouts, however, rarely reach the forest canopy or reproductive status, and the species no longer plays an important ecological and economic role in Eastern forests.

Due to the ecological function and historical importance of the American chestnut, there has long been substantial interest in developing blight-resistant trees for reintroduction in eastern U.S. forests. Many approaches to mitigating the impacts of chestnut blight have been attempted, including developing hypovirulent strains of the blight to use as a biocontrol, intercrossing pure American chestnuts to promote natural blight resistance, using genetic engineering tools to create transgenic chestnuts, and developing a disease resistant hybrid of American and Asian chestnuts through backcross breeding (Diskin et al., 2006; Fei et al., 2007; Joesting et al., 2009; Jacobs et al., 2013; Newhouse et al., 2014). As a result of these efforts, blight-resistant trees may soon be ready for reintroduction (Jacobs, 2007; Dalgleish & Swihart, 2012; Newhouse et al., 2014), and in the near future, there may be opportunities for public land managers in the eastern U.S. to support restoration efforts through research, demonstration, education, or restoration plantings on public lands (Lellis, 2006; Sherald, 2011).

Understanding the current distribution and ecological status of naturally occurring American chestnuts can inform chestnut-related management actions in a number of ways (e.g., clarifying current and historical significance of chestnut to specific sites or regions, identifying habitats that are appropriate for chestnut reintroduction, informing surveys for flowering chestnuts to be included in breeding programs). To this end, we inventoried extant American chestnuts in National Park Service (NPS) units in the National Capital Region (NCR), in Washington, DC and nearby parts of Maryland, Virginia, and West Virginia. The objectives of this study were to: (1) create a database of living American chestnut that includes information related to the location, size, health, presence of blight symptoms, reproductive status, site conditions, and local habitat for each tree, (2) summarize the frequency of American chestnut trees with respect to height, diameter at breast height, incidence of blight, and reproduction, and (3) summarize U.S. National Vegetation Classification (USNVC) associations ("vegetation types") and habitat characters associated with inventoried trees. We expect that a better understanding of the current distribution and ecology of surviving trees will inform management decisions in the NCR National Parks and beyond.

MATERIALS AND METHODS

Study Area and Site Selection

We surveyed eleven NPS units in the NCR: Antietam National Battlefield, Catoctin Mountain Park, Chesapeake & Ohio Canal National Historical Park, George Washington Memorial Parkway, Harpers Ferry National Historical Park, Manassas National Battlefield Park, Monocacy National Battlefield, National Capital Parks - East, Prince William Forest Park, Rock Creek Park, and Wolf Trap National Park for the Performing Arts (Fig. 1). The NCR spans four physiographic provinces (from west to east these include: Ridge and Valley, Blue Ridge, Piedmont, and Coastal Plain) and a

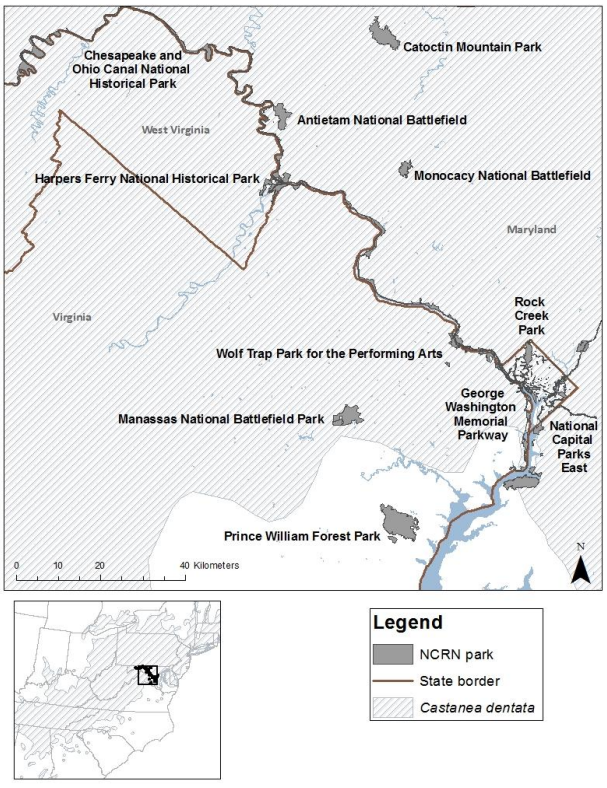

Fig. 1. Location of eleven National Capital Region (NCR) National Park Service units that were included in the American chestnut (*Castanea dentata*) survey. The hatched area is the species' approximate historical range (Little, 1977), and the inset identifies the NCR in the context of the entire historical range.

wide diversity of habitats, from alluvial forests and wetlands to upland oak-hickory forests.

Much of the NCR falls within the native range of the American chestnut, which spanned as far south as Mississippi and Alabama, west into Tennessee, and as far north as Maine and southern Ontario (Little, 1977; Tindall et al., 2004). Russell's (1987) summary of the pre-blight range and habitat affinity of the American chestnut found that the species was: present in the Piedmont and Blue Ridge of Virginia (although less common in the limestone valleys, Appalachian Plateau, or Coastal Plain), a dominant species in the Ridge and Valley and Blue Ridge of western Maryland, and common on hillsides in West Virginia. American chestnut was also reported in Coastal Plain forests of Anne Arundel, Calvert, Charles, and Prince George's counties in southern Maryland (Zon, 1904). Chestnuts were common across a wide elevational range in the mid-Atlantic region, and only a few habitats, including pure stands of hemlock and white oak, swamp forests, and forests on limestone-derived soils, were essentially devoid of chestnuts (Russell, 1987).

Survey sites were assembled from previous vegetation-related research in the NCR (e.g., Schmit et al., 2014) and personal observations of natural resource managers and local native plant enthusiasts (e.g., members of the Maryland Native Plant Society). We also targeted habitats known to be associated with American chestnuts, such as ridges and slopes with well-drained, acidic soils (Russell, 1987; Stephenson et al., 1991). Sites were surveyed during the growing season (May-October) in 2014. Trees were marked with stainless steel tags labeled with a unique identifying number, and Universal Transverse Mercator coordinates (NAD83) were recorded for each tree using a hand-held GPS. To document the surveyed areas, we recorded tracklines with the GPS unit and used ArcMap to create a 10 m buffer around these tracklines to estimate the total area searched.

Tree Characteristics

We measured diameter at breast height (dbh) of all stems ≥ 1 cm dbh and identified the crown class for each individual following the methods described in Schmit et al. (2014). Crown class refers to the position and height of the tree canopy compared to its neighbors and provides a relative measure of the amount of sunlight a tree receives. Crown classes include: open-grown, dominant, co-dominant, intermediate, overtopped, light gap exploiter, and edge tree. We recorded height using a ruler for trees < 2 m and a laser range finder for trees ≥ 2 m.

American chestnuts have frequently been found to occur as stems sprouting from the stumps of old trees (Paillet, 2002). As such, we recorded the presence and diameter of stumps associated with living stems. We checked each individual for evidence of reproduction, including flowers (catkins), fruits (burs), seeds, or nearby seedlings. We visually inspected each tree for symptoms of the chestnut blight, including the presence of sunken or swollen cankers and orange stromata on the trunk. We compared mean dbh and mean height of reproductive versus non-reproductive trees and of blighted versus non-blighted trees with Student's t-tests. We also assessed each tree for conditions that might impact survivorship (e.g., presence of heart-rot, bark damage, buck rub, and beaver damage) and recorded the presence of re-sprouts at the base of a stem. As an indicator of White-tailed Deer (*Odocoileus virginianus*) browse pressure on chestnuts, we recorded whether stems were browsable (the maximum height of deer browse is approximately 1.5 m; Oswalt et al., 2006) and the presence of deer browse.

Site Characteristics

We recorded the slope and aspect of the immediate area around each tree. Following the completion of field sampling, we overlaid chestnut locations on NPS vegetation maps to extract the USNVC association mapped to each location (Jennings et al., 2009; Hazler et al., 2012) and identified the associations that were most commonly associated with extant American chestnuts. We then summarized the areal extent of these vegetation types in the NCR as a coarse estimate of the potential American chestnut habitat in the region. We extracted elevation values for each tree from a 3 m digital elevation model of the region and summarized the frequency of chestnut trees with respect to elevation.

RESULTS

We found 234 living American chestnut trees in nine of eleven NPS units of the National Capital Region (all except Antietam National Battlefield and Manassas National Battlefield Park). Most of the NCR parks occur within the historical range of American chestnut (Fig. 1), but at least five trees found at Prince William Forest Park are outside of the range estimated by Little (1977). None of the inventoried trees was associated with an old stump. The majority were small trees, with dbh values ranging from 1.5 to 42.5 cm (mean = 7.3 cm) and heights ranging from 1.4 to 23.9 m (mean = 6.8 m) (Figs. 2a and 2b). Most were understory

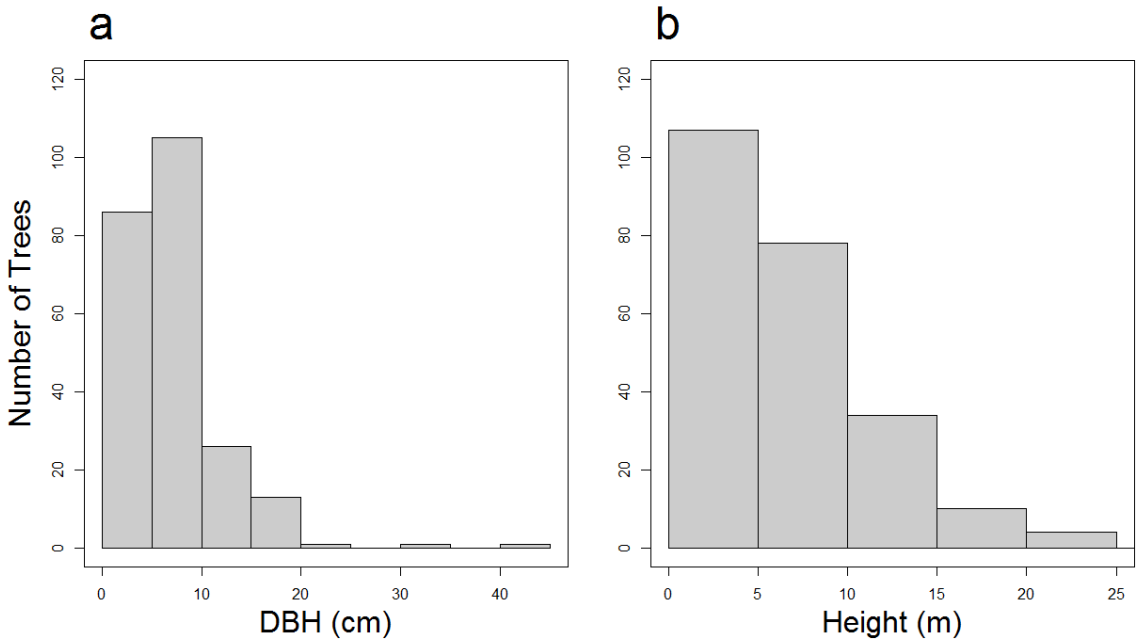

Fig. 2. Frequency of American chestnut trees with respect to (a) dbh and (b) height.

trees (91% of trees were classified as "overtopped" in the field), and only one tree reached the forest canopy (i.e., co-dominant crown class). Of the remaining trees, 5% were classified as light gap exploiters, 3% were classified as intermediate, and < 1% was classified as an edge tree. We found evidence of reproduction at seven trees, and these trees were larger than non-reproductive trees (dbh: t = -3.25, df = 6.035, p = 0.02, height: t = -2.78, df = 6.23, p = 0.03, Figs. 3a and 3c).

We found at least one visual symptom of chestnut blight fungus on 26 trees (11%), and similar to patterns of reproduction, blighted trees tended to be larger in terms of both dbh and height (dbh: t = -2.91, df = 26.68, p = 0.007, height: t = -1.85, df = 30.17, p = 0.07, Figs. 3b and 3d). About half of the sampled trees (54%) had re-sprouts growing from their base, which suggests many of them were responding to other stressors. The most commonly observed tree conditions (and number of trees on which they were observed) included: bark damage (99), large dead branches (90), advanced decay/heart-rot (35), primary branch broken (14), and buck rub (13). Of the 177 trees identified as browsable, 140 (80%) showed evidence of deer browse.

We found American chestnuts in a variety of topographic settings (Figs. 4 and 5), but they were most frequent on moderately sloped sites (mean = 24%) of W-NW and NE aspects and across a range of elevations (mean = 264 m). Chestnuts occurred in all four physiographic provinces (Valley and Ridge, Blue Ridge, Piedmont, and Coastal Plain) and were most frequently found in vegetation types dominated by *Quercus* spp. (particularly *Q. montana* L.) and heath species (Ericaceae). American chestnuts were most commonly mapped to the following USNVC associations (with number of trees and USNVC's CEGL identification code): Central Appalachian/ Northern Piedmont Chestnut Oak Forest (51, CEGL006299), Central Appalachian Basic Oak-Hickory Forest (46, CEGL008514), Central Appalachian Dry Chestnut Oak-Northern Red Oak/ Heath Forest (42, CEGL008523), and Central Appalachian Dry-Mesic Chestnut Oak-Northern Red Oak Forest (40, CEGL006057). Other associations where more than ten American chestnut trees were found included: Mid-Atlantic Mesic Mixed Hardwood Forest (16, CEGL006075), Low-Elevation Mixed Oak/ Heath Forest (11, CEGL008521), and Northern Piedmont Small-Stream Floodplain Forest (11, CEGL006492). The map units representing these vegetation types cover 6750 ha (> 30% of the total NCR area that has been classified to a USNVC vegetation type), suggesting that a substantial proportion of the NCR could be considered potential American chestnut habitat. We estimate that the total area covered by this survey was 450 ha.

DISCUSSION

Despite decades of impacts due to chestnut blight, a substantial number of American chestnuts persist in the

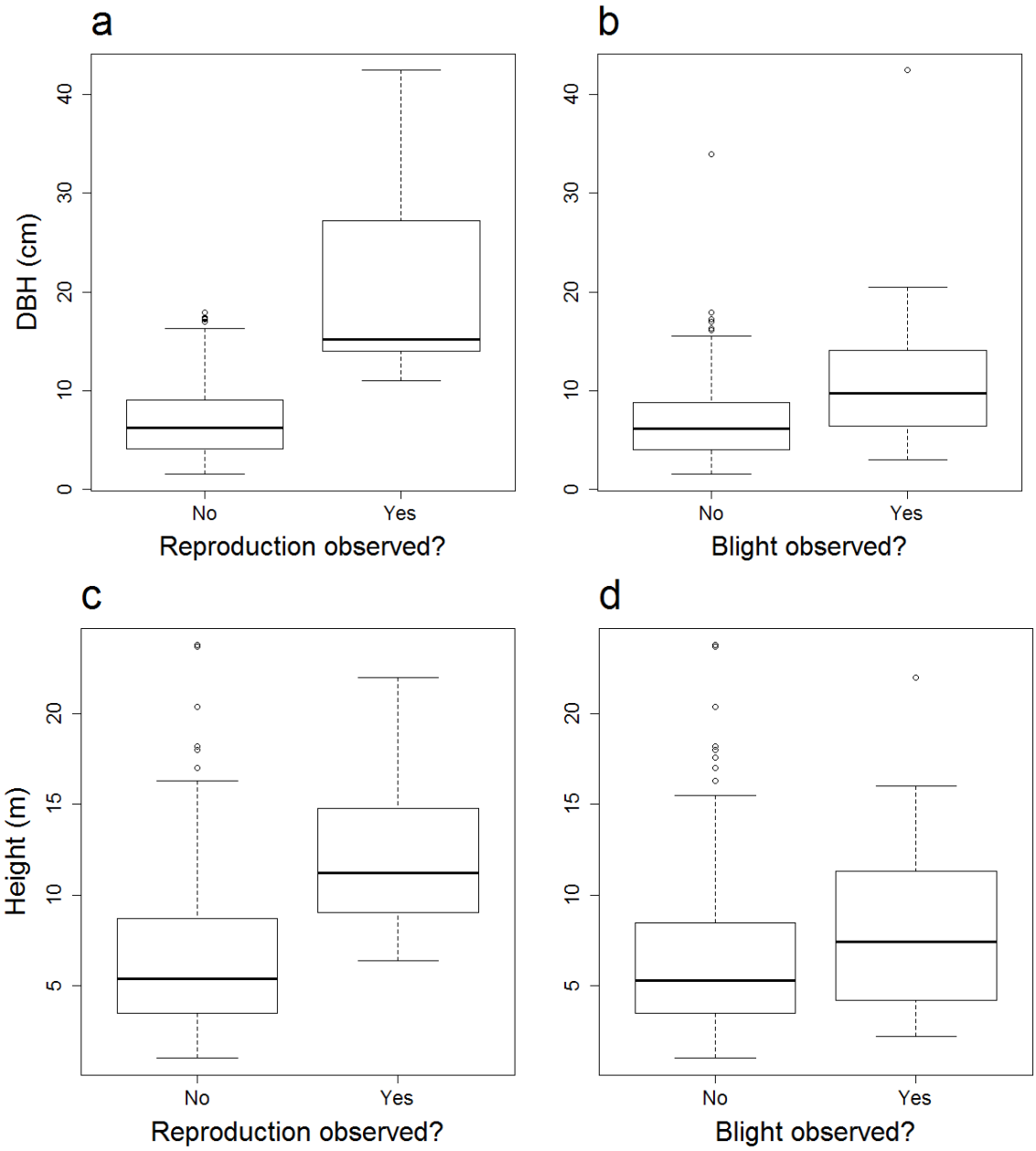

Fig. 3. The incidence of reproduction (flowers or fruits) and visual blight symptoms of American chestnut trees with respect to tree dbh (a and b) and height (c and d).

National Capital Region. Frequent re-sprouts of this species in forest understories have been documented elsewhere in the eastern U.S., although NCR trees were generally larger than those previously reported. An inventory of American chestnuts in upland forests of western Virginia, for example, found that most living stems did not exceed 2.5 cm dbh and that stems measuring > 6.3 cm dbh were uncommon (Stephenson et al., 1991). Likewise, a study in Mammoth Cave National Park in Tennessee found that 86.9% of living American chestnuts had a dbh < 2.5 cm and only 0.7% exceeded 10 cm; in terms of height, 90.6% of the chestnut trees were < 3 m and only 2.1% were > 6 m (Fei et al., 2007). In contrast, many of the NCR chestnut trees were larger: 18% of NCR trees had a dbh > 10 cm and 44% were taller than 6 m (Fig. 2).

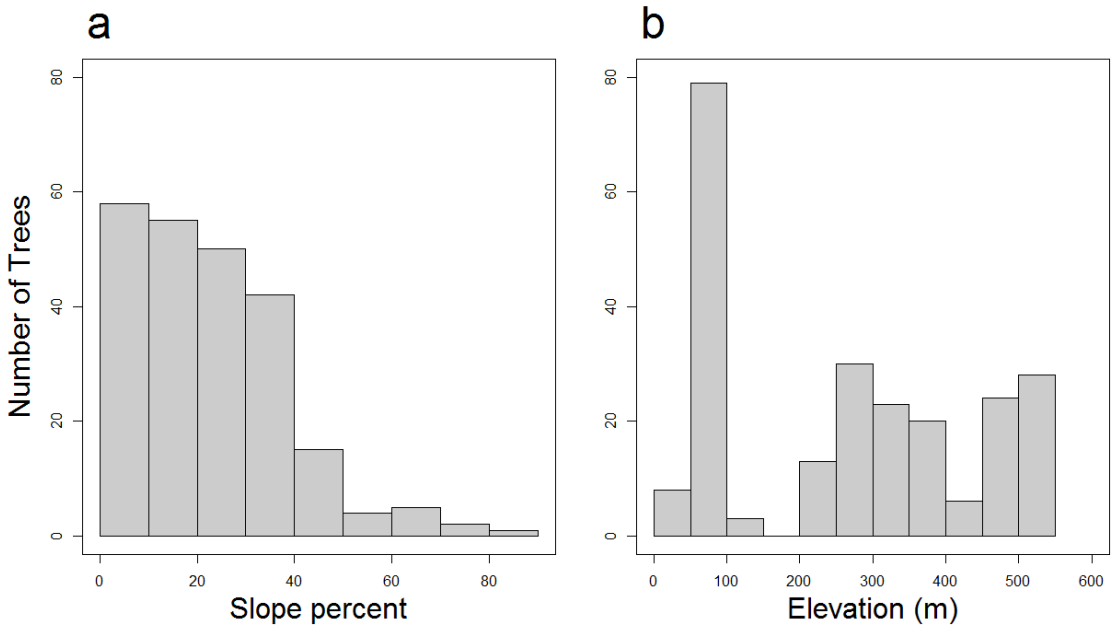

Fig. 4. Frequency of American chestnut trees with respect to (a) slope percent and (b) elevation.

Larger American chestnuts are more likely to be infected with the chestnut blight, which typically kills re-sprouts by the time they attain a height of 15 m and a dbh of 20 cm (Paillet, 2002). Indeed, NCR trees with visual symptoms of blight were larger than those without (Figs. 3b and 3d), but we also found relatively large trees that did not appear to be infected (e.g., 10 trees > 15 m tall had no visual symptoms of blight). Overall, visual symptoms of blight were uncommon among NCR chestnuts (11% displayed visual symptoms), although our estimate of blight infection may be conservative because some infected trees may not have had visual symptoms. Nevertheless, our estimate of blight frequency is well within those previously reported: southern Ontario – 30% (Tindall et al., 2004), Ridge and Valley province of Virginia – 15% (Burke, 2011), and Tennessee – 2% (Fei et al., 2007). We found no evidence of former, large tree stumps associated with the inventoried trees, which suggests that if these tree are re-sprouts, they may have originated from trees that were seedlings or saplings prior to the blight epidemic. Alternatively, stumps of the original trees may have rotted and no longer be detectable. Previous inventories in Virginia and New England found that few extant chestnuts were associated with former, large trees, and that little evidence remains of previous canopy trees in the form of logs or stumps (Paillet, 1988; Stephenson et al., 1991).

NCR chestnuts were found on hillsides of moderate slopes, consistent with previously reported site descriptions (Russell, 1987; Fei et al., 2007), although they were associated with a wider range of aspects than previously reported. Chestnuts in the mountains of the Ridge and Valley province in Virginia, for example,

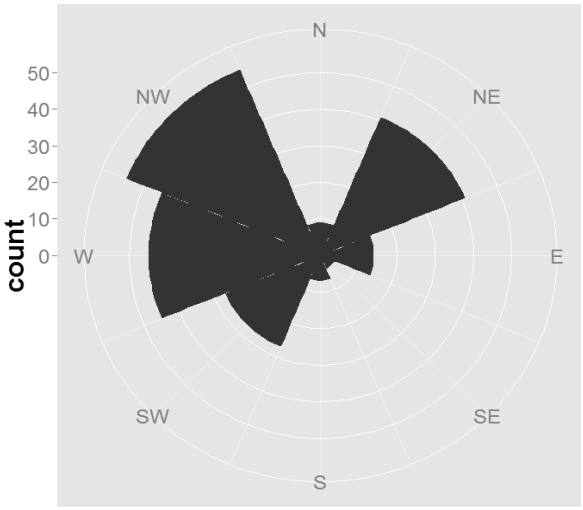

Fig. 5. Frequency of American chestnut trees with respect to aspect, summarized using a rose diagram. Each “pie piece” (or bin) represents 45 degrees. For example, the bin labeled “N” represents a total of 45 degrees or 22.5 degrees on either side of North (0 or 360 degrees). The radius of each “pie piece” equals the number of American chestnut trees found in each bin with each concentric ring equaling ten trees.

commonly occur on southern to western-facing slopes (Stephenson et al., 1991; Burke, 2012). We found a substantial number of individuals in similar sites, as well as on northeastern-facing slopes. NCR chestnuts were most commonly associated with vegetation types dominated by a mix of *Quercus* spp., including *Q. montana* (chestnut oak), *Q. rubra* L. (northern red oak), and *Q. alba* L. (white oak), and shrubs in the heath family (Ericaceae), including *Kalmia latifolia* L. (mountain laurel), *Vaccinium* spp. (blueberries), and *Gaylussacia* spp. (huckleberries). The frequent co-occurrence of American chestnut and ericaceous shrubs is well-supported (Russell, 1987; Stephenson et al., 1991). We found *K. latifolia* was a particularly good indicator of potential chestnut habitat in the field, likely reflecting its association with acidic soils (Russell, 1987). The apparent absence of chestnut at Antietam National Battlefield is likely due to the limestone-derived soils that dominate this park, consistent with previous inventories showing American chestnut is mostly absent from these soils (Russell, 1987; Tindall et al., 2004).

Although American chestnuts were the focus of this inventory, we also encountered many Allegheny chinkapins (*C. pumila* (L.) P. Miller), the only other *Castanea* species native to North America, as well as exotic species Chinese chestnuts (*C. mollissima* Blume) and Japanese chestnuts (*C. crenata* Siebold & Zucc.). These exotic individuals might be associated with old homesteads or might be the escaped progeny of planted trees in developed areas. Some of these exotic species were present in the natural areas where we found *C. dentata* re-sprouts, suggesting that there is some potential for hybridization among *Castanea* species in the region.

Implications for Restoration

We expect this inventory will inform American chestnut management and restoration activities in the mid-Atlantic region. Some of the approaches used to develop blight-resistant plant material for restoration (e.g., breeding programs) will need to use as many unrelated *C. dentata* individuals at each generation as possible to effectively sample native genetic diversity. Furthermore, the use of parent trees from the region where progeny are to be planted will be important for promoting local adaptation (Jacobs et al., 2013). Given that we searched approximately 7% of likely chestnut habitat (i.e., 450 ha of 6750 ha mapped to associated USNVC vegetation types), there are likely to be many more naturally occurring chestnuts in the NCR than we documented. All of the NPS units in the NCR have vegetation maps that include USNVC associations wherever possible. To maximize efficiency and success of efforts to find reproductive trees, future inventory work might focus on the vegetation types identified in this paper.

Despite promising developments in the pursuit of American chestnut restoration, many challenges remain on the path to success. First, not all approaches to developing blight-resistant chestnuts are equally accepted by the restoration community. Breeding programs that hybridize American and Asian chestnuts to confer blight-resistance to the American chestnut, for example, are considered controversial and biologically risky by some, since this approach would require introducing genes from a non-native species into natural habitats. Potential consequences include transfer of non-native genes to sexually compatible native trees, which might confer a competitive advantage and result in invasive behavior, or unanticipated impacts to native organisms that interact with the hybrid trees. Second, deer browse is a major stressor of eastern deciduous forests and frequently limits forest regeneration (Russell, 2001; McShea, 2012). Approximately 80% of browsable chestnuts in this study were browsed. In contrast, only 27% of the browsable saplings (woody plants with dbh $\geq$ 1 cm and < 10 cm) occurring in > 400 permanent vegetation plots in the NCR parks were browsed during the last surveys of these plots (Schmit et al., 2014). Test plantings of American chestnuts in national forests have also identified deer browse as a major challenge for restoration efforts (Clark et al., 2014). Finally, many large-scale ecological changes over the last century (e.g., introduction of exotic pests and pathogens, fire suppression, climate change) may not be favorable to chestnut reintroduction (Jacobs et al., 2013; Clark et al., 2014). Further field-testing of blight-resistant trees will be needed to develop strategies to mitigate these challenges (Jacobs et al., 2013).

SUMMARY

The American chestnut is still frequently encountered as an understory tree in the forests of the mid-Atlantic region, and as long as the root systems of these trees persist, there is no immediate threat of extinction. We expect this inventory will inform decisions about whether and how to proceed with demonstration plantings or restoration activities (e.g., selecting appropriate sites for plantings) and will guide continued efforts to survey for surviving trees and for the elusive blight-resistant individual which could substantially improve the speed and efficacy of breeding programs.

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