AMERICAN CHESTNUT AND FIRE:

IMPLICATIONS FOR RESTORATION

A Thesis

by

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ABSTRACT

Formerly the most dominant canopy tree species throughout much of eastern North America, the American chestnut (*Castanea dentata* (Marsh.) Borkh.) has since been decimated by the chestnut blight (*Cryphonectria parasitica* (Murr.) Barr.) and relegated to scattered understory sprouts. Providing a large, reliable seed crop and high quality timber, the American chestnut was an iconic keystone species, unrivaled in its ecological influence and economic value. Since its demise, however, continued efforts have been made to develop effective chestnut blight resistance and prepare blight-resistant chestnut hybrids for reintroduction in the wild. This project is concerned with the optimal management and habitat conditions for American chestnut within the broader goal of restoration. Does American chestnut sprout regeneration benefit from fire? How does its response to fire vary according to topography? With our incomplete understanding of chestnut fire ecology and geography, this study aims to evaluate the regeneration and distribution of American chestnut sprouts in recently burned areas of a mountainous landscape in the Ridge and Valley province of the central Appalachian Mountains in Virginia.

Transects divided into sections were selected in prescribed burn units and areas of wildfire to sample for chestnut response to fire. Observed chestnuts in sections were tallied, with the first in sight measured for additional response variables to gauge vitality: live height, number of live stems, blight infection, total stem diameter, average stem diameter, and shoot-to-root ratio. Characteristics of the fire regime and terrain (environmental variables) were then related to these response variables to determine how chestnut sprouts respond to fire and topography: burned/unburned, canopy cover proportion, number of burns, time since last burn, mean time between successive burns, Heat Load Index, Topographic Wetness Index, and Topographic Position Index. Response variables were averaged by environmental categories or correlated directly to environmental observational pairs. Various statistical tests were used for each comparison between response variable vs. environmental variable depending on the nature of the data involved.

The results of this study suggest a complex pattern of American chestnut sprout regeneration in response to fire, with some response variables more or less important in explaining the effect of each fire regime environmental variable. Among the response variables that appear to be positively related to chestnut vitality, there was no indication that increasing fire severity, occurrence, and/or frequency was a detriment to chestnut vitality. Conversely, there was no indication that increasing fire severity, occurrence, and/or frequency reduced the prevalence of blight infection. There were few significant relationships between chestnut vitality and the DEM-derived GIS terrain variables, suggesting that chestnut is well adapted to a variety of slope positions and environmental conditions. Ultimately, American chestnut vitality in early stages of growth is strongly controlled by light availability, and fire can be an important component of restoration.

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NOMENCLATURE

USFS	United States Forest Service
FFS	Fire and Fire Surrogate project
GWJeff NF	George Washington and Jefferson National Forests
SO	Supervisor's Office
TNC	The Nature Conservancy
NPS	National Park Service
TACF	The American Chestnut Foundation
BC_3F_3	Third backcross-bred generation of blight-resistant chestnut
ACCF	American Chestnut Cooperators' Foundation
NOAA	National Oceanic and Atmospheric Administration
NCEI	National Centers for Environmental Information
GHCN	Global Historical Climatology Network
DRC	Diameter at root collar
NDVI	Normalized difference vegetation index
USGS	United States Geological Survey
3DEP	3D Elevation Program
TNM	The National Map
DEM	Digital elevation model
GIS	Geographic information system(s)

HLI	Heat Load Index
TWI	Topographic Wetness Index
TPI	Topographic Position Index

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1. INTRODUCTION

Ever since the demise of the American chestnut, continued efforts have been made to develop chestnut blight resistance and restore the species to its former dominance of the forests of eastern North America. Once blight-resistant chestnuts are ready for large scale reintroduction, however, what are the optimal management strategies and habitat conditions to ensure their success? How does disturbance play a role in creating conditions conducive to chestnut growth and survival? While much work has focused on cultivating blight resistance, our lack of knowledge of fundamental chestnut ecology still prevents us from being effective stewards of this magnificent tree. A landscape-scale approach that relates chestnut vitality to the diverse patchwork of disturbance regimes, environmental conditions, and topography throughout its range is needed within the broader goal of restoration.

1.1 History and Significance of American Chestnut

American chestnut (*Castanea dentata* (Marsh.) Borkh.) was once dominant throughout the hardwood forests of eastern North America (Braun, 1950; Delcourt and Delcourt, 1983), comprising up to half of the canopy trees and the majority of biomass in parts of its native range (Stephenson, 1986; Russell, 1987; Burnham, 1988; Foster *et al.*, 2002; Jacobs *et al.*, 2013). The “Redwood of the East” was found from the Coastal Plain of Mississippi to the coasts of Maine and from the interior forests of Indiana to New

York City, encompassing an area of over 800,000 km^2 (Saucier, 1973). Providing a reliable seed crop and high quality timber, the American chestnut was an important foundation tree species, unrivaled in its ecological influence and economic value (Paillet, 1982; Delcourt and Delcourt, 1998; Wallace *et al.*, 2001; Ellison *et al.*, 2005; Dalgleish and Swihart, 2012).

The American chestnut was perhaps best known for its abundant production of sweet-tasting chestnuts, consumed by wildlife, used to fatten livestock, and a commodity for humans (Frothingham, 1912; Zeigler, 1920; Hawley and Hawes, 1925; Hepting, 1974). So flavorful was its nut that the species was often called "sweet chestnut" (Van Fleet, 1914). Chestnuts were a major food source for forest wildlife, up to 6,000 of which could be produced by a single mature tree (Paillet and Rutter, 1989) and providing a more reliable mast than oaks and hickories every year due to its late flowering (Diamond *et al.*, 2000; Dalgleish and Swihart, 2012; Wang *et al.*, 2013). These prolific nuts were harvested by Native Americans and settlers to be eaten (Clapper and Gravatt, 1943; Youngs, 2000), provided a substantial source of income for many living in the Appalachians (Zon, 1904), and became profitable to be sold in major cities at the turn of the twentieth century (Wang *et al.*, 2013). American chestnut, despite only contributing about 1 percent of the United States' hardwood lumber supply at the height of its production (Youngs, 2000), still proved to have an outsized influence on local economies, particularly in the heart of its range where it was the most dominant: the Appalachian Mountains (Buttrick, 1925; Hepting, 1974).

Chestnut was integral to the pre-industrial way of life in the upland American South. American chestnut could grow up to 5 feet in diameter and 120 feet in height (Buttrick, 1925), estimated to comprise 15 billion board feet (25%) of the timber volume in the southern Appalachian region (Saucier, 1973). A versatile, straight-form, fast-growing, and rot-resistant product, chestnut lumber was commonly crafted for a variety of uses in the Appalachians and beyond as walls, roofs, fence posts, rails, poles, paneling, trim, tables, chairs, cribs, coffins, firewood, and charcoal (Emerson, 1846; Ashe, 1911; Hawley and Hawes, 1912; Detwiler, 1915; Buttrick, 1925; Brown and Panshin, 1940; Hepting, 1974). Additionally, tannins extracted from chestnut could be used for tanning leather and proved vital to its manufacturing (Ashe, 1911; Anagnostakis, 1987; Youngs, 2000). American chestnut was arguably the most valuable single tree species of its time in the Appalachians, with far-reaching benefits to animals and humans alike.

In the first decade of the twentieth century, the stately, shady chestnut trees of the Bronx Zoo were found to be dying (Merkel, 1906). A deadly airborne canker fungus accidentally introduced likely from China or Japan had been discovered that girdled and killed the beloved American chestnut (Merkel, 1906; Anagnostakis, 1987). This chestnut blight (*Cryphonectria parasitica* (Murr.) Barr.), spread by wind, the feet of birds, insects, and mammals, and the movement of humans, proceeded to infect and destroy chestnut through common bark wounds caused by insects, birds, and natural cracks (Hepting, 1974; Burnham, 1988; Anagnostakis, 2001b). Root rot caused by another exotic pathogen, ink disease (*Phytophthora cinnamomi* (Rands)), also killed chestnuts primarily in lower, warmer, and wetter areas in the southern portion of its range (Crandall *et al.*, 1945; Woods, 1953; Rhoades *et al.*, 2003). With little to no natural resistance to these diseases, by mid-century the American chestnut had been functionally extirpated as a canopy tree throughout its range and relegated to scattered understory sprouts (Whittaker, 1956; Stephenson *et al.*, 1991; Griffin, 2000; Anagnostakis, 2001b, a, 2012; Dalgleish *et al.*, 2016).

The demise of the mighty American chestnut is regarded as the worst ecological disaster in post-glacial eastern North American history (Jacobs, 2007), leading to a vast restructuring of the forests where it once dominated (Stephenson, 1986; Parker *et al.*, 1993; Vandermast and Van Lear, 2002). American chestnut was regarded as a foundation species for its influence on forest community dynamics and ecosystem processes, particularly with regards to the resource provided by its seed and its role in nutrient cycling (Ellison *et al.*, 2005; Dalgleish and Swihart, 2012). Its loss greatly altered the availability and reliability of mast for wildlife throughout its range, likely contributing to the more unstable community dynamics of eastern North American forests today (Kelly *et al.*, 2008; Dalgleish and Swihart, 2012). Variability in the rodent population based on the availability of mast, for example, can influence the prevalence of gypsy moth outbreaks and risk of Lyme disease to humans (Jones *et al.*, 1998; Ostfeld *et al.*, 2006). The eastern deciduous forest is now dominated by oaks and hickories that we are familiar with today (Stephenson, 1986; Paillet, 2002), with chestnut found in the understory recurrently sprouting from existing root systems, succumbing to blight before reaching sexual maturity, dying back, and re-sprouting over the course of 10-40 years

(Paillet, 1984; Russell, 1987; Griffin, 1989; Stephenson *et al.*, 1991; Parker *et al.*, 1993; Anagnostakis, 2001b, a; Paillet, 2002). This cycle of sprout dieback and regrowth will continue indefinitely until effective resistance to chestnut blight can be developed and implemented across the landscape.

Continued efforts have been made by a variety of agencies and organizations to combat chestnut blight ever since its discovery in 1904 (Jacobs *et al.*, 2013). Early attempts to prevent the spread of chestnut blight through quarantine and tree removal were largely ineffective (Hepting, 1974; Anagnostakis, 2012), and breeding programs in the decades following by the U.S. Department of Agriculture (USDA) and later Connecticut Agricultural Experiment Station (CAES) failed to produce a blight-resistant hybrid (Beattie and Diller, 1954; Berry, 1978; Burnham *et al.*, 1986). More recent work, however, has shown promise in developing effective resistance to the blight. These efforts have progressed in parallel through biological control, breeding, and genetic engineering, with a variety of strategies in place for the greatest chance of successful restoration of American chestnut (Jacobs *et al.*, 2013; Wang *et al.*, 2013).

Hypovirulence, a virus infection of chestnut blight (Milgroom and Cortesi, 2004), was discovered in blight cankers on chestnut trees outside of its native range in 1976 (Jaynes and Elliston, 1980). Research showed that this infection could be effective in reducing the lethal effects of chestnut blight (Griffin *et al.*, 1983; Anagnostakis, 2001a), raising hopes for its use in blight control (Jaynes and Elliston, 1980). Unfortunately, however, these hypovirus strains failed to disperse between trees and blight cankers in experimental trials, rendering them ineffective to control chestnut blight at a meaningful scale (Griffin, 2000; Milgroom and Cortesi, 2004). Biological control through hypovirulence may still be used in chestnut restoration as a complement to other strategies (Anagnostakis, 1987; Griffin, 2000), but is not a practical solution itself.

Developments in the last couple of decades have made blight control more feasible than ever before through the inter-species breeding efforts led by The American Chestnut Foundation (TACF). While the American Chestnut Cooperators Foundation (ACCF) contributes to breeding efforts as well by propagating the low natural intra-species blight resistance of native American chestnut (Jacobs *et al.*, 2013), the most promising and prominent breeding program is conducted by TACF (Anagnostakis, 2001b; Hebard, 2005; Wang *et al.*, 2013). Since 1983, TACF has been successively backcross breeding American chestnut with the blight-resistant Chinese chestnut (*Castanea mollissima*) to create blight-resistant chestnut hybrids that still maintain the desired morphological traits (growth form, leaf characteristics, etc.) of pure American chestnut (Burnham *et al.*, 1986; Burnham, 1988; Diskin *et al.*, 2006; Anagnostakis, 2012). TACF has bred multiple generations of chestnut hybrids, leading to the most advanced blight-resistant hybrid to date, BC_3F_3, 15/16th pure American chestnut (Wang *et al.*, 2013; Clark *et al.*, 2014a). Initial testing of restoration BC_3F_3 trees has indicated they largely maintain the desired traits of American chestnut (Diskin *et al.*, 2006; Clark *et al.*, 2011), but research continues today to determine whether this hybrid will remain sufficiently resistant to blight and ecologically similar to pure American chestnut as it ages both in the orchard and in the wild (Hebard, 2005; Clark *et al.*, 2011; Clark *et al.*, 2012c; Wang *et al.*, 2013; Clark *et al.*, 2016).

Another promising development in blight control efforts has been the genetic engineering work led by the State University of New York College of Environmental Science and Forestry at Syracuse (SUNY-ESF). Multiple genotypes of American chestnut have been transgenically engineered for blight resistance using a wheat gene, which produces an enzyme that prevents chestnut blight from developing its lethal cankers (Merkle *et al.*, 2007; Pijut *et al.*, 2011; Newhouse *et al.*, 2014). Several challenges exist, however, to this approach that remain to be solved regardless of its efficacy (Strauss *et al.*, 2009; Jacobs *et al.*, 2013). It is unclear whether the public will accept a widely spread genetically modified organism (GMO) on public lands as the solution to restoring American chestnut (Jacobs, 2007; Merkle *et al.*, 2007), and this genetically modified chestnut has yet to be approved by the U.S. Food and Drug Administration (FDA), Environmental Protection Agency (EPA), and other regulatory agencies (Jacobs *et al.*, 2013). Despite the science and technology being adequate, resolving the social and ethical questions that would arise and developing the institutional capacity to cost effectively mass produce and distribute backcross-bred and/or genetically engineered chestnuts remain significant obstacles to reintroduction.

Large-scale restoration of American chestnut is on the horizon in the twenty-first century, with new genetic discoveries and technologies enabling the integration and refinement of blight control approaches (Kubisiak *et al.*, 1997; Wheeler and Sederoff, 2009; Jacobs *et al.*, 2013). In addition, silvical studies of the response of planted seedlings and extant sprouts to various environmental factors are emerging, providing valuable information that can help guide restoration efforts and maintain genetic diversity (McCament and McCarthy, 2005; Clark *et al.*, 2010; Clark *et al.*, 2011; Clark *et al.*, 2012a; Clark *et al.*, 2012b; Clark *et al.*, 2012c; Fields-Johnson *et al.*, 2012; Griscom and Griscom, 2012; Clark *et al.*, 2016). However, despite the focused and sustained efforts to make chestnut resistant to blight, research to determine optimal habitat conditions and management practices for reintroduction of blight-resistant stock is still lacking (Jacobs *et al.*, 2013). The extirpation of American chestnut as a mature canopy tree prior to modern forest ecology and environmental science has left many questions of the species' niche unanswered (Griffin, 2000; Paillet, 2002; Jacobs, 2007; Clark *et al.*, 2014a). Much of what we do know of chestnut ecology comes from historical, qualitative descriptions or observations of planted populations outside the native range of chestnut that were affected later or less by chestnut blight (Paillet, 1982, 1984; Paillet and Rutter, 1989). The long-term, strategic forest management of public lands with limited resources to promote the sustained success of blight-resistant chestnut must be informed by a more extensive evaluation of how chestnut responds to pertinent environmental controls.

1.2 Role of Fire

Fire, both natural and anthropogenic in origin, has historically been a key component of forest ecosystems in eastern North America. Frequent fire favors species with life history traits suited to periodic disturbance, including oaks with thick bark and vigorous sprouting ability, and pines with serotinous cones requiring heat to release seed (Abrams, 1992; Williams, 1998; Nowacki and Abrams, 2008). These species benefit from or require the reduced competition from more mesophytic, fire-intolerant species (Glitzenstein *et al.*, 2003; Nowacki and Abrams, 2008). Studies of fire history have shown that frequent burning occurred prior to, during, and after Euro-American settlement throughout much of the Appalachians until the early-mid twentieth century (Brose *et al.*, 2001; Lafon *et al.*, 2017). Native Americans used fire as a method of controlling plants and animal habitat, creating open canopy forests with a diverse understory of grasses and forbs (Black *et al.*, 2006; Abrams and Nowacki, 2008). These and subsequent disturbances promoted fire-adapted oak and pine species that dominate many of the Appalachian forests we are familiar with today (Abrams, 1992; Delcourt and Delcourt, 1998; Lafon *et al.*, 2017).

Frequent burning continued under European settlement through the nineteenth century as forests were cleared for agriculture and to feed the ever-increasing industrial demand for forest resources (Pyne, 1982; Williams, 1989; Fowler and Konopik, 2007). In the rural upland South, extensive burning was culturally engrained and often essential to survival in the frontier economy (Pyne, 1982; Lafon *et al.*, 2017). As the wave of industrial logging and railroads quickly spread southward throughout the central and southern Appalachians in the late nineteenth and early twentieth centuries (Williams, 1989), burning was frequent and widespread as leftover debris from logging operations ignited, often causing destructive wildfires (Allen, 1935; Clarkson, 1964; Pyle and Schafale, 1988; Lafon, 2010). By the Great Depression, nearly everywhere throughout the region had been logged, scarring even the most remote and inaccessible landscapes (Pyne, 1982; Williams, 1989; Dombeck *et al.*, 2004).

With the devastation wrought by industrial logging and associated fires in the Appalachians and beyond, land owners and the general public became increasingly concerned with the loss of forest resources, declining watershed function, and threats to forest regeneration (Dellasala *et al.*, 2004; Dombeck *et al.*, 2004). As fire was increasingly viewed as a threat to society, officials initiated aggressive fire suppression policies to preserve forest lands across the United States (Pyne, 1982; Sarvis, 1993). With growing land ownership and resources, fire suppression became the primary goal of the U.S. Forest Service, with officials subscribing to an “all fires out by 10 am” policy (Pyne, 1982; Sarvis, 1993; Pyne, 2001; Dombeck *et al.*, 2004). These ongoing efforts were largely successful, restoring formerly burned-over forests and changing public attitudes toward fire, as exemplified by the success of the Smokey the Bear public awareness campaign (Williams, 1989; Dombeck *et al.*, 2004; Lafon *et al.*, 2017). For the majority of the twentieth century and largely still today, fire suppression is standard policy for all fires across all levels of government, supported by the vast majority of the general public.

The widespread implementation of fire suppression policies in the early-mid twentieth century marked a departure from previous patterns of fire and has resulted in changes to forests adapted to frequent disturbance. Many xerophytic oak- and pine-dominated forests transitioned from open woodlands to closed canopies composed of more fire-intolerant, mesophytic species such as maples, beeches, and hemlocks (Cho and Boerner, 1991; Abrams *et al.*, 1995; Abrams, 1998; Cowell, 1998). This shift towards more shade-tolerant trees and closed canopy forests increased the amount of woody plants while reducing the amount of understory vegetation after canopy closure (Harrod and White, 1999; Nowacki and Abrams, 2008; Considine *et al.*, 2013). The fire-oak hypothesis has emerged, suggesting that oaks are superiorly fire-adapted, fire is essential to many oak ecosystems, and that more fire is often needed to regenerate oak stands (Abrams, 1992; Brose *et al.*, 2001; Nowacki and Abrams, 2008; McEwan *et al.*, 2011; Arthur *et al.*, 2012). Recognizing the importance of fire to and deteriorating conditions for fire-adapted, shade-intolerant species, many scientists and land managers have increasingly promoted and implemented the use of prescribed fire across the landscape in recent decades (Brose and Van Lear, 1998; Dey and Hartman, 2005; Dey and Fan, 2009; Arthur *et al.*, 2012; Schwartz *et al.*, 2016).

With American chestnut set to be restored in largely oak-dominated forests in this context and with chestnut's associations with oak, the fire-oak hypothesis serves as a useful guide for evaluating how chestnut responds to fire. The relationship between chestnut and fire remains poorly understood, with the effects of removing fire from chestnut-dominated forests being eclipsed by the devastation of the chestnut blight. While it is clear that frequent and sometimes severe fire benefits oak forests, it is unclear whether chestnut-restored forests would similarly benefit from the same disturbance regime. Understanding the dynamics of chestnut's response to fire is essential to use fire effectively as a management tool in chestnut restoration. The importance of such research is underscored as prescribed fire is increasingly being used to reduce stand densities, improve wildlife habitat, and promote regeneration of oak and pine throughout the native range of chestnut. The increasing prevalence of wildfires in the Appalachians fueled by a warming climate further highlights the need for a thorough understanding of how fire influences the foundation species to be restored throughout the region so as to more appropriately manage wildfire for the benefit of chestnut-dominated forests and vice versa.

1.3 What We Know of Chestnut Disturbance Ecology

Historical observations and current insights suggest that chestnut was associated with a variety of forest types and is adapted to a broad range of environmental conditions throughout its range (Hawley and Hawes, 1912; Russell, 1987; Jacobs *et al.*, 2013). Mature chestnut could be found in more mesic lower-mid slopes and valleys (Mattoon, 1909; Ashe, 1911; Crandall *et al.*, 1945) as well as more xeric mid-upper slopes and ridges where it was most dominant at mid elevations (Ashe, 1911; Whittaker, 1956; Russell, 1987; Stephenson *et al.*, 1991). However, with chestnut more susceptible to ink disease in moister and more sheltered environments downslope, live chestnut sprouts are most commonly found today in the drier and more exposed portions of its native range associated with forests dominated by oak (Stephenson *et al.*, 1991; Anagnostakis, 2001b; Nowacki and Abrams, 2008; Anagnostakis, 2012), to which chestnut is closely taxonomically related (Kremer *et al.*, 2007). Oaks' adaptations to disturbance that increase its competitive advantage have been extensively studied and well documented in upland forests (Nowacki and Abrams, 2008; Johnson *et al.*, 2009; Brose *et al.*, 2013), suggesting that chestnut may share similar adaptations (Belair, 2014).

To evaluate the oak-chestnut association, recent work has begun to examine the similarities and differences between their respective disturbance ecologies, with indications that chestnut shares some comparable life-history characteristics to oak and is likely adapted to disturbance (Russell, 1987; Foster *et al.*, 2002; Wang *et al.*, 2013). Historical accounts, anecdotal evidence, and studies of extant populations all report that American chestnut sprouts dramatically in response to increased light following disturbance, growing faster than surrounding species (Mattoon, 1909; Hawley and Hawes, 1912; Frothingham, 1924; Paillet, 1984; Jacobs and Severeid, 2004; McEwan *et al.*, 2006), and becoming less competitive in the presence of competing vegetation (Griffin *et al.*, 1991). One study found similar rates of mortality caused by fire between oak and chestnut species prior to the effects of chestnut blight becoming severe (McCarthy and Sims, 1935). However, despite the evidence suggesting chestnut's similar response to disturbance, the species also appears to harbor unique traits compared to oak that distinguish its disturbance ecology. First, chestnut bark is not as thick as oaks', which could have a negative effect on survival following establishment (Hawley and Hawes, 1912; Russell, 1987). Additionally, while some historical descriptions suggest chestnut was relatively shade intolerant (Frothingham, 1912; Hawley and Hawes, 1925), recent research and the persistence of understory sprouts indicate that chestnut can tolerate low-light environments, more characteristic of shade tolerant, late-successional species (Paillet, 1982, 2002; Wang *et al.*, 2006). Under the low light of closed canopies, understory chestnut sprouts can adapt by growing out like a shrub more than up like a tree to maximize surface area used for photosynthesis (Paillet, 1984, 2002). Chestnut's shade tolerance characteristics remain under debate, however, with field and greenhouse studies providing inconclusive evidence as to the most appropriate classification (Wang *et al.*, 2006; Joesting *et al.*, 2007, 2009). What remains clear of chestnut growth strategy is that sprouts can persist and adapt under closed canopies (Paillet, 1982; King, 2003; McCament and McCarthy, 2005; Joesting *et al.*, 2009), yet grow prodigiously to exploit canopy gaps similar to pioneer species (Boring *et al.*, 1981; Paillet, 1982, 1984; Griffin, 1989; Paillet and Rutter, 1989; Billo, 1998; Paillet, 2002; Clark *et al.*, 2010; Clark *et al.*, 2012a).

Further investigation is needed to differentiate the presumed similarities of chestnut to oak from empirical and descriptive evidence specific to American chestnut. The species' preferential allocation of resources may be the key to understanding why chestnut responds to environmental factors the ways it does. Existing root system development and seedling size appear to be controlling factors in the ability for wild sprouts and planted seedlings to compete when light is limited (Wang *et al.*, 2013; Clark *et al.*, 2014b). Field research has shown that blight is more prevalent on chestnuts under disturbed, open canopies than shaded, closed canopies, whereas among infected trees surviving, removal of competition is beneficial to survival (Griffin and Elkins, 1986; Griffin, 1989; Reynolds and Burke, 2011; Griscom and Griscom, 2012; Wang *et al.*, 2013). These effects on chestnut health could be partially explained by preferential growth response, as chestnut has been shown to allocate fewer resources to aboveground stem growth (i.e. total biomass) in high light environments (Wang *et al.*, 2006; Anagnostakis, 2007). Chestnut's overall higher shoot-to-root ratio relative to oaks in different light environments, however, suggests that the species' vigorous sprouting response to light may deplete the nutrient reserves needed to repeatedly re-sprout following frequent disturbance (Latham, 1992; Belair, 2014).

The body of literature reviewed here suggests that active forest management will be required to maintain the viability of blight-resistant chestnut in early stages of development as part of reintroduction efforts (McCament and McCarthy, 2005). It remains to be seen, however, if chestnut responds similarly to fire as oak or is marked by traits conducive to a different fire regime. While early reports suggested that chestnut is harmed by fire (Hough, 1878; Baker, 1884; Buttrick and Holmes, 1913; Hawley and Hawes, 1925; Russell, 1987), some sediment records indicate an increase in chestnut pollen following fire (Paillet, 2002). Only since 2005 has the impact of fire on chestnut regeneration been empirically evaluated, with largely inconclusive results to date (McCament and McCarthy, 2005; Belair, 2014; Clark *et al.*, 2014b; Jarrett *et al.*, 2016). These studies (two of which are published) have provided the first modern insights into how chestnut sprouts respond to fire and how fire might be implemented as part of American chestnut restoration.

McCament and McCarthy (2005) evaluated the response of planted pure American chestnut to multiple prescriptions (including fire) at mixed-oak forest sites representing the Central Hardwoods region as part of the pre-existing silvicultural experiments of the Forest Service Fire and Fire Surrogate (FFS) project in southeastern

Ohio. Growth parameters including total biomass, biomass of individual tree components, basal diameter, stem height, root length, leaf area, and specific leaf area were measured and survival monitored over the course of two growing seasons following the recent treatments of (1) prescribed fire, (2) thinning, and (3) a combination of the two. While survival did not significantly vary among treatments, the planted seedlings' growth response was positively correlated with the increasing canopy light caused by each treatment, with thinning being more effective than burning at opening the canopy. Light from removing trees in the canopy above was shown to initiate a stronger growth response than removal of competing vegetation below from burning. It should be noted that the focus of this study was on the differences between thinning and burning treatments, light environments did not significantly change following planting (i.e. no burning or thinning occurred after planting), burn severity was uniform and low, and no extant wild chestnut sprouts in the treatment blocks were involved. However, the greatest seedling growth response observed in this study was in a treatment including fire, informing the authors' recommendation of prescribed fire as an appropriate tool as part of creating high-light environments for optimizing chestnut growth.

Since the 2005 FFS study, fire-chestnut research has shifted towards evaluating the effects of fire following planting and on extant sprouts, allowing for more informative results (Belair, 2014; Clark *et al.*, 2014b; Jarrett *et al.*, 2016). Clark *et al.* (2014b) monitored growth and survival of planted pure American chestnut on the Cumberland Plateau of Tennessee, but saw different results than did McCament and McCarthy (2005). The authors hypothesized that high frequency and/or high intensity burning could be detrimental to chestnut, but that low frequency, low intensity surface fires may be beneficial. A broader suite of treatments was used in this study, including thinning, clearcutting, and burning both before and after planting in a variety of combinations. Complex combinations of measured explanatory variables were used to model the primary responses of survival, height, and deer browse, of which the former two are of most relevance here. The results of this study indicated that seedling survival was not hindered by low light (consistent with previous studies demonstrating chestnut's shade tolerance), but that survival was significantly positively related to canopy cover, though with tree height at planting decreasing this effect. Fire was shown to have a non-significant, negligible effect on survival following regeneration. In regards to seedling growth as measured by height, fire had a non-significant, negligible effect when prescribed both before and after planting, while canopy cover at planting was significantly positively related. The positive relationship of canopy cover to survival may be explained by increasing competition (Griscom and Griscom, 2012), but is surprising considering modern studies have shown chestnut vitality to benefit from open canopies (Latham, 1992; Wang *et al.*, 2006; Clark *et al.*, 2012a). However, even more surprising in this study is the positive relationship of canopy cover with height, alone in contradicting a large body of knowledge previously reviewed of chestnut's prolific sprouting ability following canopy opening. The finding that prescribed fire did not have a significant effect on seedling height is the first empirical evidence that suggests chestnut may be vulnerable to fire, i.e. fire many interfere with chestnut vitality.

Unfortunately, however, the presence of a host of major confounding variables, acknowledged by the authors, call into question the utility of the results of this study.

The limitations of the Clark *et al.* (2014b) study are vitally important to recognize when interpreting its results and the authors' recommendations based on them. The authors advise against using prescribed burning as a management tool in areas containing chestnut based on their findings that fire had either a neutral or negative effect on chestnut growth and survival, citing the current difficulty and expense of acquiring planting stock. However, this suggestion is informed from results affected by a low sample size, lack of burn replication, unplanned human hand-thinning of vegetation, tornado, severe drought, and other substantial deviations from the original experimental design resulting from these confounding factors. Acknowledging the confounding factors in their study, Clark *et al.* (2014b) state that "Future research with more replication is needed to confirm or reject predictions made in this study, particularly regarding seedling response to various environmental conditions and silvicultural treatments, including prescribed burning." Much still remains to be known about chestnut fire ecology.

Forthcoming results (unpublished) from another study since 2005 provide empirical evidence of planted chestnuts' response to low-intensity surface fire in the early stages of succession in a more controlled setting than that of Clark *et al.* (2014b). Belair (2014) conducted a fire simulation study in the Central Till Plain region of Indiana (outside chestnut's native range) on planted seedlings of pure American and hybrid chestnut as well as red oak. The effects of initial seedling size, light environment, and various physiological ecological characteristics on seedling height, diameter, and survival were evaluated after one growing season following aboveground stem mortality (topkill) induced using burn chambers (i.e. simulated prescribed fire), with potential effects of topography minimized. It was hypothesized that seedling height and diameter would be positively correlated with planted size and amount of light, but that planted size would have a greater influence on sprout regrowth than light environment (canopy openness). It was further hypothesized that red oak regrowth would be greater than that of chestnuts based on its larger root-to-shoot ratio. The results of this study indicate that despite chestnut seedlings' early and vigorous re-sprouting response following topkill, height and diameter of red oak seedlings were greater than that of chestnut, and that initial seedling size had a greater influence on sprout height and diameter than did canopy openness. The results further indicated that chestnut was more vulnerable to fire than oak based on its sprouts' point of attachment near ground level compared to red oak's further below ground, as well as its lower nutrient reserves and smaller root system. The author recommends that prescribed fire should be more delayed with chestnut than oak, as his evidence appears to suggest that chestnut is more vulnerable to fire and requires a longer fire-free period to establish than oak.

The specific site conditions for where the seedlings were planted in the Belair (2014) study are particularly important to consider in evaluating its results and interpretations. The lower total growth of chestnut compared to red oak may be explained by the light environment, unaltered following the simulated fire. The canopy cover was high to moderate at each stand in the study (approximately 83% at two of the stands and 44% at the third) during the seedlings' regrowth, with red oak having a statistically significantly greater amount of light available than chestnut (an average of approximately 63% canopy cover for red oak versus 81% for chestnut). While acknowledging that canopy openness is an important component to chestnut seedling success, the author did not control for this factor in his study. Consequently, chestnut's observed adaptations to fire may have been effected by the stand light environment in this study. Chestnut produced more individual sprouts (i.e stems) than red oak in the month immediately following burning, though with no difference at the end of the first growing season (end of the study). While compared growth rates to red oak following fire did not solely determine the recommendation of the author for more limited application of fire, the observed growth of multiple sprouts rather than singular investment in one sprout may have been a function of chestnut's known adaptation to be able to persist in low light under closed canopies. The overall response of chestnut to fire must be similarly evaluated in different (and high) light environments, particularly considering chestnut's known strong response to increasing light.

The Belair (2014) study accordingly does not offer satisfactory insight into chestnut's resiliency and response to fire at later stages of succession and in varying environmental conditions that differentiate it from oak fire ecology. The author acknowledges this limitation by concluding "Future studies should focus on the longer-term effects of seedling size, canopy openness and vigor on sprout's growth rate and probability of canopy recruitment following topkill." The author's study does, however, provide a detailed, fine-scale evaluation of the differences between chestnut and oak regrowth immediately following fire, and further explores the effects of competition at varying levels of the forest that may be critical in determining optimal reintroduction habitat and management at varying stages of succession. In addition, the latest known study of the effects of fire on chestnut (results forthcoming) offers the first insights of extant sprout regeneration in response to fire, based on measurements made of the same trees both before and after burning in Shenandoah National Park using a rigorous National Park Service (NPS) sampling protocol (Jarrett *et al.*, 2016).

The modern chestnut-fire literature to date (McCament and McCarthy, 2005; Belair, 2014; Clark *et al.*, 2014b; Jarrett *et al.*, 2016), while offering a promising start, still ultimately raises more questions than it answers. Solid evidence still has yet to be presented demonstrating that chestnut is or is not significantly more or less adapted to fire than oak. The methods and experimental design for each study vary significantly and suffer from a lack of replication encompassing a more representative variety of site conditions within the native range of American chestnut. Further, the most reliable results are over the shortest time frames. Broader-scale approaches that relate chestnut vitality to the diverse patchwork of disturbance regimes, environmental conditions, and topography found throughout chestnut's native range are needed. Only through a thorough investigation of both planted and extant chestnut fire ecology and geography can we know how and where to plant and manage blight-resistant chestnut.

1.4 Research Questions and Study Objectives

Does American chestnut sprout regeneration benefit from fire? How does its response to fire vary according to topography? With our understanding of chestnut fire geography incomplete, this study aims to evaluate the regeneration and distribution of American chestnut sprouts in recently burned areas of a heterogeneous, mountainous landscape. More specifically, how does varying fire severity, occurrence, and frequency affect the vitality of extant American chestnut sprouts in the Ridge and Valley province of the central Appalachian Mountains? How does varying incident radiation, topographic moisture, and slope position affect these same sprouts' response? The following objectives are intended to answer these questions:

1. Quantify variations in chestnut vitality as measured by abundance, height, stem count, stem diameter at root collar (DRC), stem mortality, presence of chestnut blight, and shoot-to-root ratio (SRR).
2. Determine chestnut response to fire from Objective 1 by comparing the responses between burned and unburned areas, across varying levels of canopy cover (i.e. as a rough proxy for burn severity), for areas burned different numbers of times, over time since last burn, and with varying time between successive burns.
3. Determine the effect of digital elevation model (DEM)-derived Heat Load Index (HLI), Topographic Wetness Index (TWI), and Topographic Position Index (TPI) on the quantified response of Objective 1.

The following are general hypotheses about the relationship between chestnut vitality response and environmental variables:

1. Increasing fire severity, occurrence, and frequency benefit or are neutral to chestnut sprout vitality as indicated by:
    a. Increased or no change in abundance
    b. Increased or no change in height
    c. Increased or no change in number of stems
    d. Increased or no change in stem diameter
    e. No change in presence of blight
2. Chestnut vitality response to fire will be greatest in areas with the following terrain characteristics:
    a. Mid slopes and upper slopes
    b. Moderate to high incident radiation (heat load)
    c. Low topographic moisture

These objectives and hypotheses allow for a descriptive analysis of American chestnut sprouts at a variety of locations that can be used to inform our understanding of the habitat conditions and disturbance regimes most beneficial to chestnut, and how they compare to those known to most benefit oak species. Results of this study may be applied to maintain genetic diversity of existing chestnut root systems and make recommendations for maximizing success of chestnut reintroduction once proven blight-resistant stock becomes widely available.

2. METHODS

2.1 Study Areas

Study areas were chosen for this project that contained a high concentration of prescribed burn units, areas of wildfire, and observed chestnut sprouts on public and private preserve land in the central Appalachian Mountains. After consulting with personnel of the U.S. Forest Service (USFS) George Washington and Jefferson National Forests (GWJeff NF) Supervisor's Office and The Nature Conservancy (TNC) Allegheny Highlands Program, three study areas were identified that matched these criteria: (1) Fenwick, (2) Warm Springs, and (3) Massanutten (Figure 1). Each study area is located in the Ridge and Valley province of the Appalachian Mountains of central-western Virginia, characterized by distinct seasonality with average temperatures ranging from ~2° C (35.6° F) in winter to ~23° C (73.4° F) in summer at the lower elevations and the majority of precipitation falling in the spring and summer (NCDC, 2012).

The Fenwick study area [37° 36’ N, 80° 3’ W; approximate elevation range 450-975 m (1,500-3,200 ft.)] is located in the northeastern corner of Craig County and neighboring western extent of Botetourt County within the Eastern Divide Ranger District of the Jefferson National Forest (Figure 2). The Warm Springs study area [37° 58’ N, 79° 49’ W; approximate elevation range 580-1280 m (1,900-4,200 ft.)] is located in southern Bath County along Warm Springs Mountain within the Warm Springs Ranger District of the George Washington National Forest and The Nature Conservancy (TNC) Warm Springs Preserve (Figure 3). Warm Springs provided one of the largest and most developed landscape-level prescribed burning initiatives in the region as part of the Central Appalachians Fire Learning Network. The Massanutten study area [38° 36’ N, 78° 38’ W; approximate elevation range 305-855 m (1,000-2,800 ft.)] is located along the western edges of Page County in the Massanutten range within the Lee Ranger District of the George Washington National Forest (Figure 4). All three study areas provided accessible burn units with documented, diverse fire history and encompassed a wide variety of canopy conditions and terrain features of interest for this project.

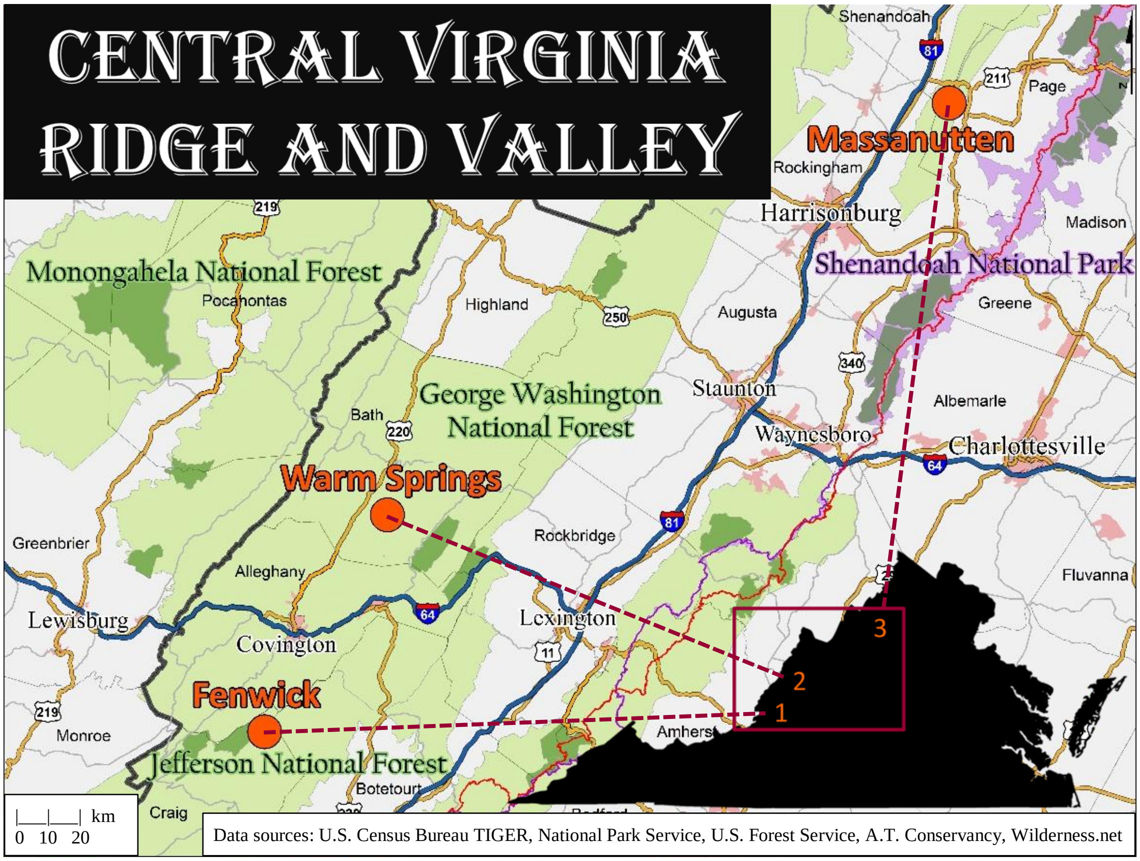

Figure 1. Map of all three study areas in central-western Virginia, (1) Fenwick, (2) Warm Springs, and (3) Massanutten.

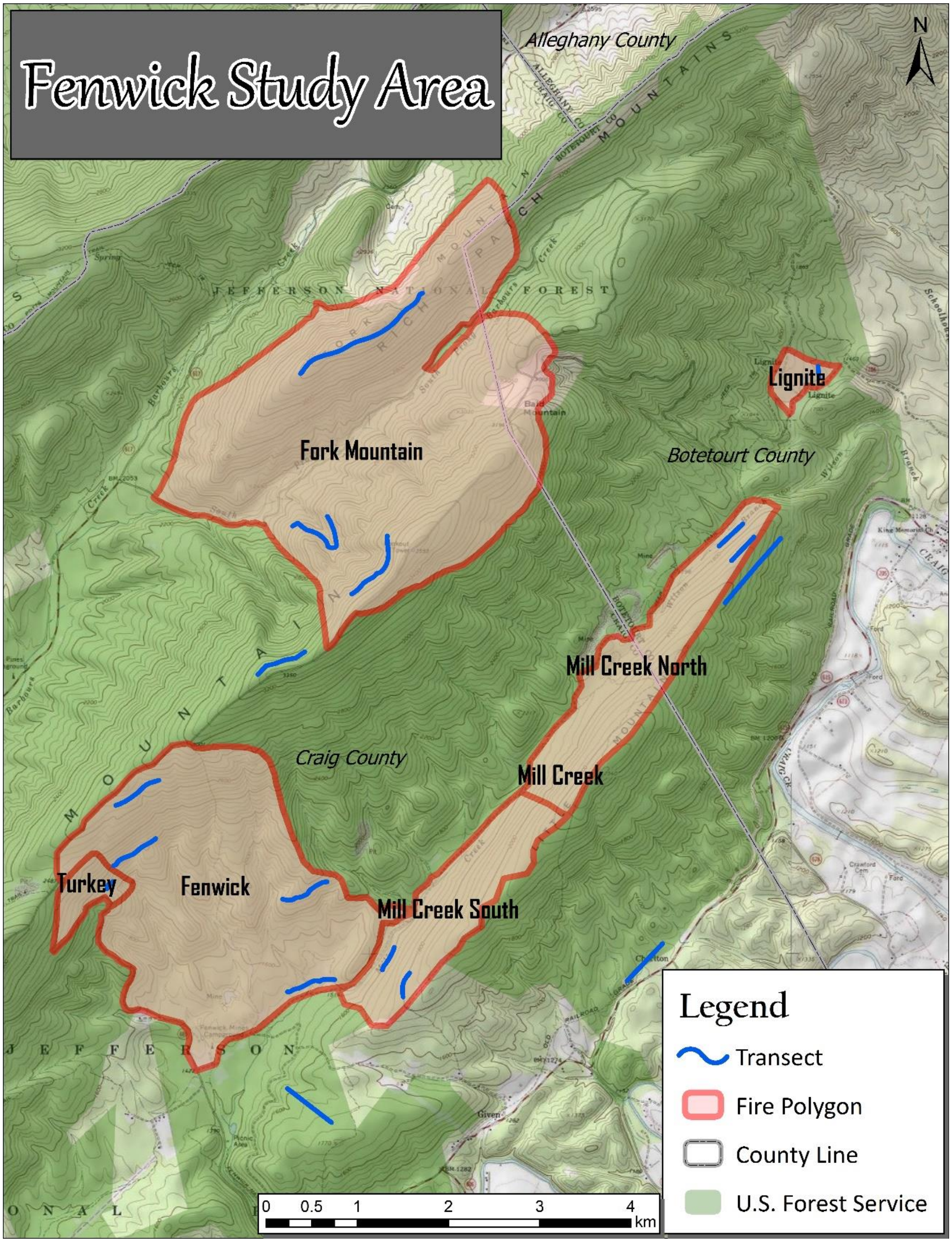

Figure 2. Map of Fenwick study area in central-western Virginia.

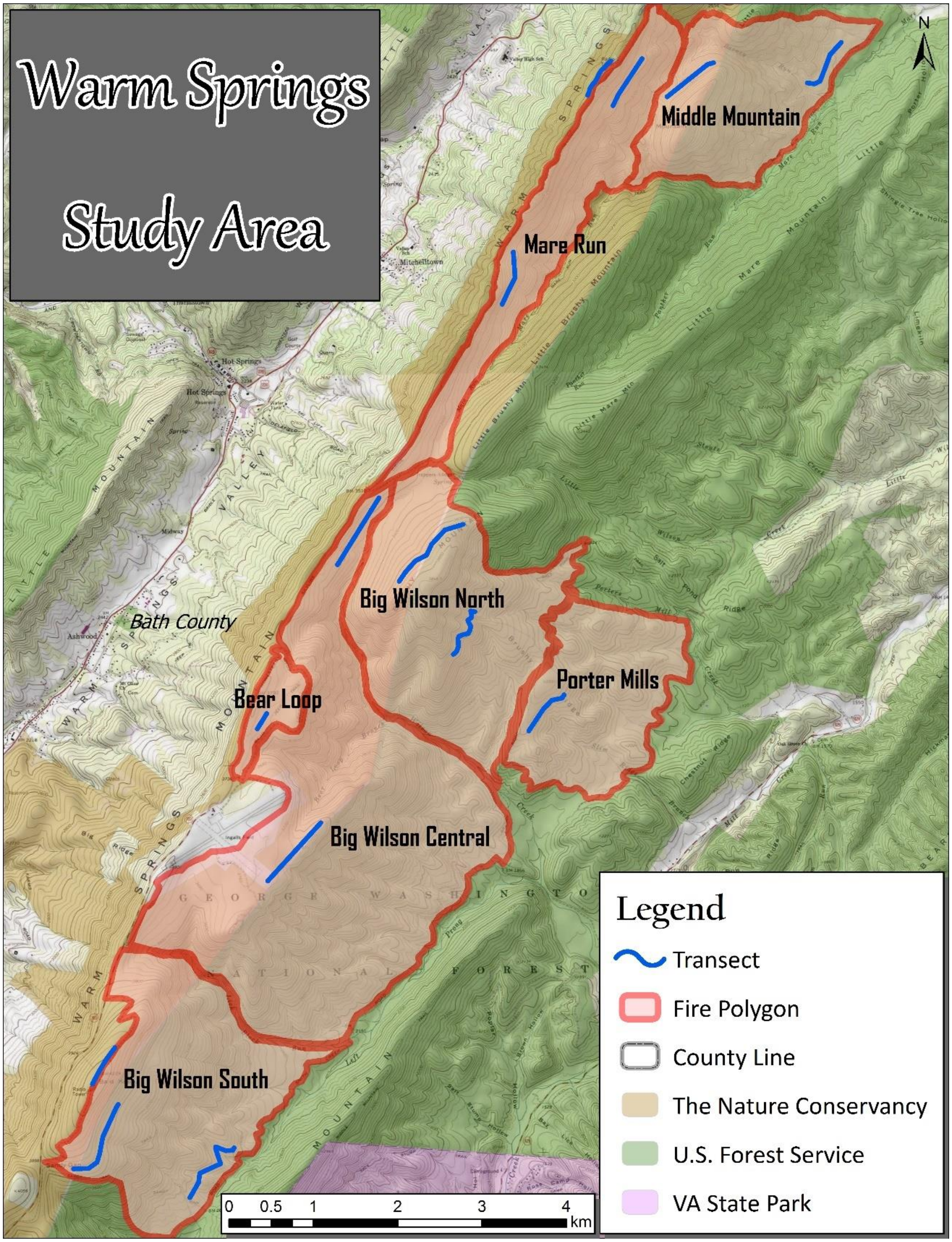

Figure 3. Map of Warm Springs study area in central-western Virginia.

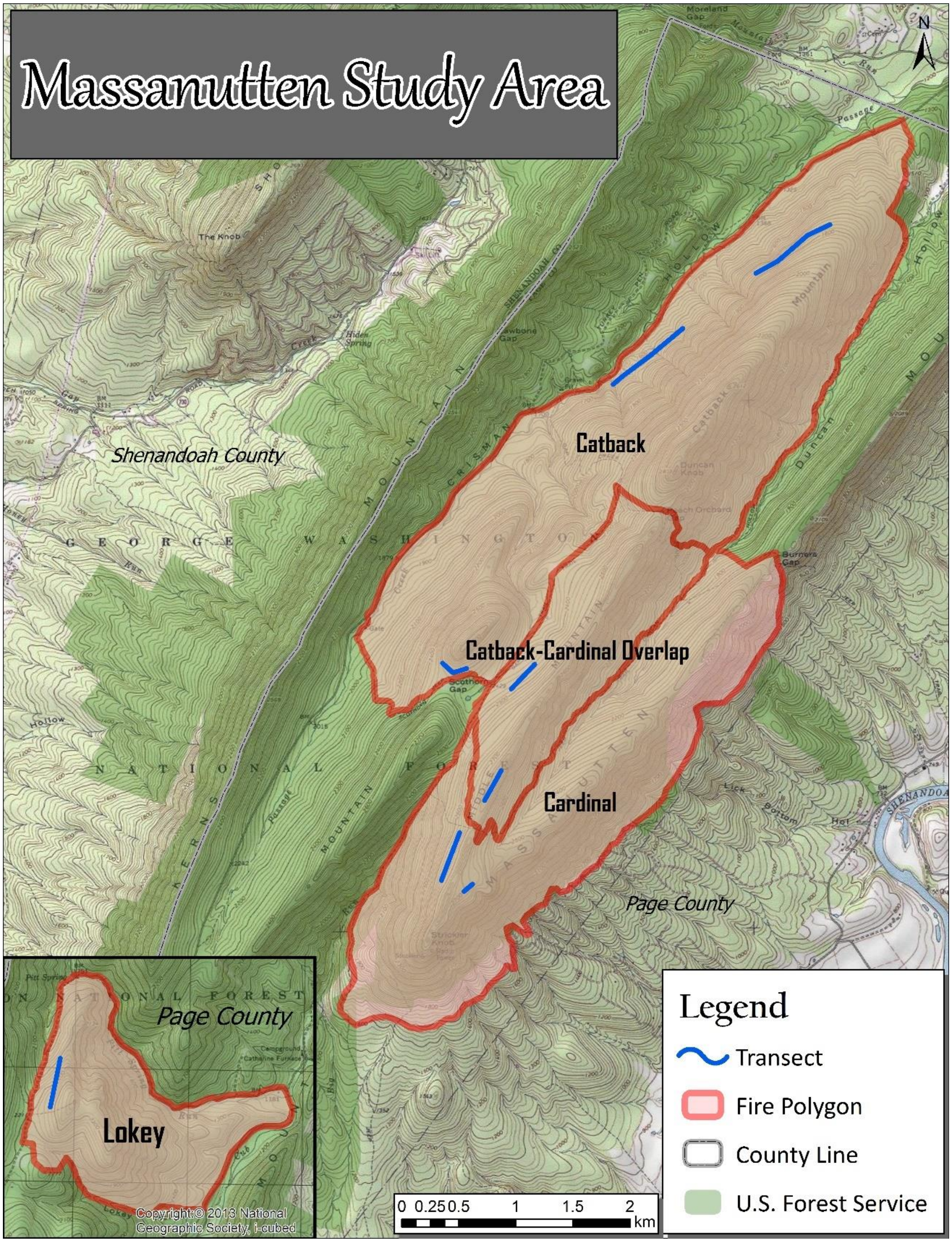

Figure 4. Map of Massanutten study area in central-western Virginia.

2.2 Sampling Design

The locations of prescribed burn units and areas of wildfire were provided as shapefile polygons from the U.S. Forest Service George Washington and Jefferson National Forests (GWJeff NF) Supervisor's Office. These polygons and associated attributes were cross-checked with other data from the Forest Service and The Nature Conservancy (TNC) to ensure their integrity, particularly with respect to burn dates, sizes, and extents. Dozens of fire polygons were selected across all study areas to provide a large sampling base to choose from for conducting fieldwork. Transects were drawn within each fire polygon using ArcMap, proportional in length to the area of the polygon [1.5 m (4.92 ft.) of transect length per 0.40 ha (1 ac) of the polygon]. Additionally, several 500 m (1,640.42 ft.) transects were drawn in unburned areas adjacent to the fire polygons to serve as a control. Transects were located to capture the diversity of terrain as represented in each study area: on ridges, slopes, and valleys; at high, mid, and low elevations; on north-, east-, south-, and west-facing slopes; etc. A transect sampling design was chosen based on individual chestnut sprouts as the unit of response, the intent to measure chestnut response across the landscape, and having one field season to collect data.

With transects created, points were generated every 25 m (82.02 ft.) along them to delineate sections and mid-points of sections to sample chestnuts from. Due to transect lengths being proportional to fire polygon areas, point spacing varied between the last two points (i.e. at the end) of each transect. Transects were divided into 50 m (164.04 ft.) sections (Figure 5), with start and end points as every other 25 m (82.02 ft.)

point (except for the shorter end sections to maintain proportionality). Each section was given a width of 50 m (164.04 ft.) [25 m (82.02 ft.) on either side of transect], giving each 50 m (164.04 ft.) section an area of 2,500 m^2 (26,909.78 $ft.^2$). With the necessary lines and points generated and georeferenced, we were ready to navigate to the transect sections in the field and take measurements.

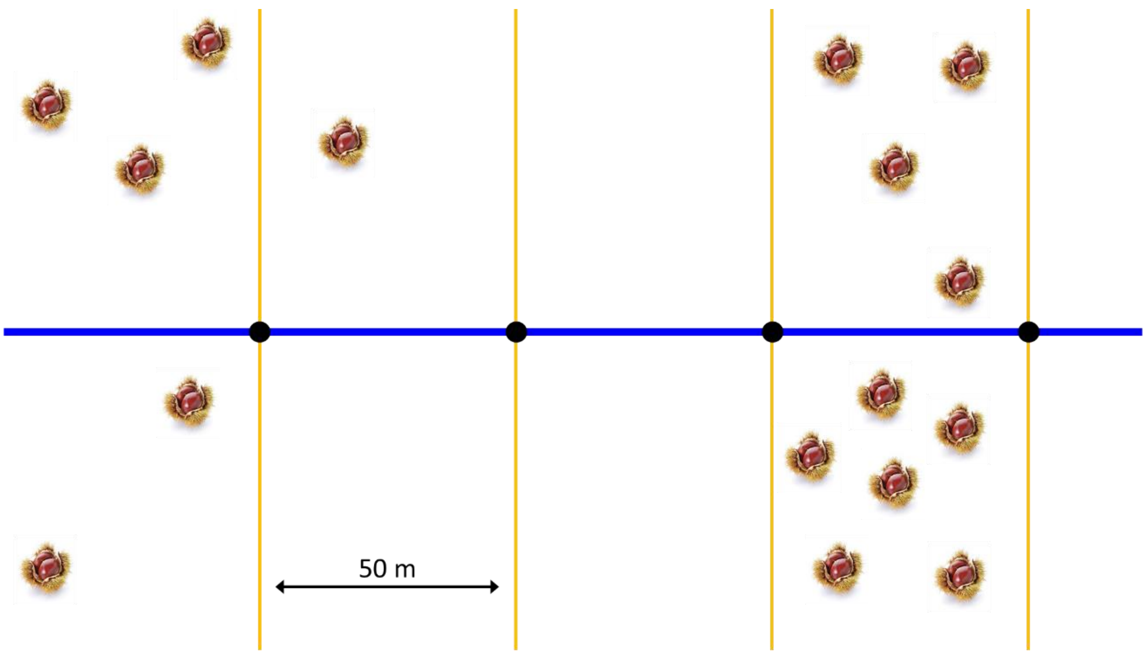

Figure 5. Graphical representation of transects and transect sections delineated as part of sampling design. Yellow lines designating section edges not to scale with transect center line (blue line).

2.3 Field Methods

Fieldwork was conducted over 16 days in May, July, August, and October 2016 with the assistance of several undergraduates and recent graduates of both Texas A&M

University and Virginia Tech. Due to the constraints of weather, available funding, available assistance, the nature of the work involved, and some unforeseen circumstances, many identified transects were not sampled from, and some transects had to be cut short (i.e. fewer sections were sampled from than it contained). A total of 1,782 stems from 230 trees in 438 sections of 39 transects within and outside of 16 burn units across the 3 study areas were measured.

All chestnut trees within the transect width were tallied for each section to determine abundance, with time spent in advance to practice identifying the species. The first chestnut in sight was then measured for each section, the primary unit of response for subsequent analysis. The response variables measured for individual chestnut trees to gauge vitality include the following: height of tallest live stem, height of tallest dead stem (if taller than tallest live stem), number of stems, stem diameter at root collar (DRC), stem mortality, and presence of blight on live stems. Environmental variables slope and canopy cover were measured for each tree as well. Measured trees were flagged with tape and their location recorded using a basic GPS unit. Location accuracy was relatively low with the GPS equipment used compared to more sophisticated systems, but with the combination of flagging tape and waypoint, measured trees can be re-located if needed.

Height was measured using a 3.05 m (10 ft.) PVC pole marked with 15.24 cm (6 in.) gradations, which when extended from the hand of the measurer, provided a quick and reliable means to determine height for trees usually less than 8 m (26.25 ft.), and often less than 5 m (16.40 ft.). The nature of extant chestnut dieback and regrowth made using a pole a feasible option for measuring such low heights. To determine the diameter at root collar (DRC) for each stem of each measured tree, digital calipers were used with the precision of 0.1 mm. The digital calipers were frequently re-calibrated to ensure accurate measurements. Slope was measured in degrees perpendicular to the prevailing contour using a clinometer. Finally, canopy cover was estimated using a spherical densiometer, a concave mirror subdivided into a grid of 24 squares approximating a circle (Figure 6). The canopy cover relative measure was derived from counting the number of imaginary dots in the grid (4 per square for 96 total) covered by vegetation (not including the measured tree itself). Canopy cover estimates were always made standing three paces to the north of the measured tree. Throughout the fieldwork, the same team members made the same measurements as often as possible to minimize measurement error. The team member with the GPS unit called out frequent course adjustments to keep the team traveling along the transect center line, and announced the beginnings and ends of transect sections.

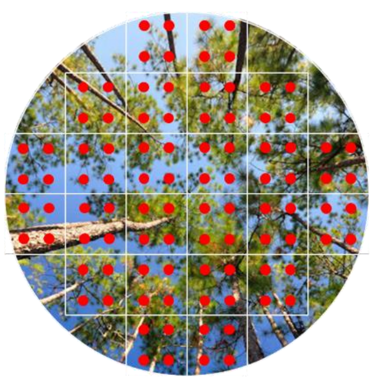

Figure 6. Grid of imaginary dots on spherical densiometer mirror used to estimate canopy cover.

2.4 Data

2.4.1 Response Variables

Data collected in the field were subsequently processed to control for quality, convert to metric units, standardize by other variables, create new variables, and extract the most meaningful variables for analysis. All data were entered and organized within a Microsoft Access relational database to preserve the hierarchical structure of the data (Figure 7) and query the data according to desired criteria. Due to the unknown cause of mortality to the individual standing dead stems measured (e.g. topkilled by fire or girdled by blight after re-sprouting), height of tallest live stem (live height) and number of live stems were used as response variables for analysis, excluding height and stem counts involving dead stems. Further, presence of chestnut blight was aggregated to the tree level (present/absent) as blight was confounded with stem mortality. Stem diameter at root collar (DRC) was measured as a proxy for root system development, to which total stem diameter at root collar (total DRC) of chestnut has been shown to be highly correlated (Jacobs and Severeid, 2004; Clark *et al.*, 2010; Clark *et al.*, 2012b).

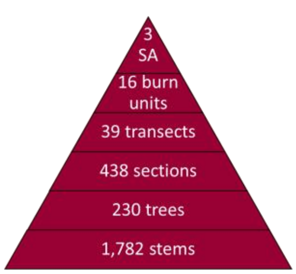

Figure 7. Hierarchical structure of field data. "SA" stands for study areas.

A new response variables was created from the field data to evaluate relative biomass allocation in different parts of the tree, which has been shown to vary under different environmental conditions (Latham, 1992; Wang *et al.*, 2006). Shoot-to-root ratio (SRR) (as derived from total stem DRC) was calculated by the following formula:

$$SRR = \left(\frac{Live\ height}{Total\ DRC}\right) \times 100$$

With the field data compiled, the response variables chosen for analysis included the following: (1) Tally, (2) Live height (LH), (3) Number of live stems (NLS), (4) Blight infection (BI), (5) Total diameter at root collar (TDRC), (6) Average diameter at root collar (AvgDRC), and (7) Shoot-to-root ratio (SRR). Each response variable was standardized by section length, time since burn, and/or canopy cover (or not standardized) according to which technique was appropriate (Figure 8).

Standardization by section length (for tallies) was calculated using the following formula:

$$[standardized\ tally] = \frac{Tally}{section\ length} \times 100$$

Standardization by time since last burn was calculated using the following formula:

$$[standardized\ response\ variable] = \frac{[response\ variable]}{time\ since\ burn} \times 1{,}000$$

Standardization by canopy cover was calculated using the following formula:

$$[standardized\ response\ variable] = response\ variable \times ([canopy\ cover\ \%] + 1)$$

Response variables standardized by time since burn and canopy cover were only used when the other factor (time since burn or canopy cover) was held constant, and vice versa. In some cases, tallies were standardized by both section length and time since burn.

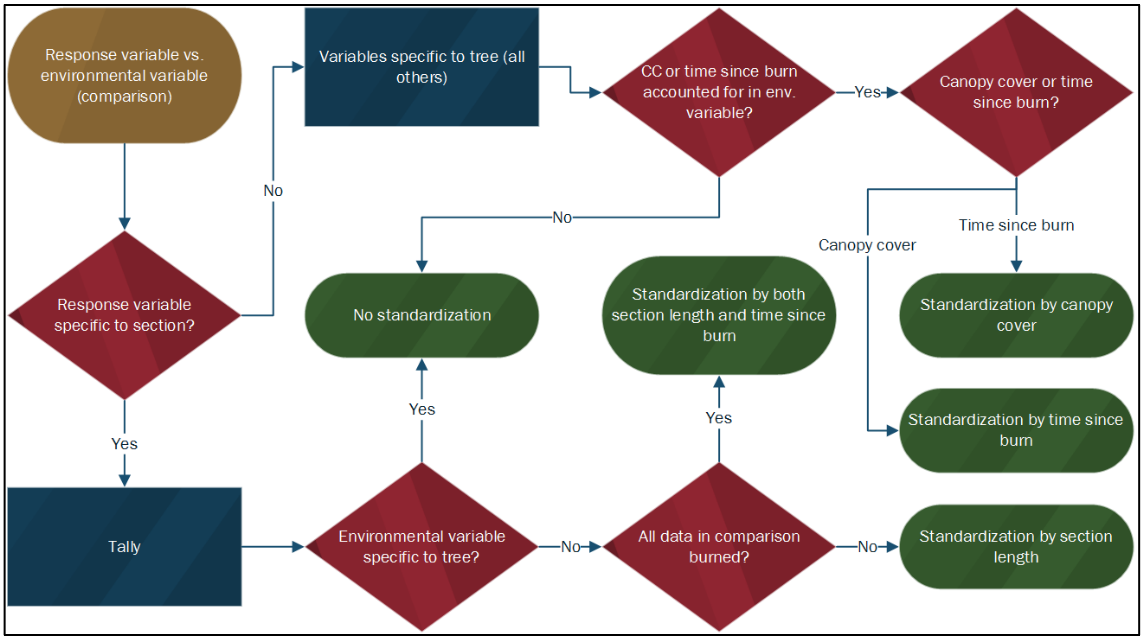

Figure 8. Flow chart illustrating decision-making process for determining what standardization to use (if any) for response variables. The dark yellow oval represents the starting point for a particular comparison of a response variable vs. an environmental variable. The maroon diamonds represent decisions to make in regard to the nature of the data involved. The dark blue rectangles represent a response variable or type of response variable. The dark green ovals represent particular standardizations (or no standardization) of the data, the ending points of the decision-making process.

2.4.2 Environmental Variables

Environmental variables to relate to measured chestnut response were compiled based on the known fire regime, using data collected in the field, and from data derived from digital elevation models (DEMs) in a geographic information system (GIS). The environmental categories and variables chosen for analysis included the following: (1) Burned/unburned, (2) Canopy cover proportion, (3) Number of burns, (4) Growing season days since last burn (Time since last burn), (5) Mean time between successive burns, (6) Heat Load Index (HLI), (7) Topographic Wetness Index (TWI), and (8) Topographic Position Index (TPI).

2.4.2.1 Fire Regime Variables

Fire regime variables not collected in the field were derived using supplemental data to the shapefile polygons provided by the U.S. Forest Service (USFS) George Washington and Jefferson National Forests (GWJeff NF) Supervisor's Office and climatological data from the National Oceanic and Atmospheric Administration (NOAA) National Centers for Environmental Information (NCEI) Global Historical Climatology Network (GHCN) through their GIS Map Portal. Transect sections collected within the boundaries of fire polygons counted in the burned category, whereas transect sections collected outside the polygons counted as unburned. Areas in the latter category may have burned prior to the establishment of the USFS modern prescribed fire and wildfire database, but were considered unburned for purposes of this project. Number of burns (ranging from 0-4) were determined based on the number of unique overlapping areas of fire polygons containing transect sections. The fire regime of transect sections were categorized according to the cumulative geometries of fire polygons containing them, not by individual fire polygons when more than one covered a particular transect.

Time since last burn represented the cumulative number of growing season days between the date of the last burn of fire polygons and the sample date. Growing season days were determined as days between the last frosts of spring and first frosts of fall, with frost days defined as days in which the minimum temperature was at or below 0° C (32° F). The nearest weather stations to each study area with reliable data for the time frame of interest were chosen as the data sources of daily minimum temperatures. The Roanoke weather station [Station ID: USW00013741; 37° 19' N, 79° 58' W; elevation 358.1 m (1,174.87 ft.)] provided data for the Fenwick study area, Hot Springs weather station [Station ID: USC00444128; 38° 0' N, 79° 50' W; elevation 681.5 m (2,235.89 ft.)] for the Warm Springs study area, and both the Fort Valley [Station ID: USR0000VFVA; 38° 50' N, 78° 24' W; elevation 243.8 m (799.87 ft.)] and Woodstock [Station ID: USC00449263; 38° 54' N, 78° 28' W; elevation 205.7 m (674.87 ft.)] weather stations for the Massanutten study area. Mean time between successive burns was determined using the same daily minimum temperature data, calculated as the average number of growing season days between successive burns for areas covered by multiple fire polygons.

Time since last burn and mean time between successive burns were classified based on average growing season length between 1995-2015, with cumulative growing season days divided by the average number of growing season days for the closest weather station over that period. Different numbers of classes and classes using natural breaks were also evaluated, but five average growing season classes for time since last burn and three average growing season classes for mean time between successive burns proved to be the most informative and meaningful classifications for each response variable based on lack of continuity, sample sizes in each category, and interpretability.

Table 1. Classification criteria used for Time since last burn (TSB) and Mean time between successive burns (AvgTBSB) fire regime environmental variables based on number of average growing seasons between 1995-2015.

Class	Number of average growing seasons	
	TSB	AvgTBSB
1	≤ 2	≤ 4
2	2-3	4-5
3	3-4	> 5
4	4-5	
5	> 5	

Additionally, raw canopy cover dot count out of 96 collected in the field was multiplied by 1.04 to obtain a proportion, and was used as a rough proxy for burn severity. With the heterogeneity of fire effects within fire polygons, canopy cover proportion provided a standardized inverse gradient of burn severity, with lower canopy cover indicating higher burn severity and higher canopy cover indicating lower burn severity. Non-fire extraneous disturbances cannot be completely accounted for using this method; therefore, canopy cover proportion must be interpreted as the light environment as can be created by fire, not true burn severity. As a proxy for burn severity, canopy cover proportion nevertheless served as a logistically feasible compromise between the high temporal resolution of remotely sensed vegetation change [e.g. as quantified by changes in the normalized difference vegetation index (NDVI)] and the high spatial resolution and accuracy of fisheye lens hemispherical images processed by image analysis software. Canopy cover proportion was treated as a continuous variable for purposes of analysis rather than being categorized, allowing for a finer scale evaluation in relation to each response variable. Spearman rank-order correlation was used for all canopy cover comparisons, except for blight infection (logistic regression used for binary response variable), as none of the response variables were both normally distributed and homoscedastic.

2.4.2.2 DEM-Derived GIS Terrain Variables

Digital elevation models (DEMs) were downloaded from the United States Geological Survey (USGS) 3D Elevation Program (3DEP) through The National Map (TNM) viewer as the source data for products derived from them. Various ArcGIS tools, the ArcGIS Spatial Analyst extension, and add-ons to ArcGIS for Desktop were used to project, clip, generate, and classify raster datasets of DEM derivatives used to compile the terrain environmental variables chosen for analysis: Heat Load Index (HLI), Topographic Wetness Index (TWI), and Topographic Position Index (TPI). Each of these variables were normalized on a scale of 0-1, and then classified into six classes based on standard deviation distance from the mean (and slope for TPI). Different numbers of classes and classes using natural breaks were also evaluated, but six standard deviation classes for HLI and TWI, and six modified standard deviation classes for TPI according to the classification method of Weiss (2001), proved to be the most informative and meaningful classifications for each response variable based on sample sizes in each category and interpretability (Table 2).

Table 2. Classification criteria used for Heat Load Index (HLI), Topographic Wetness Index (TWI), and Topographic Position Index (TPI) according to established methods. SD = standard deviation and M = mean.

Class	HLI & TWI	TPI Landform	TPI (Weiss, 2001)
1	≤ -SD	Valley	< -SD
2	> -SD & ≤ -½SD	Lower Slope	≥ -SD & < -½SD
3	> -½SD & ≤ M	Flat Area	≥ -½SD & ≤ ½SD, slope ≤ 5°
4	> M & ≤ ½SD	Mid Slope	≥ -½SD & ≤ ½SD, slope > 5°
5	> ½SD & ≤ SD	Upper Slope	> ½SD & ≤ SD
6	> SD	Ridge	> SD

2.4.2.2.1 Heat Load Index

Raw, untransformed aspect is a poor variable for quantitative analysis due to the circular nature of aspects close together (e.g. 359° and 1°, both virtually north) being far apart in value (in this example, 358°). Therefore, transformation of aspect is necessary to make it a meaningful variable. With the interpretation of aspect related to incoming solar radiation (i.e. different facing slopes receive different amounts of sunshine), Heat Load Index (HLI) was used to transform aspect for analysis, calculated using the ArcGIS Geomorphometry and Gradient Metrics Toolbox (Evans *et al.*, 2014b). HLI is a linearized aspect using a standard estimate of potential annual direct incident radiation, with values scaled symmetrically along the northeast-southwest axis, ranging from 0 on northeast-facing slopes to 1 on southwest-facing slopes (Figure 9) (Beers *et al.*, 1966;

McCune and Keon, 2002). HLI also takes into account latitude and slope, with areas at higher latitudes and on steeper slopes assigned a lower HLI value on slopes with the same aspect, calculated for each raster cell using the following formula:

$$hli = 0.039 + [0.808 * \cos(l) * \cos(\theta)] - [0.196 * \sin(\theta)] - [0.482 * \cos\big(f(\alpha)\big) * \sin\big(f(\alpha)\big)]$$

Components of this formula include the following:

$\alpha\ =\ slope\ (radians)$, $l\ =\ latitude$, $\theta\ =\ slope\ (radians)$, and $f(\alpha) = \left|\pi - \left|\alpha - \frac{5\pi}{4}\right|\right|$

(Evans *et al.*, 2014b). Though HLI does not account for cloud cover, atmospheric variations, and shading from surrounding terrain, it remains a useful measure of relative incident radiation over time across landscapes.

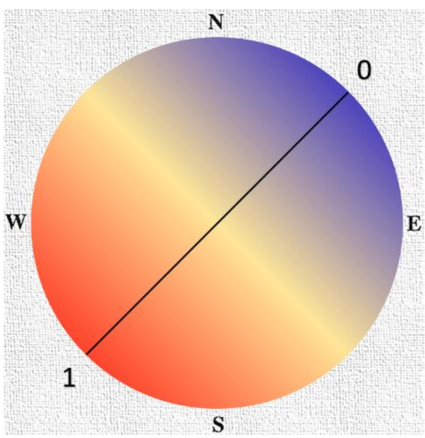

Figure 9. Representation of HLI overlaid on a compass.

2.4.2.2.2 Topographic Wetness Index

If HLI is an indicator of normal incident radiation over time, Topographic Wetness Index (TWI) is an indicator of normal wetness over time. TWI is a cumulative measure of moisture from drainage on heterogeneous landscapes (i.e. corrugated, not flat), a function of slope and upslope contributing area (Moore *et al.*, 1993; Gessler, 1995). Highest TWI values are found in the flattest areas with the largest upslope contributing area (drainage) flowing into the raster cell, whereas lowest TWI values are found in the steepest and highest areas with the lowest upslope contributing area (Figure 10). TWI was calculated based on a sequential process involving intermediate derivatives of flow direction, flow accumulation, and contributing area, calculated using the TauDEM program (Tarboton, 2015; Cooley, 2016) according to the following formula:

$$twi = \ln\left(\frac{\alpha}{\tan(\theta)}\right)$$

Components of this formula include the following:

$\alpha = catchment\ area = [(flow\ accumulation + 1) * (pixel\ area\ in\ m^2)]$ and $\theta = slope\ (radians)$ (Evans *et al.*, 2014b).

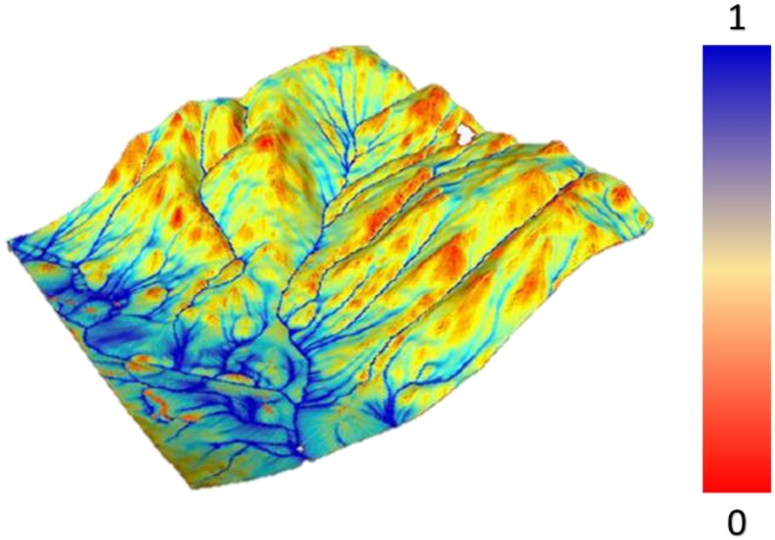

Figure 10. Representation of TWI on a mountainous landscape (Gallay, 2013).

2.4.2.2.3 Topographic Position Index

Subjective classification of slope position (e.g. choice of valley vs. mid slope vs. ridgetop by looking at a topographic map) may be useful in some cases, but Topographic Position Index (TPI) provides a more robust and objective method to accomplish this task. TPI is a measure of relative position along a slope, intuitive to how we encounter a landscape with lowest values in sheltered valleys and depressions and highest values on exposed ridgetops (Weiss, 2001; De Reu *et al.*, 2013). TPI was calculated using Raster Calculator in ArcGIS Spatial Analyst by subtracting the average elevation within a 1000 m (3,280.84 ft.) radius from the elevation value at each raster cell: $tpi = elevation - [average\ elevation\ within\ window]$ (Figure 11) (Esri, 2015). TPI was then classified based on distance from the mean and slope according to the criteria of Table 2, with landform classes of (1) Valley, (2) Lower Slope, (3) Flat Area, (4) Mid Slope, (5) Upper Slope, and (6) Ridge (Figure 12 and Figure 13) (Weiss, 2001).

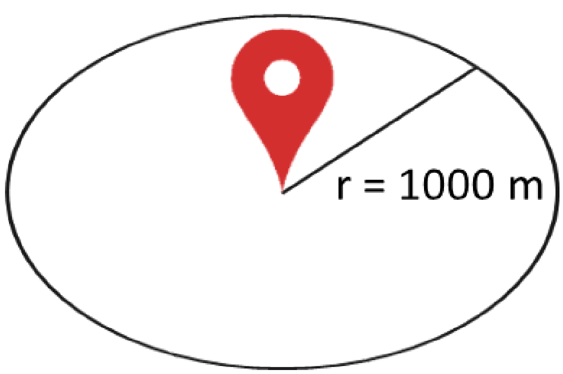

Figure 11. Representation of window used for calculating TPI.

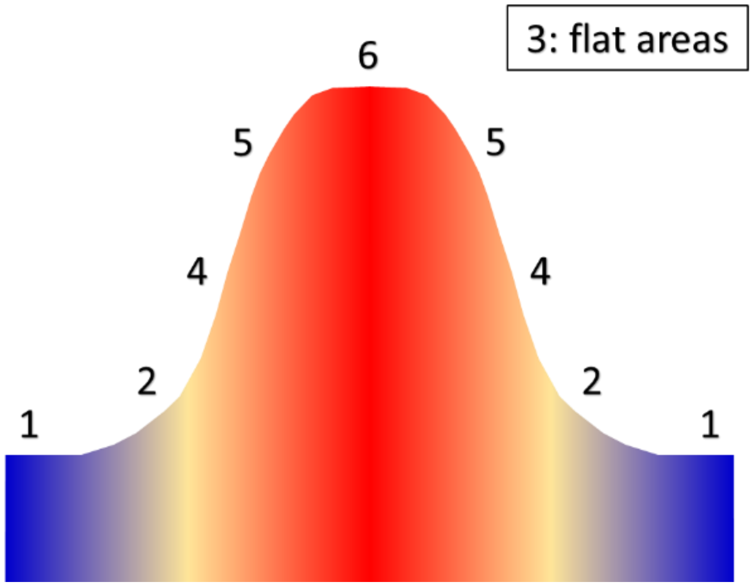

Figure 12. Distribution of TPI classes along a slope position gradient.

A circular window with a 1000 m (3,280.84 ft.) radius was chosen for analysis based on (a) meta-comparison of TPI class distribution using ten different radii of 10, 25, 50, 100, 250, 500, 1000, 2000, 5000, and 10000 m (32.81; 82.02; 164.04; 328.08; 820.21; 1,640.42; 3,280.84; 6,561.68; 16,404.2; and 32,808.4 ft) (Table 13 and Figure 31 in the Appendix) (Naito, 2017), (b) the same window size and shape used for TPI in another GIS analysis of a study in similar terrain and discussion with its author familiar with the region (Evans *et al.*, 2014a; Evans, 2017), and (c) subjective evaluation of the maps generated of TPI classes using each window radius length. While it was difficult to interpret the graph of (a), there did appear to be less variation in class distribution while not underestimating flat areas at the 1000 m (3,280.84 ft.) radius length (Figure 31 in the Appendix). Additionally, the map of TPI classes generated using the 1000 m (3,280.84 ft.) radius length was the most intuitive based on my experience in the field of the areas represented. Smaller radius sizes overestimated mid slopes, not capturing enough of the slope position extremes, whereas larger radius size underestimated the ridges and valleys, not capturing enough of the slope position mid range.

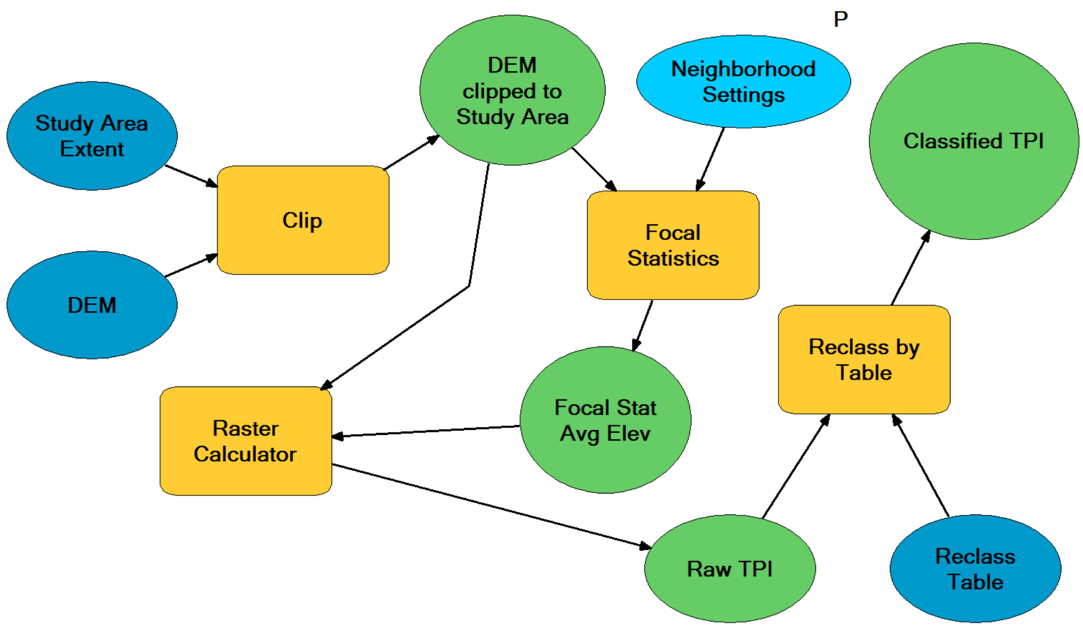

Figure 13. ArcGIS ModelBuilder diagram of process used to calculate and classify Topographic Position Index (TPI).

2.4.3 Comparative Analyses and Statistical Tests Used

With response variables and environmental variables calculated and compiled, making comparisons among groups and fitting models to evaluate chestnut's vitality became possible. Response variables were averaged by environmental categories or correlated directly to environmental observational pairs. Various statistical tests were used to evaluate whether sections and trees exhibited different vitality characteristics under varying environmental conditions. Comparisons between variables and specific hypotheses are listed below in Table 3. In some comparisons, environmental variables were sub-categorized to further control for extraneous factors. Additionally, comparisons were not made between the DEM-derived GIS terrain variables (HLI, TWI, and TPI) and the derivative response variable shoot-to-root ratio (SRR) as they did not seem meaningful for purposes of analysis.

Table 3. Hypotheses for all comparisons of response variables vs. environmental variables. Fire regime environmental variables: 1F, 2F, 3F, 4F, and 5F. DEM-derived GIS terrain variables: 6T, 6T-tsb, 7T, 7T-tsb, 8T, and 8T-tsb. "F" refers to fire regime variables, "T" refers to terrain variables, and "-tsb" refers to sub-categorization by burned sections sampled 3-5 average growing seasons (AGS) since last burn (tsb: time since burn). "↑" indicates increases; "↓" indicates decreases; "→" indicates no change if preceded by forward slash "/", otherwise indicates levels off (i.e. approaches asymptote). See Table 12 in the Results (section 3.9) for an evaluation of each of these hypotheses. Further, see Table 14 and Table 15 in the Appendix for detailed results of these analyses.

Environmental Variable	Response Variable	Hypothesis (H_a)
(1F) Burned/unburned	(1) Tally	Burned ≥ unburned
	(2) Live height (m)	Burned ≥ unburned
	(3) Number of live stems	Burned ≥ unburned
	(4) Blight infection %	No significant difference

Table 3 Continued

Environmental Variable	Response Variable	Hypothesis (H_a)
(1F) Burned/unburned	(5) Total DRC (mm)	Burned ≥ unburned
	(6) Average DRC (mm)	Burned ≥ unburned
	(7) Shoot-to-root ratio	Burned ≥ unburned
(2F) Canopy cover proportion (CC)	(2) Live height (m)	↑ as CC ↓
	(3) Number of live stems	↓/→ as CC ↓
	(4) Blight infection %	↑ as CC ↓
	(5) Total DRC (mm)	↑ as CC ↓
	(6) Average DRC (mm)	↑ as CC ↓
	(7) Shoot-to-root ratio	↑ as CC ↓
(3F) Number of burns (NB)	(1) Tally	↑/→ as NB ↑
	(2) Live height (m)	↑/→ as NB ↑
	(3) Number of live stems	↑/→ as NB ↑
	(4) Blight infection %	→ as NB ↑
	(5) Total DRC (mm)	↑/→ as NB ↑
	(6) Average DRC (mm)	↑/→ as NB ↑
	(7) Shoot-to-root ratio	↑/→ as NB ↑
(4F) Time since last burn (TSB)	(1) Tally	↑ then → with ↑ TSB
	(2) Live height (m)	↑ then → with ↑ TSB
	(3) Number of live stems	↑ with ↑ TSB
	(4) Blight infection %	↑ then → with ↑ TSB
	(5) Total DRC (mm)	↑ then → with ↑ TSB
	(6) Average DRC (mm)	↑ with ↑ TSB
	(7) Shoot-to-root ratio	↑ then → with ↑ TSB
(5T) Mean time between successive burns (AvgTBSB)	(1) Tally	↓ with ↑ AvgTBSB
	(2) Live height (m)	↓ with ↑ AvgTBSB
	(3) Number of live stems	↑/→ with ↑ AvgTBSB
	(4) Blight infection %	↓ with ↑ AvgTBSB
	(5) Total DRC (mm)	↓ with ↑ AvgTBSB
	(6) Average DRC (mm)	↓ with ↑ AvgTBSB
	(7) Shoot-to-root ratio	↓ with ↑ AvgTBSB
(6T) HLI	(1) Tally	↑ as HLI ↑
	(2) Live height (m)	↑ as HLI ↑
	(3) Number of live stems	↓/→ as HLI ↑
	(4) Blight infection %	↑ as HLI ↑
	(5) Total DRC (mm)	↑ as HLI ↑

Table 3 Continued

Environmental Variable	Response Variable	Hypothesis (H_a)
(6T) HLI	(6) Average DRC (mm)	↑ as HLI ↑
(6T-tsb) HLI	(1) Tally	↑ as HLI ↑
	(2) Live height (m)	↑ as HLI ↑
	(3) Number of live stems	↓/→ as HLI ↑
	(4) Blight infection %	↑ as HLI ↑
	(5) Total DRC (mm)	↑ as HLI ↑
	(6) Average DRC (mm)	↑ as HLI ↑
(7T) TWI	(1) Tally	↓ as TWI ↑
	(2) Live height (m)	↓ as TWI ↑
	(3) Number of live stems	↑/→ as TWI ↑
	(4) Blight infection %	↓ as TWI ↑
	(5) Total DRC (mm)	↓ as TWI ↑
	(6) Average DRC (mm)	↓ as TWI ↑
(7T-tsb) TWI	(1) Tally	↓ as TWI ↑
	(2) Live height (m)	↓ as TWI ↑
	(3) Number of live stems	↑/→ as TWI ↑
	(4) Blight infection %	↓ as TWI ↑
	(5) Total DRC (mm)	↓ as TWI ↑
	(6) Average DRC (mm)	↓ as TWI ↑
(8T) TPI	(1) Tally	↑ as TPI ↑
	(2) Live height (m)	↑ as TPI ↑
	(3) Number of live stems	↑ as TPI ↑
	(4) Blight infection %	↑ as TPI ↑
	(5) Total DRC (mm)	↑ as TPI ↑
	(6) Average DRC (mm)	↑ as TPI ↑
(8T-tsb) TPI	(1) Tally	↑ as TPI ↑
	(2) Live height (m)	↑ as TPI ↑
	(3) Number of live stems	↑ as TPI ↑
	(4) Blight infection %	↑ as TPI ↑
	(5) Total DRC (mm)	↑ as TPI ↑
	(6) Average DRC (mm)	↑ as TPI ↑

Statistical tests for significance were chosen based on the nature of the independent (environmental) variables and dependent (response) variables involved, and whether the data met the assumptions of normality, homoscedasticity, and independence required to use parametric tests. All dependent variables (and therefore associated errors) were assumed to be independent based on the nature of the field data collection. Normality was assessed using a Shapiro-Wilk normality test in combination with a histogram and Q-Q plot. Homoscedasticity was assessed using a Fisher's F-test, non-constant error variance test, Bartlett's test, and/or plot of studentized residuals vs. fitted values as appropriate. The following flow chart depicts the process used to determine the statistical test for significance to use for each analysis (Figure 14). Transformations of the response variable were used in some instances for which the transformed data met the parametric test assumptions (Table 14 and Table 15 in the Appendix).

Figure 14. Flow chart illustrating decision-making process for determining which statistical test for significance to use based on the nature of the data involved. The red oval represents the starting point for a particular comparison of a response variable vs. an environmental variable. The dark blue diamonds represent decisions to make in regard to the nature of the data involved. The orange rectangles represent a meta-analysis step, i.e. a subset of methods used to make a determination for how to proceed. The dark purple parallelograms represent a way to modify the data in order to meet particular test assumptions. The green rectangles represent particular statistical tests for significance to use, the ending points of the decision-making process.

3. RESULTS

3.1 Burned/Unburned

All chestnut responses were higher in burned sections than unburned sections, though only the differences in abundance and number of live stems were statistically significant (Figure 15). Group averages between burned and unburned sections are listed by response variable in Table 4, along with section and tree sample sizes for each group.

Table 4. Burned/unburned group averages by response variable. * denotes response variable was standardized by section length (*SL), time since last burn (*TSB), both section length and time since burn (*DTSB), or canopy cover proportion (*CC). Bold group averages denote a statistically significant difference at the α=0.05 level. Superscript λ following response variable denotes a transformation was used. Corresponding detailed results can be found in Table 14 and Table 15 in the Appendix.

	Group Averages	
Response Variable	**Unburned**	**Burned**
Section Sample Size	*65*	*373*
Tree Sample Size	*10*	*220*
(1) Tally (*SL)	**4.68**	**17.38**
(2) Live height (m)$^{\lambda}$	2.33	2.88
(3) Number of live stems	**3.40**	**5.15**
(4) Blight infection prop.	0.10	0.16
(5) Total DRC (mm)	122.4	183.5
(6) Average DRC (mm)$^{\lambda}$	22.3	23.1
(7) Shoot-to-root ratio$^{\lambda}$	2.23	3.14

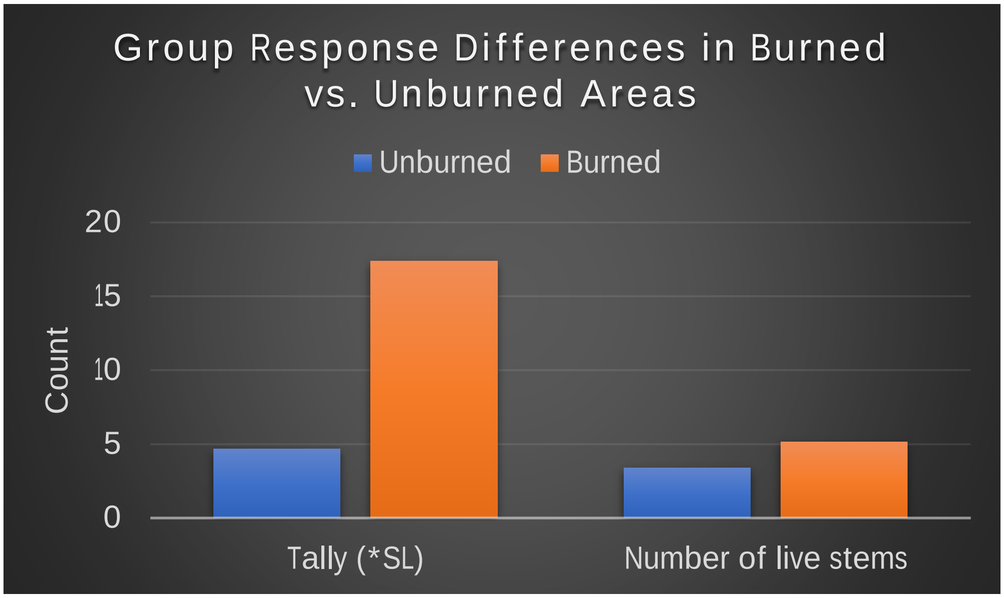

Figure 15. Average chestnut tally and number of live stems in burned vs. unburned areas. * denotes response variable was standardized by section length (*SL). Both comparisons are statistically significant (α=0.05) using Gamma and Poisson regression, respectively.

3.2 Canopy Cover Proportion

Canopy cover proportion was significantly correlated with all response variables specific to tree and in burned sections except for shoot-to-root ratio (SRR). Among these significant correlations, canopy cover proportion was positively correlated with each response variable. Significant Spearman correlations are plotted in the figures below.

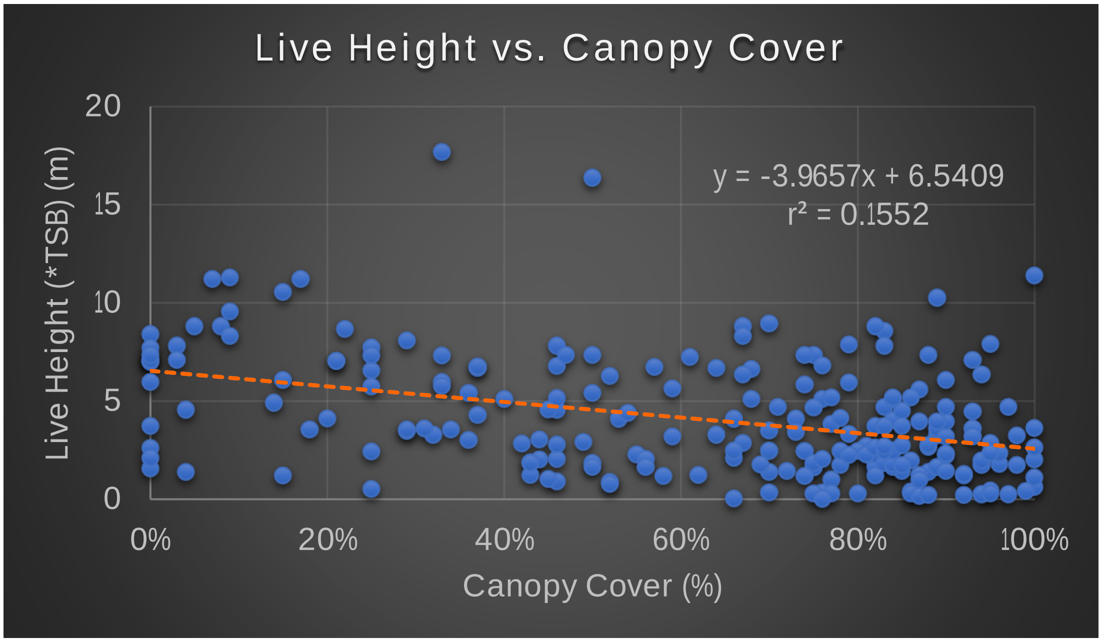

Figure 16. Live height (m) vs. canopy cover proportion (%). Statistically significant (α=0.05) using Spearman correlation. * denotes response variable was standardized by time since last burn (*TSB).

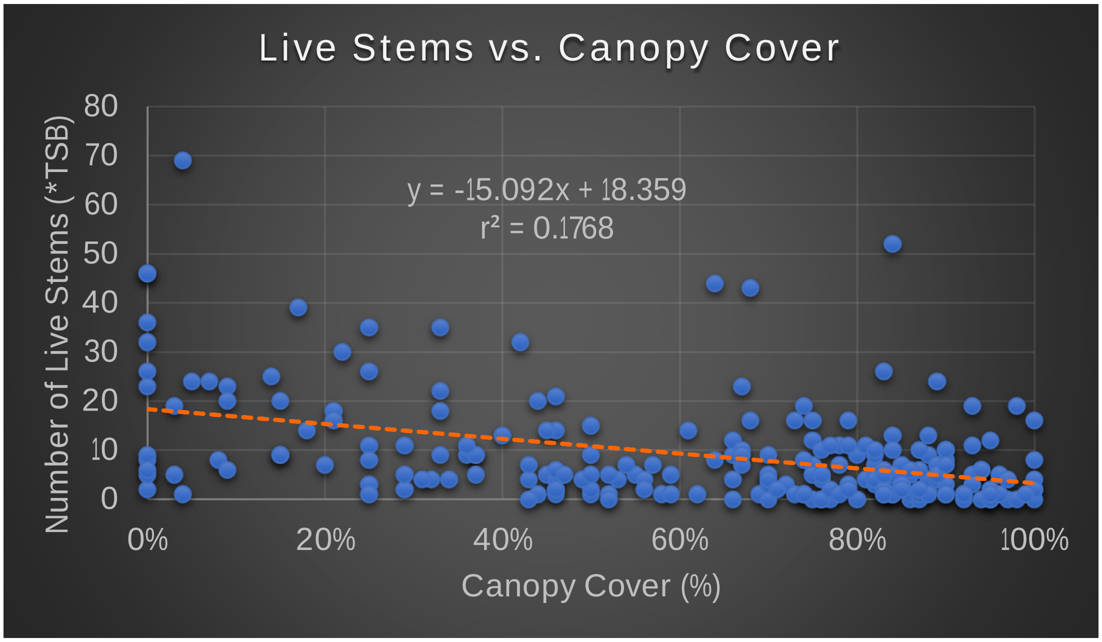

Figure 17. Number of live stems vs. canopy cover proportion (%). Statistically significant (α=0.05) using Spearman correlation. * denotes response variable was standardized by time since last burn (*TSB).

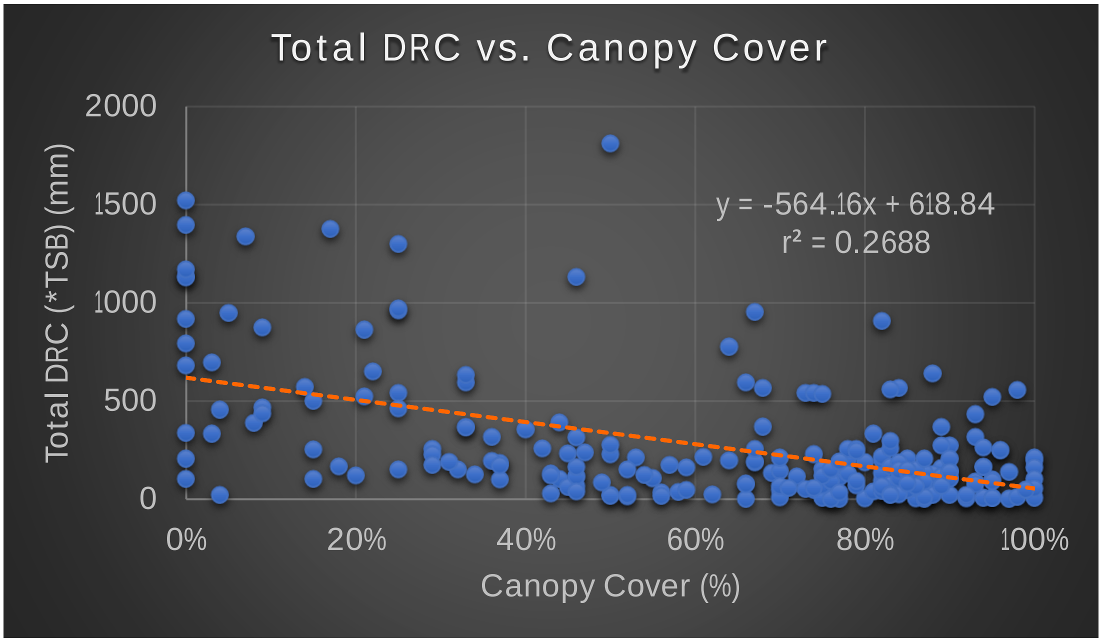

Figure 18. Total diameter at root collar (DRC) (mm) vs. canopy cover proportion (%). Statistically significant (α=0.05) using Spearman correlation. * denotes response variable was standardized by time since last burn (*TSB).

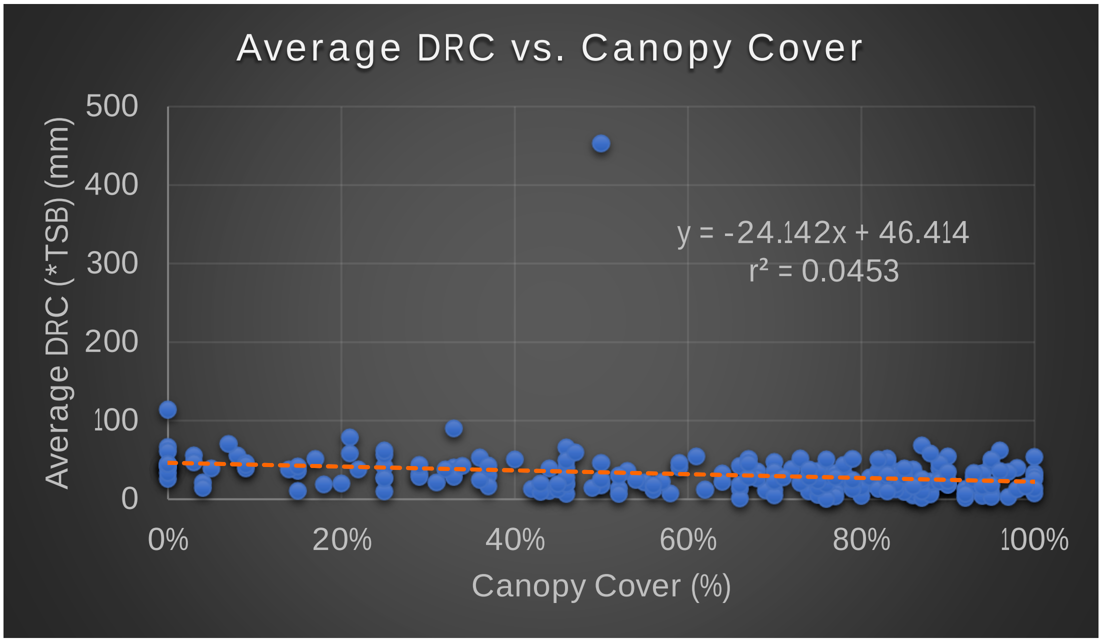

Figure 19. Average diameter at root collar (DRC) (mm) vs. canopy cover proportion (%). Statistically significant (α=0.05) using Spearman correlation. * denotes response variable was standardized by time since last burn (*TSB).

3.3 Number of Burns

Chestnut responses varied widely among number of burns, with different trends apparent for different response variables. Only the comparisons of number of live stems and blight infection to number of burns were statistically significant (Figure 20). Group averages among sections burned 0-4 times are listed by response variable in Table 5, along with section and tree sample sizes for each group.

Table 5. Number of burn group averages by response variable. * denotes response variable was standardized by section length (*SL), time since last burn (*TSB), both section length and time since burn (*DTSB), or canopy cover proportion (*CC). Bold group averages denote a statistically significant difference at the α=0.05 level. Superscript λ following response variable denotes a transformation was used. Corresponding detailed results can be found in Table 14 and Table 15 in the Appendix.

	Group Averages				
Number of Burns	**0 burns**	**1 burn**	**2 burns**	**3 burns**	**4 burns**
Section Sample Size	*65*	*222*	*49*	*88*	*14*
Tree Sample Size	*10*	*123*	*31*	*57*	*9*
(1) Tally (*SL)	4.68	16.76	24.75	16.30	8.14
(2) Live height (m)$^{\lambda}$	2.33	2.92	2.53	2.82	3.94
(3) Number of live stems	**3.40**	**4.44**	**4.97**	**6.37**	**7.89**
(4) Blight infection prop.	**0.10**	**0.11**	**0.10**	**0.23**	**0.56**
(5) Total DRC (mm)	122.4	175.4	146.8	212.2	238.6
(6) Average DRC (mm)	22.3	25.8	18.0	19.8	23.9
(7) Shoot-to-root ratio$^{\lambda}$	2.23	3.46	3.03	2.65	2.23

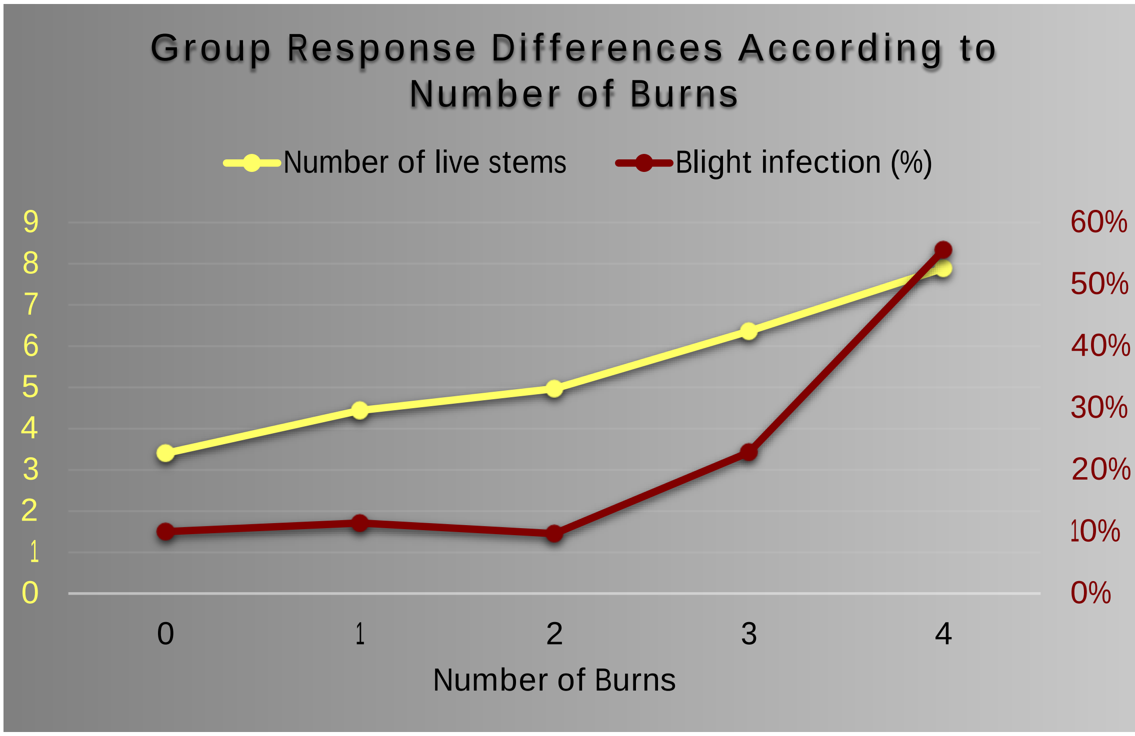

Figure 20. Average number of live stems (yellow line) and blight infection (%) (maroon line) in areas burned 0-4 times. Both comparisons are statistically significant (α=0.05) using Quasipoisson and logistic regression, respectively.

3.4 Time Since Last Burn

While chestnut response varied with increasing time since last burn in burned sections for most comparisons, it did not significantly differ between many growing season classes within those comparisons and for blight infection and total DRC. Therefore, while there was significant change in chestnut response over time in most comparisons, there was not necessarily significant change in chestnut response among different time since last burn classes in the same comparison. Group averages among each time since last burn average growing season class are listed by response variable in Table 6, along with section and tree sample sizes for each group.

Table 6. Time since last burn group averages by response variable. * denotes response variable was standardized by section length (*SL), time since last burn (*TSB), both section length and time since burn (*DTSB), or canopy cover proportion (*CC). Bold group averages denote a statistically significant difference at the α=0.05 level. Superscript λ following response variable denotes a transformation was used. Superscript letters (a, b, c, d) designate pairwise comparisons, with a significant difference between group averages not sharing the same letter. Corresponding detailed results can be found in Table 14 and Table 15 in the Appendix.

	Group Averages				
Average Growing Season (AGS) Class	**(1) ≤ 2**	**(2) 2-3**	**(3) 3-4**	**(4) 4-5**	**(5) > 5**
Section Sample Size	*5*	*101*	*77*	*98*	*92*
Tree Sample Size	*5*	*50*	*60*	*57*	*48*
(1) Tally (*SL)	**34.80**	**19.90**	**19.99**	**23.23**	**5.24**
(2) Live height (*CC) (m)	**1.91^{ab}**	**3.25^{a}**	**5.10^{c}**	**4.40^{ab}**	**5.69^{bc}**
(3) Number of live stems (*CC)	**10.63^{ab}**	**10.51^{a}**	**8.68^{ac}**	**6.51^{bc}**	**4.84^{b}**
(4) Blight infection prop. (*CC)	0.00	0.17	0.35	0.20	0.33
(5) Total DRC (*CC) (mm)	120.5	259.1	276.8	252.9	314.5
(6) Average DRC (*CC) (mm)	**14.2^{a}**	**25.3^{b}**	**31.8^{c}**	**43.8^{c}**	**49.6^{d}**
(7) Shoot-to-root ratio (*CC)$^{\lambda}$	**4.18^{ab}**	**2.73^{a}**	**5.36^{b}**	**5.50^{b}**	**7.89^{b}**

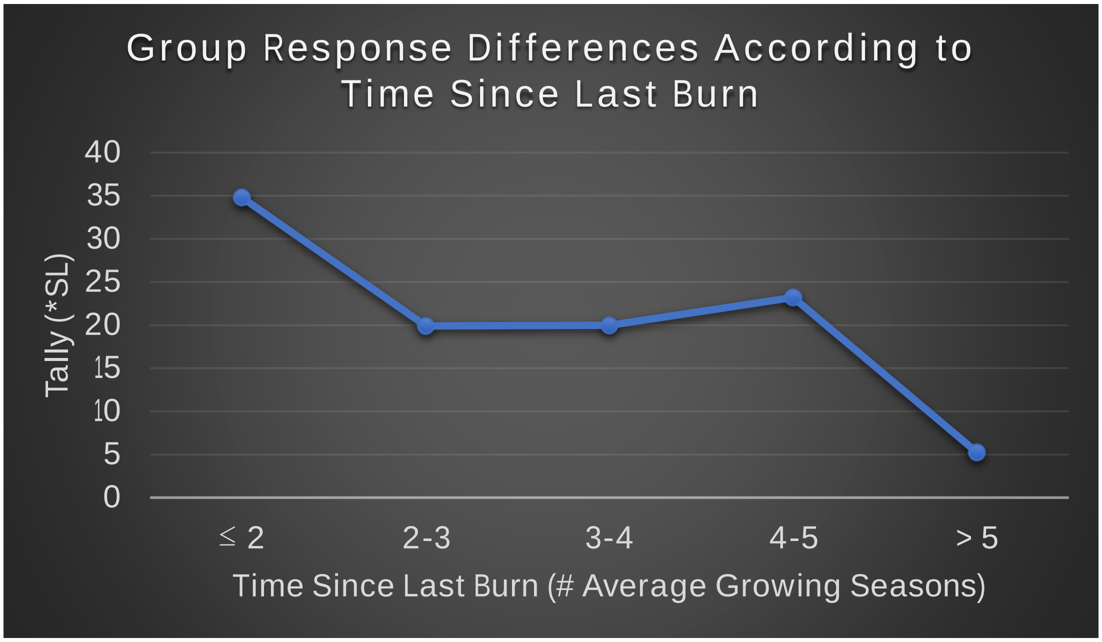

Figure 21. Average chestnut tally in burned areas by time since last burn average growing season class. Statistically significant (α=0.05) using Gamma regression. * denotes response variable was standardized by section length (*SL).

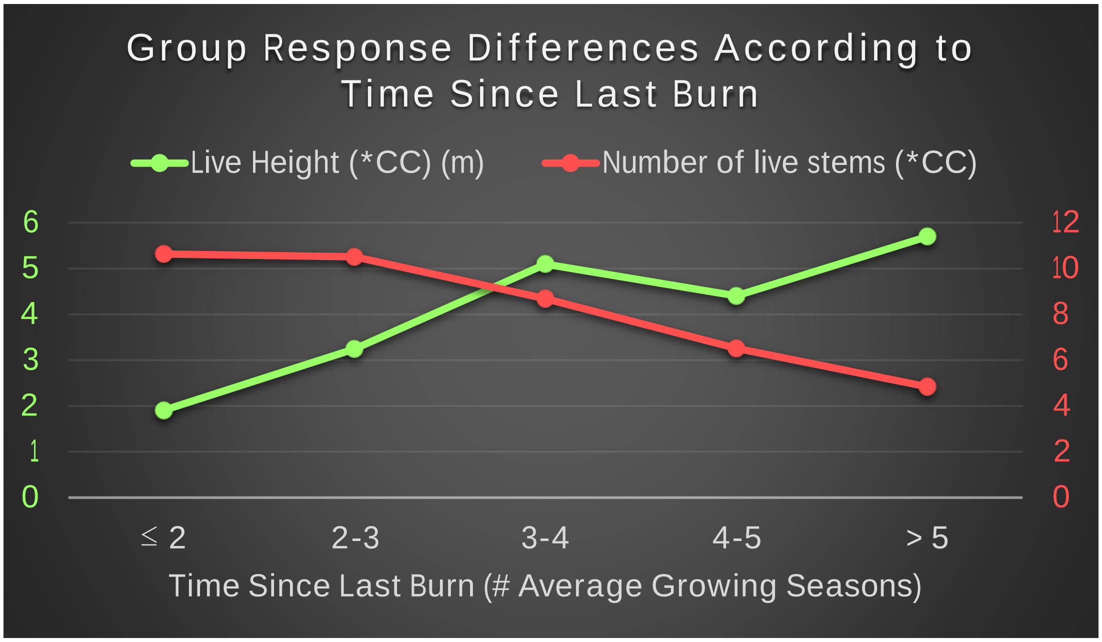

Figure 22. Average live height (m) (light green line) and number of live stems (light red line) in burned areas by time since last burn average growing season class. Both comparisons are statistically significant (α=0.05) using a Kruskal-Wallis test. * denotes response variable was standardized by canopy cover proportion (*CC).

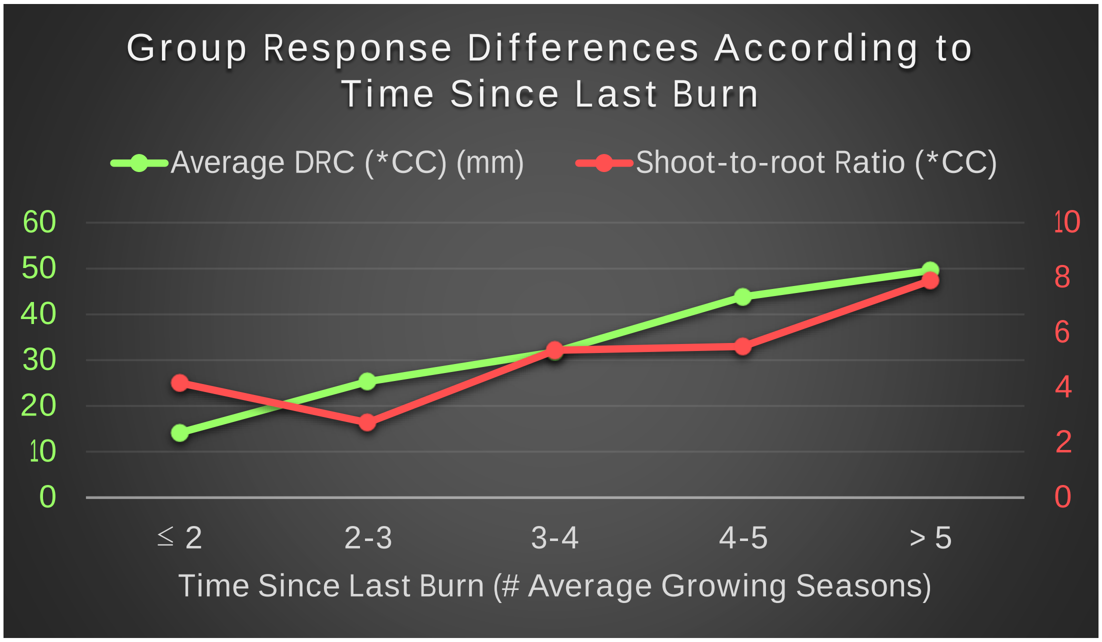

Figure 23. Average of average diameter at root collar (DRC) (mm) (light green line) and shoot-to-root ratio (light red line) in burned areas by time since last burn average growing season class. Both comparisons are statistically significant (α=0.05) using a Kruskal-Wallis and one-way ANOVA test with log-transformed data, respectively. * denotes response variable was standardized by canopy cover proportion (*CC).

3.5 Mean Time Between Successive Burns

Chestnut response varied with mean time between successive burns in burned sections for most comparisons, but it did not significantly differ between all pairs of growing season classes within those comparisons and for blight infection and average DRC. Therefore, while there were significant differences in chestnut response at varying fire return intervals in most comparisons, there were not necessarily significant differences in chestnut response among different fire return interval classes in the same comparison. Group averages among each mean time between successive burns average growing season class are listed by response variable in Table 7, along with section and tree sample sizes for each group.

Table 7. Mean time between successive burns group averages by response variable. * denotes response variable was standardized by section length (*SL), time since last burn (*TSB), both section length and time since burn (*DTSB), or canopy cover proportion (*CC). Bold group averages denote a statistically significant difference at the α=0.05 level. Superscript λ following response variable denotes a transformation was used. Superscript letters (a, b, c, d) designate pairwise comparisons, with a significant difference between group averages not sharing the same letter. Corresponding detailed results can be found in Table 14 and Table 15 in the Appendix.

	Group Averages		
Average Growing Season (AGS) Class	**(1) ≤ 4**	**(2) 4-5**	**(3) > 5**
Section Sample Size	*38*	*73*	*40*
Tree Sample Size	*30*	*45*	*22*
(1) Tally (*DTSB)	**76.18**	**29.09**	**16.66**
(2) Live height (m)	**2.86**[ab]	**3.18**[a]	**2.08**[b]
(3) Number of live stems	**6.80**	**6.87**	**3.41**
(4) Blight infection prop.	0.27	0.24	0.09
(5) Total DRC (mm)$^{\lambda}$	**199.1**[a]	**223.3**[a]	**126.2**[b]
(6) Average DRC (mm)	19.6	20.6	17.7
(7) Shoot-to-root ratio	**1.97**[a]	**2.70**[ab]	**3.85**[b]

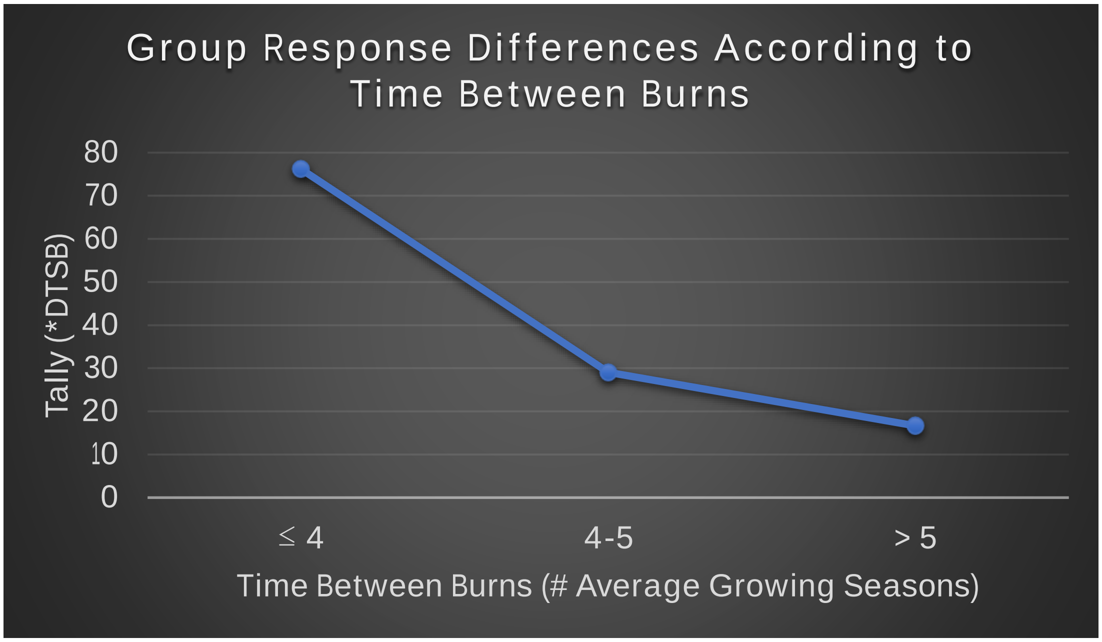

Figure 24. Average chestnut tally (standardized by section length and time since burn) in areas burned multiple times by mean time between successive burns average growing season class. Statistically significant (α=0.05) using Gamma regression. * denotes response variable was standardized by both section length and time since burn (*DTSB).

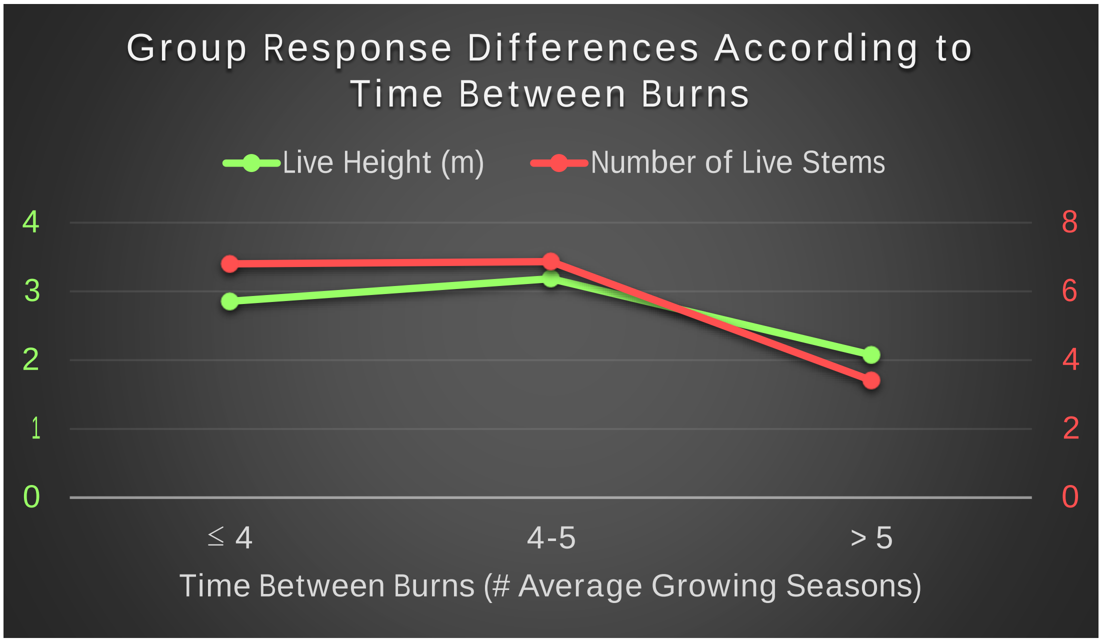

Figure 25. Average live height (m) (light green line) and number of live stems (light red line) in areas burned multiple times by mean time between successive burns average growing season class. Both comparisons are statistically significant (α=0.05) using a Kruskal-Wallis test and Quasipoisson regression, respectively.

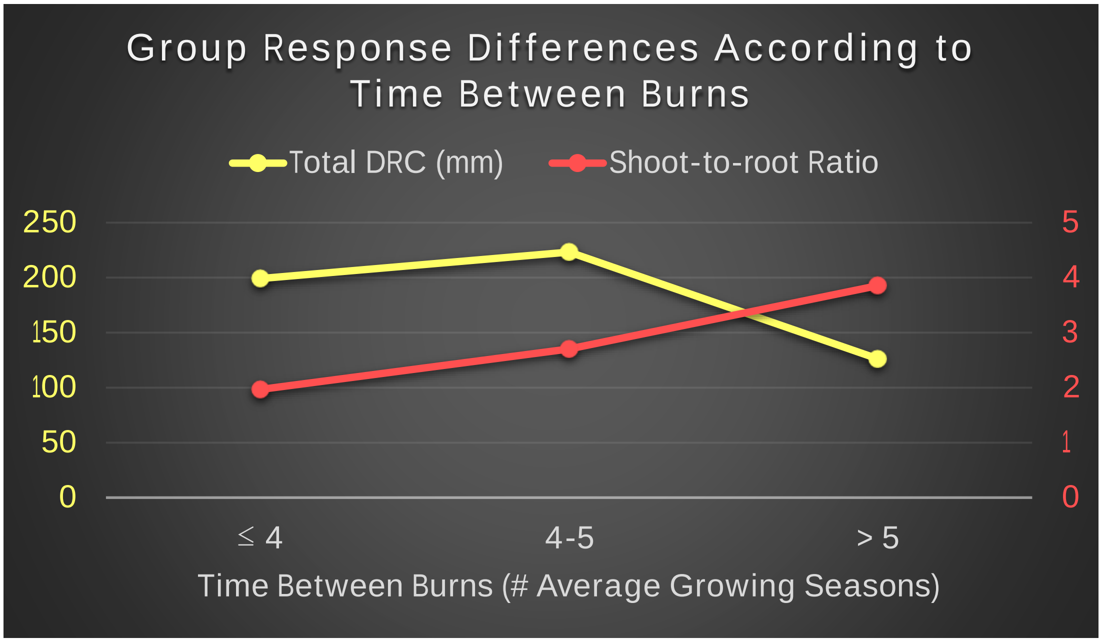

Figure 26. Average total diameter at root collar (DRC) (mm) (yellow line) and shoot-to-root ratio (light red line) in areas burned multiple times by mean time between successive burns average growing season class. Both comparisons are statistically significant (α=0.05) using a one-way ANOVA with log-transformed data and Kruskal-Wallis test, respectively.

3.6 Heat Load Index

Despite the variations in chestnut response observed in different Heat Load Index (HLI) classes, there were no significant differences for any comparison with a particular response variable. Additionally, there were no significant differences for any comparisons when filtered for time since last burn and with canopy cover held constant among burned sections. Group averages among each HLI class (both unfiltered and filtered by time since last burn) are listed by response variable in Table 8, along with section and tree sample sizes for each group.

Table 8. Heat Load Index (HLI) group averages by response variable both unfiltered and filtered by time since last burn. * denotes response variable was standardized by section length (*SL), time since last burn (*TSB), both section length and time since burn (*DTSB), or canopy cover proportion (*CC). Bold group averages denote a statistically significant difference at the α=0.05 level. Superscript λ following response variable denotes a transformation was used. Superscript letters (a, b, c, d) designate pairwise comparisons, with a significant difference between group averages not sharing the same letter. Corresponding detailed results can be found in Table 14 and Table 15 in the Appendix.

	Group Averages					
Heat Load Index (HLI) Class	**1**	**2**	**3**	**4**	**5**	**6**
Section Sample Size	*41*	*73*	*115*	*87*	*64*	*58*
Tree Sample Size	*20*	*34*	*52*	*49*	*44*	*31*
(1) Tally (*SL)	14.83	16.22	12.90	17.67	17.31	14.93
(2) Live height (m)	2.94	2.70	2.91	2.87	2.44	3.45
(3) Number of live stems	6.65	4.76	5.63	4.53	4.27	5.48
(4) Blight infection prop.	0.15	0.12	0.13	0.18	0.07	0.32
(5) Total DRC (mm)	173.2	174.4	181.6	166.5	167.5	233.2
(6) Average DRC (mm)	22.6	20.8	20.1	21.2	27.0	27.9
	Group Averages					
Heat Load Index (HLI) Class: 3-5 Avg GS since last burn	**1**	**2**	**3**	**4**	**5**	**6**
Section Sample Size	*12*	*24*	*63*	*41*	*29*	*6*
Tree Sample Size	*8*	*17*	*37*	*27*	*24*	*4*
(1) Tally (*SL)	16.67	22.60	16.70	30.73	25.30	4.67
(2) Live height (*CC) (m)	5.87	4.23	4.59	4.86	4.50	7.11
(3) Number of live stems (*CC)	7.19	6.76	8.16	8.16	6.16	12.38
(4) Blight infection prop. (*CC)	0.22	0.29	0.26	0.36	0.13	0.89
(5) Total DRC (*CC) (mm)	231.7	193.9	242.5	299.8	287.4	476.9
(6) Average DRC (*CC) (mm)	39.9	34.2	30.9	34.3	51.9	47.5

3.7 Topographic Wetness Index

Despite the variations in chestnut response observed in different Topographic Wetness Index (TWI) classes, only the comparison with tally was statistically significant. However, when the data was subset to include only the mid-range of time since last burn (3-5 average growing seasons) for burned sections and standardized by canopy cover proportion, comparisons with live height, number of live stems, total DRC, and average DRC became statistically significant, though not among all pairwise comparisons. Group averages among each TWI class (both unfiltered and filtered by time since last burn) are listed by response variable in Table 9, along with section and tree sample sizes for each group.

Table 9. Topographic Wetness Index (TWI) group averages by response variable both unfiltered and filtered by time since last burn. * denotes response variable was standardized by section length (*SL), time since last burn (*TSB), both section length and time since burn (*DTSB), or canopy cover proportion (*CC). Bold group averages denote a statistically significant difference at the α=0.05 level. Superscript λ following response variable denotes a transformation was used. Superscript letters (a, b, c, d) designate pairwise comparisons, with a significant difference between group averages not sharing the same letter. Corresponding detailed results can be found in Table 14 and Table 15 in the Appendix.

	Group Averages					
Topographic Wetness Index (TWI) Class	**1**	**2**	**3**	**4**	**5**	**6**
Section Sample Size	*50*	*75*	*104*	*100*	*67*	*42*
Tree Sample Size	*29*	*32*	*45*	*50*	*44*	*30*
(1) Tally (*SL)	**6.58**	**15.33**	**11.86**	**19.76**	**20.40**	**17.38**
(2) Live height (m)	2.89	3.11	2.89	2.74	2.60	3.08
(3) Number of live stems	5.28	4.72	4.49	5.14	5.93	4.80
(4) Blight infection prop.	0.28	0.22	0.07	0.14	0.09	0.23
(5) Total DRC (mm)	173.4	224.0	154.3	195.0	139.9	218.5

Table 9 Continued

Topographic Wetness Index (TWI) Class	**1**	**2**	**3**	**4**	**5**	**6**
(6) Average DRC (mm)	22.3	27.8	22.4	25.0	18.7	22.8
	Group Averages					
Topographic Wetness Index (TWI): 3-5 Avg GS (AGS) since last burn	**1**	**2**	**3**	**4**	**5**	**6**
Section Sample Size	*11*	*14*	*36*	*60*	*31*	*23*
Tree Sample Size	*9*	*9*	*20*	*37*	*22*	*20*
(1) Tally (*SL)	11.64	20.43	24.00	26.76	14.84	20.53
(2) Live height (*CC) (m)$^{\lambda}$	**8.41**^{a}	**4.88**^{ab}	**4.61**^{ab}	**3.94**^{b}	**4.34**^{b}	**5.19**^{ab}
(3) Number of live stems (*CC)	**16.05**^{a}	**6.38**^{ab}	**8.51**^{ab}	**6.80**^{b}	**6.44**^{b}	**6.33**^{b}
(4) Blight infection prop. (*CC)	1.02	0.18	0.09	0.24	0.22	0.33
(5) Total DRC (*CC) (mm)	**534.7**^{a}	**239.3**^{ab}	**250.8**^{b}	**275.0**^{b}	**183.9**^{b}	**241.0**^{b}
(6) Average DRC (*CC) (mm)	**44.9**^{a}	**36.0**^{ab}	**38.8**^{ab}	**39.3**^{b}	**31.7**^{ab}	**37.6**^{ab}

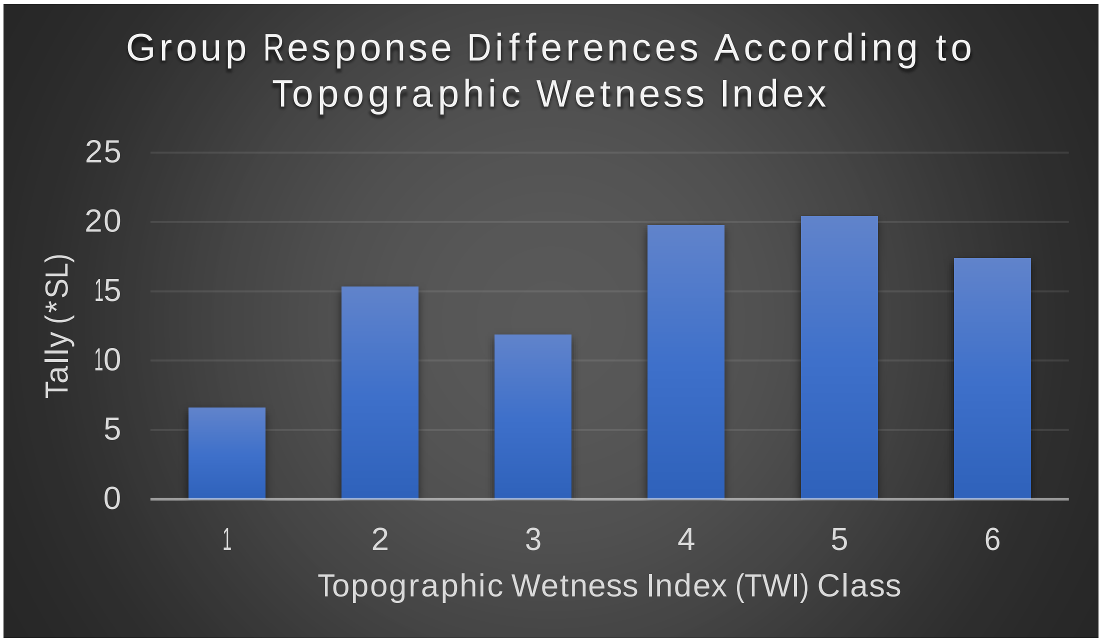

Figure 27. Average chestnut tally by Topographic Wetness Index (TWI) class. Statistically significant (α=0.05) using Gamma regression. * denotes response variable was standardized by section length (*SL).

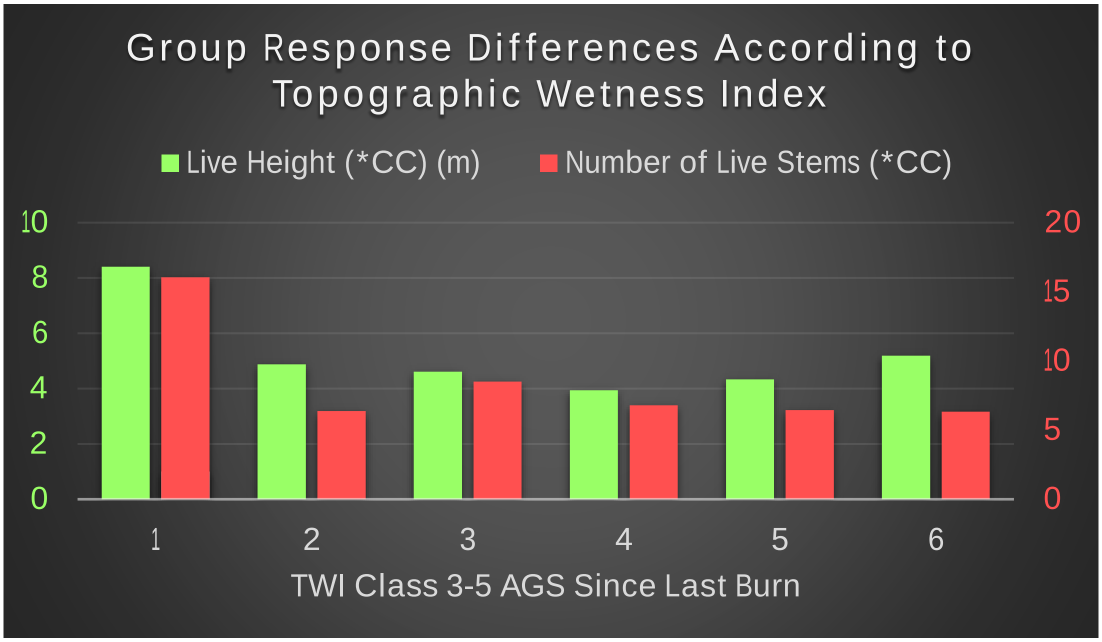

Figure 28. Average live height (m) (light green series) and number of live stems (light red series) in burned areas 3-5 average growing seasons (AGS) since last burn by Topographic Wetness Index (TWI) class. Both comparisons are statistically significant (α=0.05) using a one-way ANOVA with log-transformed data and Kruskal-Wallis test, respectively. * denotes response variable was standardized by canopy cover proportion (*CC).

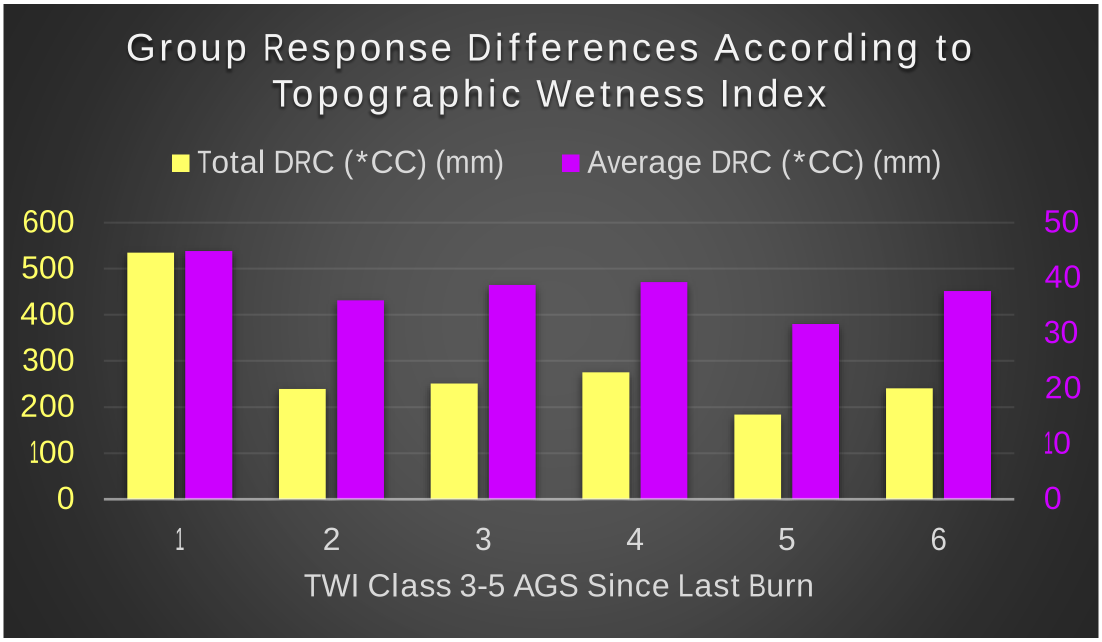

Figure 29. Average total diameter at root collar (DRC) (mm) (yellow series) and of average diameter at root collar (DRC) (mm) (purple series) in burned areas 3-5 average growing seasons (AGS) since last burn by Topographic Wetness Index (TWI) class. Both comparisons are statistically significant (α=0.05) using a Kruskal-Wallis test. * denotes response variable was standardized by canopy cover proportion (*CC).

3.8 Topographic Position Index

Among the variations in chestnut response observed in different Topographic Position Index (TPI) classes, as with TWI, only the comparison with tally was statistically significant. When the data was subset to include only the mid-range of time since last burn (3-5 average growing seasons) for burned sections and standardized by canopy cover proportion, no comparisons were statistically significant. Group averages among each TPI class (both unfiltered and filtered by time since last burn) are listed by response variable in Table 10, along with section and tree sample sizes for each group.

Table 10. Topographic Position Index (TPI) group averages by response variable both unfiltered and filtered by time since last burn. * denotes response variable was standardized by section length (*SL), time since last burn (*TSB), both section length and time since burn (*DTSB), or canopy cover proportion (*CC). Bold group averages denote a statistically significant difference at the α=0.05 level. Superscript λ following response variable denotes a transformation was used. Superscript letters (a, b, c, d) designate pairwise comparisons, with a significant difference between group averages not sharing the same letter. Corresponding detailed results can be found in Table 14 and Table 15 in the Appendix.

	Group Averages					
Topographic Position Index (TPI) Class	**(1) Valley**	**(2) Lower Slope**	**(3) Flat Area**	**(4) Mid Slope**	**(5) Upper Slope**	**(6) Ridge**
Section Sample Size	*52*	*46*	*4*	*61*	*55*	*220*
Tree Sample Size	*20*	*29*	*0*	*28*	*23*	*130*
(1) Tally (*SL)	**9.08**	**4.58**	**0.00**	**8.67**	**15.60**	**21.44**
(2) Live height (m)	3.07	3.14	n/a	2.82	3.26	2.69
(3) Number of live stems	4.50	4.97	n/a	5.29	6.43	4.91
(4) Blight infection prop.	0.10	0.14	n/a	0.14	0.22	0.16
(5) Total DRC (mm)	124.5	182.5	n/a	183.5	246.9	176.9
(6) Average DRC (mm)	18.9	25.0	n/a	21.1	33.4	21.8
	Group Averages					
Topographic Position Index (TPI): 3-5 Avg GS (AGS) since last burn	**(1) Valley**	**(2) Lower Slope**	**(3) Flat Area**	**(4) Mid Slope**	**(5) Upper Slope**	**(6) Ridge**
Section Sample Size	*16*	*10*	*0*	*32*	*35*	*82*
Tree Sample Size	*16*	*9*	*0*	*15*	*15*	*62*
(1) Tally (*SL)	28.38	2.82	n/a	11.92	12.12	30.83
(2) Live height (*CC) (m)	5.01	6.02	n/a	5.37	5.34	4.22
(3) Number of live stems (*CC)$^{\lambda}$	7.04	3.75	n/a	10.33	7.30	7.76
(4) Blight infection prop. (*CC)	0.22	0.00	n/a	0.43	0.10	0.34
(5) Total DRC (*CC) (mm)	207.7	135.4	n/a	356.3	355.8	254.9
(6) Average DRC (*CC) (mm)	32.5	42.9	n/a	36.8	64.0	32.1

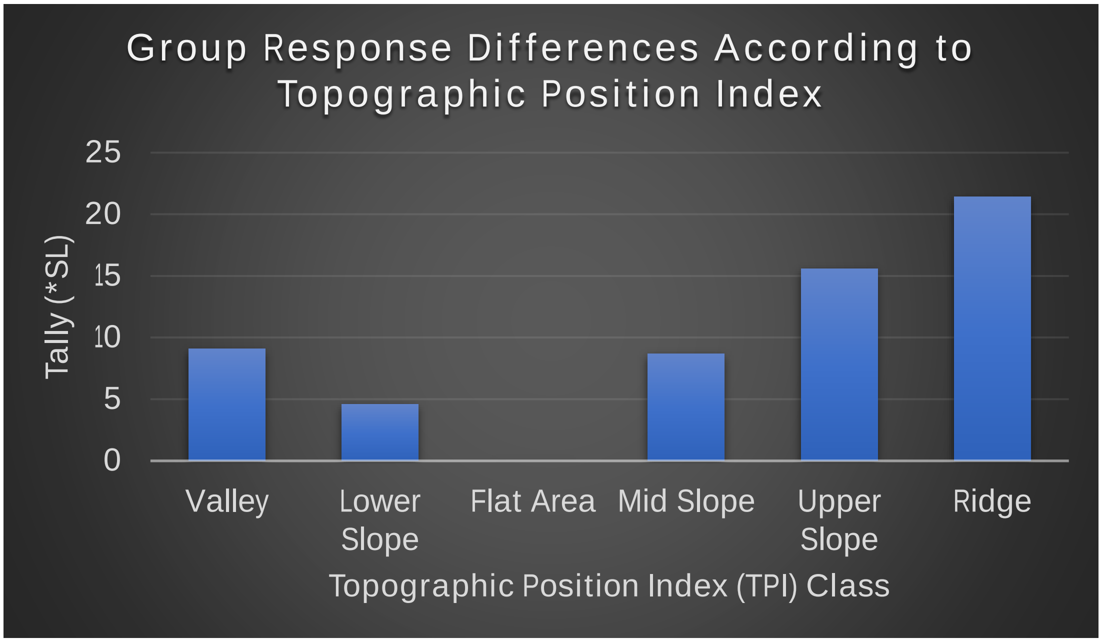

Figure 30. Average chestnut tally (standardized by section length) by Topographic Position Index (TPI) class. Statistically significant (α=0.05) using Gamma regression. * denotes response variable was standardized by section length (*SL).

3.9 Summary of Results and Evaluation of Hypotheses

Based on the results of the analyses presented in sections 3.1-3.8, Table 12 summarizes the overall trends for each environmental variable vs. response variable comparison and whether the evidence supports rejecting the null hypothesis (H_0) generated as the opposite of the (alternate) hypotheses presented prior to analysis in Table 3. Three separate determinations for each hypothesis were possible, as reflected by the "Reject H_0?" attribute in Table 12: (1) "Yes" indicates supporting evidence to reject H_0 and accept H_a, (2) "Fail" indicates lack of supporting evidence to reject H_0 (but does not necessarily require accepting H_0), and (3) "No" indicates supporting evidence not to reject, i.e. to accept H_0 (color coded green, yellow, and red, respectively).

Table 11. Summary of results of all tested comparisons of response variables vs. environmental variables.

	Environmental Variable	Response Variable						
		1	2	3	4	5	6	7
		Tally	Live height	Number of live stems	Blight %	Total DRC	Average DRC	Shoot-to-root ratio
1F	Burned/unburned	**Burned > unburned**	Burned > unburned	**Burned > unburned**	Burned > unburned	Burned > unburned	Burned > unburned	Burned > unburned
2F	Canopy cover proportion	n/a	**↑ as CC ↓**	**↑ as CC ↓**	**↑ as CC ↓**	**↑ as CC ↓**	**↑ as CC ↓**	↓ as CC ↓
3F	Number of burns	↑ then ↓ as NB ↑	Mixed / ~ ↑ as NB ↑	**↑ as NB ↑**	**~ ↑ as NB ↑**	Mixed / ~ ↑ as NB ↑	Mixed / not discernible	↑ then ↓ as NB ↑
4F	Time since last burn	**Mixed / not discernible**	**↑ then → with ↑ TSB**	**↓ with ↑ TSB**	↑ then → with ↑ TSB	↑ then → with ↑ TSB	**↑ with ↑ TSB**	**Mixed / ~ ↑ w/ ↑ TSB**
5F	Mean time between burns	**↓ with ↑ AvgTBSB**	**Mixed / not discernible**	**Mixed / not discernible**	↓ with ↑ AvgTBSB	**Mixed / not discernible**	Mixed / not discernible	**↑ with ↑ AvgTBSB**
6T	HLI	Mixed / not discernible	Mixed / not discernible	Mixed / not discernible	Mixed / not discernible	Mixed / not discernible	Mixed / not discernible	n/a
6T-tsb	HLI [tsb]	Mixed / not discernible	Mixed / not discernible	Mixed / not discernible	Mixed / not discernible	Mixed / ~ ↑ as HLI ↑	Mixed / not discernible	n/a
7T	TWI	**Mixed / not discernible**	Mixed / not discernible	Mixed / not discernible	Mixed / not discernible	Mixed / not discernible	Mixed / not discernible	n/a
7T-tsb	TWI [tsb]	Mixed / not discernible	**Mixed / not discernible**	**Mixed / not discernible**	Mixed / not discernible	**Mixed / not discernible**	**Mixed / not discernible**	n/a
8T	TPI	**↓ then ↑ as TPI ↑**	Mixed / not discernible	Mixed / not discernible	Mixed / not discernible	Mixed / not discernible	Mixed / not discernible	n/a
8T-tsb	TPI [tsb]	↓ then ↑ as TPI ↑	↑ then ↓ as TPI ↑	Mixed / not discernible	Mixed / not discernible	Mixed / not discernible	Mixed / not discernible	n/a

Table 12. Results of all tested comparisons of response variables vs. environmental variables, including the alternate hypothesis (H_a), null hypothesis (H_0), result, statistical significance, and whether the analysis supports rejecting H_0 for each. Number of live stems: "# of live stems"; Shoot-to-root ratio: SRR. Bold "Yes" for "Stat Sig?" attribute indicates statistical significance detected at the α=0.05 level; "No" indicates no statistical significance. Corresponding detailed results can be found in Table 14 and Table 15 in the Appendix.

Env. Variable	Response Variable	Hypothesis (H_a)	Null Hyp. (H_0)	Result	Stat Sig?	Reject H_0?
(1F) Burned/ unburned	(1) Tally	Burned ≥ unburned	Burned < unburned	Burned > unburned	**Yes**	Yes
	(2) Live height (m)	Burned ≥ unburned	Burned < unburned	Burned > unburned	No	Fail
	(3) # of live stems	Burned ≥ unburned	Burned < unburned	Burned > unburned	**Yes**	Yes
	(4) Blight infection %	No sig. difference	Burned ≠ unburned	Burned > unburned	No	Yes
	(5) Total DRC (mm)	Burned ≥ unburned	Burned < unburned	Burned > unburned	No	Fail
	(6) Avg DRC (mm)	Burned ≥ unburned	Burned < unburned	Burned > unburned	No	Fail
	(7) SRR	Burned ≥ unburned	Burned < unburned	Burned > unburned	No	Fail
(2F) Canopy cover proportion (CC)	(2) Live height (m)	↑ as CC ↓	↓/→ as CC ↓	↑ as CC ↓	**Yes**	Yes
	(3) # of live stems	↓/→ as CC ↓	↑ as CC ↓	↑ as CC ↓	**Yes**	Fail
	(4) Blight infection %	↑ as CC ↓	↓/→ as CC ↓	↑ as CC ↓	**Yes**	Yes
	(5) Total DRC (mm)	↑ as CC ↓	↓/→ as CC ↓	↑ as CC ↓	**Yes**	Yes
	(6) Avg DRC (mm)	↑ as CC ↓	↓/→ as CC ↓	↑ as CC ↓	**Yes**	Yes
	(7) SRR	↑ as CC ↓	↓/→ as CC ↓	↓ as CC ↓	No	Fail
(3F) Number of burns (NB)	(1) Tally	↑/→ as NB ↑	↓ as NB ↑	↑ then ↓ as NB ↑	No	Fail

Table 12 Continued

Env. Variable	Response Variable	Hypothesis (H_a)	Null Hyp. (H_0)	Result	Stat Sig?	Reject H_0?
(3F) Number of burns (NB)	(2) Live height (m)	↑/→ as NB ↑	↓ as NB ↑	Mixed / ~ ↑ as NB ↑	No	Fail
	(3) # of live stems	↑/→ as NB ↑	↓ as NB ↑	↑ as NB ↑	**Yes**	Yes
	(4) Blight infection %	→ as NB ↑	↑↓ as NB ↑	~ ↑ as NB ↑	**Yes**	Fail
	(5) Total DRC (mm)	↑/→ as NB ↑	↓ as NB ↑	Mixed / ~ ↑ as NB ↑	No	Fail
	(6) Avg DRC (mm)	↑/→ as NB ↑	↓ as NB ↑	Mixed / not discernible	No	Yes
	(7) SRR	↑/→ as NB ↑	↓ as NB ↑	↑ then ↓ as NB ↑	No	Fail
(4F) Time since last burn (TSB)	(1) Tally	↑ then → with ↑ TSB	Not ↑, → with ↑ TSB	Mixed / not discernible	**Yes**	Fail
	(2) Live height (m)	↑ then → with ↑ TSB	Not ↑, → with ↑ TSB	↑ then → with ↑ TSB	**Yes**	Yes
	(3) # of live stems	↑ with ↑ TSB	↓ with ↑ TSB	↓ with ↑ TSB	**Yes**	Fail
	(4) Blight infection %	↑ then → with ↑ TSB	Not ↑, → with ↑ TSB	↑ then → with ↑ TSB	No	Fail
	(5) Total DRC (mm)	↑ then → with ↑ TSB	Not ↑, → with ↑ TSB	↑ then → with ↑ TSB	No	Fail
	(6) Avg DRC (mm)	↑ with ↑ TSB	↓ with ↑ TSB	↑ with ↑ TSB	**Yes**	Yes
	(7) SRR	↑ then → with ↑ TSB	Not ↑, → with ↑ TSB	Mixed / ~ ↑ with ↑ TSB	**Yes**	Fail
(5T) Mean time between successive burns (AvgTBSB)	(1) Tally	↓ with ↑ AvgTBSB	↑/→ with ↑ AvgTBSB	↓ with ↑ AvgTBSB	**Yes**	Yes
	(2) Live height (m)	↓ with ↑ AvgTBSB	↑/→ with ↑ AvgTBSB	Mixed / not discernible	**Yes**	Fail

Table 12 Continued

Env. Variable	Response Variable	Hypothesis (H_a)	Null Hyp. (H_0)	Result	Stat Sig?	Reject H_0?
(5T) Mean time between successive burns (AvgTBSB)	(3) # of live stems	↑/→ with ↑ AvgTBSB	↓ with ↑ AvgTBSB	Mixed / not discernible	**Yes**	Fail
	(4) Blight infection %	↓ with ↑ AvgTBSB	↑/→ with ↑ AvgTBSB	↓ with ↑ AvgTBSB	No	Fail
	(5) Total DRC (mm)	↓ with ↑ AvgTBSB	↑/→ with ↑ AvgTBSB	Mixed / not discernible	**Yes**	Fail
	(6) Avg DRC (mm)	↓ with ↑ AvgTBSB	↑/→ with ↑ AvgTBSB	Mixed / not discernible	No	Fail
	(7) SRR	↓ with ↑ AvgTBSB	↑/→ with ↑ AvgTBSB	↑ with ↑ AvgTBSB	**Yes**	Fail
(6T) HLI	(1) Tally	↑ as HLI ↑	↓/→ as HLI ↑	Mixed / not discernible	No	Fail
	(2) Live height (m)	↑ as HLI ↑	↓/→ as HLI ↑	Mixed / not discernible	No	Fail
	(3) # of live stems	↓/→ as HLI ↑	↑ as HLI ↑	Mixed / not discernible	No	Fail
	(4) Blight infection %	↑ as HLI ↑	↓/→ as HLI ↑	Mixed / not discernible	No	Fail
	(5) Total DRC (mm)	↑ as HLI ↑	↓/→ as HLI ↑	Mixed / not discernible	No	Fail
	(6) Avg DRC (mm)	↑ as HLI ↑	↓/→ as HLI ↑	Mixed / not discernible	No	Fail
(6T-tsb) HLI	(1) Tally	↑ as HLI ↑	↓/→ as HLI ↑	Mixed / not discernible	No	Fail
	(2) Live height (m)	↑ as HLI ↑	↓/→ as HLI ↑	Mixed / not discernible	No	Fail
	(3) # of live stems	↓/→ as HLI ↑	↑ as HLI ↑	Mixed / not discernible	No	Fail
	(4) Blight infection %	↑ as HLI ↑	↓/→ as HLI ↑	Mixed / not discernible	No	Fail
	(5) Total DRC (mm)	↑ as HLI ↑	↓/→ as HLI ↑	Mixed / ~ ↑ as HLI ↑	No	Fail
	(6) Avg DRC (mm)	↑ as HLI ↑	↓/→ as HLI ↑	Mixed / not discernible	No	Fail

Table 12 Continued

Env. Variable	Response Variable	Hypothesis (H_a)	Null Hyp. (H_0)	Result	Stat Sig?	Reject H_0?
(7T) TWI	(1) Tally	↓ as TWI ↑	↑/→ as TWI ↑	Mixed / not discernible	**Yes**	Fail
	(2) Live height (m)	↓ as TWI ↑	↑/→ as TWI ↑	Mixed / not discernible	No	Fail
	(3) # of live stems	↑/→ as TWI ↑	↓ as TWI ↑	Mixed / not discernible	No	Fail
	(4) Blight infection %	↓ as TWI ↑	↑/→ as TWI ↑	Mixed / not discernible	No	Fail
	(5) Total DRC (mm)	↓ as TWI ↑	↑/→ as TWI ↑	Mixed / not discernible	No	Fail
	(6) Avg DRC (mm)	↓ as TWI ↑	↑/→ as TWI ↑	Mixed / not discernible	No	Fail
(7T-tsb) TWI	(1) Tally	↓ as TWI ↑	↑/→ as TWI ↑	Mixed / not discernible	No	Fail
	(2) Live height (m)	↓ as TWI ↑	↑/→ as TWI ↑	Mixed / not discernible	**Yes**	Fail
	(3) # of live stems	↑/→ as TWI ↑	↓ as TWI ↑	Mixed / not discernible	**Yes**	Yes
	(4) Blight infection %	↓ as TWI ↑	↑/→ as TWI ↑	Mixed / not discernible	No	Fail
	(5) Total DRC (mm)	↓ as TWI ↑	↑/→ as TWI ↑	Mixed / not discernible	**Yes**	Fail
	(6) Avg DRC (mm)	↓ as TWI ↑	↑/→ as TWI ↑	Mixed / not discernible	**Yes**	Fail
(8T) TPI	(1) Tally	↑ as TPI ↑	↓/→ as TPI ↑	↓ then ↑ as TPI ↑	**Yes**	Fail
	(2) Live height (m)	↑ as TPI ↑	↓/→ as TPI ↑	Mixed / not discernible	No	Fail
	(3) # of live stems	↑ as TPI ↑	↓/→ as TPI ↑	Mixed / not discernible	No	Fail
	(4) Blight infection %	↑ as TPI ↑	↓/→ as TPI ↑	Mixed / not discernible	No	Fail
	(5) Total DRC (mm)	↑ as TPI ↑	↓/→ as TPI ↑	Mixed / not discernible	No	Fail

Table 12 Continued

Env. Variable	Response Variable	Hypothesis (H_a)	Null Hyp. (H_0)	Result	Stat Sig?	Reject H_0?
(8T) TPI	(6) Avg DRC (mm)	↑ as TPI ↑	↓/→ as TPI ↑	Mixed / not discernible	No	Fail
(8T-tsb) TPI	(1) Tally	↑ as TPI ↑	↓/→ as TPI ↑	↓ then ↑ as TPI ↑	No	Fail
	(2) Live height (m)	↑ as TPI ↑	↓/→ as TPI ↑	↑ then ↓ as TPI ↑	No	Fail
	(3) # of live stems	↑ as TPI ↑	↓/→ as TPI ↑	Mixed / not discernible	No	Fail
	(4) Blight infection %	↑ as TPI ↑	↓/→ as TPI ↑	Mixed / not discernible	No	Fail
	(5) Total DRC (mm)	↑ as TPI ↑	↓/→ as TPI ↑	Mixed / not discernible	No	Fail
	(6) Avg DRC (mm)	↑ as TPI ↑	↓/→ as TPI ↑	Mixed / not discernible	No	Fail

4. CONCLUSIONS

4.1 Chestnut Response to Fire

The results of this study suggest a complex pattern of American chestnut sprout regeneration in response to fire, with some response variables more or less important in explaining the effect of each fire regime environmental variable. Among the response variables that appear to be positively related to chestnut vitality [(1) Tally, (2) Live height, (3) Number of live stems, (5) Total DRC, and (6) Average DRC], there was no indication that increasing fire severity, occurrence, and/or frequency was a detriment to chestnut vitality. Conversely, there was no indication that increasing fire severity, occurrence, and/or frequency reduced the prevalence of (4) Blight infection, negatively related to chestnut vitality. Chestnut response as quantified by (7) Shoot-to-root ratio provided further information to evaluate chestnut's response to fire.

More chestnut trees and chestnuts with more live stems were found in burned than in unburned transect sections (Table 4 and Figure 15), suggesting that fire is beneficial to chestnut abundance and elicits more vigorous re-sprouting than in undisturbed areas. However, the lack of significant differences detected for the remaining response variables (Table 4) indicates that other environmental factors have a stronger influence on them than the dichotomous effect of burning, particularly in regards to live height, total DRC, and average DRC which are significantly negatively correlated with canopy cover proportion (Table 14 and Table 15 in the Appendix). This pattern is unsurprising given what we know of chestnut's strong response to light aboveground (Paillet, 1982, 1984; Griffin, 1989; Paillet and Rutter, 1989; Billo, 1998; Paillet, 2002; Jacobs and Severeid, 2004; McEwan *et al.*, 2006; Clark *et al.*, 2010; Clark *et al.*, 2012a) and allocation of resources in different light environments (Paillet, 1982; Wang *et al.*, 2006; Anagnostakis, 2007; Joesting *et al.*, 2009). Presence of chestnut blight not being significantly different in burned vs. unburned sections (Table 4) but being significantly negatively correlated with canopy cover (Table 14 and Table 15 in the Appendix) also supports previous studies of blight prevalence in high light environments (Griffin *et al.*, 1991). The ability of chestnut to resist chestnut blight may be impaired by the increased proportion of resources devoted to stem growth in response to high light availability (Latham, 1992). From this evidence (or lack thereof), we can see that the occurrence of fire only begins to explain the patterns observed.

Number of live stems increasing with increasing light was contrary to expectations as it was thought that chestnut would prefer singular stem growth at the expense of the overall number of stems in high light environments. This result suggests a more even growth pattern (i.e. less relative importance of height) with increasing light than was expected. As was a common sight in the field, chestnuts under open canopies were not only taller than chestnuts under closed canopies, but were also wider with more stems. These growth patterns, at least in the early stages of succession, suggest that the more open canopy conditions created by more severe prescribed burns and wildfires are beneficial to chestnut establishing dominance, but also may cause chestnut sprouts to be more susceptible to blight. It remains unclear whether the advantage of increased growth offsets the disadvantage of decreased health and under what environmental conditions. Other factors in relation to fire must be considered, however, as canopy cover alone does not determine the importance of fire in creating an environment conducive to chestnut growth.

The non-significant effects of number of burns on chestnut abundance, height, stem diameter, and shoot-to-root ratio in conjunction with the significant, positive effect on number of live stems (Table 5) suggests that repeated fire occurrence is not necessarily a detriment to chestnut vitality. If repeated fire occurrence impaired the re-sprouting ability of chestnut, we would expect a negative relationship with increasing number of burns. Simultaneously, as with canopy cover, blight infection generally increased with increasing number of burns. Therefore, even if chestnut sprouting is not negatively affected by repeated fire occurrence, its susceptibility to blight may be. These statistically significant results should be interpreted with caution, however, due to the low sample size of the category with the most burns (n=9). Future work with a more even distribution of sample sizes between areas burned various numbers of times will provide better insights into how repeated fire occurrence affects chestnut vitality.

In addition to being a variable by which other response variables can be standardized, time since last burn is an environmental variable itself for evaluating chestnut response to fire, providing a temporal view of chestnut growth patterns following fire. There were no significant differences among time since last burn classes only for blight infection (unlike with number of burns) and total DRC (as with number of burns), suggesting that these responses may not necessarily increase linearly over time and that other factors (e.g. canopy cover) have a larger influence on them, particularly in later stages of succession. The resources chestnut root systems must devote to frequent re-sprouting due to mortality caused by blight is likely altering their development, as indicated by no clear trend over time found with total stem diameter. The growth patterns varied significantly for the remaining response variables with time since last burn. With chestnut abundance, there was no clearly discernible pattern with increasing time since burn, though there did seem to be a general decrease over time (Figure 21). Lower abundance in later time classes may suggest the decreased competitive ability of chestnut when the canopy eventually closes following a moderate to severe fire that opened the canopy. In contrast to the pattern observed with canopy cover where both live height and number of live stems significantly increased with increasing light, the direction of the response varied for these two variables with increasing time since burn with canopy cover held constant: live height generally increased (may be leveling off toward the end) while number of live stems decreased (Figure 22). This would suggest that chestnut focuses its growth over time on its main stem at the expense of the smaller stems that sprouted around it soon after the last fire. This pattern is further supported by the significant positive relationships found with average stem diameter and shoot-to-root ratio. The picture that emerges of chestnut growth following fire is one of (a) initial vigorous re-sprouting with many stems, but (b) eventual concentration of growth in the main stem as expressed by increasing height and average stem diameter but no change in total stem diameter.

Response differences among mean time between successive burns classes for areas burned multiple times provide insights into how chestnut vitality is affected by varying fire return intervals. If more frequent fire was a detriment to chestnut vitality, impairing the species' ability to re-sprout following fire, we would expect a positive relationship between chestnut response and time between burns. Due to the nature of the burn history of the areas sampled for this project and associated sample sizes in different classes, the most meaningful classification of time between burns (three classes based on average growing seasons; Table 1) also made it difficult to determine trends in relation to each response variable. Though all comparisons were significant except for blight infection and average DRC, clear trends were only apparent with tally and shoot-to-root ratio (Table 7). There is not enough information to determine whether the significant differences detected for live height, number of live stems, and total DRC are positively or negatively related to time between burns. While there was no significant relationship for blight infection, chestnut abundance decreased with increasing time between burns (Figure 24), suggesting that infrequent fire may actually hinder the chances of chestnut success. Conversely, shoot-to-root ratio increased with increasing time between burns (Figure 26), appearing to mirror the growth strategy apparent with increasing time since last burn of increasing investment in the main stem.

4.2 Influence of Terrain

Unlike with the response patterns observed in relation to fire regime, there were few significant relationships between chestnut vitality and the DEM-derived GIS terrain variables. Even with the most meaningful classification of each terrain variable, there was often no discernible trend with increasing heat load, topographic moisture, and slope position. This absence of a clear pattern suggests that chestnut is well adapted to a variety of slope positions and environmental conditions, supporting the historical accounts we have of the former dominance of chestnut in the eastern deciduous forest across the landscape. Despite the broad niche of chestnut, however, a few clues remain from the comparisons across terrain conditions that may indicate where chestnut performs the best. It is important to consider the influence of terrain in American chestnut restoration, for even the best management prescriptions may fail to produce the desired result if applied in the wrong places.

There were no significant differences for any response variable comparisons with Heat Load Index (HLI) (Table 8), whether standardized by canopy cover and time since burn or not. While it was expected that transect sections on slopes and aspects receiving higher direct incident radiation would have larger and more abundant chestnuts, chestnuts sampled in this project showed no preference for such portions of the landscape. Such a result underscores the importance of canopy openness to chestnut sprout success, as chestnuts cannot benefit from increased sunshine under closed canopies. In this scenario trapped in low light conditions, chestnuts on gentle, southwest-facing aspects at lower latitudes would show no different growth patterns than chestnuts on steep, northeast-facing aspects at higher latitudes. While canopy cover still appears to be the largest single controlling factor of chestnut growth as the tree exists today, Heat

Load Index may prove more useful in evaluating chestnut response when restoration enables blight-resistant chestnuts to reach the canopy in the future.

Wetter parts of the landscape with larger upslope contributing areas lining drainages and riparian corridors were expected to have fewer and smaller chestnut sprouts due to the increased competition from mesophytic vegetation. However, even among the comparisons with significant differences for Topographic Wetness Index (TWI) (tally and each except for tally and blight infection with time since burn sub-classes), there were no discernible patterns (Table 9). While several of the largest chestnut responses were found in the lowest TWI class, the decrease from class 1 to 2 did not continue as the classes increased [this may suggest the influence of outliers in class 1 with a small sample size (n=9)]. The same lack of relationship existed correspondingly with Topographic Position Index (TPI), but with one notable, statistically significant exception (Table 10). Though chestnut abundance was higher in valleys than lower slopes, it steadily increased with increasing slope position thereafter (minus flat areas, which were nearly non-existent among the transect sections sampled) (Figure 30). This result suggests that chestnut can adapt to sheltered environments but is better suited to the more exposed parts of a mountainous landscape: upper slopes and ridges. Such portions of the landscape are also less conducive to root rot caused by ink disease, which has less tolerance for drier, colder conditions found at higher elevations (Rhoades *et al.*, 2003). Therefore, even if chestnut sprouts on upper slopes and ridges do not grow taller and larger than chestnuts at lower slope positions, their increased abundance in these portions of the landscape suggest the importance of implementing management prescriptions there (cf. Griscom and Griscom, 2012). With the right prescriptions implemented to maintain canopy conditions favorable to chestnut in its early stages of growth, it would be expected that chestnuts in areas of higher heat load would be more successful in reaching the canopy.

4.3 Conclusions and Management Implications

Based on the evidence presented, the primary takeaways from this study can be summarized as follows:

- American chestnut vitality in early stages of growth is strongly controlled by light environment, with the tallest and largest chestnuts found in the most open canopy conditions.
- The more open canopy conditions (and potentially injuries sustained) caused by more severe fire results in a higher incidence of chestnut blight infection.
- Fire regime, and resulting canopy conditions, have a greater effect on chestnut vitality than the surrounding topography.
- American chestnuts are the most abundant at the highest slope positions, and terrain should be considered in restoration efforts to maximize the benefits of management prescriptions.
- High fire severity, occurrence, and/or frequency does not necessarily harm chestnut, and can benefit chestnut by opening the canopy and removing competition.

The lack of a significant relationship between canopy cover and shoot-to-root ratio (SRR) suggests that chestnut root systems (and thereby re-sprouting ability) may be harmed by injuries sustained from repeated and/or severe fire: chestnut may not be able to allocate adequate resources to belowground growth in low light environments before and after fires that do not significantly increase the light available that are commensurate to the resources it allocates to aboveground growth in high light environments. If a fire does not open the canopy enough such that chestnut can capitalize with its aboveground response, there may be little to no benefit of fire to chestnut. Ultimately, the light environment both before and after prescribed burning must be carefully considered when determining how and when to implement fire in stands of planted blight-resistant chestnut, and with what other management prescriptions to use it with. For example, it may not be desirable or feasible to remove the canopy of a mature forest through severe fire or a clearcut in many areas prior to planting due to the high costs and risks involved. Silvicultural treatments such as a shelterwood harvest with midstory removal, however, can be adequately effective in increasing the light environment for chestnuts while also keeping competition in check (Belair, 2014). Therefore, there may be some advantages in establishing chestnut seedlings in stands of low understory competition but full canopies (Griscom and Griscom, 2012). To maximize the chances of successful blight-resistant chestnut establishment, management strategy should focus on the following within the existing forest mosaic:

- Creating canopy gaps through selective harvesting where needed to stimulate initial chestnut growth.

- Keeping understory mesophytic vegetation in check in xerophytic environments through periodic surface prescribed fire.

Future work of the effects of fire on chestnut will provide further insights into how, when, and where various fire severities and frequencies should be applied to planted chestnut seedlings.

4.4 Future Work

The work presented here and of McCament and McCarthy (2005), Belair (2014), Clark et al. (2014b), and Jarrett et al. (2016) is only the beginning of research in chestnut fire ecology and geography. The insights that we have gained from these studies provide the theoretical and methodological framework to conduct more rigorous and complex analyses over longer periods of time that will allow us to determine the precise effects of varying characteristics of fire on pure, hybrid, planted, and extant chestnut growth, health, dispersal, and survival in varying landscapes, climates, forest types, soils, and with varying moisture and nutrient availability. Direct comparisons with other tree species, knowing the existing biomass prior to burning, utilizing a plot-based approach, and establishing long-term monitoring plots will minimize extraneous factors and make comparisons more meaningful, i.e. a truer reflection of reality. The short temporal nature of extant chestnut sprout dieback and regrowth will require tightly-controlled and frequent sampling to detect small variations in chestnut vitality that might not otherwise be detected. Research should be conducted at a variety of scales from fine-scale physiology to regional-scale climatology, and at all scales in between. The interacting effects of other types of natural and anthropogenic disturbances besides fire such as insect outbreaks, deer browse, invasive species, drought, and extreme weather events must also be considered. Specifically, future work should address the following questions:

- Does increased light availability necessarily lead to greater establishment and dominance at all stages of growth?
- If chestnut is more susceptible to harmful pathogens in higher light environments, are larger chestnuts better or less able to resist them and ultimately survive?
- Are there ways to alter burning techniques prescribed for oak-dominated forests to improve habitat conditions for chestnut while still maintaining the benefits for oak species?
- Do some life history characteristics of chestnut conferring an advantage in frequently and/or severely burned environments (e.g. vigorous sprouting ability, prolific early growth in response to light) compensate for others that may be a disadvantage (e.g. shallower dormant buds than oak, thinner bark)? If so, how and at what levels of fire severity and frequency and in what stages of growth?
- Do chestnut leaves more facilitate or impede burning? If the former, how do the presence and density of chestnuts influence the behavior of fire in a particular stand?

- How long of a fire-free period under what light environment(s) is required for chestnut to gain dominance before chestnut is sufficiently able to survive what severities of fire?
- When chestnut reaches sexual maturity, is chestnut more successful reproducing with increased growth in higher light environments or moderate growth in moderate light environments? I.e. does the preferential allocation of resources to stem growth in high light environments diminish resources that would have otherwise been utilized for flowering and fruiting?

As we begin to answer these questions, let us always maintain a sense of awe for the majestic tree that the American chestnut was, is, and will be, and that our efforts are only a small part of a much larger story.

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Table 13. TPI classification using different circular window radii.

	r = 10 m		r = 25 m		r = 50 m		r = 100 m	
	Mean	0.00	**Mean**	0.00	**Mean**	0.00	**Mean**	0.00
	SD	0.21	**SD**	0.89	**SD**	1.89	**SD**	5.08
	Min	-12.21	**Min**	-16.38	**Min**	-21.21	**Min**	-36.81
	Max	13.17	**Max**	14.73	**Max**	20.09	**Max**	40.58
Class	**Lower**	**Upper**	**Lower**	**Upper**	**Lower**	**Upper**	**Lower**	**Upper**
1	-12.21	-0.21	-16.38	-0.89	-21.21	-1.89	-36.81	-5.08
2	-0.21	-0.11	-0.89	-0.45	-1.89	-0.95	-5.08	-2.54
3	-0.11	0.11	-0.45	0.45	-0.95	0.95	-2.54	2.54
4	-0.11	0.11	-0.45	0.45	-0.95	0.95	-2.54	2.54
5	0.11	0.21	0.45	0.89	0.95	1.89	2.54	5.08
6	0.21	13.17	0.89	14.73	1.89	20.09	5.08	40.58
	r = 250 m		**r = 500 m**		**r = 1000 m**		**r = 2000 m**	
	Mean	0.01	**Mean**	0.03	**Mean**	0.06	**Mean**	-0.11
	SD	12.50	**SD**	23.12	**SD**	40.60	**SD**	64.20
	Min	-75.67	**Min**	-118.14	**Min**	-173.41	**Min**	-239.89
	Max	91.54	**Max**	161.13	**Max**	251.06	**Max**	343.04
Class	**Lower**	**Upper**	**Lower**	**Upper**	**Lower**	**Upper**	**Lower**	**Upper**
1	-75.67	-12.49	-118.14	-23.09	-173.41	-40.54	-239.89	-64.31
2	-12.49	-6.24	-23.09	-11.53	-40.54	-20.24	-64.31	-32.21
3	-6.24	6.26	-11.53	11.59	-20.24	20.36	-32.21	31.99
4	-6.24	6.26	-11.53	11.59	-20.24	20.36	-32.21	31.99
5	6.26	12.51	11.59	23.15	20.36	40.66	31.99	64.09
6	12.51	91.54	23.15	161.13	40.66	251.06	64.09	343.04

Table 13 Continued

	r = 5000 m		r = 10000 m	
	Mean	-1.45	**Mean**	-6.83
	SD	109.89	**SD**	152.79
	Min	-247.08	**Min**	-303.93
	Max	488.85	**Max**	568.04
Class	**Lower**	**Upper**	**Lower**	**Upper**
1	-247.08	-111.34	-303.93	-159.62
2	-111.34	-56.40	-159.62	-83.23
3	-56.40	53.50	-83.23	69.57
4	-56.40	53.50	-83.23	69.57
5	53.50	108.44	69.57	145.96
6	108.44	488.85	145.96	568.04

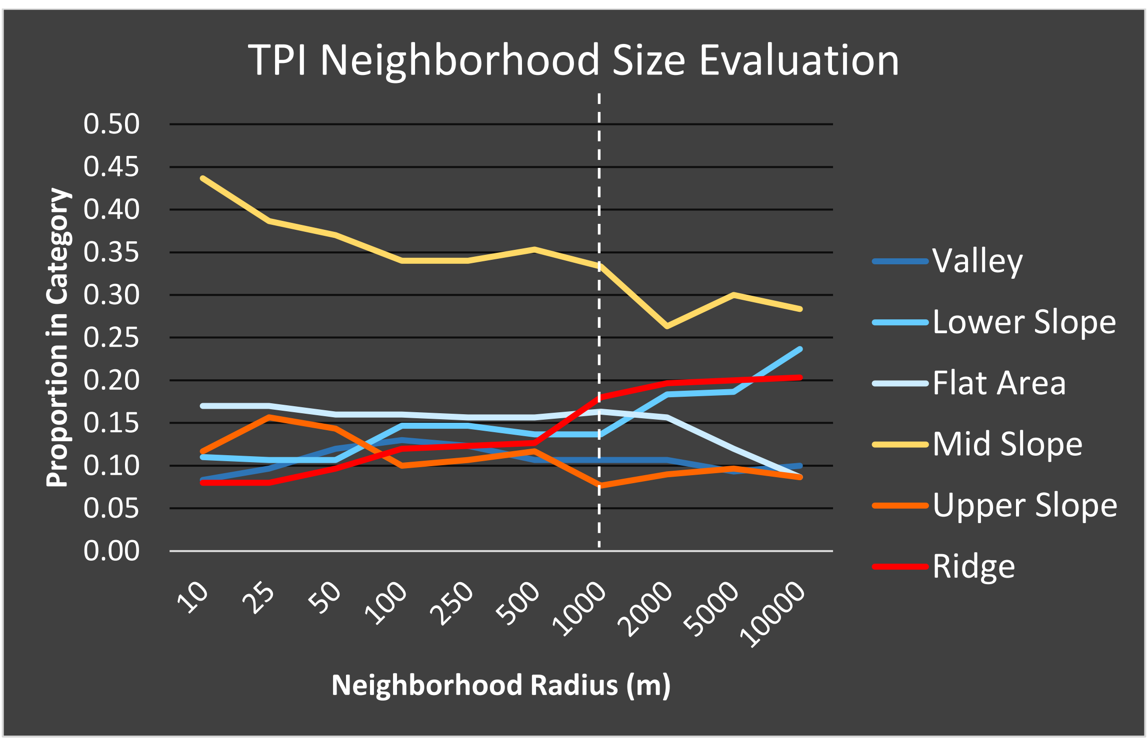

Figure 31. Proportion of landscape in each TPI class with increasing radius size. White vertial dotted line indicates radius selected.

Table 14. All tested comparisons of response variables vs. environmental variables, including whether each met parametric test assumptions and the statistical test for significance used. Fire regime environmental variables: 1F, 2F, 3F, 4F, and 5F. DEM-derived GIS terrain variables: 6T, 6T-tsb, 7T, 7T-tsb, 8T, and 8T-tsb. "F" refers to fire regime variables, "T" refers to terrain variables, and "-tsb" refers to sub-categorization by burned sections sampled 3-5 average growing seasons (AGS) since last burn (tsb: time since burn). Live height: LH, Number of live stems: NLS, Blight infection: BI, Total DRC: TDRC, Average DRC: ADRC, and Shoot-to-root ratio: SRR. * denotes response variable was standardized by section length (added 1 to avoid zeros) (*SL+1), time since last burn (*TSB), both section length and time since burn (*DTSB+1), or canopy cover proportion (*CC). Unique comparison code is a unique identifier assigned to each comparison of a response variable vs. an environmental variable. "Meet parametric?" attribute indicates whether the untransformed response variable met the assumptions of normality and homoscedasticity required to use parametric tests or for Poisson and logistic regression, whether the data was not over-dispersed. "Meet w/ transformation?" attribute indicates whether a transformed response variable met the same assumptions, with the transformation used in parentheses if the answer was yes.

Environmental Variable	Response Variable (*std)	Unique Comparison Code	Meet para-metric?	Meet w/ transfor-mation?	Statistical Test Used
(1F) Burned/ unburned	(1) Tally (*SL+1)	1Fx1-SL	n/a	n/a	Gamma regression
	(2) LH	1Fx2	No	Yes (Log)	Independent t-test
	(3) NLS	1Fx3	Yes	n/a	Poisson regression
	(4) BI	1Fx4	Yes	n/a	Logistic regression
	(5) TDRC	1Fx5	No	No	Mann-Whitney U test
	(6) ADRC	1Fx6	No	Yes (Sqrt)	Independent t-test
	(7) SRR	1Fx7	No	Yes (Log)	Independent t-test
(2F) Canopy cover proportion (CCP)	(2) LH (*TSB)	2Fx2-TSB	No	n/a	Spearman correlation

Table 14 Continued

Environmental Variable	Response Variable (*std)	Unique Comparison Code	Meet para-metric?	Meet w/ transfor-mation?	Statistical Test Used
(2F) Canopy cover proportion (CCP)	(3) NLS (*TSB)	2Fx3-TSB	No	n/a	Spearman correlation
	(4) BI	2Fx4	Yes	n/a	Logistic regression
	(5) TDRC (*TSB)	2Fx5-TSB	No	n/a	Spearman correlation
	(6) ADRC (*TSB)	2Fx6-TSB	No	n/a	Spearman correlation
	(7) SRR (*TSB)	2Fx7-TSB	No	n/a	Spearman correlation
(3F) Number of burns (NB)	(1) Tally (*SL+1)	3Fx1-SL	n/a	n/a	Gamma regression
	(2) LH	3Fx2	No	Yes (Log)	One-way ANOVA
	(3) NLS	3Fx3	No	n/a	Quasipoisson regression
	(4) BI	3Fx4	Yes	n/a	Logistic regression
	(5) TDRC	3Fx5	No	No	Kruskal-Wallis test
	(6) ADRC	3Fx6	No	No	Kruskal-Wallis test
	(7) SRR	3Fx7	No	Yes (Log)	One-way ANOVA
(4F) Time since last burn (TSB)	(1) Tally (*SL+1)	4Fx1-SL	n/a	n/a	Gamma regression
	(2) LH (*CC)	4Fx2-CC	No	No	Kruskal-Wallis test
	(3) NLS (*CC)	4Fx3-CC	No	No	Kruskal-Wallis test
	(4) BI	4Fx4	Yes	n/a	Logistic regression

Table 14 Continued

Environmental Variable	Response Variable (*std)	Unique Comparison Code	Meet para-metric?	Meet w/ transfor-mation?	Statistical Test Used
(4F) Time since last burn (TSB)	(5) TDRC (*CC)	4Fx5-CC	No	No	Kruskal-Wallis test
	(6) ADRC (*CC)	4Fx6-CC	No	No	Kruskal-Wallis test
	(7) SRR (*CC)	4Fx7-CC	No	Yes (Log)	One-way ANOVA
(5F) Mean time between successive burns (AvgTBSB)	(1) Tally (*DTSB+1)	5Fx1-DTSB	n/a	n/a	Gamma regression
	(2) LH	5Fx2	No	No	Kruskal-Wallis test
	(3) NLS	5Fx3	No	n/a	Quasipoisson regression
	(4) BI	5Fx4	Yes	n/a	Logistic regression
	(5) TDRC	5Fx5	No	Yes (Log)	One-way ANOVA
	(6) ADRC	5Fx6	Yes	n/a	One-way ANOVA
	(7) SRR	5Fx7	No	No	Kruskal-Wallis test
(6T) HLI	(1) Tally (*SL+1)	6Tx1-SL	n/a	n/a	Gamma regression
	(2) LH	6Tx2	No	No	Kruskal-Wallis test
	(3) NLS	6Tx3	No	n/a	Quasipoisson regression
	(4) BI	6Tx4	Yes	n/a	Logistic regression
	(5) TDRC	6Tx5	No	No	Kruskal-Wallis test
	(6) ADRC	6Tx6	No	No	Kruskal-Wallis test

Table 14 Continued

Environmental Variable	Response Variable (*std)	Unique Comparison Code	Meet para-metric?	Meet w/ transfor-mation?	Statistical Test Used
(6T-tsb) HLI	(1) Tally (*SL+1)	6T-tsbx1-SL	n/a	n/a	Gamma regression
	(2) LH (*CC)	6T-tsbx2-CC	No	No	Kruskal-Wallis test
	(3) NLS (*CC)	6T-tsbx3-CC	No	No	Kruskal-Wallis test
	(4) BI	6T-tsbx4	Yes	n/a	Logistic regression
	(5) TDRC (*CC)	6T-tsbx5-CC	No	No	Kruskal-Wallis test
	(6) ADRC (*CC)	6T-tsbx6-CC	No	No	Kruskal-Wallis test
(7T) TWI	(1) Tally (*SL+1)	7Tx1-SL	n/a	n/a	Gamma regression
	(2) LH	7Tx2	No	No	Kruskal-Wallis test
	(3) NLS	7Tx3	No	n/a	Quasipoisson regression
	(4) BI	7Tx4	Yes	n/a	Logistic regression
	(5) TDRC	7Tx5	No	No	Kruskal-Wallis test
	(6) ADRC	7Tx6	No	No	Kruskal-Wallis test
(7T-tsb) TWI	(1) Tally (*SL+1)	7T-tsbx1-SL	n/a	n/a	Gamma regression
	(2) LH (*CC)	7T-tsbx2-CC	No	Yes (Log)	One-way ANOVA
	(3) NLS (*CC)	7T-tsbx3-CC	No	No	Kruskal-Wallis test
	(4) BI	7T-tsbx4	Yes	n/a	Logistic regression

Table 14 Continued

Environmental Variable	Response Variable (*std)	Unique Comparison Code	Meet para-metric?	Meet w/ transfor-mation?	Statistical Test Used
(7T-tsb) TWI	(5) TDRC (*CC)	7T-tsbx5-CC	No	No	Kruskal-Wallis test
	(6) ADRC (*CC)	7T-tsbx6-CC	No	No	Kruskal-Wallis test
(8T) TPI	(1) Tally (*SL+1)	8Tx1-SL	n/a	n/a	Gamma regression
	(2) LH	8Tx2	No	No	Kruskal-Wallis test
	(3) NLS	8Tx3	No	n/a	Quasipoisson regression
	(4) BI	8Tx4	Yes	n/a	Logistic regression
	(5) TDRC	8Tx5	No	No	Kruskal-Wallis test
	(6) ADRC	8Tx6	No	No	Kruskal-Wallis test
(8T-tsb) TPI	(1) Tally (*SL+1)	8T-tsbx1-SL	n/a	n/a	Gamma regression
	(2) LH (*CC)	8T-tsbx2-CC	No	No	Kruskal-Wallis test
	(3) NLS (*CC)	8T-tsbx3-CC	No	Yes (Log)	One-way ANOVA
	(4) BI	8T-tsbx4	Yes	n/a	Logistic regression
	(5) TDRC (*CC)	8T-tsbx5-CC	No	No	Kruskal-Wallis test
	(6) ADRC (*CC)	8T-tsbx6-CC	No	No	Kruskal-Wallis test

Table 15. Detailed results of all tested comparisons of response variables vs. environmental variables, including what transformation was used (if any), the statistical test for significance used, and the test statistic/estimate and p-value for that test. Unique comparison code refers to the unique identifier assigned to each comparison of a response variable vs. an environmental variable in Table 14. Bold p-values indicate significance at the α=0.05 level. "Significant pairwise comparisons" attribute indicates which classes were significantly different than the other class in the comparison pair of two classes at a time.

Unique Comparison Code	Trans-formation Used	Statistical Test Used	Test statistic/ estimate	p-value	Significant pairwise comparisons
1Fx1-SL	None	Gamma regression	-0.12172	**0.00**	n/a
1Fx2	Natural log	Independent t-test	-0.84781	0.40	n/a
1Fx3	None	Poisson regression	0.4161	**0.02**	n/a
1Fx4	None	Logistic regression	0.5322	0.62	n/a
1Fx5	None	Mann-Whitney U test	1040.5	0.77	n/a
1Fx6	Square root	Independent t-test	0.13565	0.89	n/a
1Fx7	Natural log	Independent t-test	-0.47715	0.63	n/a
2Fx2-TSB	None	Spearman correlation	-0.3661292	**0.00**	n/a
2Fx3-TSB	None	Spearman correlation	-0.3741365	**0.00**	n/a
2Fx4	None	Logistic regression	-1.3721	**0.02**	n/a
2Fx5-TSB	None	Spearman correlation	-0.4180592	**0.00**	n/a
2Fx6-TSB	None	Spearman correlation	-0.2940619	**0.00**	n/a
2Fx7-TSB	None	Spearman correlation	0.05733876	0.40	n/a

Table 15 Continued

Unique Comparison Code	Trans-formation Used	Statistical Test Used	Test statistic/ estimate	p-value	Significant pairwise comparisons
3Fx1-SL	None	Gamma regression	-0.00674	0.16	n/a
3Fx2	Natural log	One-way ANOVA	1.62	0.20	n/a
3Fx3	None	Quasipoisson regression	0.1878	**0.00**	n/a
3Fx4	None	Logistic regression	0.5375	**0.00**	n/a
3Fx5	None	Kruskal-Wallis test	5.0122	0.29	n/a
3Fx6	None	Kruskal-Wallis test	7.1735	0.13	n/a
3Fx7	Natural log	One-way ANOVA	1.541	0.22	n/a
4Fx1-SL	None	Gamma regression	0.012157	0.01	n/a
4Fx2-CC	None	Kruskal-Wallis test	26.659	0.00	Between **1-3**, **2-3**, **2-5**, **3-4**
4Fx3-CC	None	Kruskal-Wallis test	35.209	0.00	Between **2-4**, **2-5**, **3-5**
4Fx4	None	Logistic regression	0.113	0.49	n/a
4Fx5-CC	None	Kruskal-Wallis test	4.2663	0.37	n/a
4Fx6-CC	None	Kruskal-Wallis test	42.173	0.00	Between ALL except 3-4
4Fx7-CC	Natural log	One-way ANOVA	7.07	0.00	Between **2-3**, **2-4**, **2-5**
5Fx1-DTSB	None	Gamma regression	0.020987	**0.00**	n/a
5Fx2	None	Kruskal-Wallis test	6.3095	**0.04**	Between **2-3**

Table 15 Continued

Unique Comparison Code	Trans-formation Used	Statistical Test Used	Test statistic/ estimate	p-value	Significant pairwise comparisons
5Fx3	None	Quasipoisson regression	-0.2636	**0.03**	n/a
5Fx4	None	Logistic regression	-0.5076	0.15	n/a
5Fx5	Natural log	One-way ANOVA	3.547	**0.03**	Between **1-3**, **2-3**
5Fx6	None	One-way ANOVA	0.726	0.49	n/a
5Fx7	None	Kruskal-Wallis test	6.2881	**0.04**	Between **1-3**
6Tx1-SL	None	Gamma regression	-0.001223	0.74	n/a
6Tx2	None	Kruskal-Wallis test	7.4325	0.19	n/a
6Tx3	None	Quasipoisson regression	-0.04304	0.27	n/a
6Tx4	None	Logistic regression	0.1591	0.20	n/a
6Tx5	None	Kruskal-Wallis test	6.1993	0.29	n/a
6Tx6	None	Kruskal-Wallis test	5.8539	0.32	n/a
6T-tsbx1-SL	None	Gamma regression	-0.002726	0.52	n/a
6T-tsbx2-CC	None	Kruskal-Wallis test	6.8968	0.23	n/a
6T-tsbx3-CC	None	Kruskal-Wallis test	6.4909	0.26	n/a
6T-tsbx4	None	Logistic regression	0.06843	0.73	n/a
6T-tsbx5-CC	None	Kruskal-Wallis test	7.3995	0.19	n/a

Table 15 Continued

Unique Comparison Code	**Trans-formation Used**	**Statistical Test Used**	**Test statistic/ estimate**	**p-value**	**Significant pairwise comparisons**
6T-tsbx6-CC	None	Kruskal-Wallis test	4.6128	0.46	n/a
7Tx1-SL	None	Gamma regression	-0.008552	**0.02**	n/a
7Tx2	None	Kruskal-Wallis test	2.2469	0.81	n/a
7Tx3	None	Quasipoisson regression	0.0187	0.62	n/a
7Tx4	None	Logistic regression	-0.1158	0.32	n/a
7Tx5	None	Kruskal-Wallis test	1.9044	0.86	n/a
7Tx6	None	Kruskal-Wallis test	10.608	0.06	n/a
7T-tsbx1-SL	None	Gamma regression	-0.0001236	0.97	n/a
7T-tsbx2-CC	Natural log	One-way ANOVA	3.44	**0.01**	Between **1-4**, **1-5**
7T-tsbx3-CC	None	Kruskal-Wallis test	14.373	**0.01**	Between **1-4**, **1-5**, **1-6**
7T-tsbx4	None	Logistic regression	-0.1873	0.27	n/a
7T-tsbx5-CC	None	Kruskal-Wallis test	15.305	**0.01**	Between **1-3**, **1-4**, **1-5**, **1-6**
7T-tsbx6-CC	None	Kruskal-Wallis test	14.853	**0.01**	Between **1-4**
8Tx1-SL	None	Gamma regression	-0.019392	**0.00**	n/a
8Tx2	None	Kruskal-Wallis test	4.6759	0.32	n/a
8Tx3	None	Quasipoisson regression	0.005783	0.89	n/a

Table 15 Continued

Unique Comparison Code	Trans-formation Used	Statistical Test Used	Test statistic/ estimate	p-value	Significant pairwise comparisons
8Tx4	None	Logistic regression	0.09636	0.48	n/a
8Tx5	None	Kruskal-Wallis test	3.1801	0.53	n/a
8Tx6	None	Kruskal-Wallis test	2.1253	0.71	n/a
8T-tsbx1-SL	None	Gamma regression	-0.006792	0.08	n/a
8T-tsbx2-CC	None	Kruskal-Wallis test	5.6387	0.23	n/a
8T-tsbx3-CC	Natural log	One-way ANOVA	1.202	0.28	n/a
8T-tsbx4	None	Logistic regression	0.1914	0.30	n/a
8T-tsbx5-CC	None	Kruskal-Wallis test	5.4066	0.25	n/a
8T-tsbx6-CC	None	Kruskal-Wallis test	3.3879	0.50	n/a