

# Resurrecting the Lost Flames of American Chestnut

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## ABSTRACT

Loss of native foundation tree species to introduced pests profoundly alters the structure and function of many forest ecosystems. Recent advances to resurrect or prevent the loss of species by developing resistant hybrids hold promise, but uncertainty remains about the potential impacts of introducing a novel genotype on ecological processes, such as fire. A classic example of a non-native, pathogen-caused loss of a foundation species is American chestnut (*Castanea dentata*), a species now functionally extinct from the eastern US but undergoing experimental trials to resurrect the species with a putatively disease-resistant genotype. We compared the litter flammability among American chestnut, Chinese chestnut (*C. mollissima*), and a population of first intercross, third-generation backcrossed hybrid (BC<sub>3</sub>F<sub>2</sub>) using laboratory burning experiments. Litter flammability of American chestnut was consistently greater than Chinese chestnut, whereas the hybrid had an intermediate flammability or more closely resembled Chinese chestnut flammability by some mea-

asures. Greater flammability in American chestnut was associated with a longer leaf structure with greater curling when dry. American chestnut had flammability properties consistent with other pyrophytic species present in contemporary fire-prone ecosystems. The loss of American chestnut may have altered litter flammability of some eastern US forest ecosystems, a result more commonly associated with compositional changes in conjunction with fire exclusion and other disturbances. Resurrecting American chestnut with a hybrid genotype may mitigate this change in areas where less flammable species have replaced American chestnut. Resurrection of lost foundation species through introduction of resistant genotypes may represent a resounding ecological success story, but unanticipated changes to ecological processes, such as fire, should be considered.

**Key words:** fire ecology; disease resistance; global change; litter flammability; mesophication; restoration; resurrection ecology.

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## HIGHLIGHTS

- American chestnut litter is remarkably flammable based on laboratory experiments.
- The backcross hybrid (BC<sub>3</sub>F<sub>2</sub>) generally had similar or slightly lower litter flammability than American chestnut.
- Loss of American chestnut may have contributed to reduced fire frequency.

## INTRODUCTION

Numerous forest ecosystems have experienced substantial reduction or loss related to non-native insect and pathogen outbreaks (Ellison and others 2005; Aukema and others 2010). Many of these events have long been a strong driver of change in forests locally and globally (Elton 1958), dramatically altering forest structure and composition that can directly and indirectly disrupt key ecosystem functions, such as nutrient cycling, primary productivity, and natural disturbance processes (Liebhold and others 1995; Lovett and others 2006; Metz and others 2013). These impacts are especially concerning when forest loss impacts foundation species whose traits define and structure ecosystem dynamics and promote locally stable conditions (Dayton 1972; Ellison and others 2005). Given the rapid increases in global trade and travel (Levine and D'Antonio 2003; Aukema and others 2010) and increasing global temperatures related to climate change (Sturrock and others 2011; Weed and others 2013), forest loss from non-native, invasive pests and pathogens are projected to continue over the coming decades and may result in the extirpation or extinction of some tree species.

These events have prompted forest scientists and managers to seek creative solutions to recover lost or declining species through promoting resistance. Recent successes in developing resistant genotypes, through phenotypic selection, hybridization with related species, or genetic engineering, hold promise to resurrect functionally extirpated or extinct species to their native ecosystems (Sniezko 2006). Introducing resistant genotypes for a species that has long been absent can serve as a successful example of resurrection ecology (also referred to "de-extinction") and provide potential insight into other species that are or may go extinct in the near future. Yet, successful resurrection of a species is contingent on the replacement genotype serving as an adequate ecological proxy of the lost species (Shapiro 2017), requiring examination of the broader ecological impacts of reintroduction (Sherkow and Greely 2013).

Resurrecting species through the introduction of novel genotypes may alter ecological processes in unintended or undesired ways (Whitham and others 2003, 2006). Numerous studies on terrestrial ecosystems have found that intraspecific differences in plant genotypes can have cascading impacts on higher-order ecological processes, such as community assembly, nutrient dynamics, and disturbance regimes (Bailey and others 2004; Sch-

weitzer and others 2004). Given the preponderance of fire-prone forests globally, there is a need to consider the influence of novel genotypes on fire behavior and effects in these ecosystems.

Feedbacks between vegetation traits and fire regimes regulate ecological processes in many fire-prone ecosystems (Beckage and others 2009; Veldman and others 2013). In most forested ecosystems, the predominant driver of surface fire behavior is senesced leaf litter and fine woody fuels (Rothermel 1983). Many studies have determined that tree litter from frequent-fire forest types often has greater flammability (Fonda 2001; Kane and others 2008; Engber and Varner 2012), which has been closely linked to individual leaf traits and litter fuelbed properties. Typically, tree species with larger or longer leaves (among other traits) will have fuelbed densities conducive to greater oxygen permeation that promote greater flame lengths, faster flaming times, and greater fuel consumption (Scarff and Westoby 2006; Engber and Varner 2012; Kreye and others 2013; Varner and others 2015b). Additionally, leaf traits and associated litter fuelbed traits can influence the moisture content and drying rates that can affect litter flammability (Kreye and others 2013, 2018). Changes in the leaf traits of litter fuelbeds may have implications on the flammability of fire-prone ecosystems (Mola and others 2014; Varner and others 2017; Kreye and others 2018), and shifts in composition have been linked with altered fire regimes (Brooks and others 2004).

One of the earliest examples of extensive tree mortality in the USA was chestnut blight, a disease caused by the fungus *Cryphonectria parasitica*. Since the pathogen was first detected in the early twentieth century (Murrill 1906), American chestnut (*Castanea dentata*) has been eliminated from the overstory throughout its historical range and almost exclusively persists as small understory resprouts (Anagnostakis 1987), rendering the species as functionally extinct (Saterberg and others 2013). Prior to its loss, American chestnut comprised as much as 25% of the trees and 36% of the basal area across large areas of the eastern hardwood forest (Foster and others 2002; Elliott and Swank 2008; Wang and others 2013). This species also regulated numerous ecological processes (for example, productivity, decomposition, and nutrient cycling; Paillet 2002) and provided important ecosystem services (for example, lumber, fence post, and food resources; Youngs 2000), contributing to its characterization as a foundation species (Ellison and others 2005; Jacobs and others 2013).

Forest managers are considering large-scale reforestation and restoration plantings of putatively disease-resistant American chestnut seedlings produced through backcross hybridization with blight-resistant Chinese chestnut (*C. mollissima*) (Steiner and Carlson 2006; Jacobs 2007). Although ongoing work holds much promise, the effectiveness and feasibility of a large-scale effort still presents challenges (Clark and others 2014, 2016; Steiner and others 2017). Recent research has advanced our understanding of the performance of disease-resistant chestnut genotypes (Clark and others 2012, 2016; Brown and others 2014; Knapp and others 2014; Pinchot and others 2015), although the potential impacts of these novel genotypes on ecological processes and other factors have been largely unexamined (Jacobs 2007; Jacobs and others 2013).

Although the fire ecology of American chestnut is not well resolved (Foster and others 2002), multiple lines of evidence suggest that many eastern hardwood forests that contained American chestnut had historically experienced litter-driven surface fires, with relatively low incidences of stand-replacing crown fires. Pre-blight fire return intervals conservatively ranged from 3 to 13 years (Guyette and others 2012; Brose and others 2014; Stambaugh and others 2015; Varner and others 2016; Lafon and others 2017). As a result, managers continue to promote the use of prescribed fire in many of the forests where American chestnut could be reintroduced (Brose and others 2014). However, any strong differences in litter flammability between American chestnut hybrids and the functionally extinct species could promote undesired conditions that alter the flammability of the ecosystem with potential negative ecological or economic impacts.

The aim of this study was to examine differences in chestnut litter flammability of a backcross hybrid genotype ( $BC_3F_2$ ) in comparison with a pure American and a pure Chinese chestnut through laboratory drying and burning trials. The specific objectives were: (1) to determine whether leaf and flammability characteristics differed among the three chestnut types; (2) to determine the leaf traits most associated with litter flammability characteristics among the three chestnut types; and (3) to examine the litter flammability of American chestnut in context with other species from fire-prone forests. The results of this study will provide critical information into the past and future fire ecology of American chestnut and eastern North American hardwood forests, and the potential ecological consequences of resurrecting a func-

tionally extinct species that holds insights for other resurrected species in fire-prone ecosystems.

## METHODS

We collected litter samples from eight replicate trees per chestnut type: American chestnut (*C. dentata*); Chinese chestnut (*C. mollissima*); and third-generation backcrossed hybrid ( $BC_3F_2$ ). Trees were part of the Purdue University Hardwood Tree Improvement and Regeneration Center chestnut breeding program in partnership with the American Chestnut Foundation. The  $BC_3F_2$  trees originated from open-pollinated  $BC_3F_1$  trees from multiple families within a single plantation. Litter was collected in September 2015 from several planting sites within a 10 km radius of West Lafayette, Indiana, USA. Plantations were composed of either widely spaced (3 m) open-canopy trees or more narrowly spaced (1 m), closed-canopy trees. All sampled trees were 9 years old at the time of litter collection. The backcross hybrid and most pure American chestnut collections were from small, healthy trees ranging from 10 to 15 cm in diameter at breast height (1.3 m; dbh), whereas one American chestnut and all Chinese chestnut were 15–35 cm in dbh.

All approximately – 100 g samples were collected from recently fallen or loosely attached, sun and shade leaves on each individual tree and placed in paper bags. Samples were oven-dried at 40°C for 24 h. Leaf trait measurements were taken from 15 leaves randomly selected from each replicate. Leaf edge thickness was measured using electronic calipers, and curl depth was measured as the height of a dry leaf above a flat surface to the nearest millimeter (Engber and Varner 2012). These same sample leaves were then wetted and flattened between two heavy flat surfaces and allowed to dry. Afterward, leaf length, maximum width, area, and perimeter were measured using WinFOLIA image processing software (Regent Instruments, Quebec, Canada). Leaf volume was calculated by multiplying leaf thickness by the surface area of one side. Surface area-to-volume ratio was calculated by dividing leaf thickness by two (Mauseth 2000), and specific leaf area was calculated by dividing leaf area by dry mass.

Litter burning trials were conducted in the Humboldt State University Wildland Fire Laboratory using standard methods (Fonda 2001). Relative humidity ranged from 58.0% to 70.3% and air temperatures ranged from 20°C to 26°C at the time of the burning. Burning trials consisted of approximately 15 g of litter from each replicate per

chestnut type (24 total trials). Each litter sample was evenly distributed as a fuelbed over a 35 cm × 35 cm lattice of xylene-soaked cotton strings on a stainless-steel platform. A 2.75 m × 2.75 m fume hood above the platform generated a constant draw of 15–20 cm s<sup>-1</sup>, though we detected no airflow at the fuelbed. Prior to ignition, fuelbed depth was measured to the nearest mm from four locations (7 cm from each corner of the fuelbed). Strings were ignited from all sides and a timer was started at litter ignition. Maximum flame height was visually estimated to the nearest cm using a vertical ruler placed just behind the burning platform. Flaming time was measured as the duration from litter ignition to flaming extinction, and smoldering time was measured as the duration from flaming extinction to smoldering extinction. Both flaming time and smoldering time were recorded to the nearest second. Percent litter consumption was calculated as the proportion of the initial litter mass consumed (Eq. 1).

$$\text{Consumption}(\%) = \frac{(\text{litter mass} - \text{residual mass})}{\text{litter mass}} \times 100 \quad (1)$$

Fuelbed drying was measured over a 72-h period under laboratory conditions. After drying at 40°C for 24 h, 15 g from five of the replicates per chestnut type was used to create litter beds for the desorption trials. Litter beds were soaked in a water bath for 24 h, then removed, and consistently agitated to remove excess surface water on the leaves before being placed in 24 × 24 × 4 cm pre-weighed aluminum pans with 36 holes (5 mm diameter) spaced 25 mm apart. Each pan was elevated on wooden slats to allow drainage of any residual water. At this time, we recorded the wet weight of the litter to calculate the initial moisture content (Kreye and others 2013). Litter beds were allowed to air-dry under laboratory conditions that were controlled by a dehumidifier (Frigidaire FFAD7033R1, Charlotte, North Carolina, USA). Relative humidity and air temperature throughout the drying experiments were somewhat constant, ranging from 43% to 50% and 23°C to 24°C, respectively. Litter beds were weighed at half hour intervals for the first 4 h, every hour for the next 20 h, and intermittently until the moisture content stabilized over multiple intervals. Percent moisture content was calculated for each time step (Eq. 2):

$$m_t = \frac{(\text{litter mass}_t - \text{litter mass}_{\text{od}})}{\text{litter mass}_{\text{od}}} \times 100, \quad (2)$$

where  $m_t$  is moisture content at time  $t$ , litter mass<sub>*t*</sub> is fuel mass at time  $t$ , and litter mass<sub>od</sub> is oven-dried fuel mass. Based on percent moisture content, we calculated the relative moisture content of a litter bed for each time step (Eq. 3; Fosberg and others 1970):

$$E = \frac{(m_t - m_f)}{(m_i - m_f)}, \quad (3)$$

where  $E$  is relative moisture content,  $m_i$  is initial moisture content, and  $m_f$  is final moisture content.

Response time ( $\tau$ ) of each litter bed was determined using piecewise regression with the *segmented* package (Muggeo 2008). Response time represents the time a fuel particle or fuelbed takes to reach 63% of the equilibrium moisture content. Shorter response times indicate fuels that dry and gain moisture faster than fuels with longer response times. The natural log of relative moisture content ( $E$ ) was separated into two linear sections: initial and final time lag (Nelson and Hiers 2008) based on the calculated break point determined by the piecewise regression. Response time for each litter bed was calculated algebraically using the regression equation of the relationship between time and  $\log E$  for the initial time lag, where  $E = 0.368$  (Eq. 4).

$$\tau = \frac{\log(E)}{\text{slope}} - \text{intercept} \quad (4)$$

## Data Analysis

Leaf traits, drying characteristics (initial moisture content, response time), and flammability measurements were compared among the three chestnut types using a one-way analysis of variance (ANOVA) followed by Bonferroni (all pair-wise) multiple comparison tests when significant differences were detected. Chestnut types were compared using the nonparametric Kruskal–Wallis one-way ANOVA on ranks followed by the Dunn test to determine differences among chestnut types because data did not meet parametric test assumptions. Univariate correlations among all leaf traits and flammability measures were completed using simple linear regression and assessed for violations of test assumptions. We also conducted a multivariate analysis of all flammability measurements among chestnut types using principal com-

ponents analysis with the *prcomp* function in the *vegan* package (Oksanen and others 2017). A permutation multivariate analysis of variance test was conducted to detect a chestnut type effect followed by a Tukey HSD test with a Bonferroni correction factor to detect pair-wise differences among types. Although flammability measures have been correlated in other studies (Engber and Varner 2012), only flaming time and consumption were significantly correlated in our dataset ( $r^2 = 0.59$ ,  $p < 0.0001$ ). Subsequently, we compared the relationship between leaf traits and flammability scores using the *envfit* function in the *vegan* package (Oksanen and others 2017) and report all significant relationships ( $\alpha = 0.1$ ) based on 999 permutations. Analyses were all completed using R statistical software (R Development Core Team 2017).

## RESULTS

Although the backcross hybrid is expected to be 94% genetically similar to American chestnut, there were significant differences in litter flammability during the laboratory experiment (Table 1). American chestnut had 18% taller flames ( $p = 0.005$ ; Figure 1) and 32% shorter flaming times ( $p = 0.006$ ) than Chinese chestnut. The hybrid litter flammability was either similar to Chinese chestnut (for example, maximum flame height) or had intermediate values between American and Chinese chestnut (for example, flaming time). Chinese chestnut and the backcross hybrid had approximately 10% lower initial moisture content than American chestnut but did not differ significantly ( $p = 0.204$ ). Response time also did not differ significantly among chestnut types



Figure 1. Laboratory burn demonstrating the flame heights of American chestnut (*Castanea dentata*). The average maximum flame height for all observations was 98.9 cm (range = 91–106 cm).

( $p = 0.206$ ), but Chinese chestnut had more than a 50% lower value than either American chestnut or the hybrid.

Differences in leaf traits among chestnut types were also observed (Table 2), some of which related to variation in flammability. Chinese chestnut

**Table 1.** Mean (Standard Error) Litter Flammability and Moisture Characteristics by Chestnut Type

	American chestnut ( <i>C. dentata</i> )	Backcross hybrid	Chinese chestnut ( <i>C. mollissima</i> )	$\chi^2$	<i>p</i>
<i>Litter flammability</i>					
Maximum flame height (cm)	98.9 (1.9) <sup>a</sup>	87.9 (2.6) <sup>b</sup>	83.8 (3.6) <sup>b</sup>	10.70	<b>0.005</b>
Flaming time (s)	25.3 (1.0) <sup>b</sup>	29.0 (1.5) <sup>ab</sup>	37.2 (4.1) <sup>a</sup>	10.26	<b>0.006</b>
Smoldering time (s)	238.7 (31.7)	201.8 (16.0)	201.4 (15.3)	0.38	0.829
Consumption (%)	91.3 (0.6) <sup>ab</sup>	92.0 (0.5) <sup>a</sup>	88.5 (1.4) <sup>b</sup>	6.39	<b>0.041</b>
<i>Litter moisture characteristics</i>					
Initial moisture content (%)	285.9 (24.2)	265.6 (12.0)	243.0 (5.3)	1.91	0.204
Response time (h)	6.9 (1.4)	8.0 (2.2)	4.0 (0.2)	3.16	0.206

Comparisons are based on a Kruskal–Wallis nonparametric one-way ANOVA ( $df = 2, 21$ ), using the Dunn test to determine differences among chestnut types. Significant differences in characteristics are depicted in bold, with differences among types denoted with superscripted letters.

**Table 2.** Mean (Standard Error) Leaf and Fuelbed Characteristics by Chestnut Type

Characteristics	American chestnut ( <i>C. dentata</i> )	Backcross hybrid	Chinese chestnut ( <i>C. mollissima</i> )	<i>F</i>	<i>p</i>
Dry mass (g)	0.52 (0.03)	0.48 (0.04)	0.52 (0.04)	0.97	0.617
Max leaf length (cm)	18.8 (0.6) <sup>a</sup>	17.2 (0.4) <sup>ab</sup>	16.6 (0.6) <sup>b</sup>	4.71	<b>0.020</b>
Max leaf width (cm)	6.3 (0.3) <sup>a</sup>	5.5 (0.2) <sup>b</sup>	6.7 (0.2) <sup>a</sup>	7.62	<b>0.003</b>
Leaf thickness (mm)	0.152 (0.005)	0.159 (0.003)	0.150 (0.007)	1.51	0.471
Leaf curl (mm)	32.8 (2.7)	27.6 (1.3)	27.6 (2.0)	1.62	0.221
Leaf perimeter (cm)	60.3 (3.9)	52.7 (1.6)	50.8 (1.4)	3.39	0.053
Surface area-to-volume ratio (cm <sup>2</sup> /cm <sup>3</sup> )	134.1 (4.5)	127.8 (2.6)	138.4 (5.8)	1.07	0.360
Perimeter-to-surface area ratio (cm/cm <sup>2</sup> )	0.85 (0.03) <sup>ab</sup>	0.95 (0.03) <sup>a</sup>	0.75 (0.04) <sup>b</sup>	10.36	<b>0.006</b>
Specific leaf area (cm <sup>2</sup> /g)	161.3 (8.1) <sup>a</sup>	126.4 (4.1) <sup>b</sup>	148.4 (4.7) <sup>a</sup>	11.32	<b>0.003</b>
Fuelbed depth (cm)	5.3 (0.6)	5.1 (0.3)	4.8 (0.5)	0.30	0.754

Comparisons are based on a one-way ANOVA ( $df = 2, 21$ ) with a Tukey HSD multiple comparison test. Significant differences in characteristics are depicted in bold, with differences among types denoted with superscripted letters.

had a 13.2% shorter maximum leaf length than American chestnut. The backcross hybrid had an intermediate length but was narrower than either American or Chinese chestnut (Figure 2). Perimeter-to-surface area ratio was the highest for the hybrid and was significantly greater than Chinese chestnut, which had the lowest values. Maximum leaf length was the leaf trait most associated with flammability measures and had a positive relationship with flame height ( $r^2 = 0.32$ ,  $p = 0.004$ ),



**Figure 2.** Representative leaves that highlight measured differences in litter characteristics among American chestnut (left), backcross hybrid (center), and Chinese chestnut (right).

where American chestnut had longer leaves and taller flame heights compared to Chinese chestnut, with the backcross hybrid having intermediate values (Figure 3). Fuelbeds of American chestnut were deeper than the hybrid or Chinese chestnut but did not differ among species ( $p = 0.754$ ). Flaming time was negatively associated with leaf curling ( $r^2 = 0.22$ ,  $p = 0.02$ ) and consumption was negatively associated with leaf thickness ( $r^2 = 0.18$ ,  $p = 0.04$ ) and fuelbed depth ( $r^2 = 0.17$ ,  $p = 0.049$ ), but none of these characteristics differed significantly among chestnut types. Differences in flammability were detected among chestnut types when examined in a multivariate analysis ( $F = 3.9$ ,  $p = 0.002$ ). Consistent with the univariate analyses, American chestnut had taller flames, shorter flaming times, longer smoldering times, and greater consumption compared to Chinese chestnut and the backcross hybrid (Figure 4). Differences in the multivariate flammability scores among chestnut types corresponded with maximum leaf length ( $r^2 = 0.37$ ,  $p = 0.007$ ), leaf curl ( $r^2 = 0.29$ ,  $p = 0.025$ ), and leaf perimeter ( $r^2 = 0.31$ ,  $p = 0.03$ ).

## DISCUSSION

To our knowledge, this is the first study to examine the potential changes in flammability associated with the loss of a foundation species and the implications of resurrecting a genetically similar, disease-resistant genotype. Resurrection of American chestnut through the introduction of a disease-resistant hybrid would likely serve as an acceptable ecological proxy with respect to litter flammability because the American chestnut and

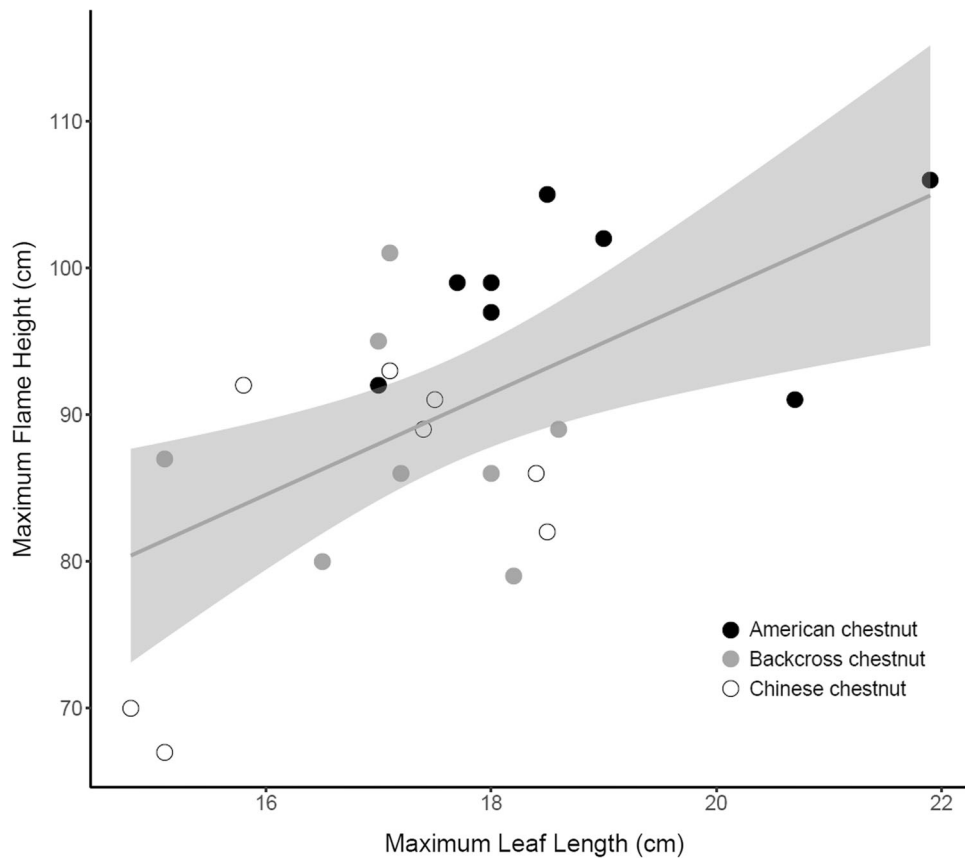
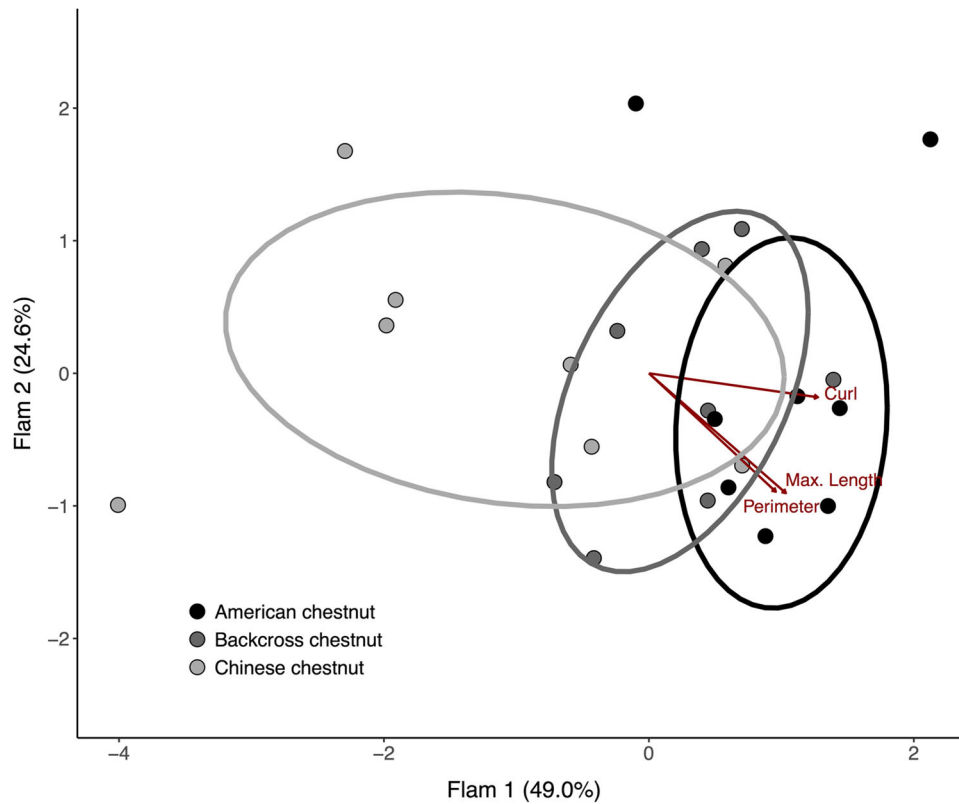


Figure 3. Positive relationship ( $r^2 = 0.32$ ,  $p = 0.004$ ) between maximum leaf length and maximum flame height by chestnut type.

the backcross hybrid burned similarly. Where differences were detected (for example, maximum flame height), these did not seem to be strictly related to differences in leaf traits among the chestnut types. However, consideration of flammability across multiple measures indicated that the backcross hybrid might confer a slight dampening of flammability relative to American chestnut. These findings suggest that selection of disease-resistant genotypes may also consider, among others (for example, Diskin and others 2006), traits that can promote litter flammability (for example, maximum leaf length, curl) most similar to the pure American chestnut. The specific impacts to flammability will also depend on the particular families (that is, genotypes), and the level of intercross used to develop the resistant hybrids, which we did not examine, warrants further research. For instance, our results were based on a first intercross of third-generation backcross hybrids ( $BC_3F_2$ ) instead of the recommended use of a third generation to confer pathogen resistance (Steiner and others 2017). In addition, the culling of less resistant  $BC_3F_2$  parent plants is still ongoing

and the process of selecting the final resistant genotypes in the resurrection of American chestnut may result in differences in litter flammability, suggesting the need for follow-up research.

Previous research that has examined compositional changes in American chestnut forest types before and after blight-induced mortality has mostly shown substantial increases in mesophytic tree species such as maples (*Acer* spp.) (for example, Keever 1953; Agrawal and Stephenson 1995; Myers and others 2004; Hawkins 2006; Elliott and Swank 2008), although in some locations pyrophytic oak (for example, *Quercus alba*) or hickory species (for example, *Carya glabra*) replaced American chestnut (Korstian and Stickel 1927; McCormick and Platt 1980). The degree to which the replacement species would dampen or facilitate regional fire regimes needs more examination, but a recent study by Varner and others (2017) found that changes in flammability were contingent on the litter characteristics of the replacing species, where replacement by mesophytes had a stronger dampening effect on flammability. Based on our results of substantive litter flammability during



**Figure 4.** Separation of chestnut types along two flammability axes. Each type differed in flammability based on a PERMANOVA test ( $F = 3.9$ ,  $p = 0.002$ ). The first PCA axis (Flam1) explained 49.0% of the variation in flammability and was negatively associated with flaming time (FlmT;  $r = -0.67$ ) and positively associated with consumption (Cnsm;  $r = 0.6$ ). The second PCA axis (Flam2) explained 24.1% of the variation in flammability and was positively associated with smoldering time (SmlT;  $r = 0.94$ ). A third flammability axis (not shown) explained 21.8% and was positively associated with maximum flaming height (FlmH;  $r = 0.7$ ). The ellipses represent 68% of the data for each chestnut type. The maroon join plots refer to relative strength of significant relationships among leaf traits and flammability scores.

laboratory experiments, we propose that the loss of American chestnut significantly contributed to reduced ignition and spread of fires in chestnut forests now dominated by mesophytic species. These impacts would likely be exacerbated when the loss of American chestnut was coupled with decreases in other pyrophytic species (for example, oak and hickory species; Nowacki and Abrams 2008).

Resurrection of American chestnut through the introduction of a disease-resistant backcross hybrid has the potential to influence several ecological processes in these forests, including the potential restoration of their historic fire regimes. The slight dampening in flammability in the backcross hybrid compared to American chestnut may cause reduced ignition and fire spread where introduced, yet other traits may confer persistence. Similar to American chestnut, the hybrid is capable of basal resprouting following fire and other disturbances (Wang and others 2013; Belair and others In press). Recent evidence has shown that resprouting of

BC<sub>3</sub>F<sub>2</sub> and BC<sub>3</sub>F<sub>2</sub> hybrids following dieback of planted seedlings was similar to American chestnut, but less vigorous than Chinese chestnut (Thomas-Van Gundy and others 2017) though specific responses to fire have not yet been examined. Persistence of the hybrid will also depend on the rate and amount of bark produced. Some have suggested that American chestnut may have relatively thin bark (for example, Ashe 1912); however, these studies are largely based on anecdotal observations, focused on smaller individuals (that is, seedlings and saplings), and occurred during a time period that predated the concept of fire ecology, thus indicating a need to quantify bark thickness within and among chestnut types. American chestnut and the backcross hybrid litter dried at moderate rates and burned with substantial flammability (Table 1), relatively consistent with many other pyrophytic species (that is, species with rapidly drying and combustible litter) from fire-prone ecosystems. For instance, maximum flame



height for American chestnut litter was just below 100 cm, values similar to or exceeding pyrophytic pines and oaks from historically fire-prone ecosystems in the southeastern US. These maximum flame height values were consistent with eastern white oak (*Quercus alba*; 98.7 cm) and were greater than longleaf pine (*Pinus palustris*; 92.3 cm) and shortleaf pine (*Pinus taeda*; 78 cm) (Varner and others 2015a). American chestnut litter also had a mean time lag of 6.9 h, indicating moderate drying rates that were slightly higher than other pyrophytic species, such as eastern white oak (4.3 h) and shortleaf pine (3.4 h) (Kreye and others 2013).

The importance of fire to American chestnut is not well understood, and conflicting reports are abundant in the literature (for example, McEwan and others 2011; Lafon and others 2017). The high flammability of American chestnut litter observed in our study contributes further evidence that American chestnut has a suite of traits to promote persistence in a frequent-fire forest. The species is a prolific resprouter, capable of producing numerous, fast-growing basal sprouts and can rapidly respond to new growing space caused by disturbances (Belair and others 2014). The degree of shade tolerance has differed widely among studies (Niinemets and Valladares 2006; Wang and others 2006), but most indicate that American chestnut regeneration is moderately shade tolerant and highly plastic in response to disturbance (Rhoades and others 2009; Knapp and others 2014; Belair and others 2018). Larger trees that would occupy the overstory of fire-frequent forests may have traits that better allow them to persist under these conditions, such as lower shade tolerance, higher drought tolerance, and greater bark thickness.

Our observations of American chestnut flammability provide additional support that oak-chestnut forests historically experienced a frequent-fire regime (Guyette and others 2012; Stambaugh and others 2015; Varner and others 2016; Lafon and others 2017). A comprehensive review of existing fire scar studies throughout much of the former American chestnut range highlighted a high-frequency fire regime with historic fire return intervals prior to 1900 between 4 and 13 years (Lafon and others 2017). Native American ignitions were likely the primary source for maintaining such a historically frequent-fire regime (Hessl and others 2011; Aldrich and others 2014); however, models reconstructing historic fire frequency based on climate–fire relationships independent of contributions from human ignitions also corroborate a frequent-fire regime for oak-chestnut forests (Guyette and others 2012;

Stambaugh and others 2015). The mixture of fire-resistant and fire-neutral traits, with fire history evidence aside, suggests the possibility that the fire regime of forests containing American chestnut ranged from moderate to high frequency, depending on the climate, topographic conditions, co-occurring tree species, and other factors for a given site.

Given our findings that American chestnut has characteristics consistent with other pyrophytic species, we propose that the loss of this foundation species may have contributed to the known reductions in fire frequency of these forests following fire exclusion in the early to mid-1900s (Guyette and others 2012; Lafon and others 2017). A positive feedback mechanism termed “mesophication” posits that the prolonged exclusion of fire shifted forest structure and composition from lower density, shade-intolerant, pyrophytic species to higher density communities of shade-tolerant, mesophytic (fire-sensitive) species in many eastern US forests (Nowacki and Abrams 2008). The increased presence of mesophytes promotes a greater proportion of litter that retains more moisture and has lower flammability (Kreye and others 2013, 2018), further promoting less flammable conditions and reducing the incidence of fire. In forests containing American chestnut, mesophication could have been facilitated by the loss of American chestnut to blight that reduced the proportional dominance of pyrophytes and their more flammable litter (McEwan and others 2011), though more investigation is needed.

Understanding the potential changes in litter flammability due to chestnut blight has important implications for other non-native pathogens introduced to fire-prone forests. Two modern examples of non-native pathogens that have resulted in substantial tree mortality include laurel wilt (*Raffaelea lauricola*) that affects red bay (*Persea burbonia*) and other members of the Lauraceae in southeastern US. (Fraedrich and others 2008), and sudden oak death (*Phytophthora ramorum*) that affects tanoak (*Notholithocarpus densiflorus*) and some true oaks (*Quercus* spp.) in California and Oregon (Rizzo and Garbelotto 2003). Although these species have not yet become functionally extinct, they both, among others, have high potential to spread throughout the species’ ranges over the coming decades (Meentemeyer and others 2011; Kendra and others 2013). Previous research has focused on the potential impacts of pathogen-induced mortality on changes in fuel characteristics (Forrestel and others 2011; Kuljian and Varner 2013) and the observed synergistic interactions between patho-

gen-induced and fire-induced tree mortality (Metz and others 2011, 2013). Our study provides one means to anticipating potential impacts to changes and the hopeful resurrection of these species through introduction of resistant genotypes.

Resurrection of American chestnut would serve as a resounding ecological success story of a species that has been functionally extinct for nearly a century and potentially could provide many lost or degraded ecosystem services in hardwood forests of eastern North America. American chestnut litter is quite flammable and loss of this species conceivably contributed to inhibition of fire and the greater abundance of mesophytic species in some forests. Reintroduction of a disease-resistant hybrid, with subtly dampened fire behavior compared to American chestnut, may still increase flammability in these forests, but broader ecological implications of the functional differences between American chestnut and hybrid genotypes are not well understood. Insights from this study and others will be needed to adequately assess the broader ecological consequences of resurrecting the once-iconic American chestnut, with the potential to inform the resurrection of other foundation species in frequent-fire ecosystems.

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