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Stand and site characteristics affect the probability of stump sprouting in some eastern North American hardwoods

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ABSTRACT

Stump sprouting is a widespread phenomenon in North American hardwood tree species following logging or severe crown damage from natural disturbances such as fire, wind, or insect attack. However, other than the effects of species and tree size, factors that influence the probability of sprouting are not well understood. Data from harvested stands in Pennsylvania and Connecticut, USA, were used to evaluate the effects of several variables on stump sprouting frequencies measured within the first year after cutting for several oak and other hardwood species. After adjusting for species and diameter of the "parent" tree (ortet), clearcut harvests were found to result in a higher frequency of sprouted stumps than shelterwood harvests or crop tree releases. In addition, the probability of sprouting was higher for trees in the Ridge and Valley province of Pennsylvania vs. the Appalachian Plateaus, and in general it was higher on dry vs. moist sites. After accounting for all measured variables, there remained statistically significant stand-to-stand differences in sprouting frequency that arose from unknown causes. Results should temper expectations of stump sprout contributions to regeneration stocking that are based on simple models derived from a small number of stands or a limited geographic area. On the stand-level basis at which most managers work, the actual contribution of sprouts to future stand development may vary widely from modeled expectations.

1. Introduction

Many tree species can produce new shoots and branches from long-dormant buds in response to damage from natural disturbances such as fire, wind, or insect attack. These buds originate from meristems in leaf axils and grow outward to remain just below the bark as the stem increases in diameter. All angiosperm trees in temperate climates have the capacity to sprout from dormant buds (Del Tredici 2001), but it is much stronger in some species than others (White 1991; Del Tredici 2001; Keyser and Loftis 2015). Although resprouting is probably an ancient adaptation to destructive agents, the relationship between sprouting potential and ecological conditions can be complex (Lamont et al. 2019), and dormant buds may serve other adaptive purposes such as increasing seedling longevity in shaded, understory conditions where dieback may occur in the absence of actual damage (reviewed by Del Tredici 2001).

Within the tree canopy, sprouts from dormant buds can contribute importantly to crown renewal following the decline or death of branches, but it is sprouts from the stumps of top-killed trees that have received most research attention. Stump sprouts often grow vigorously into replacement trees (Wendel 1975; Loftis and McGee 1993; Johnson et al. 2002; Knapp et al. 2017). Species that readily stump-sprout can dominate regeneration following stand-replacement disturbances such as fire (Brown 1960; Swan 1970), windthrow (Peterson and Pickett 1991; Cooper-Ellis et al. 1999), and logging (McIntyre 1936; Liming and Johnson 1944; Beck and Hooper 1986; Arthur et al. 1997; Cook et al. 1998). For these reasons, stump sprouting has considerable ecological and silvicultural significance. In eastern North America, sprouting is of particular interest in oak-dominated stands because stump sprouts can be an important supplement to oak seedling regeneration, which on a regional basis is failing to sustain oak dominance levels following stand harvests (Abrams 2003; Fei et al. 2011; Dey 2014; Knott et al. 2019).

Sprout contributions to future stocking are often anticipated in

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Table 1
Stands, species, and harvest treatments represented in stump sprout data sets by study. Sample sizes for each species are shown in parentheses.

Study (data set)	Number of stands	Species	Harvest treatment (residual basal area)
Connecticut (CT) (Ward and Williams 2018)	13	red maple (520), white oak (96), northern red oak (137), black oak (136)	Clearcut (no residual) vs. Crop Tree Release (6–17 m^2ha^{-1})
Pennsylvania (PA1) (Fei and Steiner 2009)	54 (central and northern PA)	red maple (1531), American beech (203), blackgum (229), white oak (272), chestnut oak (675), northern red oak (429), black oak (146)	Clearcut (1–5 m^2ha^{-1}) vs. Shelterwood (6–23 m^2ha^{-1})
Pennsylvania (PA2) (Royo et al. 2016)	17 (northern PA)	red maple (157), American beech (236)	Shelterwood (6–21 m^2ha^{-1})

silvicultural guidelines for managing and harvesting oak-dominated stands (Sander et al. 1984; Brose et al. 2008; Steiner et al. 2008). Typically, the probability that a stump will sprout is modeled as a function of species and size class because of the well-known tendency for sprouting to vary among species and decline as tree size (or age) increases (Johnson 1975; Johnson 1977; Dey et al. 1996; Weigel and Peng 2002; Matula et al. 2012; Šplíchalová et al. 2012; Keyser and Loftis 2015; Knapp et al. 2017; Ward and Williams 2018). However, estimates of sprouting probability have often differed greatly from one study to another, suggesting that factors other than species and size may importantly affect sprouting behavior (see, for example, Johnson 1977; Cook et al. 1998; Weigel and Peng 2002; Fei and Steiner 2009; Sands and Abrams 2009; Keyser and Zarnoch 2014; Ward and Williams 2018). Such influences, if present, are not well understood, although several studies have shown an effect of site quality or topographic position on sprout production (Johnson 1977; Lynch and Bassett 1987; Weigel and Peng 2002, Dinh et al. 2018), and there is some evidence (reviewed below) that the intensity of harvest (or retained basal area) can affect sprouting behavior. It would be important to know the degree to which models of stump-sprout contributions to regeneration can be significantly influenced by stand-level effects, and we are aware of no studies in which sprouting probability is examined across stands or regions while controlling for species and tree size. Here we use data from three studies in the northeastern United States to examine the effects of stand, physiographic region, and stand- and site-related variables on the probability that a cut stump will sprout.

2. Materials and methods

Data on the presence or absence of live sprouts on cut stumps were assembled from three studies in two U.S. states, Pennsylvania (studies PA1 and PA2) and Connecticut (CT) (Table 1). Altogether, data were available for a total of seven species: red maple (*Acer rubrum* L.), American beech (*Fagus grandifolia* Ehrh.), blackgum (*Nyssa sylvatica* Marsh.), white oak (*Quercus alba* L.), chestnut oak (*Q. montana* Willd.), northern red oak (*Q. rubra* L.), and black oak (*Q. velutina* Lam.). Each study encompassed multiple stands distributed over a large area: about 4,000 km^2 in CT, 13,000 km^2 in PA1, and 6,500 km^2 in PA2. Each stand was treated with a single harvest regime (PA2) or one of two regimes (in CT and PA1) that left different levels of residual basal area (BA), either clearcuts vs. shelterwood cuts or clearcuts vs. crop tree release treatments (Table 1). Although the data sets were assembled to meet individual study objectives, they are similar in the following respects: 1) the presence or absence of at least one living sprout on a stump was determined within one year following harvest, timed so that sprouts could be observed on all stumps capable of sprouting and before natural mortality caused the loss of some; 2) stumps were sampled at random with respect to the independent variables considered here; and 3) all stumps within a stand could be treated as independent observations. Tree size was recorded as diameter at breast height (1.37 m, DBH) or stump diameter, and stump diameters were converted to DBH according to the following equation derived from PA1 data ($n \geq 30$ for each species):

$$\ln(\mathrm{DBH}) = 0.226 + 0.868^{*}\ln(\mathrm{D}),$$

where D = stump diameter (cm)

Model coefficient of determination was 0.90, and the addition of species as a categorical variable did not significantly improve model fit. Only data from trees ≥ 5 cm DBH were used for analyses.

For all Pennsylvania stands (PA1 and PA2), we determined site moisture regime using Iverson's (1997) integrated moisture index (IMI), which is a composite measure of topographic shading, flow accumulation of water downslope, landscape curvature, and water-holding capacity of the soil. We were interested in IMI both as a measure of site quality (Zahner 1968; Kozlowski 1971; Carmean 1975; Kramer 1986; Hinckley et al. 1991) and as a surrogate indicator of wildfire frequency, hypothesizing that sprouting would be most common on intrinsically drier (and presumably more fire-prone) sites (Lamont et al. 2019). IMI values, which can range from 1 to 100, were obtained from a raster map of Pennsylvania projected to a resolution of ~ 11 m, where each raster cell is assigned an IMI value (Peters et al. 2013). IMI values were averaged for all raster cells within the boundary of each stand, and stands were assigned to site moisture classes based upon the classification scheme of Peters et al. (2013): Xeric (IMI < 35), Intermediate ($35 \leq$ IMI ≤ 50), and Mesic (IMI > 50). Additionally, PA1 stands were classified by physiographic province, Appalachian Plateaus or Ridge and Valley. These provinces, which coincide in Pennsylvania with distinct ecoregions (Bailey 1995), distinguish two sets of stands whose sites differ climatically, geologically, and floristically. The fact that we had many stands in each offered the opportunity to test whether sprouting behavior within a species differed according to broadly defined ecological conditions.

The presence or absence of at least one living sprout on a stump was modeled as a function of DBH, harvest treatment (CT and PA1 only, see Table 1), physiographic province (PA1 only), and moisture class (PA1 and PA2 only), all of which were treated as fixed effects. Analyses were performed separately for each species within a study for which we had data from ≥ 29 stumps per harvest treatment, province, or moisture class. Data were analyzed by general linear regression using a "logit" link function in which the response variable is represented by the log odds of the sprouting probability:

$$\ln\frac{P_s}{1-P_s} = B_0 + B_{1i} + B_2{}^{*}x + \varepsilon, \quad (1)$$

where P_s = the probability that a stump will produce at least one sprout; B_0 = null intercept (reference harvest treatment, physiographic province, or moisture class); B_{1i} = intercept increment for the ith alternative harvest treatment, physiographic province, or moisture class; B_2 = common slope coefficient; and x = DBH. All analyses were performed separately for each species and study combination, except that PA1 and PA2 stands were combined for analyses involving moisture class.

In addition, similar but mixed-effect models were run with stand added as a random variable to test whether stand significantly affected P_s after accounting for measurable fixed effects:

$$\ln\frac{P_s}{1-P_s} = B_0 + B_{1i} + u_j + B_2{}^{*}x + \varepsilon, \quad (2)$$

Where Ps, B_0, B_{1i}, B_2, and x are defined as above and u_j = the random intercept for the jth stand. Fixed-effect variables were included only if

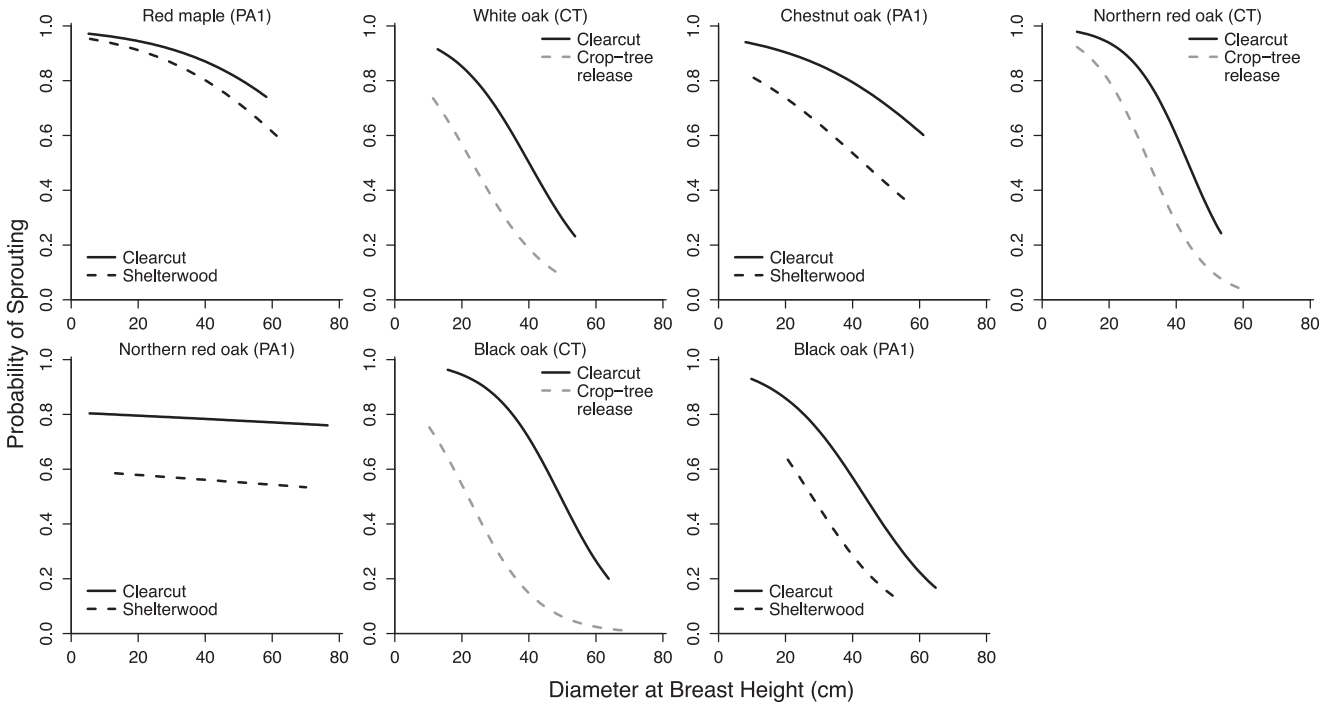

Fig. 1. The probability of stump sprouting as a function of DBH and harvest treatment by species and study. The effect of harvest treatment was significant ($P < 0.05$) in every instance. DBH was significant for all species and studies except for northern red oak in PA1.

they were significant in the previous analysis. For these analyses, we examined only study and species combinations where the species was present in at least 5 stands (Harrison et al. 2018) with a minimum of 10 stumps per stand (Austin and Leckie 2018). It should be noted that the data restrictions described for both models (Equations (1) and (2)) precluded analyses that included all fixed and random effects and precluded some comparisons that are suggested by Table 1 (e.g., a comparison of harvest treatments for blackgum in PA1).

In all analyses, the significance of fixed-effect variables was evaluated via likelihood ratio tests between full and reduced models (Meloun and Militký 2011). The significance of stand effects was tested using an approximate restricted likelihood ratio test with "normalized" penalized quasi-likelihood estimation and 10,000 simulations (Chen 2019a). The random effect standard deviation was derived via general linear mixed models fit using restricted maximum likelihood (Chen 2019b). Intercepts for individual harvest treatments, physiographic provinces, and moisture classes were not compared due to the likelihood of unobserved heterogeneity existing among classes (Mood 2010).

3. Results

Where harvest treatment comparisons were possible, sprouting probabilities for red maple and white, chestnut, northern red, and black oaks were consistently higher ($P < 0.05$) in clearcuts compared to shelterwood or crop tree release treatments that left residual stands with reduced BA but substantial levels of overhead shade (Fig. 1, Table S1). The P_s advantage in clearcuts varied by DBH, but at 40 cm[1] it ranged in absolute percentages from 7% for red maple in PA1 (clearcut vs. shelterwood) to 57% for black oak in CT (clearcut vs. crop tree release). For all other species, the advantage was 22% to 32%. As expected, P_s declined with increasing DBH in all comparisons involving harvest treatment, although the decline was non-significant ($P > 0.05$) for northern red oak in PA1 stands. We found no significant harvest treatment effect on sprouting of white oak in PA1 stands or sprouting of American beech and blackgum.

Stumps were more likely to sprout in the Ridge and Valley physiographic province than in the Appalachian Plateaus ($P < 0.05$) for red maple and white, chestnut, and northern red oaks (Fig. 2, Table S2). The difference ranged from 11% (red maple) to 31% (chestnut oak) for trees 40 cm in diameter. Again, the effect of DBH was not significant for northern red oak. We found no significant effect of physiographic province on sprouting of black oak.

Sprouting probabilities for stumps in PA1 and PA2 stands varied according to moisture regime ($P < 0.05$) for American beech, blackgum, and chestnut, northern red, and black oaks. In general, the pattern was for P_s to be higher on drier vs. moister sites (Fig. 3, Table S3). Where comparisons for 40-cm stumps were possible (all species except blackgum), the range of P_s between moisture classes was 11 to 24% depending on species, and in every case sprouting was more likely for stumps on the drier of the two classes of sites bracketing the range (Fig. 3). However, a regular pattern of diminishing P_s from xeric to intermediate sites, or xeric to intermediate to mesic (where present), did not occur in blackgum and northern red oak, which sprouted best on intermediate sites. Moisture class was not significantly associated with P_s for red maple and white oak.

When the random variable "stand" was added to fixed-effect models, it was significant ($P < 0.05$) in nearly every case, indicating the presence of unknown stand effects on P_s after accounting for DBH, harvest treatment, physiographic province, or moisture regime (Table 2). Results are also shown for models based upon only stand and DBH for those instances where the influence of other fixed-effect variables could not be examined due to data limitations. In these cases, also, the random effect of stand was significant.

4. Discussion

The likelihood of stump sprouting in northeastern U.S. hardwoods varied with species, tree size, harvesting intensity, physiographic region, and site moisture regime. After accounting for these variables,

[1] For illustrative purposes. 40-cm trees are commonly found in stands that are considered mature and harvestable, and they are a representative source of sprout regeneration for the next stand.

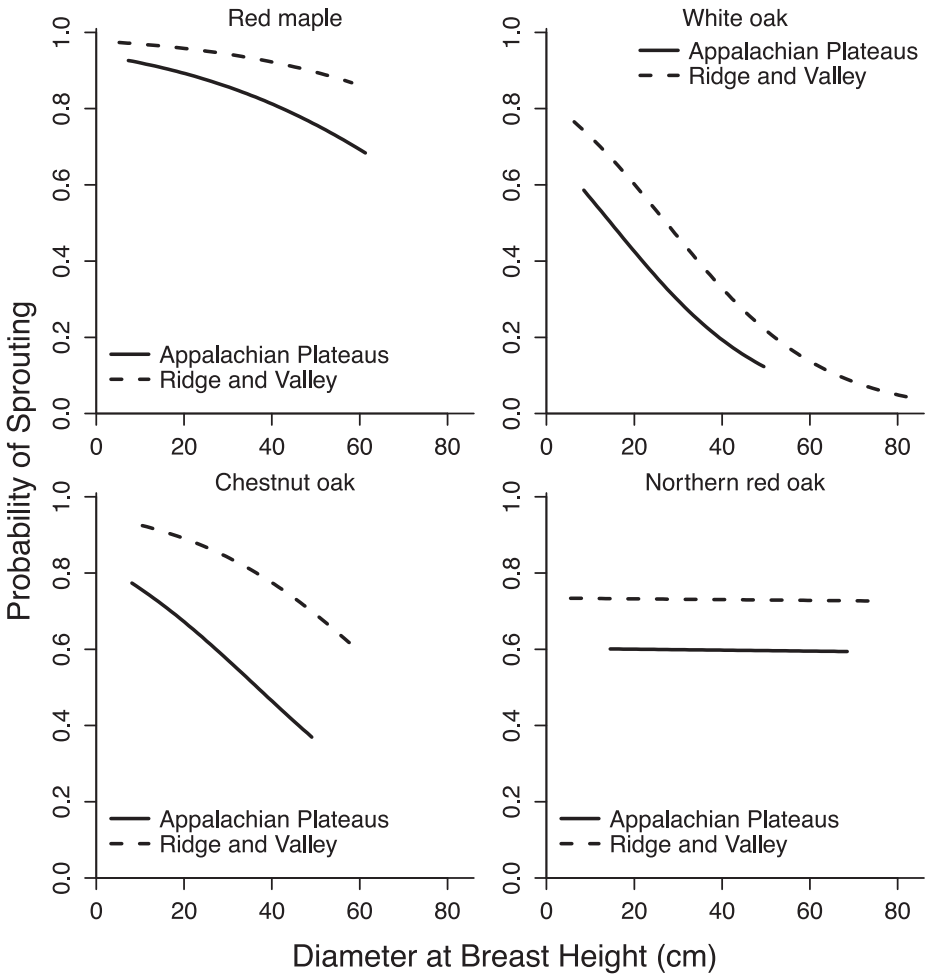

Fig. 2. The probability of stump sprouting as a function of DBH and physiographic province in PA1 stands. The effect of physiographic province was significant ($P < 0.05$) for all species. DBH was significant ($P < 0.05$) for all species except northern red oak.

additional variation in sprouting frequency across stands demonstrated the presence of other site-level factors that we were unable to identify. In general, P_s was greater following clearcut versus other harvesting methods, it was greater in the Ridge and Valley physiographic province of Pennsylvania compared to the Appalachian Plateau, and it was greater on drier versus wetter sites. Not all species responded identically to these factors, however.

As expected, P_s declined as tree size increased for all species except American beech. Compared with oaks and blackgum, both American beech and red maple retained high sprouting frequencies into the larger diameter classes (>~40 cm). Basal sprouting is regarded primarily as an adaptation to fire (Bond and Midgley 2003, Cocking et al. 2014, Nemens et al. 2018, Lamont et al. 2019), and in the region of study fire is the most common natural disturbance that would cause sprouting. These oak species, and blackgum, become relatively resistant to light fires as their bark thickens with age, and this is regarded as an important ecological process in oak ecosystems (Abrams 1992, Brose et al. 2014, Varner et al. 2016). With their thicker bark, mature trees of these species are less dependent upon sprouting to persist in fire prone areas (Bond and Midgley 2003). Red maple and beech have thinner bark, even when mature, and reliance on sprouting from dormant buds following a fire event may be an important survival adaptation even in large trees of these two species. The fact that P_s increased with the size of beech trees is unusual but not unique to this study (Knapp et al. 2017), and it could be the result of dormant meristems branching (i.e., proliferating) as they grow outward to maintain their position just outside the xylem (Wilson 1968; Del Tredici 2001, Meier et al. 2012).

Where harvest treatment comparisons were possible, P_s for red maple and most oak species was greater in clearcuts than in stands treated with shelterwood harvests (PA1) or crop tree releases (CT). Clearcut stands averaged 9.5 and 11.0 m^2ha^{-1} less BA than their more lightly harvested counterparts in PA1 and CT, respectively, and this difference was evidently large enough that P_s was significantly depressed where residual BA was greater. This has practical importance because retention of residual trees is frequently a recommendation in regeneration prescriptions, and it appears that retention of residual BA carries a cost in the sprouting potential of those stumps that are cut. The existing literature on this topic is scarce, and results have been mixed. Atwood et al. (2009) reported similar results for the same species and similar levels of residual BA as in our study. Other studies have shown mixed results or no effect of harvest treatment (or BA retention) on the P_s of oaks and associated species (Gardiner and Helmig 1997; Dey and Jensen 2002; Lockhart and Chambers 2007; Keyser and Zarnoch 2014; Keyser and Loftis 2015; Knapp et al. 2017). However, direct comparisons between the last-named studies and ours are problematic because of differences in species coverage and because most employed BA treatment levels very different from ours, either within a much narrower range or beyond the highest levels we examined, both of which might understandably result in no detectable effect (Gardiner and Helmig 1997; Keyser and Zarnoch 2014; Keyser and Loftis 2015; Knapp et al. 2017). If P_s increases as residual BA decreases, it is presumably because lower BA levels create more light availability near the forest floor. Light is known to induce epicormic sprouting from dormant buds on the trunk (Blum 1963, Smith 1965), which is the same process that produces sprouts from

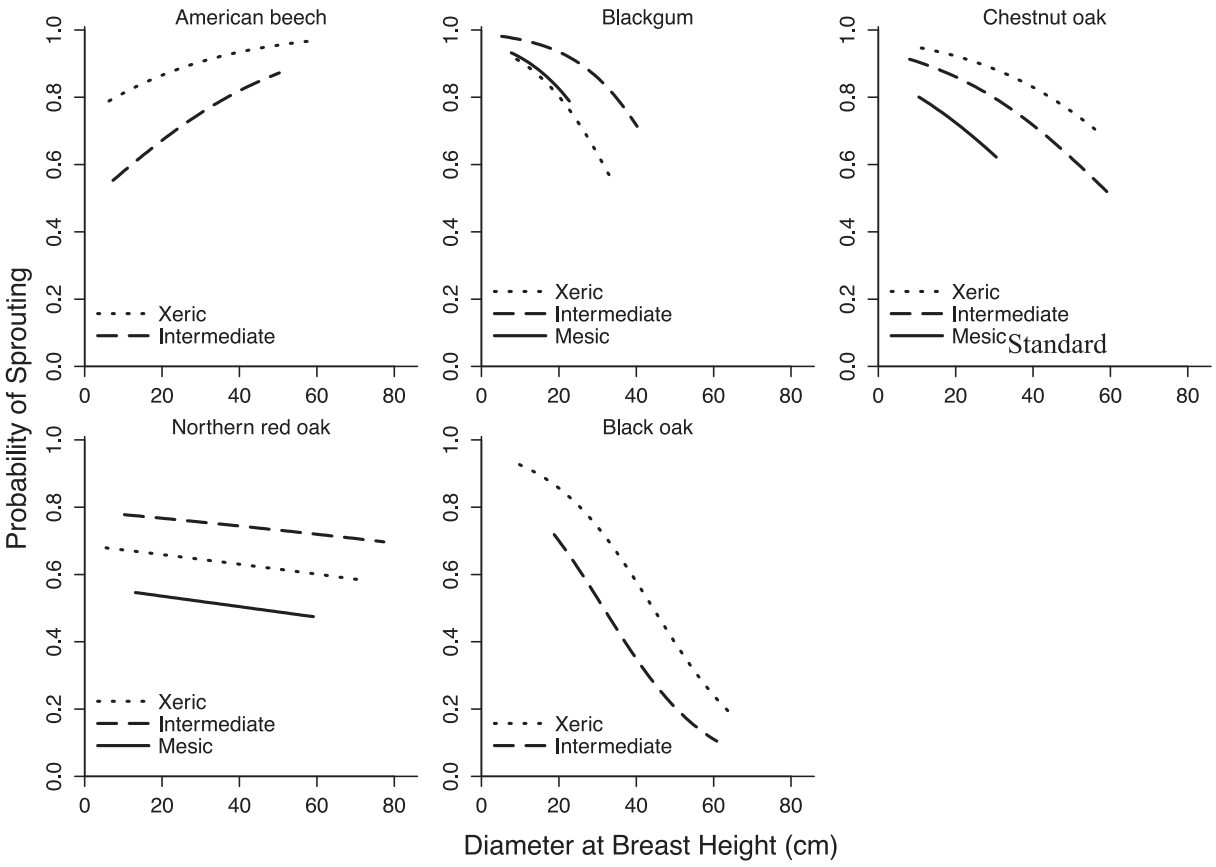

Fig. 3. Sprouting probabilities for stumps as a function of DBH and moisture class for stands in Pennsylvania. The effects of moisture regime were significant ($P < 0.05$) for all species. DBH was significant for all species except northern red oak.

Table 2
Random stand effects (standard deviations of intercepts, u_j) in linear mixed models of stump sprouting probabilities as a function of stand plus the fixed effects of DBH, harvest treatment, physiographic province, and moisture regime (Equation (2)). Intercept variation between stands within a study is significant in all models at $P < 0.05$ (approximate restricted likelihood ratio test) unless otherwise indicated (ns).

Model Variables	Species	Study	Stands	Standard Deviation
Stand, DBH	red maple	CT	7	0.358
		PA2	7	3.041
Stand, Harvest[1]	northern red oak	PA1	14	0.957
Stand, Province[1]	northern red oak	PA1	14	1.380
Stand, Moisture Class[1]	northern red oak	PA1	14	1.183
Stand, DBH, Harvest	red maple	PA1	47	1.198
	white oak	CT	5	<0.001(ns)
	chestnut oak	PA1	27	1.637
	northern red oak	CT	5	0.239 (ns)
Stand, DBH, Province	red maple	PA1	47	1.163
	white oak	PA1	9	0.727
	chestnut oak	PA1	27	1.690
Stand, DBH, Moisture Class	American beech	PA1 + PA2	14	1.631
	blackgum	PA1	9	1.962
	chestnut oak	PA1	27	1.620

[1] DBH omitted from analyses because it was not a significant effect in models that did not include stand as a variable.

morphologically identical dormant buds at stump height (Del Tredici 2001; Meier et al. 2012). Controlled experiments involving the shading of small, cut stumps (<13 cm in diameter) have demonstrated that shading reduces the production of sprouts on oak stumps of that size (Vogt and Cox 1970). Studies have also shown that sprouting of California black oak (*Q. kelloggii*) following wildfires increases with fire severity, presumably because overstory mortality of large conifers in high burn severity locations increased forest floor light conditions (Cocking et al. 2014, Nemens et al. 2018).

In general, each species sprouted more frequently on drier vs. moister sites, but the pattern was not consistently monotonic in comparisons across all three moisture classes. Taking moisture regime as a measure of both site quality (Zahner 1968; Kozlowski 1971; Carmean 1975; Kramer 1986; Hinckley et al. 1991) and vulnerability to wildfire (Guyette et al. 2012), sprouting was generally higher on sites with lower productivity and a greater likelihood of fire disturbance. In addition, we found that P_s was consistently higher in the Ridge and Valley vs. Appalachian Plateaus physiographic provinces, and similar observations have been reported for these two provinces in Virginia and West Virginia, just to the south of our study region in Pennsylvania (Atwood et al. 2009). Compared with the Appalachian Plateaus, the vegetation of the Ridge and Valley is more xerophytic and forest fires historically more frequent (Guyette et al. 2012). Regionally, studies of the relationship between sprouting and site quality have yielded inconsistent results (Johnson 1977; Lynch and Bassett 1987; Kays et al. 1988; Weigel and Peng 2002; Keyser and Loftis 2015). Globally, at identical disturbance frequencies, sprouting is expected to be ecologically more advantageous as site productivity declines (Bellingham and Sparrow 2000). It has been suggested that selection for sprouting is controlled by interactions between disturbance frequency, disturbance severity, and site productivity because carbon is allocated to resprouting potential at the expense of

growth and seed production, which can be more advantageous strategies on productive sites (Bellingham and Sparrow 2000). Under this model, in contrast to the obvious expectation, sprouting potential is not necessarily maximized on those sites with the most frequent or severe disturbances. Similarly, in a review of the literature, Lamont et al. (2011) showed that the overall pattern, across species and habitats, was a decline in capacity to sprout as fires became less frequent. But the trend varied among individual productivity gradients, and most showed disproportionate increases in sprouting as productivity declined. This complexity was amplified in the current study by our use of a single variable as a surrogate for both site quality and wildfire frequency. Whatever the specific ecological advantages, the effect of site moisture regime on sprouting frequency was large enough to have important management implications if stump sprouts are relied upon to supplement seedling regeneration.

Results show that P_s can be affected by site characteristics, management regime, regional factors, and perhaps historical legacies of disturbance frequency. Together, these and other variables (e.g., Kays et al. 1988; Babeux and Mauffett 1994) may confound expectations of stump sprouting if those expectations are based on simple models derived from a small and geographically limited sample of stands. Even after accounting for modeled variables in the current study, stand-to-stand differences in sprouting frequency remained significant and large. For example, for a predicted P_s of 0.70 at the intercept, and using the average standard deviation of stand intercepts presented in Table 2, $P_s \pm 1\sigma$ encompasses a range of sprouting frequencies from 0.35 to 0.91 that could not be statistically explained by variables measured in this study. Those variables advance our understanding of sprouting behavior. But on the stand-level basis at which most managers work, expectations must be tempered by an understanding of underlying uncertainties, especially if regeneration success following harvest is projected to depend heavily upon stump sprouting.

CRediT authorship contribution statement

Jennifer M. Nieves: Methodology, Validation, Formal analysis, Writing – original draft. **Jeffrey S. Ward:** Conceptualization, Investigation, Funding acquisition, Writing – review & editing. **Alejandro A. Royo:** Investigation, Writing – review & editing, Funding acquisition. **Marc E. McDill:** Writing – review & editing, Project administration. **Jesse K. Kreye:** Writing – review & editing. **Kim C. Steiner:** Conceptualization, Methodology, Writing – original draft, Supervision, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

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