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Effects of oak wilt (*Bretziella fagacearum*) on post harvest *Quercus* regeneration

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ABSTRACT

Oak wilt is a serious disease affecting oaks, especially those in the red oak group. Despite concern around a lack of oak regeneration and increasing mortality from oak wilt, there has been little effort to connect the two in relation to common forest management practices to regenerate oak. Oak management commonly includes clearcut harvesting, particularly within lower quality sites where sprouting is a viable regeneration method, but also where oak wilt is most problematic. We found that clearcut harvesting that encompassed pockets of oak wilt infected trees did not facilitate expansion or long-term perpetuation of oak wilt, but rather could serve as a containment mechanism for oak wilt. We found that stumps around 30 cm produced the greatest number of sprouts and that relatively minor differences in stump size determined if a stump was initially viable or never produced sprouts. Strong effects of stump size, and sprouting ability, remained significant drivers of survival (and mortality) over an extended 10-year period. Forest practices for oak on poor sites, such as those we studied, tend to be managed on short rotations which is likely well suited to capturing the maximum sprouting ability and long-term survival of oaks to regenerate stands.

1. Introduction

Oaks (*Quercus* spp.) are frequently a dominant species in eastern North America with important ecological and economic roles (Johnson et al., 2002; Fralish, 2004; Ellison et al., 2005). Oak cover types comprise half of forest lands in the eastern United States, but difficulties regenerating oak are common (Lorimer, 1993, Atwood et al., 2009) with high potential for future replacement by later successional species (Knoot et al., 2010). These difficulties are most pronounced in the Central Hardwoods Region (Fralish, 2003), which has lost oak abundance, as measured by importance value, on 81% of forested areas (Fei et al., 2011). In southern Wisconsin, two species of red oaks (*Quercus rubra*, *Q. velutina*) have declined nearly 50% since 1950 (Rogers et al., 2008) and oaks are predicted to decline further in the next generation of canopy trees (Taylor and Lorimer, 2003). Sustaining oak as a viable resource will require the ability to both regenerate and recruit oak into the overstory as dominant mature trees (Dey, 2014).

The prospects for continued oak dominance may be best on dry sites where shade tolerant competitors are often less abundant (Taylor and Lorimer, 2003). Clearcutting has been successful in regenerating oak on sites of average or lower productivity (Site Index ca. 50–60, Carmean et al., 1989) with managers often relying on stump sprouting. In stands originating from clearcutting, stump sprouts typically comprise anywhere from 50 to 75% of oak basal area in dominant positions (Gould et al., 2002; Morrissey et al., 2008). Stump sprouts are a source of oak on higher quality sites as well due to problems of greater competitive exclusion of advanced oak reproduction in these sites (Dey, 2014). Stump sprouts have a large established root system with stored resources (Johnson et al., 2002) allowing growth rates that can compete well during canopy closure and stem exclusion stages; however, regenerating oak is typically more difficult in higher quality sites.

Ironically, where we have our greatest chance for advanced reproduction of oak, on lower quality sites with dry, sandy soils, (Schwartz and Demchik, 2015) we also have the most pronounced problems of mortality due to the oak wilt pathogen (Juzwik, 2009). Oak wilt (*Bretziella fagacearum*, formerly *Ceratpcystis fagacearum*), is considered the most important disease affecting oaks in the eastern United States (Juzwik et al., 2011). The oak wilt fungus is spread overland by insect transmission into fresh wounds, or, more commonly, below ground by root graft transmission (Bruhn and Heyd, 1992). Below ground spread of oak wilt occurs over greater distances in shallow, sandier soils, because of higher levels of root grafting with these conditions (Gillespie and True, 1959, Bruhn et al., 1991, Evans et al., 2016). The fungus disrupts water and nutrient conducting channels and members of the red oak group (e.g., *Q. rubra*, *Q. velutina*, and *Q. ellipsoidalis*) are particularly susceptible to oak wilt with leaves wilting and

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falling rapidly once infected and tree death usually within two months. The white oak group (e.g., *Q. alba*, and *Q. macrocarpa*) is not as susceptible to oak wilt due to anatomical and physiological features such as increased tyloses and greater drought tolerance (Jacobi and MacDonald, 1980).

Despite growing concern around advanced oak reproduction and increasing mortality from oak wilt there has been little effort to connect the two in relation to common forest management practices to regenerate and maintain oak. Tyron et al., (1983) compared oak seedlings and sprouts between infected and uninfected parts of oak wilt stands and found no differences. In the study, they focused on oak regeneration within openings created by oak wilt, not in relation to harvest. There has not been an evaluation of the effects of oak wilt measuring changes in the same stands over 10 years. The spread of oak wilt is often highly variable and the roots of infected red oaks can harbor and transmit the fungus via root grafts for years after tree death (Tyron et al., 1983, Bruhn et al., 2003, Gleason and Mueller, 2005). Thus, a longer-term view of this issue is important and can inform forest operations in fundamental ways. We do not know, for example, if oak wilt negatively influences advanced reproduction in oak and/or spreads in a harvested stand, which conceivably could accelerate forest succession toward shade-tolerant and/or non-canopy-forming species such as black cherry (*Prunus serotina*) and box elder (*Acer negundo*, McCune and Cottam, 1985). Alternatively, clearcutting stands with oak wilt could essentially serve as an oak wilt control measure helping to maintain oak.

Oak wilt harvest guidelines in Wisconsin specify that managers cannot rely on stump sprouts for reproduction in stands where oak wilt is present. The guidelines do allow harvest in high transmission risk periods if reproduction is by seed source (WI DNR 2018). This flexibility was adopted based on the results from the studies by Tyron et al. (1983) and a 5-year interim data analysis of this study. Root grafts of oak seedlings to infected root systems is unlikely within the time the pathogen is viable (5–6 years) thus seedlings likely pose a lessor risk of transmission (WI DNR 2018). Oak wilt has become a major constraint impacting foresters and timber professionals' ability to operate, particularly in summer months when accumulated constraints are greatest on timber harvesting (Evans et al., 2016). However, oak wilt transmission to seedlings that become root grafted to infected root systems of stumps that remain viable would indicate a need for more, rather than less, conservative harvest guidelines.

This project was a long-term (10 year) analysis of oak wilt impacts on regeneration of red oak (*Quercus* spp.) dominated stands. Our objectives were to evaluate the effects of oak wilt on post-harvest regeneration dynamics for stump sprout, and seed origin oaks most susceptible to oak wilt. Specifically, our primary hypothesis was that stumps sprout origin oak reproduction would be reduced in oak wilt pockets over time whereas seed reproduction would be unaffected due to a lack of root grafting.

2. Methods

2.1. Study area

We conducted our research in Juneau, Adams, and Waushara Counties in the Central Sands Ecological Landscape of Wisconsin (Fig. 1, WI DNR 2015). The Central Sands are a nearly level expanse of well-drained glacial lacustrine and outwash sands. Historically, the Central Sands were primarily scrub oak - jack pine (*Pinus banksiana*) barrens with frequent fire disturbance. The landscape today is comprised primarily of xeric upland pine and oak forest (> 60% of forest land area) and is the most heavily forested landscape in southern Wisconsin (WI DNR 2018). Oaks have the highest importance value (average of relative dominance and relative density) of any tree species in the Central Sands, but for some species, including northern red oak (*Q. rubra*), average annual removals exceed growth rates (USFS, 2009). Sites were very dry and nutrient poor oak stands with low site productivity (SI < 50) and are typically managed with short rotation ages (70–90). Oak overstory species typically include northern pin oak (*Q. ellipsoidalis*), black oak (*Q. velutina*), red oak (*Q. rubra*), all in the red oak group, as well as bur (*Q. macrocarpa*), and white oak (*Q. alba*) in the white oak group. The forest products and processing industry is one of the largest economic sectors in the state and region. The Central Sands ecological landscape represents a best-case scenario in terms of oak regeneration and a worst-case scenario in terms of prevalence and spread of oak wilt with nearly level, deep, sandy soils (that facilitate root grafting), high oak basal areas and pronounced prevalence of oak wilt.

2.2. Data collection

We identified ten stands that contained oak wilt just prior to commercial clearcut harvesting in 2007, marked the center of each oak wilt pocket, and recorded their locations. Following harvest, we placed 1–2, 10 m radius plots within the boundaries of oak wilt pockets ($n = 18$) in each of the ten stands. We confirmed the presence of oak wilt for multiple trees in each oak wilt plot included in the study with laboratory isolation procedures (Pokorny, 1999). Oak wilt pockets were well established with multiple actively wilting trees extending beyond our 10 m radius plots and all marked stumps were highly likely to be root grafted and contain oak wilt (Bruhn and Heyd, 1992). We paired oak wilt plots with randomly placed control plots (absent of oak wilt) located > 45 m away from oak wilt plots ($n = 17$). These areas were well beyond root graft distance to oak wilt pockets (Bruhn and Heyd, 1992) and were systematically searched during active oak wilt season with no sign of oak wilt. Within each 10 m plot we marked all oak stumps with a permanent identification tag, recorded species group (red or white) and measured stump diameters. We collected data annually from 2007 to 2010, then in 2012, 2015, and 2017. The data included whether stumps were alive or dead, number of sprouts for each live stump, and we measured all living sprouts in 2017.

Additionally, we established four 1 or 2 m radius sub-plots (2 m radius if there were less than four seedlings within a 1 m radius subplot) 6 m from plot centers in the four cardinal directions within each 10 m plot and permanently marked them. Within subplots we recorded and marked oak seedlings (≤ 30 cm tall) and saplings (> 30 cm tall) by group (red or white) and in 2017, ten years post-harvest, we counted all seedling and sapling size woody stems of all species. We also estimated percent cover class of Pennsylvania sedge (*Carex pensylvanica*) within subplots at this time. Pennsylvania sedge is a native species that can form dense understory mats limiting seed regeneration of hardwoods (Abrams et al., 1985, Powers and Nagel, 2009).

2.3. Data analysis

To understand potential differences in mortality of stump sprouts over time we used survival analysis which analyzes time to death, in our case of stumps in plots within ($n = 125$) and outside ($n = 137$) of oak wilt pockets. Survival analysis offered several advantages with our dataset. The first is that it allowed us to retain data that is lost from view of the study over the course of a decade. For various reasons individual stumps that were lost or destroyed after years of being included in the study can be retained as censored observations informing the model until their disappearance and unknown fate. Survival analysis also allowed us to determine survival rates, and make comparisons annually over a 10-year period rather than just after 10 years alone. Annual survival estimates could be important if, for example, initial differences observed diminished over time or a lack of difference initially observed became more amplified. Our methods can distinguish not only if, but when such differences may have occurred.

We used the Cox proportional hazards regression model, which is a semiparametric model that provides easy to interpret information

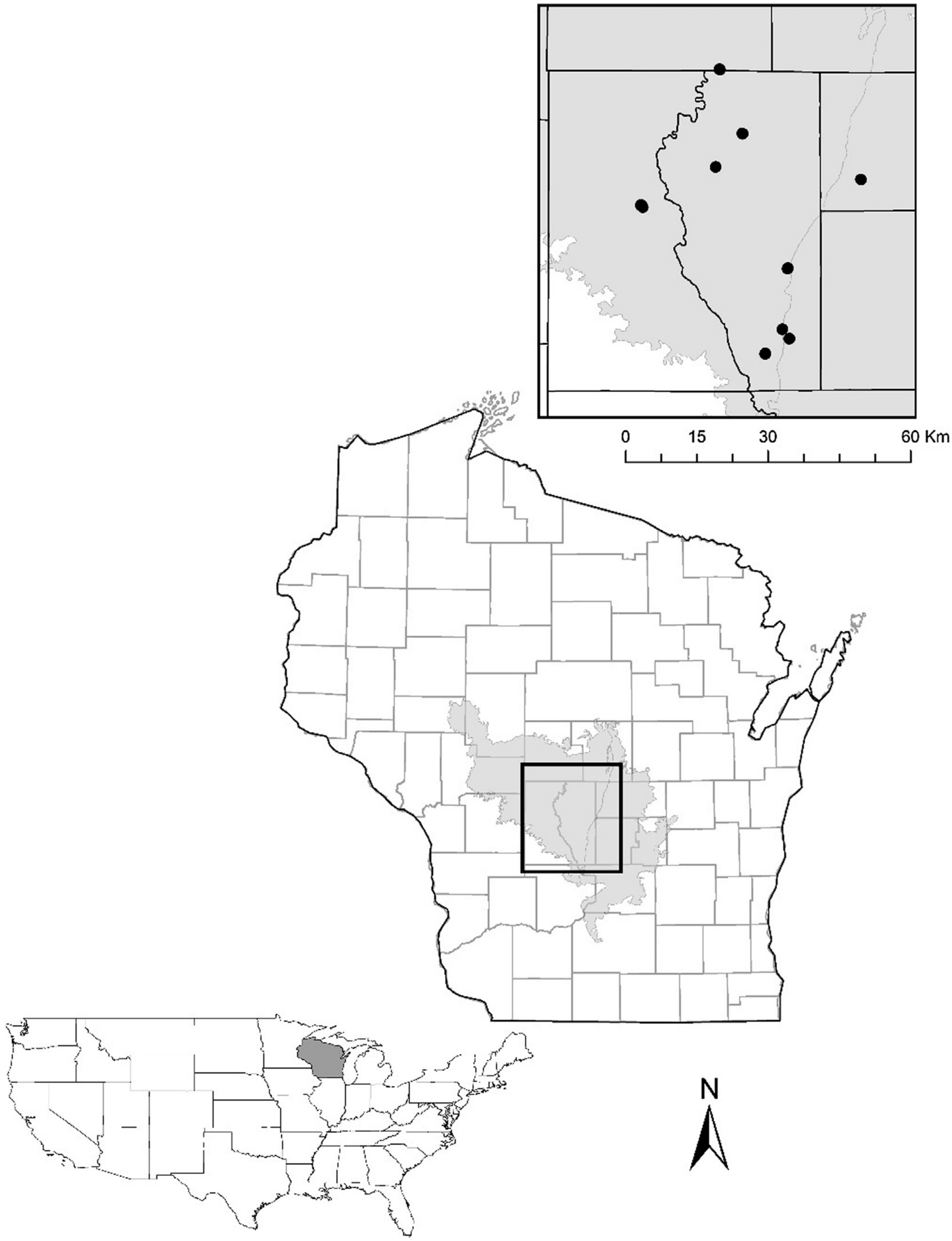

Fig. 1. Location of study sites (n = 10) in the Central Sands ecological landscape (light gray area) of Wisconsin, USA.

regarding the relationship of the hazard function to predictor variables. In our case, we included stump diameters at the time of harvest (2007) and the maximum number of sprouts produced by a stump as covariates in our Cox proportional hazards model. Regression models for survival analysis attempt to estimate parameters which describe the relationship between predictors and the hazard rate, allowing parameters (βs) to take on any value, while preserving the non-negative hazard rate (Hosmer et al., 2008). This is commonly addressed by parameterizing the hazard function as:

$$h(t|x) = \exp(\beta_0 + \beta_1 x)$$

Cox survival probabilities are adjusted using the mean value of each covariate across both control and oak wilt plot groups to focus on the impact of potential risk factors (covariates) on survival time. We also evaluated the nonparametric Gehan-Breslow survival function, which is used to determine differences in survival curves between two groups (stumps in either control or oak wilt plots). This model does not consider covariates and weights data accordingly when there are many late-survival-time-censored values. Both models were analyzed in SigmaPlot (Systat Software, San Jose, CA).

To understand seed source regeneration, we analyzed the percent cover of sedge as well as seedling and sapling density of all woody species for data we collected in 2017 at the subplot level using a multivariate analysis of variance procedure (MANOVA; SAS Version 9.4, SAS Institute Inc., Cary, NC). We used MANOVA because we were interested in comparing potential differences between control and oak

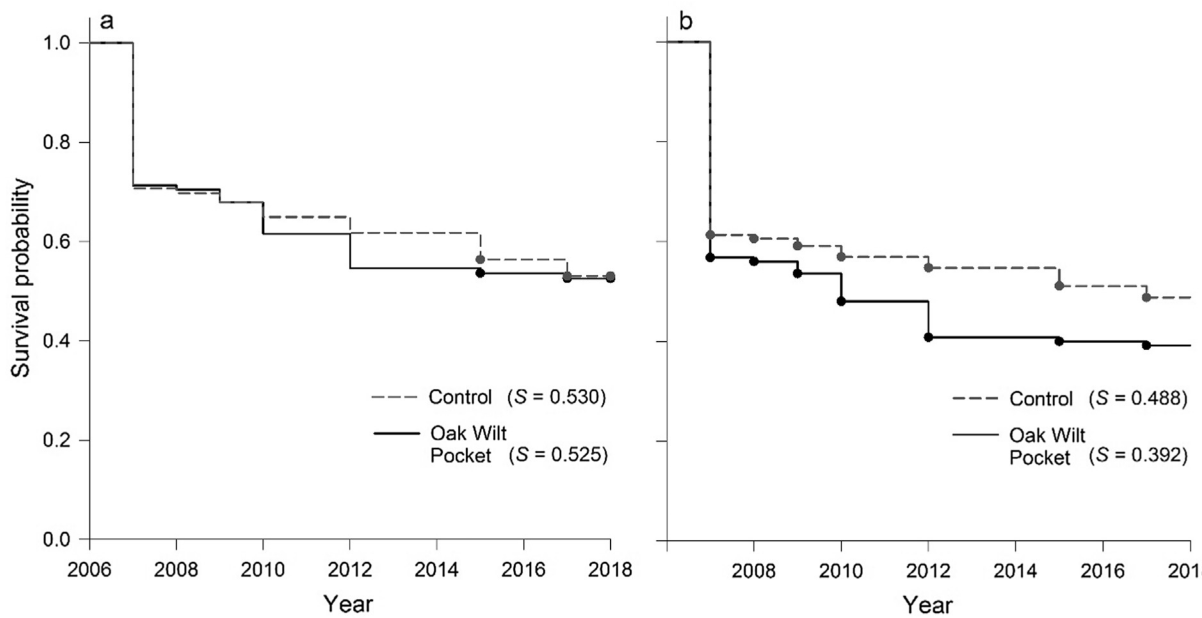

Fig. 2. Survival curves for stumps in control (n = 137) and oak wilt plots (n = 125) from 2007 (time of harvest) through 2017. Graph includes (a) Cox proportional hazards (PH) covariate adjusted survival function, and (b) Gehan-Breslow survival function. The Cox PH model focuses on the impact of potential risk factors (covariates) on survival time, while the Gehan-Breslow model focuses on differences between control and pocket groups.

wilt pocket subplots for multiple, conceptually and statistically related, dependent variables simultaneously (Huberty and Olejnik, 2006). We standardized measurements of stem density for subplots (collected at 1–2 m radius) by calculating the number of stems/ha. We analyzed seed reproduction (seedlings and saplings) of oak separately from other species to try and understand if potential differences in oak reproduction could be attributed, in part, to competition from other woody plants.

3. Results

3.1. Stump sprout survival

We found no differences between oak wilt and control plots in number of stumps that never sprouted or survived, mean stump diameters, the average stump sprout size, nor maximum number of sprouts produced. Similarly, there was no differences in survival between oak wilt and control plots (Fig. 2); however, both stump diameter and maximum number of stump sprouts produced were strong predictors of stump origin sprout survival (Table 1). Stump diameter is often a significant factor in determining probability of sprouting in oaks, usually with an inverse relationship between stump diameter and the number of sprouts per stump (Sands and Abrams, 2009). We observed high variability between stump diameters and sprouting, but mid-size stumps tended to be the most prolific sprouters in our study (Fig. 3).

Table 1
Cox proportional hazards survival model estimates and hazard ratios. The hazard ratio is the proportional change in hazard rate due to a unit change in a covariate.

Covariate	β	SE	Σ^2	*P*-val	Hazard ratio (HR)	HR 95% CI	HR 95% CI
Stump diameter	0.044	0.016	8.21	0.004	1.045	1.014	1.077
Maximum no. sprouts	−0.087	0.015	34.50	< 0.001	0.916	0.890	0.943

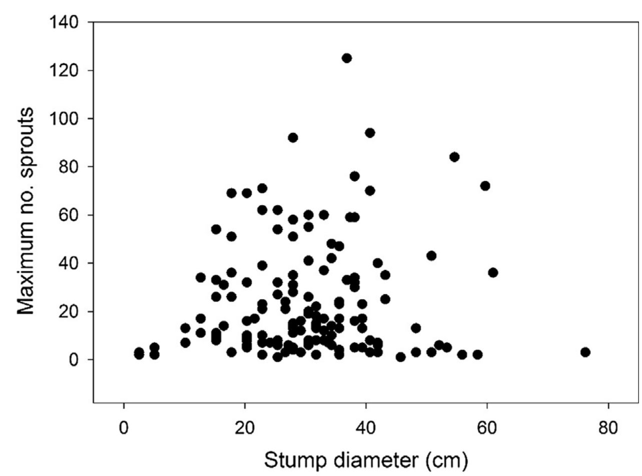

Fig. 3. Scatter plot of maximum number of sprouts produced by stump diameter for stumps that produced sprouts after harvest (n = 149).

Similarly, stumps that never produced sprouts were significantly larger (μ = 36.7 cm) than those that did (μ = 28.7 cm, Fig. 4). The maximum number of sprouts observed during the study occurred soon after harvest, usually the year of harvest (2007).

Neither the Cox, nor Gehan-Breslow method of survival analysis indicated a difference in survival between control and oak wilt plots, but final survival probabilities differed slightly between the two (Fig. 2). Gehan-Breslow survival rates were generally lower than for Cox with approximately 39–49% of stumps still surviving after 10 years while the Cox model resulted in around 53% survival over this time (Fig. 2). Differences in survival rates between models are likely in part a result of how the models handle stumps that never sprouted at the onset of the study which range from a 29% drop in survival in the Cox model to 43% in the Gehan-Breslow model. The Gehan-Breslow model assumes early survival times are known more accurately than later times and weights the data accordingly. In either case roughly one half of stumps in our study survived for the 10 years following harvest.

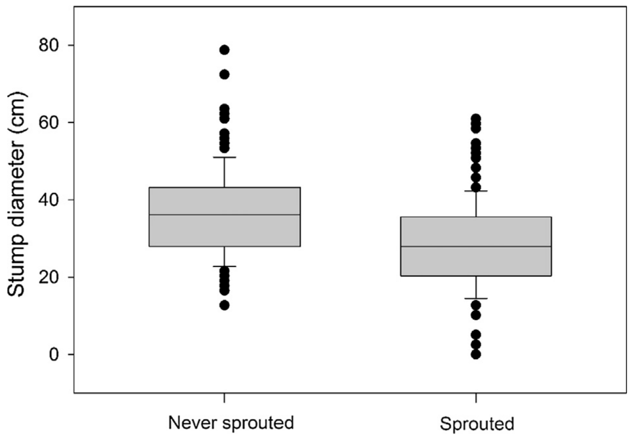

Fig. 4. Box plot comparison of stumps that either never sprouted (n = 108) or sprouted (n = 126) by stump diameter at time of harvest (2007). Stumps that never sprouted were on average significantly larger diameter (μ = 36.7 cm) than those that sprouted (μ = 28.7 cm, $P < 0.001$).

3.2. Seedling and sapling recruitment

We found no differences in seedling or sapling density between control and oak wilt plots aside from a greater number of non-oak seedlings in control plots (Table 2). Sedge cover was negatively correlated with other seedlings ($P = 0.032$), and was higher in oak wilt plots ($\bar{x}$ = 57%) as compared to control plots ($\bar{x}$ = 43%); but differences were not pronounced (Table 2). The number of seedlings and saplings for both oak and other species were positively correlated; where we found oak seedlings, there were also oak saplings, and seedlings of other species were found with saplings of other species as well ($P < 0.001$). This likely reflects subtle site differences that tend toward oak or other species and the 10-year post harvest stand initiation stage where we would expect a high number of species of all sizes where light is not yet a limiting factor.

4. Discussion

Oaks are undergoing what can be described as a regeneration crisis for a variety of reasons including a lack of fire and other disturbance processes, increased deer herbivory, and invasive pathogens (Dey, 2014). One-fourth of oak species in the United States are now considered of conservation concern (Jerome et al., 2017). Red oaks considered in this study are not yet a conservation concern, but they have declined in abundance and are particularly susceptible to effects of fire suppression and associated altered habitat, two of the leading threats to Quercus species in the U.S. (Fei et al., 2011, Jerome et al., 2017). Oak wilt has the ability to compound problems of declining oak abundance (Mcshea et al., 2007). Oak wilt is considered the most important forest disease problem in Wisconsin as well as Minnesota, Illinois, Iowa, and Texas (Juzwik, 2000). Despite the ramifications of oak wilt mortality exacerbating an already problematic issue of advanced reproduction in oak, little work has been done to understand the impacts of oak wilt on infected stump or seedling (from acorn) survival.

Oak management commonly includes clearcut harvesting, particularly within lower quality sites such as the Central Sands of Wisconsin where sprouting is a viable regeneration method for retention of oaks (Schwartz and Demchik, 2013). Regenerating oak on poor sites by sprouts has relatively high predictability as oaks are drought tolerant, have full light following harvest, and are aggressive sprouters (Johnson et al., 2002). Thus, as a forest progresses through the stand initiation stage to the stem exclusion stage, oaks have a higher chance of becoming dominant on low quality sites than on higher quality sites (Oliver and Larson, 1996; Johnson et al., 2002; Frelich, 2002). However, relying on stump sprout reproduction in the presence of widespread oak wilt carries a risk of maintaining the pathogen in the stand within viable root systems and/or that oak wilt can result in elevated mortality, poor regeneration and type conversion.

Our data indicate that after 10 years the presence of oak wilt had no discernable effect on stump origin sprout survival or seed origin reproduction (abundance of seedlings or saplings) with abundant reproduction in both cases. The only differences we found between control and oak wilt plots was higher sedge cover in oak wilt plots and more seedlings of non-oak species in control plots (Table 2). These may be related as we also observed a significant negative correlation between sedge cover and non-oak seedlings (Pearson's $r = -0.215$, $P = 0.032$). Sedge cover was common everywhere and locally very abundant ($\bar{x}$ = 51%, max cover = 88%), but did not appear to limit advanced reproduction. Seed production and establishment in oaks can also be limited by high levels of seed predation. As much as 90% of acorns are predated even in bumper crop years (Johnson et al., 2002; Schwartz and Demchik, 2013).

Deer herbivory may also limit reproduction and has been linked to low levels of advanced tree reproduction across eastern North America (Russell et al., 2001, Rooney and Waller, 2003, Sage et al., 2003). Stump sprouts can be beneficial under heavy browse pressure with faster initial growth rates than seedlings limiting the time sprouts are vulnerable to browse (Wendel, 1975). Notably, research in Pennsylvania found no effect of browse on the proportion of stumps sprouting or sprout density in hardwoods even where deer densities varied by an order of magnitude (Royo et al., 2016). This research found that the primary effect of deer browse was on sprout height (Royo et al., 2016). We did not quantify deer browse in this study or measure sprout heights, but browse did not appear to limit advanced reproduction in our sites which were well stocked with > 9000 seedlings/ha, 97% of which was oak. 2007–2013 post-harvest deer density estimates for our study region ranged from 57 to 114/km^2 (22–44/m^2) with an average of 80/km^2 (31/mi^2), mostly above target goals of 65/km^2 (25/mi^2, WI DNR 2008–2015). We considered deer herbivory to be relatively constant among oak wilt and control plots within the same clearcut stand, which was our primary unit of comparison.

Our results suggest that clearcut harvesting that encompassed pockets of oak wilt infected trees did not facilitate expansion or long-term perpetuation of oak wilt. Conversely, clearcutting may have served as an oak wilt control, or containment mechanism within infected stands. An important caveat to our work is that we did not isolate the oak wilt fungus from stumps at the conclusion of this study. We did collect data in late summer 2017, when peak levels of symptomatic trees occur, but found no symptomatic trees or sprouts. Gibbs (1980) found that survival of oak wilt fungus in branches of trees killed by oak wilt depended on the time of year the tree was killed. Successful isolation varied from 1 to 2 months in trees killed in May or June to successful isolation the following spring in trees killed later in summer (Gibbs, 1980). This suggests highly variable survival of oak wilt, but it is unclear if pathogen survival equates to viability with the ability to remain infectious. Similarly, oak wilt spread is often sporadic in nature

Table 2
Differences in dependent variables between control and oak wilt pocket subplots 10-years post clearcut harvest.

	Control (n = 45)		Pocket (n = 54)		MANOVA	
Variable	$\bar{x}$	SD	$\bar{x}$	SD	F-value	P-value
% Sedge	43.1	34.7	57.1	35.3	3.94	0.050
Oak Seedling	7694	14,831	6309	13,906	0.23	0.633
Other* Seedling	3696	7186	796	1417	8.42	0.005
Oak Sapling	18,042	20,394	17,644	24,108	0.01	0.930
Other* Sapling	12,238	17,653	10,373	11,900	0.39	0.534

* Other refers to all non-oak species in subplots based on size therefor including brush species.

with centers becoming inactive and/or expanding sporadically for unknown reasons (Juzwik et al., 2011). There remain many unknowns with the epidemiology of oak wilt. Managers must therefore balance imperfect knowledge of a pathogen associated with great uncertainty and economic losses with operational efficiencies.

Past research has determined significant effects of stump diameter on the probability of stumps producing sprouts (e.g., Johnson, 1975, Weigel and Johnson, 1998, Dey and Jensen, 2002). These studies have generally found an inverse relationship between stump size and probability of a stump producing ≥ one sprout. Sands and Abrams (2009) evaluated stump diameter and the number and size of sprouts produced, as opposed to at least a single sprout, and found more nuanced results including the greatest number of sprouts in middle (ca. 20–40 cm) size classes. We found a similar pattern, with stumps around 30 cm producing the greatest number of sprouts (Fig. 3). We also found that slight differences in stump size can mean the difference between a stump never producing sprouts or initially remaining viable (Fig. 4). Strong effects of stump size, and sprouting ability, remained significant drivers of survival (and mortality) over an extended 10-year period (Table 1, Fig. 1). Forest practices in Wisconsin for oak on poor sites, such as those we studied, tend to be managed on short rotations which is likely well suited to capturing the maximum sprouting ability and long-term survival of oaks to regenerate stands.

4.1. Management implications

Tens of thousands of oaks die annually from oak wilt in the Lake States of Minnesota, Wisconsin, and Michigan alone (Juzwik, 2009; Juzwik et al., 2011). Losses of trees to oak wilt are associated with economic losses, such and timber revenue, and decreased property values (Appel, 1995) along with other values more difficult to measure (Juzwik et al., 2011). Despite the importance of oak harvest to this region and oak wilt in posing a direct threat to this resource, there remain many unknowns around common management activities in the presence of oak wilt. Root grafts are estimated to be responsible for 90% of infections in this region (Cook, 2001; Wilson, 2005). Similarly, roots of infected red oaks can harbor and transmit the fungus through grafts for several years after tree death (Gleason and Mueller, 2005), but it is unknown, for example, how (or if) oak wilt is sustained in a clearcut harvest. In Wisconsin, oak harvest guidelines, which aim at reducing the risk of oak wilt, assume that clearcutting on future oak stocking stands where regeneration is largely of seed origin is low risk (Juzwik et al., 2010). However, where stump sprout regeneration predominates, impacts of oak wilt are assumed to be higher, but impacts remained unquantified (Juzwik et al., 2010). Our results did not show significant differences in stump sprout origin survival over time within and outside of oak wilt pockets, nor did we see signs of oak wilt in these stands after 10 years. These findings indicate that the effects of oak wilt may not *functionally* persist in these situations and common management practices may be viable even where oak wilt is common as was the case in our study sites.

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