

RESEARCH ARTICLE

Neighbours consistently influence tree growth and survival in a frequently burned open oak landscape

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Funding information

Division of Environmental Biology, Grant/Award Number: BSR/8717847, DEB/0208125, DEB/9419922 and DEB/9873673

Handling Editor: Giselda Durigan

Abstract

1. Successful management of fire-prone woody ecosystems is challenging and requires knowledge of the spatial arrangement of the trees and how the tree distribution patterns influence the nature and consequences of subsequent fires.
2. In open tree landscapes, trees are often aggregated, and the ability of trees within the clumps to survive fires plays a significant role in determining subsequent landscape dynamics. If positive interactions exist among neighbouring trees, this will help maintain the patterns of clumped trees. However, the tree-aggregated landscape will continue to exist only if the positive neighbour interactions persist consistently over time. In cases where disturbances are episodic, detecting these interactions is only possible through long-term studies.
3. Data reported here are from a 25-year study involving the annual tree censusing of a large grid-plot in a frequently burned open oak landscape dominated by *Quercus macrocarpa* and *Quercus ellipsoidalis*. The results showed that while having neighbours reduced tree growth, neighbours consistently facilitated survival, irrespective as to whether the neighbours were conspecifics or heterospecifics. Trees of all sizes in close proximity to neighbours were considerably more likely to survive fire throughout the study. This neighbour facilitation is likely the result of a reduction of both herbaceous and woody fuel within clumps.
4. *Synthesis*. This is the first study to document consistent neighbour facilitation among trees experiencing repeated stressors over an extended time period. Our findings support the literature documenting positive neighbour effects among plants in stressful and highly disturbed environments, in accordance with the stress-gradient hypothesis. While aggregated tree regeneration is typically viewed as the primary cause for the development of tree clumps in fire-prone ecosystems, our study showed that aggregated tree survival, by itself, can also be an important driver of post-fire tree clumping. Our results support the growing literature emphasizing the importance of landscape heterogeneity as a driver of resilience in fire-prone tree ecosystems, and the value of maintaining or creating this heterogeneity during forest management.

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KEYWORDS

fire, landscape ecology, neighbour facilitation, open tree landscapes, *Quercus*, stress-gradient hypothesis, tree aggregation, tree growth and survival

1 | INTRODUCTION

Successful management of fire-prone woody ecosystems is challenging and requires knowledge of the spatial arrangement of the trees (Das et al., 2008; Larson & Churchill, 2012; Meddens et al., 2018; Meyer et al., 2008) and how the tree distribution patterns influence the nature and consequences of subsequent fires (Frelich et al., 1998; Stephens et al., 2008; Turner, 1989). Tree aggregation, or clumping, is an especially common distribution pattern (Armesto et al., 1986; Condit et al., 2000; Larson & Churchill, 2012; Peterson, 2020), particularly in environments experiencing periodic fires (Bacelar et al., 2014; Moustakas, 2015; Staver et al., 2019; Tamjidi & Lutz, 2020). Clumping can provide trees a variety of benefits, including refuge from physical stress (Baumeister & Callaway, 2006; Tirado & Pugnaire, 2005), reduced susceptibility to enemies (Pineda et al., 2010) and suppression of a strong competitor (Lutz et al., 2014).

Open tree landscapes, such as savannas, parklands, brushlands, barrens, scrub and woodlands, are notably dynamic ecosystems, in which intensity, frequency and patterns of fire can determine whether the landscape is maintained or if it begins to transition into a more open or closed landscape (Hanberry et al., 2018). According to the stress-gradient hypothesis, the role of facilitation becomes increasingly important in conjunction with increasing stress (Bertness & Callaway, 1994). Fires, particularly repeated fires, represent a major type of stress for most trees. If positive neighbour interactions result in the increased survival of clumped trees during fires, then this would promote the perpetuation of the open tree landscape.

As emphasized by Brooker and Callaghan (1998), in cases where disturbances are episodic, detecting positive interactions among neighbours is only possible through long-term studies. This is especially true for studies trying to determine whether positive interactions in response to disturbances remain consistent over time. To conduct such research, a study would require a temporal scale long enough for many disturbances to occur, along with a spatial scale large enough to include many trees and tree neighbourhoods. We are not aware of any such study.

The primary purpose of this study was to determine the nature of neighbour interactions among trees in an open oak landscape experiencing frequent fires, and the extent to which these interactions are sustained over time. We were able to do this using data obtained from a large grid-plot study in which trees were censused annually for 25 years, during which time the trees experienced between 9 and 11 fires. The long-term observations allowed us to test how local tree density affects growth and survival of individuals in the face of repeated fires, and, secondarily, the extent to which these effects might be mediated by soil nitrogen and access to water.

2 | MATERIALS AND METHODS

2.1 | Study site

This research was conducted at, and with the permission of, the Cedar Creek Ecosystem Science Reserve (CCESR; Latitude: 45.401, Longitude -93.201) located in east-central Minnesota in the Anoka Sandplain, a glacial outwash area. The site is a mosaic of wetlands, old fields, and patches of oak savannas, woodlands and forests. CCESR experiences a temperate mesic climate (780-mm mean annual precipitation and 6.72°C mean annual temperature; Pellegrini et al., 2021). Except for that in a few small wetland patches, the soil in the area of CCESR where this study was conducted is of the Sartell series, excessively drained and low in organic matter and total nitrogen (Grigal et al., 1974). In this region of Minnesota, precipitation roughly equals transpiration (Grigal et al., 1974). This, combined with the soil's limited water retention capacity, means that vegetation at CCESR commonly experience drought conditions. As described by Grigal et al. (1974), within a particular climatic area, a soil's ability to supply water to plants is dependent on soil properties and the site's topographic position, with the latter influencing the quantity of water a site receives from upslope and the depth to groundwater. Due to the very slight relief in the Anoka Sandplain, CCESR has an elevation gradient of only 10m. The water table at CCESR is located at the lower end of the site's elevation gradient (Basiletti, 2018). Thus, small changes in elevation may influence a tree's access to groundwater.

Prior to European settlement, fire in this area created a patchwork of prairie, savanna and woodland habitat (Wovcha et al., 1995). Fires were suppressed following settlement resulting in the transition of many oak savannas to oak forests (Wovcha et al., 1995). An aerial photograph of the study site in 1959 showed the study site to be mostly open with scattered trees and a few larger patches of trees (Davis et al., 1997). Boundaries of the woody vegetation, openings and wetlands were digitized from this photo using Arc/Info (Environmental Systems Research Institute), showing that in 1959 open area constituted 47.6% of the study site (with 95.9% of the open area being contiguous), while the scattered woody canopy area represented 41.4% of the study site (wetland habitat constituted 11% of the area; Davis et al., 1997). A similar aerial photograph of the study site was taken in 1988 (except for a single fire in one area of the grid in 1987, no fires occurred in the study site between 1959 and 1988). This photo was also digitized, but in addition it was registered to the grid using ground targets (Davis et al., 1997). The digitized 1988 photograph documented the substantial decline in open area (23.8% of the study site in 1988) and increase in woody canopy (65.8% of the 1988 study site, with 95.6% of the canopy area being contiguous; Davis et al., 1997). Some tree landscapes have been described as alternative stable state

environments in which open canopy states (e.g. savanna) and closed canopy states (e.g. forests) are viewed as generally stable, but which can rapidly alternate from one state to the other under a narrow set of conditions (tipping points; Bond, 2022; Ribeiro et al., 2021). However, the oak landscape at CCSR is better described as part of a gradient system, in which tree canopy varies continually from very low in high fire frequency sites to nearly 100% in the unburned areas.

The oak habitats at CCSR are characterized by low tree diversity. They are dominated by two species of oaks, *Quercus macrocarpa* Michx and *Quercus ellipsoidalis* E. J. Hill, accompanied by varying abundances of a small number of mesophytic species, depending on the burn frequency (Peterson & Reich, 2001). In 1964, a program of prescribed burns [ranging from controls (no burns) to nearly annual burns] was initiated at CCSR to restore and maintain oak savanna and to study the effects of fire on vegetation (Irving, 1970).

2.2 | Study grid

During 1988, one of us (MD) initiated the GLADES (Grid for Landscape Analysis and DEmographic Study) Project with the establishment of a square 16 ha grid (consisting of 1,600 10×10 m cells) in a portion of the CCSR oak savanna/woodland habitat. In 1995 and 1996, nearly 9,000 trees with a dbh (diameter at breast height) of at least 2 cm were tagged, each with a unique number. Their dbh and x, y location within the grid were also recorded (Davis, 2021). If a tree possessed multiple stems, the tag was attached only to the largest stem. However, dbh was measured and recorded for all stems of multiple-stemmed trees. A burn programme was instituted in the grid area in 1987, and the study grid contained three different burn units, with burn numbers in the units during the 25-year study (1995–2020) ranging from 9 to 11 (Davis, 2021) and mean burn frequencies ranging from one in 2.3 years to one in 2.75 years. Burns took place in late April or early May and were surface fires. *Q. macrocarpa* and *Q. ellipsoidalis* represented 90% of all the trees in 1995. All trees, including each of the stems of multiple-stemmed trees, were visited annually and their statuses (live, dead standing or dead fallen) recorded. The dbh of live stems was measured every 5 years (Davis, 2021).

2.3 | Stems versus trees

All analyses were conducted at the level of trees. For example, a tree was considered dead only if all stems were dead. Basal area of a tree consisted of the summed basal areas of all live stems. Note that while many top-killed trees resprouted, the frequent fires prevented the sprouts from persisting and replacing any killed trees (Davis, 2021).

2.4 | Growth

Growth rate was defined as the increment in dbh divided by the time between measurements. All census intervals were exactly 5 years

because censuses were carried out at the same time (late spring) each year, within 15 days. When multiple stems of a tree survived, only growth of the largest stem in the earlier census was used in analyses. If two stems were the same size, one was chosen at random.

2.5 | Growth distribution and transformation

In tree species, the distribution of growth rates among individuals within a species is typically highly right-skewed, and this was the case in the two dominant species, *Q. macrocarpa* and *Q. ellipsoidalis* (Figure 1a). It was thus necessary to transform growth, normalizing the distribution for use in statistical models relating growth to neighbourhood density. Log-transformation would be routine but is invalid in this situation due to many growth rates of exactly zero (because of millimetre resolution in dbh). In this situation, one option is to convert zeros to the smallest positive growth rate that could be measured, in this case 1 mm dbh over 5 years. However, such an arbitrary value is a problem. When growth rates are low, the exact choice of a smallest positive has a large impact, because the logarithm varies rapidly at small numbers. In saplings, growth rates are typically <1 mm year⁻¹, so arbitrarily converting 0 growth to 0.2 versus 0.1 is a large difference and can affect results.

A better transformation is the square root, or some other similar power, while maintaining any negatives. Define growth g as

$$g = \frac{s_t - s_{t-1}}{\Delta t},$$

where s_t is size (dbh) at time t and Δt is the time interval. Then the transformation T is

$$T = \begin{cases} g^k & g \geq 0 \\ -[(-g)^k] & g < 0 \end{cases},$$

where $k > 0$. If $k = 0.5$, it would be a square root transformation, but we used instead $k = 0.45$. Kenfack et al. (2014) tested skewness of T across a range of values of k . Here we tested a similar range and found $k = 0.45$ was effective at reducing skewness across a range of dbh categories (Figure 1b).

2.6 | Neighbourhood density

For each tree, we located every other tree <20 m away. This can be done efficiently in a large plot by first assigning every tree a cell number within a grid of 20×20 m. Then, inter-tree distances were calculated only for trees within the same cell or neighbouring cells. That locates every tree within 20 m but reduces enormously the number of distances calculated. The identity of all neighbours alive during any given year and within 20 m of every tree was calculated and saved.

Neighbour density was defined as the basal area of all those neighbours that were alive in any one census. Neighbour density

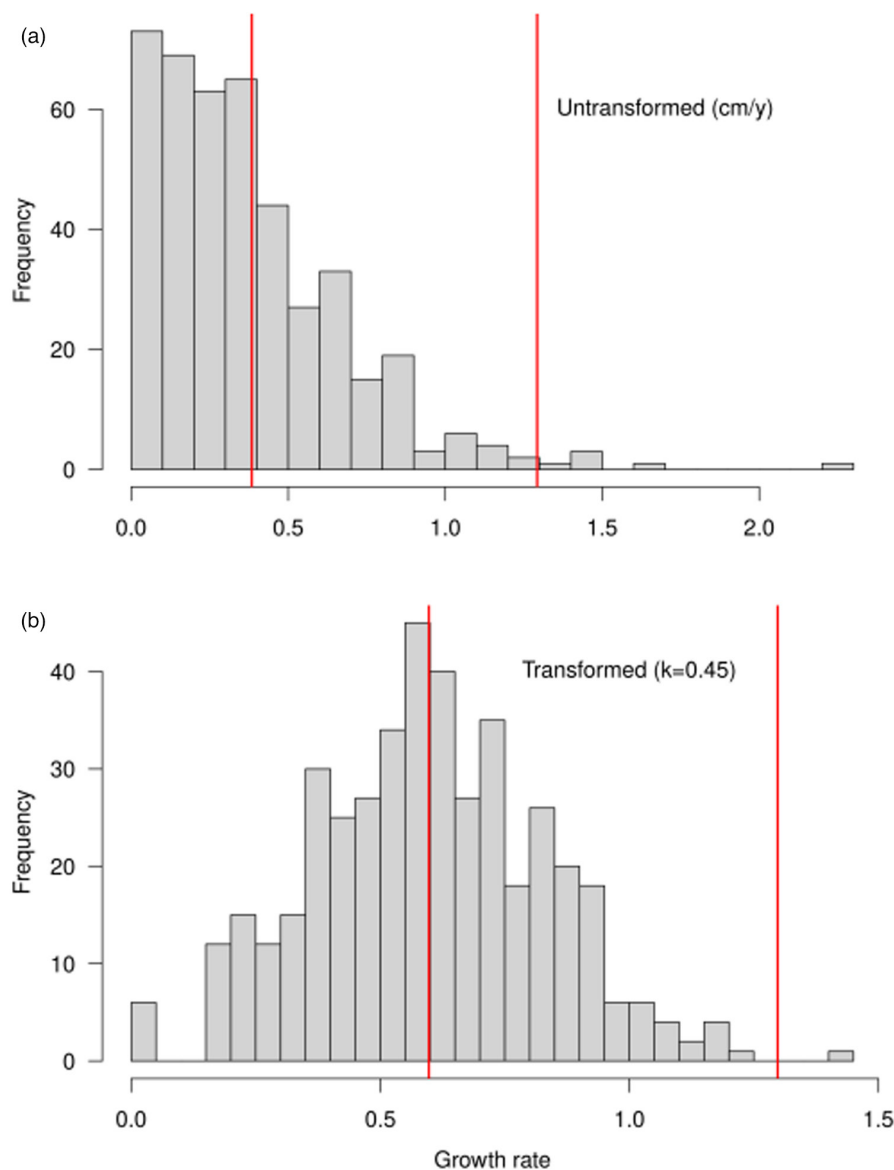


FIGURE 1 Histogram of (a) untransformed growth (dbh increment) and (b) growth transformed by the power 0.45. Vertical red lines are at the mean and 3 standard deviations above the mean. In panel B, the leftmost bar, near 0, includes the 6 trees with exactly 0 growth; in panel a, the leftmost bar includes the zeroes plus those at $g = 0.2$. Data are from *Quercus ellipsoidalis*, using growth from census 6 to 11, including stems ≥ 10 but < 20 cm dbh.

was divided into species groups. For every individual of *Q. macrocarpa*, the neighbouring basal area was considered in two categories: conspecific, meaning all basal area of neighbouring *Q. macrocarpa*, and heterospecific, that of all other species. Likewise, neighbouring basal area of every *Q. ellipsoidalis* was divided into the same two groups, conspecific (other *Q. ellipsoidalis*) versus heterospecific (all species except *Q. ellipsoidalis*). The two oak species so thoroughly dominate the study site that heterospecific basal area is nearly all due to the opposite oak. To illustrate, in 1995, the two oak species represented more than 92% of the basal area in the study grid, which increased to 95% by 2005 and to 97% by 2020 (Davis, 2021).

We further subdivided neighbours by distance, 0–5, 5–10 and 10–20 m away from a focal tree, dividing basal area by surface area of each ring. In preliminary analyses, we found no difference in the impact of neighbours within 5 m and at 5–10 m, so we combined those categories. This left four measures of neighbour density, two taxonomic (heterospecific vs. conspecific) and two distance categories.

Because neighbour density was limited to a fairly small range, no transformation was necessary, matching other analyses of local density (Comita et al., 2010; Condit et al., 1994). We chose to measure neighbourhood density in $\text{m}^2 \text{ha}^{-1}$. Specifically, we chose a magnitude of $10 \text{m}^2 \text{ha}^{-1}$ as the unit of measurement for neighbourhood density because this was close to two standard deviations (SD) of both conspecific and heterospecific density, in both distance categories, for the two abundant species. For example, the SD of neighbour density around *Q. ellipsoidalis* individuals in the four categories was between 3.5 and $8.9 \text{m}^2 \text{ha}^{-1}$ (across all five censuses); in *Q. macrocarpa*, it was $3.1\text{--}7.7 \text{m}^2 \text{ha}^{-1}$. This means that varying neighbour density by $10 \text{m}^2 \text{ha}^{-1}$ indicated an increase that covered most of the range of density.

2.7 | Environmental variables

Any effects of neighbours on plant growth and survival could be mediated by abiotic factors such as soil nutrients and water. The

primary nutrient limiting plant growth at Cedar Creek is soil nitrogen (Tilman, 1987). We did not sample soil nitrogen within and outside of tree clumps. However, in 1989, soil nitrogen was sampled in each of the 1600 grid cells. Nine soil samples were collected from each cell, mixed, dried and analysed for total N using alkaline persulfate digestion followed by NO_3 measurement on a Technicon II Autoanalyser. Since the 1988 digitized map was registered to the ground grid, it was possible to compare total N in grid cells covered by tree canopy with total N of open area grid cells.

A tree's ability to access water would also be expected to influence its vigour and potentially its vulnerability to fires. Because the water table at CCESR is quite flat, it is closer to the surface at the lower end of the site's elevation gradient (Basiletti, 2018). Therefore, small differences in elevation in this sandy soil environment affect a tree's access to water. Thus, elevation was used as a surrogate for water availability.

2.7.1 | Elevation

In 1989, Mark Hurd Corp. (no longer extant) collaborated with a local surveying company and produced a set of highly accurate and high-resolution topographic data for the site, consisting of a grid of elevation data (m above sea level) at points 3 m apart (meaning 9 points within each 10×10 m cell). The elevation designated for each cell consisted of the mean of all elevation points within the cell. Elevation ranged from a low of 278.1 m and a high of 285.6 m. Elevation was standardized by subtracting 278 m, the minimum, and dividing by 7.5, the range. This meant that the unit of elevation, as for neighbour density, represented the entire range across the plot.

For each tree, a value for soil nitrogen and elevation was assigned from the closest grid cell centre. Soil N and elevation turned out to be highly correlated ($r = -0.552$, $p < 0.0001$), and preliminary models suggested elevation was a better predictor of growth than soil N. The growth and survival models thus included elevation, but not N, as a predictor.

2.8 | Growth and survival as a function of neighbourhood density and dbh

A linear, multiple regression was used to relate growth to five variables: four measures of local neighbourhood density, and elevation. Focal trees were divided into four size categories, 2–5, 5–10, 10–20 and 20+ cm dbh (each category open on the right, so ≥ 5 and < 10 , etc.). This allowed each size category to have different responses. Stem diameter was included as a predictor within each category because growth changes considerably with size, especially in small trees. Growth was calculated in five census intervals, each lasting 5 years, and the census was included in the model as a random effect, accounting for the repeated growth measurements of the same individual trees. The models were run separately in the two species,

Q. macrocarpa and *Q. ellipsoidalis*, meaning there were eight models all told, four dbh categories in two species. The survival model was parallel in all aspects, but with logistic regression replacing linear regression.

2.9 | Parameter fitting

Regression parameters were estimated using a Bayesian Monte Carlo procedure. For growth, the model was based on a Gaussian error term; for survival, the error was binomial. The post burn-in chain of estimates produced a posterior distribution for every parameter, and statistical confidence in every parameter was estimated as 95th percentile from the posterior distributions (or 95% credible intervals). Models were run 10,000 steps, and the first 2,000 discarded as burn-in. Chains were examined visually and converged in $< 1,000$ steps. Details of the method are given elsewhere (Condit et al., 2006; Condit et al., 2007).

Results are presented as effect sizes of the four neighbourhood predictors and elevation on growth and survival of stems in each of the top three size categories. Results for the smallest size class, 2–5 cm dbh were not reported in detail because the number of trees in this size class declined substantially during the study due to their high mortality rates during the burns (no live small pin oaks remained by the end of the study), making it impossible for the models to yield reliable results for the latter time periods.

In the case of growth, these are partial regression coefficients from the linear regression (i.e. the regression parameters for each predictor); these were divided by standard deviations in each dbh class and species. Since predictors (neighbours and elevation) were standardized so one unit means approximately the entire range, a growth effect of 1.0 means that growth varied by an amount equal to its standard deviation across the full range of the predictor. Survival rates cannot be transformed with a standard deviation, but effect sizes can be transformed so that they display the change in survival across the range of a predictor. We do not report the dbh effect, since the four dbh categories allow conclusions about neighbourhood effects and tree size; dbh was in the model only as a precaution to avoid misinterpreting the density effects.

3 | RESULTS

3.1 | Soil nitrogen

Total soil N in the grid cells under tree canopy was greater than that of grid cells in open areas (tree cells: $1,020 \pm 1,040 \text{ mg kg}^{-1}$, open cells: $610 \pm 190 \text{ mg kg}^{-1}$, $t = 12.79$, $p < 0.0001$).

3.2 | Survival

Q. macrocarpa trees survived at a much higher rate than *Q. ellipsoidalis* trees during the study, and survival of both species increased

with tree size, as illustrated by the 25-year survival rates in burn unit three (*Q. macrocarpa*: <10 cm dbh 9.3%, 10–24.99 cm 48.5%, >25 cm 60.7%; *Q. ellipsoidalis*: 10 cm 0%, 10–24.99 cm 11.7%, >25 cm 13.3%).

3.2.1 | Neighbour density

In both *Q. macrocarpa* and *Q. ellipsoidalis*, neighbourhood density, both heterospecific and conspecific, was positively associated with survival likelihood and effects were consistent across dbh classes and censuses (Figures 2 and 3). The effect of neighbours did not diminish with distance. Effect sizes were often +0.5 up to +0.9. To reach effects >0.8 means survival would increase from 10% per 5 years without neighbours to 90% with dense crowding.

The two species differed in detail. Both benefited most by having *Q. macrocarpa* neighbours, that is, the conspecific effects in *Q. macrocarpa* were stronger than the heterospecific effects, but just the opposite in *Q. ellipsoidalis* (Figures 2 and 3). Note that while small sample sizes of the 2–5 cm dbh trees during the latter time intervals made it impossible to model these trees throughout the study, the survival effects of neighbours for these trees were similarly consistently positive during the first two intervals. As in the larger trees, small *Q. macrocarpa* were best protected by conspecifics, while small *Q. ellipsoidalis* were best protected by heterospecifics.

3.2.2 | Elevation

Survival generally was not significantly associated with elevation. Few tests were significant, and those that were significant were inconsistent in direction, so we omit the effect sizes.

3.3 | Growth

3.3.1 | Conspecific density

In both *Q. macrocarpa* and *Q. ellipsoidalis*, growth was consistently negatively associated with conspecific neighbour density (Figures 4 and 5). Effects reached –0.5 to –0.6, meaning that growth changed by half its standard deviation across the range of neighbour density, although most effects had lower magnitudes. The negative effect of conspecifics was consistent across censuses in both species. In both species, the impact of the nearest conspecifics, those <10 m away, was stronger than the impact of neighbours 10–20 m away, though some significant negative effects persisted at the greater distance (Figures 4 and 5).

There were differences in detail between the two species, however. In *Q. macrocarpa*, trees in the largest dbh category, ≥20 cm, were unaffected by conspecific neighbours (Figure 4); only smaller trees were inhibited. In contrast, all dbh categories in *Q. ellipsoidalis* suffered lower growth near conspecifics (Figure 5), though the 5–10 cm class in *Q. ellipsoidalis* had small samples and erratic results.

3.3.2 | Heterospecific density

The two species were quite distinct in their growth response to heterospecific neighbours. *Q. macrocarpa* growth was negatively impacted in all censuses and all dbh categories (Figure 4). In the largest dbh class (≥20 cm), the negative impact of heterospecifics contrasted with the lack of impact of conspecifics. In contrast, *Q. ellipsoidalis* growth was not affected by heterospecific neighbours (Figure 5). Effect sizes were positive more often than negative, but no effects were significantly different from zero. The small sample

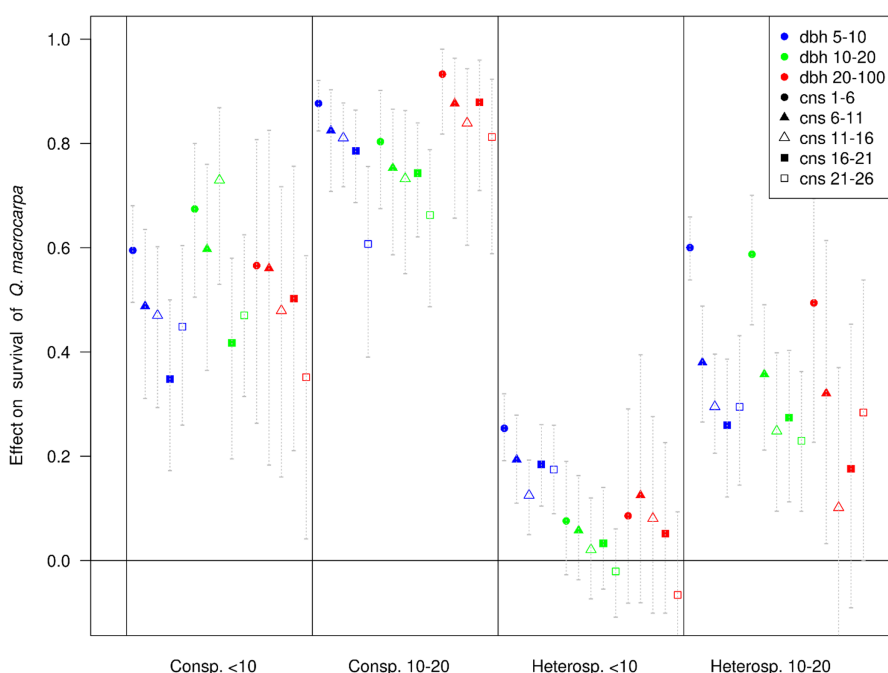


FIGURE 2 Effect sizes of four neighbourhood parameters on survival in *Quercus macrocarpa*: Conspecific basal area within 10 m (consp. <10) and at 10–20 m (consp. 10–20); heterospecific basal area within 10 m (heterosp. <10) and at 10–20 m (heterosp. 10–20). Positive effect sizes mean increased survival; negative effect sizes mean reduced survival. A single model was run for each of the three dbh classes; each included the census variable as a random effect. The three dbh classes are separated by colour, the six censuses by shape. Vertical dashed lines are 95% credible intervals, which is 95th percentile of posterior distributions of each parameter, the post-burn-in parameter chains.

FIGURE 3 Effect sizes of five parameters describing local neighbourhoods on survival in *Q. ellipsoidalis*. See Figure 2.

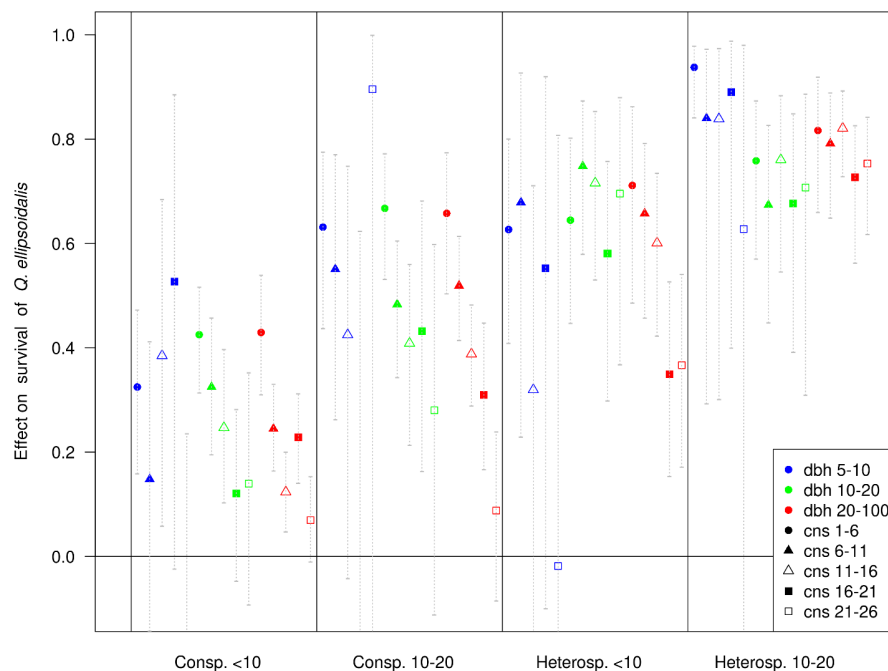
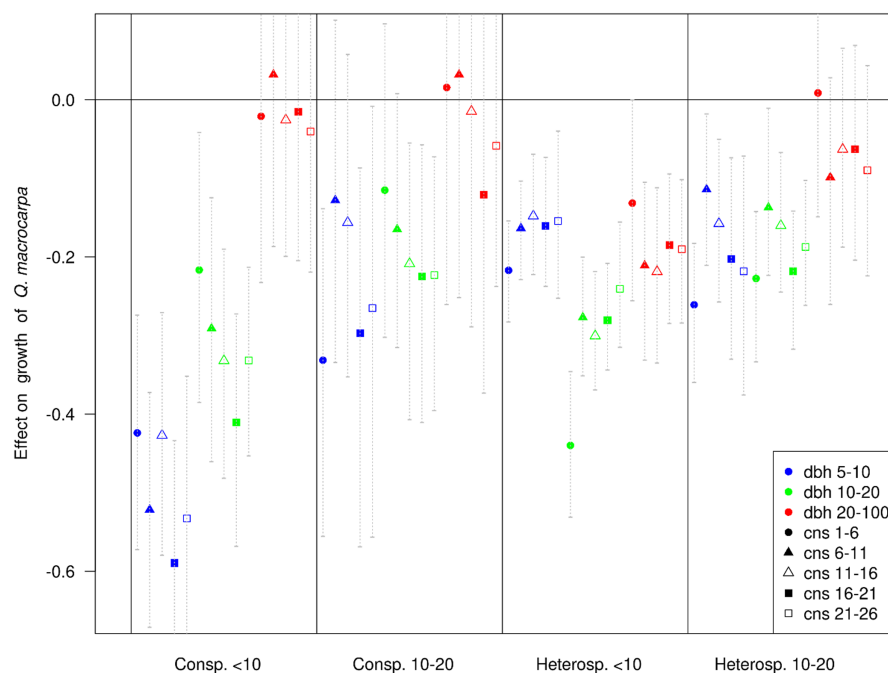


FIGURE 4 Effect sizes of four neighbourhood parameters on growth in *Quercus macrocarpa*: Conspecific basal area within 10 m (consp. <10) and at 10–20 m (consp. 10–20); heterospecific basal area within 10 m (heterosp. <10) and at 10–20 m (heterosp. 10–20). Positive effect sizes mean increased growth rates. Negative effect sizes mean reduced growth rates. A single model was run for each of the three dbh classes; each included the census variable as a random effect. The three dbh classes are separated by colour, the six censuses by shape. Vertical dashed lines are 95% credible intervals, which is 95th percentile of posterior distributions of each parameter, the post-burn-in parameter chains.



sizes of the smallest size class (2–5 cm dbh) made it difficult to discern a relationship between neighbour density and growth, but where significant, they were negative (reduced growth with more neighbours).

3.3.3 | Elevation

Elevation had a significant negative effect on growth in both species, meaning trees grew fastest at lower elevations. The effect size was around -0.1 in most cases where it was significant,

though it reached -0.3 to -0.4 in the *Q. ellipsoidalis* trees 5–10 cm in diameter.

4 | DISCUSSION

4.1 | Survival

While other studies of fire-prone environments have documented increased survival of clumped trees (Cohn et al., 2011; Trauernicht et al., 2016), this is the first study to document consistent neighbour

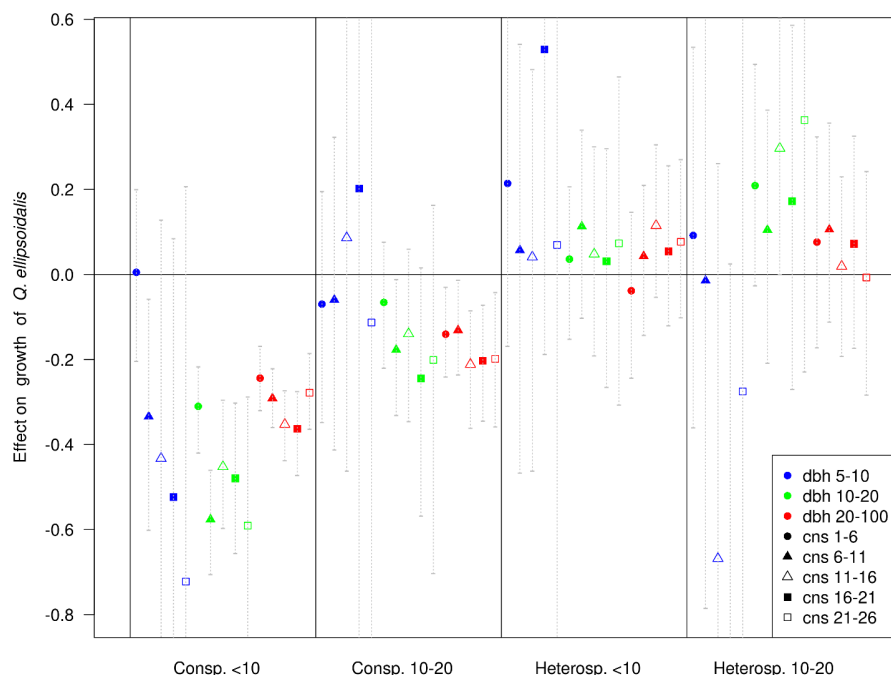


FIGURE 5 Effect sizes of five parameters describing local neighbourhoods on growth in *Quercus ellipsoidalis*. See Figure 4.

facilitation among trees experiencing repeated stressors over an extended time period. Trees of all sizes in close proximity with neighbours were considerably more likely to survive fire throughout the study. Our findings support the literature documenting positive neighbour effects among plants in stressful and highly disturbed environments (Bertness & Callaway, 1994; Brooker et al., 2008; Guo et al., 2021).

We believe two factors contributed to this neighbour facilitation in terms of survival. The first involves the reduction of herbaceous fuel under tree canopies. The decline in fire frequency and intensity, and the associated decline in tree mortality that occurs when other open tree landscapes transition to forests, has been attributed to the reduced biomass of grasses under trees, which are the primary fuel for surface fires in these environments (Archibald et al., 2009; Frost & Robertson, 1987; Hoffmann et al., 2012; Holdo, 2005). Rebertus and Burns (1997) found that tree survival in *Quercus* savannas was inversely related to grass cover. At CCESR, grass abundance is strongly negatively associated with tree canopy cover in the oak-dominated habitats (Pellegrini et al., 2021; Peterson et al., 2007). In a separate CCESR study, Wragg et al. (2018) showed that, compared to forbs, grass-dominated areas generate higher temperatures, release heat to greater heights and burn more completely. Newberry et al. (2020) found similar results in a savanna-forest ecotone in Brazil, with reduced grass biomass under trees associated with reduced ignition success, rate of spread, fire-line intensity and flame height. Thus, more neighbouring trees means less grass which, in turn, means reduced fire risk.

The second factor involves the reduction of woody fuel. While both oak species contributed to neighbour facilitation involving survival, the survival benefit of having *Q. macrocarpa* as neighbours exceeded the benefit of having neighbouring *Q. ellipsoidalis* for both species (Figures 2 and 3). We think the difference in fire

susceptibility between the two oak species may account for this difference. *Q. macrocarpa* is considered among the most fire-resistant oaks, particularly as compared to *Q. ellipsoidalis* (Frelich et al., 2015; Lorimer, 1985), and is illustrated by the much higher survival rate of *Q. macrocarpa* during this study. This means that *Q. ellipsoidalis* is more likely to serve as fuel, threatening the survival of its neighbours. Conversely, the more fire-resistant *Q. macrocarpa* is likely to impede the spread of fire, reducing the threat of fire-induced mortality among its neighbours. Belote et al. (2015) found the fire-resistant *Larix occidentalis* increased survival rates among nearby trees in a similar way.

The fact that most of the small saplings (2–5 cm) had died after 10 years does not conflict with our finding of neighbour facilitation in clumps. As is the case with all trees, seedlings and small saplings are extremely vulnerable to fire. Unless a small sapling is growing in a place where fire never reaches, chances are very low it will survive repeated fires. As described above, the survival effects of neighbours for the small saplings for both oak species were similarly consistently positive during the first two intervals. However, despite neighbour facilitation, the small saplings in clumps remained quite vulnerable to the fires, and most eventually died during the study.

If soil nitrogen and/or soil water were greater under tree clumps, it is possible these factors could have contributed to the increased survival of clumped trees. Reich et al. (2001) showed an increase in N mineralization under trees at CCESR, and our findings showed increased levels of total N in grid cells under trees compared to open area grid cells. Both set of results suggest that clumped trees may have enjoyed higher soil nitrogen conditions. However, while it is possible soil nitrogen and/or water could have been higher under clumped trees and could have contributed to increased vigour of clumped trees, then one would have expected the increased resources to have contributed positively to both tree survival and

growth. However, as shown, compared to isolated trees, while clumped trees enjoyed increased survival, they exhibited significantly reduced growth. Since these two aspects of overall tree vigour, survival and growth, manifested themselves in opposite ways in the clumps, it seems unlikely that either of these two resources had a significant influence on the survival of clumped trees.

Figures 2 and 3 suggest a possible modest decline in neighbour facilitation during the 25-year study. If the study site continues to experience frequent fires long into the future, and if clump sizes decline because of these fires, neighbour facilitation might eventually decline more substantially. However, we can confidently say that after 25 years of repeated fires, the positive clumping effect associated with survival remained strong.

Decades of studies at CCSR have documented high mortality effects of fires on trees (Pellegrini et al., 2021; Peterson & Reich, 2001; White, 1983). This also is illustrated by the results of this study. In burn unit three, only 6.2% of the trees died during the fire-free period 1995–1999. The unit was burned for the first time in 2000, and this single burn immediately increased the percent of dead trees to 33.2%. By year 10 (2005), the trees in this unit had experienced three fires, and the percent of dead oak trees had increased to 64.4%. While undoubtedly some trees in the study grid died from causes other than fires, the magnitude of these effects on tree mortality is very small compared to the mortality caused by fire.

4.2 | Growth

Growth of both species was greater at lower elevations, likely because lower elevation sites were closer to the water table and were higher in soil nitrogen.

The overall negative association between growth and conspecific neighbours for both oak species of all size classes, except for large *Q. macrocarpa* trees, is consistent with expected outcomes of intraspecific competition for resources, for example, nutrients, water and/or light (Adler et al., 2018; Yang et al., 2019). That growth in large *Q. macrocarpa* trees was not affected by neighbouring conspecifics is not surprising. They are unlikely to be overtopped by neighbouring conspecifics, and the fact that large *Q. macrocarpa* trees produce some of the deepest roots of all oaks (Deitschmann, 1965; Johnson, 1990) means they may be able to escape much of the underground competition with smaller *Q. macrocarpa* trees. Although growth in large *Q. macrocarpa* trees was not affected by conspecifics, it was negatively affected by heterospecific neighbours. This is likely due to interspecific competition with the much faster growing *Q. ellipsoidalis*, which grows (increase in dbh) three times faster than *Q. macrocarpa* (Davis, 2021). Also, at this site *Q. ellipsoidalis* typically grows taller than *Q. macrocarpa*, meaning that even large *Q. macrocarpa* trees can end up growing in the shade of *Q. ellipsoidalis*.

Unlike *Q. macrocarpa*, *Q. ellipsoidalis* growth was not affected by neighbouring heterospecifics. As emphasized above, by not serving as a good fuel, *Q. macrocarpa* is likely to impede the spread of fire. Since fire is known to reduce growth of surviving trees (Refsland

et al., 2020), *Q. macrocarpa* would be expected to provide its neighbours some protection from growth reductions due to fire, thereby perhaps cancelling out negative effects due to competition.

5 | CONCLUSIONS

We found the ability of a tree to survive fires is greatly increased when it has neighbours, either conspecific or heterospecific. Other studies of open tree landscapes experiencing fire have documented increased tree survival in clumps or groves (Cohn et al., 2011; Trauernicht et al., 2016). However, we believe our study is the first to document persistent neighbour facilitated survival in trees experiencing many fires during an extended period of time. The reduction of both herbaceous and woody fuel in tree clumps almost certainly contributed to the persistent neighbour facilitation.

Our findings support the idea that facilitation among plants occurs more commonly in severe and highly disturbed environments (Brooker & Callaghan, 1998; Walker & Chapin, 1987), in accordance with the stress-gradient hypothesis (Bertness & Callaway, 1994). The fact that survival was enhanced by neighbour facilitation, while growth was often reduced by negative neighbour interactions, is consistent with the findings from a meta-analysis of the stress-gradient hypothesis by Adams et al. (2022), which showed that increasing stress tends to result in an increase in positive ecological interactions in terms of survival but an increase in negative interactions with respect to growth.

Based on a review of 50 studies of spatial pattern in fire-frequent forests, Larson and Churchill (2012) concluded that aggregated tree regeneration is the primary cause for the development and maintenance of tree clumps in these environments. In the study reported here, due to persistent neighbour facilitation, trees survived best growing in groups. Since the frequent fires prevented any significant tree regeneration in the study area, either through sprouting or seedling recruits (Davis, 2021), the study showed that aggregated tree survival, by itself, can also be an important driver of post-fire tree clumping. The results reported here, along with those by Lutz et al. (2014) and Larson et al. (2015), emphasize the importance of documenting the spatial patterns of surviving trees following fires, in addition to those from regeneration, to gain a fuller understanding of the processes creating the observed tree spatial patterns in fire-frequent landscapes. Finally, our results support the growing literature emphasizing the importance of landscape heterogeneity as a driver of resilience in fire-prone forest ecosystems, and the importance of maintaining or creating this heterogeneity during forest management (Churchill et al., 2013).

AUTHORS' CONTRIBUTIONS

M.D. initiated and conducted the field portion of the study; R.C. performed the data analyses and produced the figures. Both co-wrote the paper.

ACKNOWLEDGEMENTS

This study could not have been conducted without the assistance of more than 40 Macalester College students, who helped set up

and monitor the woodland grid from 1988 through 2013. We thank Cathleen Nguyen, Rebecca Montgomery, and Jeannine Cavender-Bares for their censusing help during 2017–2019. We thank David Bosanko, Dale Krueger, Jim Krueger and Troy Mielke for conducting the controlled burns. Conversations with Jim Lutz and Sara Germain were very helpful during the writing of the paper. This research was supported by NSF grants BSR-8717847, DEB-9419922, DEB-9873673 and DEB-0208125 (M.D.).

CONFLICT OF INTEREST

The authors declare no conflict of interest.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/1365-2745.13906>.

DATA AVAILABILITY STATEMENT

The data are available from Dryad Digital Repository <https://doi.org/10.7291/D1SD5S> (Davis & Condit, 2022).

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How to cite this article: Davis, M. A., & Condit, R. (2022).

Neighbours consistently influence tree growth and survival in a frequently burned open oak landscape. *Journal of Ecology*, 00, 1–11. <https://doi.org/10.1111/1365-2745.13906>