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Pollen-limited reproduction in blue oak: implications for wind pollination in fragmented populations

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Abstract Human activities are fragmenting forests and woodlands worldwide, but the impact of reduced tree population densities on pollen transfer in wind-pollinated trees is poorly understood. In a 4-year study, we evaluated relationships among stand density, pollen availability, and seed production in a thinned and fragmented population of blue oak (*Quercus douglasii*). Geographic coordinates were established and flowering interval determined for 100 contiguous trees. The number of neighboring trees within 60 m that released pollen during each tree's flowering period was calculated and relationships with acorn production explored using multiple regression. We evaluated the effects of female flower production, average temperature, and relative humidity during the pollination period, and number of pollen-producing neighbors on individual trees' acorn production. All factors except temperature were significant in at least one of the years of our study, but the combination of factors influencing acorn production varied among years. In 1996, a year of large acorn crop size, acorn production was significantly positively associated with number of neighboring pollen producers and density of female flowers. In 1997, 1998, and 1999, many trees produced few or no acorns, and significant associations between number of pollen-producing neighbors and acorn production were only apparent among moderately to highly reproductive trees. Acorn production by these reproductive trees in 1997 was significantly positively associated with number of neighboring pollen producers and significantly negatively associated with average relative humidity during the pollination period. In 1998, no analysis was possible, because too few trees produced a moderate to large acorn crop. Only density of female flowers was significantly associated with acorn production of moderately to highly reproductive trees in 1999. The effect of spatial scale was also investigated by conducting analyses with pollen producers counted in radii ranging from 30 m to 80 m. The association between number of pollen-producing neighbors and acorn production was strongest when neighborhood sizes of 60 m or larger were considered. Our results suggest that fragmentation and thinning of blue oak woodlands may reduce pollen availability and limit reproduction in this wind-pollinated species.

Keywords Density-dependent reproduction · Habitat fragmentation · Pollen limitation · Wind pollination · *Quercus douglasii*

Introduction

The efficiency of pollen transfer between plants is often dependent on population density (Antonovics and Levin 1980), but studies of this relationship in tree populations have focused almost exclusively on insect-pollinated species. Long distances between individual trees can limit the movement of pollinators, resulting in reduced seed yields (Silander 1978; House 1993; Ghazoul et al. 1998) or higher proportions of self-pollinated seed (Murawski and Hamrick 1991, 1992). In wind-pollinated trees, dispersal of pollen into a volume of air typically results in pollen concentrations dropping off sharply with increasing distance from a source (Wright 1952; Gleaves 1973; Levin and Kerster 1974). However, many wind-pollinated trees produce copious amounts of pollen (Whitehead 1983), and numerous pollen grains may be present in the air even at considerable distances from a source (Caron and Leblanc 1992).

Some experimental evidence suggests that reproduction in populations of wind-pollinated trees can at times be pollen limited. *Fagus sylvatica* trees growing in isolation or in small stands were noted by Nilsson and

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Wastljung (1987) to produce a large proportion of unfilled seeds, suggesting a lack of cross-pollination. A positive correlation between population density and the proportion of filled seeds has been shown in *Pinus contorta* (Smith et al. 1988). These authors also reported a positive, though not statistically significant, correlation between the amount of pollen in the air and the proportion of filled seeds. High levels of self-pollination in *Thuja occidentalis* populations have been attributed to sparse densities and consequently low availability of outcrossed pollen (Perry and Knowles 1990). Allison (1990a) found that the proportion of filled *Taxus canadensis* seeds was related to the proximity to and amount of pollen produced by neighboring individuals. Furthermore, adding supplemental pollen to flowers increased seed production in low-density populations but not in high-density populations (Allison 1990b). Supplemental pollen has also been shown to increase seed production in populations of several *Betula* species growing at high elevations (Holm 1994), where pollen availability was presumably limited due to spatial patchiness and unfavorable weather conditions. In wind-pollinated tree species that produce variable numbers of male flowers in different years, seed production is often greatest in years of high male flower production, presumably due to greater pollen availability (Feret et al. 1982; Gysel 1958; Norton and Kelly 1988; Shibata et al. 1998).

The inter-plant distances at which pollination is impaired remain unclear, and the consequences for reproduction in wind-pollinated tree species are poorly understood. Understanding the effects of population density and spatial structure is vital for predicting the consequences of management activities and human disturbance in forested ecosystems. The goal of our study was to investigate how population fragmentation and thinning influence reproduction in the wind-pollinated blue oak, *Quercus douglasii*.

Blue oak is a small to medium sized tree endemic to California. Most abundant in the foothills surrounding the Central Valley, blue oaks are commonly found in open-canopied, nearly monospecific stands (Pavlik et al. 1991). Trees are deciduous and flower in early spring, shortly after the first leaves emerge. Although individual trees produce both male and female flowers in most years, blue oaks are likely to be primarily or exclusively outcrossing. Mating system analyses of other oak species demonstrate a high degree of outcrossing (Lumaret et al. 1991; Schwartzmann and Gerhold 1991; Bacilieri et al. 1993; Dow and Ashley 1996, 1998), and self-pollination in oaks is thought to be prevented by gametophytic self-incompatibility (Hagman 1975; Lumaret et al. 1991; Ducousso et al. 1993). In a preliminary pollen-addition experiment with blue oaks, bagged branches supplemented with pollen from other trees produced acorns whereas those exposed only to their own pollen did not (E. Knapp and K. Rice, unpublished work).

Blue oak acorns mature in the fall of the year that flowers are pollinated. Like many oak species, blue oaks exhibit mast fruiting with synchronous production of large acorn crops in some years and small crops in others (Koenig et al. 1994b). Acorn production also varies considerably among individual trees within a year, and trees with poor acorn production can be observed even in a mast year when average acorn production is high (E. Knapp, personal observation). The patterns and causes of variability in blue oak acorn production have been the subject of considerable research (Koenig et al. 1994b, 1996; Koenig and Knops 1995), as acorns are not only needed for recruitment of the next generation of trees, but are also an important source of food for many birds and mammals (Verner 1979; Block et al. 1990; Koenig and Knops 1995). Koenig et al. (1994b) found no evidence of regular cycles of acorn production in blue oak; rather, acorn production appeared to vary unpredictably across years, perhaps in response to variable weather conditions.

Although blue oaks are still an abundant and widespread tree in California, considerable habitat has been destroyed or degraded. Tens of thousands of hectares of blue oaks are lost annually to urbanization, wood cutting, and agricultural conversion (Bolsinger 1988), eliminating some stands and leaving others fragmented and thinned below their natural densities. Poor recruitment (Bolsinger 1988; Pavlik et al. 1991; Mensing 1992), possibly due in part to grazing pressure (Swiecki and Bernhardt 1998) and seedling competition with introduced weedy species (Gordon et al. 1989), also threatens the sustainability of remaining blue oak populations. If trees lost through natural mortality are not replaced, population density will decline over time even in uncut stands. The consequences of habitat fragmentation, tree cutting, and poor recruitment for pollination in this species have not been previously considered.

In this study, we examined the relationship between pollen availability and acorn production in a thinned and fragmented stand of blue oak. Our objectives were to evaluate how population density affects pollen availability and to assess the relative effects of pollen availability, weather during pollination, and female reproductive effort on acorn production.

Materials and methods

Study location and population

This study was conducted on a contiguous stand of 100 reproductively mature blue oak trees at the University of California Sierra Foothill Research and Extension Center in Yuba County, California. Trees covered an approximately 800×300 m area and elevation of the site ranged from 190 to 260 m above sea level. Selective clearing for "pasture improvement" several decades earlier had reduced the canopy cover of blue oaks from its original 60% to only 6%, leaving the remaining stand thinned and fragmented (Fig. 1). There was no evidence of successful recruitment beyond the seedling stage since the time of clearing. Understory vegetation was typical of foothill woodland and blue oak savanna communities in California, consisting mainly of exotic annual grasses with scattered exotic and native herbaceous dicots.

Trees were identified and marked with numbered aluminum tags. The spatial location of each tree in the study area and the

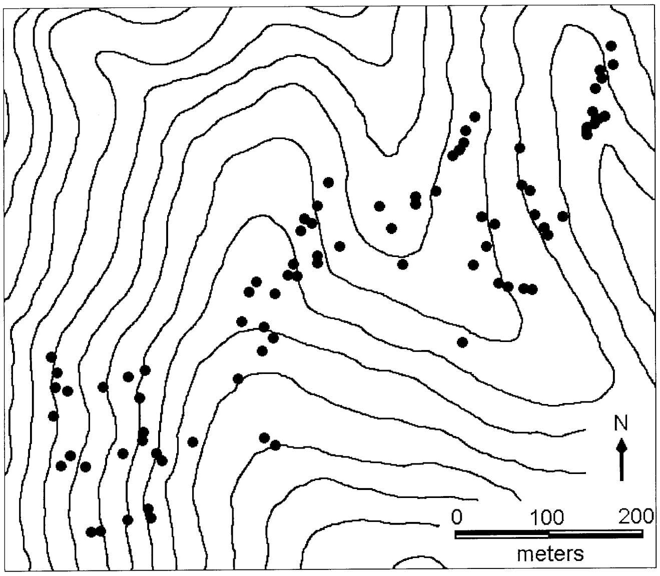

Fig. 1 Map of the study site showing *10-m contours* and the locations of all trees included in our analyses of acorn production (*filled circles*). Data were collected on 15 additional trees northeast of the area shown, but they were not included in the multiple regression analyses because of their proximity to neighbors outside the study site

nearest trees outside the study area were mapped using a Trimble TDC-1 (Trimble Navigation, Sunnyvale, Calif., USA) global positioning system (GPS). Each point was based on the average of approximately 100 differentially corrected measurements taken at 1-s intervals within 1 m of the tree's trunk. The accuracy of the measured locations was verified by overlaying the GPS points onto a composite aerial photograph of the study site using Idrisi GIS software (Clark University, 1997).

Measuring flowering and estimating pollen availability

The timing of flowering was monitored in the spring of 1997 and 1998 at approximately 3-day intervals, with dates of onset and termination of pollen release and onset of female flowering recorded for each tree. Pollen release was readily detectable by the change in color and shape of a tree's catkins. Anthers turned from yellow to green and catkins began to wither and dry almost immediately after dehiscence. The onset of female flowering was determined by inspecting five branches of each tree for open stigmas on each day of monitoring. The date at which stigmas ceased to be receptive to pollen was not always readily apparent, but we observed that stigmas darkened and lost their initial glossy, moist appearance less than a week after opening, and that female flowers on a given tree generally opened over a period of only a few days. We therefore estimated that the female flowers on any tree remained collectively receptive for 10 days following the opening of the first stigmas, a duration within the range reported for other oak species (Pjatnisky 1947, cited in Rushton 1977; Cottam et al. 1982; Lumaret et al. 1991).

After determining the timing of flowering, we estimated the availability of locally-produced pollen by counting the number of trees within 60 m that released pollen during a tree's period of stigma receptivity. The timing of individual trees' flowering was not determined in 1996 and 1999, and pollen availability in these years was estimated using the average of the numbers of pollen-producing neighbors in 1997 and 1998. Trees whose 60-m radii included neighbors outside the study area, for which dates of pollen release were unknown, were excluded from analyses of the effect of number of pollen producing neighbors on acorn production.

Female flower production was measured on each tree in 1998 and 1999. At the end of the flowering period, we sampled four branch ends (weighing approximately 25 g each) from separate locations on each tree using a pole pruner and counted the total number of female flowers present. The samples from each tree were weighed in the field and number of female flowers per gram of branch fresh weight were recorded. Female flower production in 1996 and 1997 was estimated as the average of the values determined for that tree in 1998 and 1999.

Estimating acorn production

Acorn production was evaluated in September of 1997, 1998, and 1999 using a visual survey technique developed by Koenig et al. (1994a). Two observers on opposite sides of a tree counted all acorns seen in a 15-s period; the index of acorn production was the total number counted per 30 s of observer time. Koenig et al. (1994a) demonstrated that acorn scores obtained using this method were highly correlated with results obtained using seedfall traps. Because our study was initiated after acorns had dropped in 1996, acorn production for this year was estimated by observing acorn caps remaining on trees in January 1997. Cap density was scored on a scale of 0 (none) to 5 (highest). Nearly all acorn caps fall from a tree within a year (E. Knapp, personal observation), so these estimates were unlikely to have been biased by caps produced prior to 1996.

Data analysis

We used multiple linear regression to evaluate how acorn production in each year was related to the number of pollen-producing neighbors within 60 m of each tree, female flower density, and weather during the pollination period. Because weather conditions were highly variable and the timing of each tree's flowering was closely monitored only in 1997 and 1998, weather during the pollination period was included in the analyses in just these two years. We initially considered two weather variables, average relative humidity and average temperature, that we hypothesized might affect pollen release or transfer. Only relative humidity was included in the final regression models after preliminary analyses indicated that the effect of temperature was not significant in any year.

Many trees produced few or no acorns in the latter 3 years of the study. To investigate factors affecting acorn production on trees that were at least minimally reproductive, we performed additional multiple regression analyses in 1997 and 1999 on data sets restricted to trees producing more than five acorns per 30 second count. In 1998, insufficient sample size due to low acorn production in the stand precluded such an analysis.

To examine the potential importance of pollen availability at different spatial scales, we performed additional analyses where pollen-producing neighbors were counted within radii ranging from 30 m to 80 m, in 10-m increments. We evaluated the strength of the relationship between the number of pollen producing neighboring trees and acorn production at each of these spatial scales using multiple regression, including the same variables as in the original 60-m analyses. Only trees whose largest (80 m) neighborhood radius did not include any blue oak trees outside the study area were included in these analyses. This eliminated any potential bias of fluctuating sample sizes at the different spatial scales.

Acorn counts were natural log-transformed to improve uniformity of variance and normality of the residuals. Repeatability of flowering times across years was tested using intra-class correlation coefficients. All analyses were conducted using JMP (SAS Institute 1995) and SAS (SAS Institute 1998) statistical software.

Results

Variation in flowering and acorn production

Considerable within-year variation in the timing of flowering was observed in 1997 and 1998, with as many as 28 days separating early- and late-flowering trees. Temporal separation of male and female flowering on the same tree was not generally apparent; male and female flowering was usually initiated during the same census interval. Trees began to flower in mid-February of 1997 and in mid-March of 1998, but individual trees' timing relative to others in the stand was consistent between years. Numbers of neighbors within 60 m that produced pollen during each tree's flowering period ranged from 0 to 11, and values from 1997 and 1998 were strongly correlated across years (intra-class correlation coefficient r_I=0.759, n=39, P<0.001 for the 60-m neighborhood radius). The percentage of trees with overlapping flowering intervals averaged 80% of the total number of neighboring trees present, but ranged from 100% to less than 25%.

The extent of female flower production varied among trees, with numbers of female flowers per gram of branch fresh weight ranging from 0 to 1.31 in 1998 and from 0 to 0.99 in 1999. Individual trees tended to produce similar densities of female flowers in each year, as indicated by a significant intraclass correlation across years (r_I=0.341, n=98, P<0.001).

Acorn crops were highly variable within and among years. Acorn caps were present on 90% of the trees in the stand following the 1996 season. Cap production scores ranged from 0 to 5 with a mean of 2.4 and median of 3. These observations, and reports of high acorn production in nearby stands (W. Koenig, personal communication), suggest that 1996 was a year of high reproduction (a mast year) for blue oaks in this region. Acorn production was substantially less in the following 3 years, with many trees producing few or no acorns. Acorns were observed on 61% of the trees in 1997, 34% of trees in 1998, and 63% of trees in 1999. Acorn counts from a nearby stand of trees indicated that approximately 6 times more acorns were produced per tree in 1996 than in 1997 (W. Koenig, personal communication). Mean, median, and maximum acorn counts were 3.9, 1, and 44 in 1997; 2.1, 0, and 56 in 1998; and 10.4, 3, and 71 in 1999.

Factors affecting acorn production

In 1996, the regression of acorn production on female flower density and number of pollen-producing neighbors within a 60 m radius was statistically significant (P<0.001, n=39, R^2=0.370) (Table 1). The standardized partial regression coefficients for both female flower density and number of pollen producing neighbors were significant, positive, and similar in magnitude. Trees with more pollen-producing neighbors produced larger acorn crops, as did trees with greater densities of female flowers.

The regression for 1997 included the effect of relative humidity during the pollination period in addition to female flower production and number of pollen-producing neighbors. No significant associations were detected with the full data set, containing reproductive as well as non-reproductive trees (P=0.252, n=40, R^2=0.106). When acorn production of only the more reproductive trees (those with acorn counts greater than 5) was considered, the multiple regression of acorn production on relative humidity and number of neighboring pollen producers was statistically significant (P=0.043, n=10, R^2=0.720) (Table 1). Higher acorn counts were associated with lower relative humidity during pollination and larger numbers of pollen-producing neighbors (P=0.022 and P=0.015, respectively, for the associated partial regression coefficients). Acorn production was not significantly associated with estimated female flower density in 1997.

In 1998, the regression of acorn production on relative humidity, female flower density, and number of pol-

Table 1 Multiple regression analyses of acorn production in 1996, 1997, and 1999. The independent variables in the regression are number of pollen-producing trees within a 60-m radius of the focal tree, number of female flowers per gram of branch fresh weight, and average relative humidity during the tree's pollination period (included in 1997 only). Analyses for the latter two years included only trees that were at least minimally reproductive (acorn counts greater than 5). In 1998, poor acorn production did not allow meaningful analyses

Year	Model and effects	R^2	Adjusted R^2	Standardized coefficient	F ratio	P
1996	Full model (n=39)	0.370	0.335	–	10.56	<0.001
	Number of pollen-producing neighbors			0.473	12.67	0.001
	Female flowers/g branch			0.423	10.15	0.003
1997	Full model (n=10)	0.720	0.581	–	5.15	0.043
	Number of pollen-producing neighbors			0.828	11.26	0.015
	Female flowers/g branch			–0.003	0.00	0.989
	Average relative humidity			–0.764	9.48	0.022
1999	Full model (n=15)	0.385	0.283	–	3.76	0.054
	Number of pollen-producing neighbors			0.254	1.24	0.288
	Female flowers/g branch			0.603	6.96	0.022

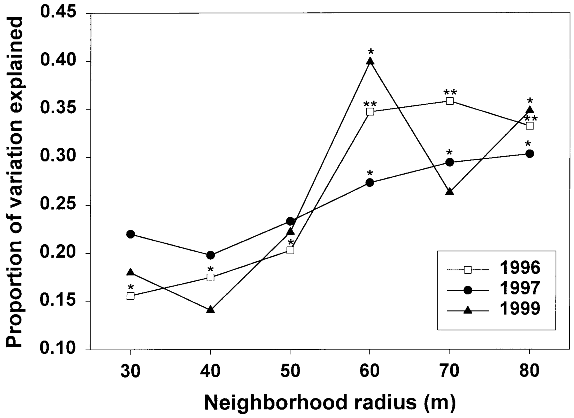

Fig. 2 Proportion of variation in acorn production explained by the number of pollen producing neighbors (the squared semipartial correlation, sr^2, obtained in multiple regression), plotted against the radius within which pollen-producing neighbors were counted. Radii for which the effect of pollen-producing neighbors was statistically significant are denoted by *($P<0.05$) and **($P<0.001$)

len producing neighbors was not statistically significant when the full data set was used ($P=0.148$, $n=39$, $R^2=0.066$). Acorn production was not significantly negatively associated with relative humidity during the pollination period ($P=0.118$) and positively associated with female flower density ($P=0.100$). The effect of pollen-producing neighbors did not approach significance in this year ($P=0.238$). Multiple regression analyses including only the moderately to highly reproductive trees was not possible in 1998 due to poor acorn production and the resulting low sample size.

In 1999, the regression of acorn production on female flower density and number of pollen producing neighbors was significant when the full data set, containing non-reproductive as well as reproductive trees, was used ($P<0.001$, $n=39$, $R^2=0.322$). With the full data set, only female flower density was significantly associated with acorn production ($P<0.001$). Trees with greater numbers of female flowers produced the most acorns. When only trees that produced a moderate to large crop of acorns were considered, the multiple regression of acorn production on female flower density and number of pollen producing neighbors was nearly significant ($P=0.054$, $n=15$, $R^2=0.385$) (Table 1). The number of female flowers was again the only variable significantly positively associated with acorn production ($P=0.022$). The partial regression coefficient for number of pollen-producing neighbors was positive but not significant ($P=0.288$).

Effect of spatial scale

The association between acorn production and the number of pollen producing neighbors was stronger at larger neighborhood sizes (Fig. 2). In multiple regression analyses for 1996, the proportion of variation in acorn production explained by the effect of pollen-producing neighbors (sr^2) increased from 0.16 when pollen producers were counted within 30 m of each tree to a maximum of 0.36 when pollen producers were counted within 70 m of each tree. The greatest increases in sr^2 occurred as the neighborhood radius was increased from 30 m to 60 m. The 70-m and 80-m neighborhoods produced little further change. In 1996, 26 trees were included the analysis, as this was the number remaining for the largest radius (80 m) after eliminating trees with neighbors outside the study area. Poor acorn production by many trees led to small sample sizes for this analysis in 1997 and 1999 ($n=7$ and $n=9$, respectively), but results from these years suggest a similar pattern of greater explanatory power for neighborhood sizes of 60 m or larger (Fig. 2).

Discussion

Stand density, pollen availability, and reproduction

Our results indicate that reproduction in this blue oak population may be limited by the availability of locally-produced pollen. During a highly reproductive year and when considering the more reproductive individuals in the stand in years with lower acorn production, trees with many pollen-producing neighbors tended to produce larger acorn crops than those that were more isolated. Associations between number of pollen-producing neighbors and acorn production were strongest for neighborhood sizes of 60 m or more in all years, suggesting that large neighborhoods were more likely to include the actual pollen parents of a tree's acorns. Trees contained within these larger neighborhoods are also less likely to be genetically related and therefore less likely to share incompatibility alleles. Relatedness may reduce pollination efficiency at the smallest spatial scales. Consistent with this possibility, Dow and Ashley (1996) found that nearest neighbors in a *Q. macrocarpa* population were rarely successful pollen parents. The apparent spatial scales of successful fertilization indicated in our study are consistent with Dow and Ashley (1998), who found that the average distance between parents in a *Q. macrocarpa* stand was 75 m.

The actual efficiency of pollen transfer between trees is sensitive to a host of complex factors such as the distance between donor and recipient, the amount of pollen produced and its temporal distribution across the flowering period, wind speed and direction, and local topography. Because we lacked complete information regarding all of these factors and their potentially complex interactions, our analyses use the simplifying assumption that all pollen-producing trees within a given radius contribute equally to pollen availability. Such simplifying assumptions would be expected to weaken the strength of the association between potential pollen availability and acorn production. Thus, the actual importance of local pollen may be even greater than our analyses indicate.

The effects of density reduction may depend on initial population density as well as the extent of thinning. While we found a positive association between the density of pollen-producing neighbors and acorn production, Healy (1997) reported that moderate thinning led to greater acorn production in a dense stand of red oak (*Q. rubra*). Reproduction in very dense stands may be limited by intraspecific competition for resources such as light and water. Thinning could conceivably promote acorn production under these circumstances if it is sufficient to reduce competition yet not drastic enough to limit pollen availability. We have observed poor acorn production in very dense blue oak stands (E. Knapp and K. Rice, personal observation), but such effects were not apparent over the range of densities examined in the present study.

Other influences on reproduction in blue oak

Weather during the pollination period may greatly affect pollen availability and reproduction in wind-pollinated species. Due to variation in flowering times within populations, different trees potentially experience different weather conditions during pollination in the same season. We found a negative association between average relative humidity during the pollination period and acorn production; this effect was statistically significant in 1997 and approached statistical significance in 1998. Atmospheric moisture can affect the aerodynamic properties of pollen grains (Whitehead 1983) and successful fertilization has been shown to be greater under low-humidity conditions in other oak species (Wolgast and Stout 1977). High humidity may reduce the amount of pollen released into the air by inhibiting dehiscence of anthers (Sharp and Chisman 1961). We have observed that blue oak catkins maturing during periods of cool, moist weather often wither without shedding pollen. High humidity is also associated with precipitation, which washes pollen from the air (Whitehead 1983). Though not indicated as significant in our study, warm temperatures may promote pollination by stimulating the growth and maturation of catkins (Sharp and Chisman 1961).

In addition to substantial within-year effects, climatic variation may account for differences in acorn production among years. In a 16-year study, Koenig et al. (1996) found that weather variables explained 48% of annual variation in blue oak acorn production. While weather may act on seed production pathways other than pollen transport, the strongest correlations between weather measurements and acorn production occurred for periods during flowering, rather than before or after (Koenig et al. 1996). The nearly complete failure of reproduction we observed in 1998 may have been due to adverse weather during the pollination period. Wet and cool weather coincided with flowering and the only reproductive trees in this year flowered during a brief multi-day dry spell.

Differences in female flower density accounted for a significant amount of the observed variation in acorn production in 1996 and 1999. Trees with more female flowers produced larger acorn crops. Trees tended to produce a similar number of female flowers in each year relative to other trees in the stand, although considerable variation existed. A link between seed production and resource availability has been suggested for several wind-pollinated tree species (Allen and Platt 1990; Sharp and Sprague 1967; Sork et al. 1993), and variation in female flower production may reflect the resource status of individual trees. Sharp and Sprague (1967) noted that trees producing a heavy crop of acorns in one year tended to produce fewer female flowers and fewer acorns in the following year. In blue oaks, acorn production has been positively associated with water availability (Koenig and Knops 1995).

The existence of multiple factors limiting acorn production of blue oaks could explain why we found the strongest association between pollen availability and acorn production in 1996, a year of high overall acorn production, while in other years a significant association was absent or could only be detected after excluding relatively non-reproductive trees. Large seed crops might only be possible under favorable conditions of weather and resource availability. If this is the case, the availability of locally-produced pollen would be most likely to limit reproduction in times and locations where the constraints imposed by other factors are not strong.

Implications of habitat fragmentation for reproduction in wind-pollinated trees

Although pollen limitation as a function of population density is still not well documented in wind-pollinated trees, the scarcity of reported examples may not be an accurate reflection of the importance of this phenomenon in natural populations. The strength of pollen limitation as a selective factor is suggested by features common to many wind-pollinated species, such as coordinated flowering, flowering prior to leafing out (reducing interference with pollen movement), highly divided stigmatic surfaces (providing larger surface areas for pollen capture), and production of large amounts of pollen (Whitehead 1983). It has also been argued that without a relatively close spacing of individuals, wind pollination would likely be too inefficient a mating system to have persisted over evolutionary time (Regal 1982; Whitehead 1983). The general absence of wind-pollinated species from tropical forests, where conspecifics are often widely separated, supports this view (Regal 1982). Although reproduction in wind-pollinated species may not be strongly pollen limited under typical conditions, pollen limitation has been reported in populations with low densities due to natural isolation (Nilsson and Wastljung 1987; Holm 1994), and in populations where the density of flowers was reduced by herbivory (Allison 1990a, 1990b). Low density in the blue oak stand we studied resulted from artificial thinning and clearing, and thus demonstrates how human-caused alterations to the spatial structure of a wind-pollinated tree population may interfere with reproduction.

Reductions in density are not unique to the population we studied. Residential development, stand thinning for pasture "improvement", and firewood harvest are common practices in blue oak woodlands. Insufficient regeneration is thought to be a widespread problem in blue oak (Bolsinger 1988; Pavlik et al. 1991; Mensing 1992), and will cause further density declines if recruitment cannot keep pace with mortality. This suggests a potentially worrisome scenario, where reduced stand density may cause the remaining trees to produce fewer acorns, possibly impairing the stand's ability to perpetuate itself. Even in populations where recruitment is not strongly limited by the size of acorn crops, negative effects would likely be experienced by animals that rely on acorns for food. Because of the wide geographic range of blue oak and the importance of blue oak woodlands as habitat for a large number of plant and animal species, this process could significantly reduce local and regional biodiversity on hundreds of thousands of hectares throughout California. Human activities are fragmenting stands and altering population densities of many other wind-pollinated tree species as well. The continued health of these populations and the ecosystems to which they contribute may depend upon maintaining tree densities adequate for efficient pollen transfer.

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