Evol Ecol (2015) 29:927–945
DOI 10.1007/s10682-015-9769-4

ORIGINAL PAPER

Impact of asymmetric male and female gamete dispersal on allelic diversity and spatial genetic structure in valley oak (*Quercus lobata* Née)

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Received: 4 January 2015 / Accepted: 13 May 2015

Abstract The distribution and abundance of genetic diversity in plant populations is initiated by sexually asymmetric propagule dispersal through pollen and seeds. Because these processes occur serially, it is not transparent how each contributes to subsequent patterns of genetic diversity. Using combined seedling/seed coat assay for naturally distributed seedlings of *Quercus lobata* Née, we extracted male and female gametic genotypes, and then assessed (wind-vectored) paternal and (gravity- and animal-vectored) maternal contributions to spatially distributed allelic diversity. We evaluated 200 naturally recruited seedlings from 4 open patches away from any adult canopies (denoted 'open'), and 174 seedlings from 14 patches immediately beneath adult canopies (denoted 'canopy'). The open patches included 19 % long distant dispersal events of >1 km while the canopy patches contained seedlings from one tree overhead. For each patch type, we partitioned average allelic diversity for six microsatellite loci for the whole study site (γ) into separate within-patch (α) and among-patch (β) components, translated into among-patch divergence (δ). We found that α-diversity resulting from seed dispersal was much less than that from pollen dispersal in both patch types, while total γ-diversity across the site was similar. Divergence (δ) among canopy patches was significantly greater than δ among open patches. We then evaluated spatial genetic autocorrelation (kinship) patterns for both open

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and canopy strata, separately for male and female gametes. Female gametes showed sharply declining kinship with increasing distance for canopy patches and modestly for open patches. In sharp contrast, male gametes from both patches showed only subtle decline of kinship, but seedlings still showed significant structure across patch types. On balance, sexual asymmetry in propagule dispersal shapes both the abundance and distribution of allelic diversity, with pollen dispersal promoting overall diversity but reducing spatial structure, but seed-dispersal reduces overall diversity and markedly increases spatial genetic structure.

Keywords Alpha and gamma diversity · Genetic diversity · Isolation by distance · Pollen dispersal · Seed dispersal · Spatial genetic structure

Introduction

For plant populations, gene flow is sequential, involving pollen dispersal, followed by seed dispersal. Once seedlings become established, the initial pattern of available genetic diversity within and among local sites has been established; subsequent opportunities for both genetic drift and local adaptation will be shaped by the balance between limited parental effective size and propagule flow (Crawford 1984; Wright 1943, 1946). Though a few species exhibit at least as much seed flow as pollen flow (e.g., Holbrook et al. 2002; Karubian et al. 2010), most tree species disperse pollen farther than seed (e.g., Chybicki and Burczyk 2010; Garcia et al. 2007; Heuertz et al. 2003; Isagi et al. 2007; Krauss et al. 2009; Moran and Clark 2012; Ravigne et al. 2006). Population structure analyses of nuclear versus maternally inherited markers support the higher gene flow through pollen than seed movement (Ennos 1994; Hamilton and Miller 2002; Sork and Smouse 2006). As the final stage of the process, however, seed dispersal has a disproportionate impact on the local effective size of recruiting populations, since it moves both female and male gametes (Crawford 1984; Garcia and Grivet 2011; Hamilton and Miller 2002). Estimating the separate contributions of pollen and seeds to gene flow becomes elusive, however, because many studies compare the two processes using different sets of individuals or markers. Overcoming that limitation, recent studies have compared haploid pollen and diploid seed dispersal by using maternally and parentally inherited tissue from the same seedlings, with an emphasis on estimating the effective number of pollen, seed, or seedling parents (Garcia et al. 2007; Grivet et al. 2009). Instead, a more precise comparison of the relative contributions of male and female parents would be to use the allelic contributions of their respective haploid contributions to the genetic diversity of naturally recruited seedling populations.

To analyze the impact of asymmetric dispersal on genetic diversity, it seems appropriate to employ recently developed methods that translate ecological diversity statistics into genetic analogues (Jost 2007, 2010; Jost et al. 2010; Nei 1973; Scofield et al. 2012; Tuomisto 2010). For example, we (Scofield et al. 2012) have demonstrated that the effective numbers of genotypes within and among local seedling patches can be translated into α, β, γ diversity measures, where α-diversity is the effective number of maternal seed sources within each patch, γ-diversity is the effective number of maternal seed sources for the entire study site, and β-diversity is the effective number of seedling patches, or the turnover rate of maternal parentage from patch to patch. We also introduced a term δ,

which is the [0, 1]-scaled pairwise maternal divergence between patches. This term provided a useful measure that allows an analysis of the level of maternal sharing among different seedling patches. We showed that different dispersal vectors generated different patterns of divergence among patches. Scofield et al. (2012) used genotypes to identify maternal seed sources, but we did not extend the study to examine either paternal genotypes or the allelic diversity consequences for recently established seedlings themselves. The patterns of spatial genetic autocorrelation among these seedlings will reflect the allelic diversity of both parental sexes, as well as isolation by (sexually-asymmetric) propagule movement (Heywood 1991; Vekemans and Hardy 2004).

Our objective here is to elucidate the contributions of sexually asymmetric dispersal of haploid gametes to seedling allelic diversity within and among patches and to assess spatial genetic structure (SGS) across the landscape, using valley oak (*Quercus lobata* Née, Fagaceae) as our study system. We have previously shown that pollen dispersal can be sufficiently restricted to create local neighborhoods (Austerlitz et al. 2004; Sork et al. 2002b) and that pollen flow creates spatial autocorrelation (Austerlitz et al. 2007). We have also shown that the pollen dispersal kernel exhibits both a high degree of local pollen flow as well as a long fat tail that can spread alleles extensively across the landscape (Pluess et al. 2009). By analyzing the genotypes of established seedlings and the maternal (pericarp) tissues of their attached acorns, we have also shown that pollen and seed dispersal are spatially asymmetric (Grivet et al. 2009). Despite the fact that seed dispersal slightly enhances the effective number of pollen parents represented in local seedling patches, it seriously constrains the effective number of seed parents in those same patches. The net patterns among established seedlings are demonstrable, but a major limitation of previous analyses has been their focus on diploid seedling patterns and the effective number of parental genotypes, rather than on the separate contributions of male and female gametes to the allelic diversity patterns within the seedlings themselves.

In this paper, we compare male and female (gametic) contributions to the allelic diversity itself, using the same seedling populations studied by Grivet et al. (2009). To assess separate male and female gametic contributions to allelic diversity, we will apply a classical diversity approach to obtain measures of α, β, and γ. We introduced this approach to compare foraging behaviors of vertebrate dispersal agents and added a measure of pairwise divergence (δ) among patches—to provide a measure of the extent to which two patches included progeny from different maternal sources (Scofield et al. 2012). We will here extend that same methodology to the post-dispersal seedlings, comparing the haploid contributions of male and female gametes for those found in open and canopy recruiting patches for both diversity metrics and spatial autocorrelation (kinship) patterns, and addressing three specific questions. (1) What is the pattern of seed dispersal into seedling patches that are proximal to (canopy) and distant from (open) maternal adults? (2) How does that dispersal differential impact allelic diversity of male versus female gametes, measured in terms of within-patch (α), among-patch (β), and total (γ) allelic diversity components, as well as the degree of allelic divergence (δ) among patches? (3) What are the consequences of sexually asymmetric (pollen and seed) dispersal for fine scale spatial genetic structure (SGS) of paternal and maternal allelic contributions to open versus canopy patches? We know from previous work (Grivet et al. 2009) that seed dispersal enhances the effective number of both male and female parents in seedling patches, and that the effective number of maternal parents is lower than that of paternal parents. Here, we test the predictions that both allelic diversity patterns and the fine scale SGS of alleles will be disproportionately shaped by sexually asymmetric (male vs. female) gametic dispersal. This focus on allele contributions, rather than effective number of parental

genotypes, yields a more precise assessment of the genetic consequences of pollen and seed dispersal, by directly comparing the haploid contributions of the two kinds of gametes, instead of comparing haploid pollen with diploid seeds.

Materials and methods

Study system

Our study site is located along the valley floor of Figueroa Creek, within the UC Santa Barbara Sedgwick Reserve in the Santa Ynez Valley (34°42′N, 120°02′W), Santa Barbara County (California, USA). This savannah habitat includes our study species valley oak (*Quercus lobata* Née) and coast live oak (*Quercus agrifolia* Née), with blue oak (*Quercus douglasii* Hook and Arn.) along the slopes. This low-density population (1–6 trees per hectare) is composed of clustered centenary adult trees, interspersed with scattered saplings and juveniles. The fine scale genetic structure of valley oak adults within this valley indicates a small amount of spatial autocorrelation within 100 m and only a trace of anisotropy (Austerlitz et al. 2007; Dutech et al. 2005). This site has been the locality of numerous studies by our research team (described below), with adult valley oaks exhaustively mapped and genotyped over about 300 ha.

Valley oak is wind pollinated and essentially 100% outcrossed (Sork et al. 2002a), with estimates of effective mean pollen dispersal distances ranging from 60 to 350 m (Austerlitz et al. 2007; Pluess et al. 2009; Sork et al. 2002b). Adult trees produce massive quantities of acorns every 4–6 years, which was the case in 2002, when seedlings were found both beneath adult trees and in areas away from any adults. With the exception of that 1 year, few seedlings have became established over the period 2001–2013 (Sork, pers. observation), due to summer drought, an absence of large acorn crops, seed predation, small rodent herbivory, and grazing by deer (Tyler et al. 2006; Zavaleta et al. 2007). Acorns are consumed, stored, and occasionally dispersed by acorn woodpeckers, *Melanerpes formicivorus* (Grivet et al. 2005; Scofield et al. 2010, 2011, 2012), as well as by small mammals such as mice (*Peromyscus* spp.) and California ground squirrels (*Spermophilus beecheyi*). A prominent avian dispersal agent, however, is the western scrub jay (*Aphelocoma coerulescens*) (Koenig et al. 2009), whose foraging and caching behavior provide a highly effective dispersal mechanism for valley oak acorns, because the birds store them beneath the soil at some distance from adults (WD Carmen, pers. comm).

Sampling design

Following the acorn season of 2002, we located and sampled tissue from newly germinated seedlings and their attached acorns throughout Figueroa Creek valley (Grivet et al. 2009) in open areas away from and beneath the canopies of acorn-producing adults (see Fig. 1). In four patches located at least 20 m away from the canopy edge of any acorn-producing adult, we selected 200 seedlings with attached acorn; we here designate those as ‘open’ patches, because they were found in open areas without any canopy cover. Given the lack of valley oak overhead, we presumed that the seedlings had been dispersed, especially since they had all emerged from buried seeds (Grivet & Sork, pers. observation). The most likely dispersal agent was the western scrub jay, because the acorns were buried singly and in a manner consistent with their reported caching behavior. Other possible

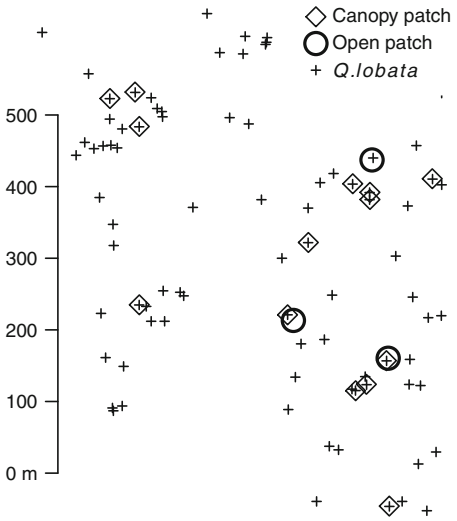

Fig. 1 Map of sampling locations of low-dispersal canopy seedling patches and a subset of high-dispersal open seedling patches and *Quercus lobata* seed source trees at Figueroa Creek valley, Sedgwick Reserve, Santa Barbara Co., CA, USA. A complete map of open patches and source trees is presented in Fig. 2a. Each canopy patch was found beneath the canopy of a *Q. lobata.* The *figure* illustrates relative spatial placement and densities of trees and patches. Given the large areal extent depicted, it should be noted that the sizes, shapes and overlaps of symbols chosen for visual clarity should not be taken to represent the sizes, shapes and overlaps of trees and patches in nature

dispersers include rodents (gray squirrels, chipmunks, and deer mice) that move seeds away from the maternal source, but usually less than 50 m, or acorn woodpeckers that could have dropped acorns en route to their granaries (Koenig et al. 2008; Scofield et al. 2011; Thompson et al. 2014).

We also sampled 14 seedling patches and 174 seedlings with attached acorns, located in patches immediately beneath the canopies of acorn-producing valley oak adults. We will henceforth refer to this patch type as a 'canopy' patch. We presumed these seedlings were derived from dispersal by gravity, but short-range dispersal by rodents is also possible, which we later confirmed by testing that assumption genetically.

Despite the lower number of patches utilized, this study will use slightly larger sample sizes of dispersed seedlings than Grivet et al. (2009), incorporating subsequent improvements in genotypic assignment (Smouse et al. 2012). We use fewer patches than Grivet et al. (2009) to ensure that the two patch types were represented by comparable sample sizes and the area in which seedlings were collected covered comparable spatial expanses. To elucidate the dispersal events that contributed each recruiting seedling, we first determined the maternal genotype, using methods described below, and then matched it to the genotype of one of the 353 mapped and genotyped adults in Figueroa valley.

DNA extraction and genotyping

DNA extraction and amplification protocols for these samples are described elsewhere (Grivet et al. 2005, 2009; Sork et al. 2002b). For this study, we used the following six nuclear microsatellite loci: MSQ4 ($K = 22$ alleles in seedlings), QpZAG1/5 ($K = 8$),

QpZAG9 ($K = 17$), QpZAG36 ($K = 8$), QrZAG11 ($K = 8$) and QrZAG20 ($K = 11$), deployed for those papers and other efforts (Dutech et al. 2005; Grivet et al. 2009; Sork et al. 2002b). To separate male and female gametes within a seedling, we used a combination of TwoGener gametic extraction (Smouse et al. 2001), and pericarp assay of the maternal genotype (Grivet et al. 2005). We converted seedling/pericarp genotypic pairs into their haploid male and female gametic genotypes. For any seedlings or pericarp tissue with four complete loci, we inferred complete genotype, using methods described in Smouse et al. (2012).

Allelic diversity measures

All diversity analyses described below were conducted in R (R Core Team 2014) and are implemented in the package **dispersalDiversity** (Scofield 2015a) and Sorklab website (http://www.eeb.ucla.edu/Faculty/Sork/Sorklab). The **readGenalex** package (Scofield 2015b) was used to read and manipulate genotype data in R.

To assess allelic diversity within patches and total across patches, we utilized the technical developments in Scofield et al. (2012), and summarized the allelic counts for each of the six microsatellite loci within the g-th patch, for male gametes, for female gametes, and for diploid seedlings, and then extracted unbiased estimates of the probability of drawing two identical alleles for any given locus from the same patch:

$$r_{gg} = \sum_{k=1}^{K} \frac{x_{gk}\left(x_{gk} - 1\right)}{n_g\left(n_g - 1\right)}, \tag{1}$$

where x_{gk} is the tally (within the g-th patch) of the k-th allele from a locus with K observed alleles, and where n_g is the total number of alleles sampled within that same patch, analogous to Simpson's (1949) unbiased estimator of species identity and as Nei's (1972; 1973) unbiased estimator of allelic identity. An additional form of unbiased diversity estimator $\left(q^*_{gg}\right)$ is due to Nielsen et al. (2003), and the interested reader is referred to Scofield et al. (2012) for further discussion of its use in measuring dispersal. We will provide examples of both estimates below.

Within each patch, we averaged the values for the six loci to obtain a per-locus average value, remembering that diploid seedlings have twice as many alleles as do the gametes. On the premise that individual patch diversities of a given type (canopy or open) are credibly homogeneous, we used a weighted estimate of the average within-patch identity, defined as:

$$\bar{r} = \sum_{g=1}^{G} \frac{\left(n_g - 1\right)}{\left(N - G\right)} \cdot r_{gg}, \tag{2}$$

where G was the number of patches and $N = \Sigma_g\,(n_g)$ was the total sample size for the patch type, measuring the probability (unweighted average over the six loci) that two randomly drawn alleles from the same patch were identical. Inverting Eq. (1) yields a natural measure of within-patch diversity for the g-th patch $\left(\alpha_g = 1/r_{gg}\right)$, basically the effective number of alleles per locus for that patch (see Jost 2007; Scofield et al. 2012). The average within-patch alpha diversity is similarly estimated by inverting Eq. (2), yielding $\alpha = (1/\bar{r})$. With our sample sizes, differences between unbiased estimators our relatively small; for open-patch male gametes $\alpha = 3.040$ from inverted r_{gg} for open-patch male gametes, but

$\alpha^* = 3.035$ from inverted q^*_{gg}. We constructed the single-patch estimates of the α_g-estimates and pooled within-patch α-diversities separately for maternal gametes, paternal gametes, and diploid seedlings, and separately for the 14 canopy and four (4) open patches.

Similarly, we obtained an unbiased measure of the allelic identity for any particular locus within the entire collection of either (canopy) or (open) patches as the probability of drawing two identical alleles from the collection, without regard to patch:

$$R_0 = \sum_{k=1}^{K} \frac{X_k(X_k - 1)}{N(N-1)}, \tag{3}$$

where (for any particular locus) X_k is the total tally of alleles of the k-th type for the whole site; we then used an unweighted average Eq. (3) over the six loci. Reciprocation again yields the total per-locus diversity ($\gamma = 1/R_0$), the effective number of alleles per average locus within the entire collection for either patch type. Both unbiased estimators produce $\gamma = 3.131$ for open-patch male gametes; we will continue by presenting results for just r_{gg}-based [Eq. (1)] estimators and note that the **dispersalDiversity** R package readily produces results for both estimators.

Testing for heterogeneous α and γ diversity metrics

To test whether α is heterogeneous between canopy or open patch types, or between male and female gametes, we deployed a non-parametric analogue of Bartlett's variance heterogeneity test (Jost 2008; Snedecor and Cochran 1989), using methods from Scofield et al. (2012). The tests are invariant with respect to the form of diversity estimator employed. We first translated the pooled within-canopy and within-open patch α-diversities among female gametes into variance analogues, as well as a pooled within-patch variance from both types of patches. We next computed Bartlett's test and bootstrapped membership among the strata in question, testing each locus individually and summing observed and bootstrapped log-likelihoods for testing across all loci; we performed 9999 bootstraps plus the observed. As is commonly observed in comparisons of genetic diversity, a significant difference at one locus, if of sufficient strength, can result in a significant difference across all loci. We compared average α-diversities for canopy and open patch types for male gametes, as well as those for male versus female gametes, using the same types of tests. Finally, we constructed analogous tests of γ-diversity for canopy versus open patch types and for male versus female gametes, using the same sort of non-parametric Bartlett's tests described in Scofield et al. (2012). When gene flow into patches is restricted, we would expect that α-diversity would be less than when gene flow is high. However, the impact of gene flow on γ-diversity is less easy to predict, because it will depend on the extent to which the accumulated patches incorporate all sources of genes. Moreover, the differences in γ-diversity between male and female gametes will depend on the sexual asymmetry of dispersal.

Inter-patch turnover and diversity

For ecological studies, $\beta = (\gamma/\alpha)$ diversity provides a traditional description of species turnover across sites and thus compositional divergence among strata (Whittaker 1960, 1972). Here, diversity of alleles within patches is α and that across the entire (valley-wide) site is γ, so β diversity represents the turnover in allelic composition from patch to patch. It is best viewed as the "effective number" of genetically (non-overlapping) patches for the site. If all patches have identical allele frequencies, then $\beta = 1$, but if each patch contains

different alleles, then β = the number of patches. The more extensive is dispersal, whether of pollen or seed, the lower is the expectation for allelic turnover.

Jost (2007) has pointed out that diversity components are limited in range by the numbers of individuals and strata sampled. For our Simpson/Nei-type measures, the minimum value is always 1, but the maximum number can depend on the sampling frame. With modest sample sizes for some patches, it is possible to miss rare alleles in the population, particularly for hyper-allelic microsatellite loci, and not all loci are equally prone to the problem. For example, at Sedgwick adult *Q. lobata* carry several alleles unobserved in seedlings collected for the present study (MSQ4, $K = 4$ novel alleles in adults; QpZAG1/5, $K = 3$; QpZAG9, $K = 6$; QpZAG36, $K = 2$; QrZAG11, $K = 4$; QrZAG20,$K = 3$). On the other hand, regardless of population diversity we can never observe more alleles than gametes. For our unbiased Nei/Simpson allelic-identity treatment in Eqs. (1) and (3), it is convenient to use maximum values that reflect the sampling scheme itself, which does not change from locus to locus. We have used $\alpha_{max} = (N - G)/G$, $\gamma_{max} = (N - G)$ and $\beta_{max} = (\gamma_{max}/\alpha_{max}) = G$ for haploid male and female gametes, and $\alpha_{max} = (2\,N - G)/G$, $\gamma_{max} = (2\,N - G)$ and $\beta_{max} = (\gamma_{max}/\alpha_{max}) = G$ for the diploid seedlings. With these limits so defined, we can compute diversity metrics scaled to have range [0, 1] (following Jost 2007) as:

$$0 \le \alpha' = \left(\frac{\alpha - 1}{\alpha}\right) \cdot \left(\frac{\alpha_{max}}{\alpha_{max} - 1}\right) \le 1, \tag{4a}$$

$$0 \le \beta' = \left(\frac{\beta - 1}{\beta}\right) \cdot \left(\frac{\beta_{max}}{\beta_{max} - 1}\right) \le 1, \tag{4b}$$

$$0 \le \gamma' = \left(\frac{\gamma - 1}{\gamma}\right) \cdot \left(\frac{\gamma_{max}}{\gamma_{max} - 1}\right) \le 1. \tag{4c}$$

These scaled metrics may make visualization and/or quantitative comparisons more convenient between groups or systems differing in overall diversity. Other scalings to [0, 1] may certainly be formulated, and care must be taken that scaling is performed consistently. The statistical testing framework developed here and in Scofield et al. (2012) is insensitive to monotonic transformations, so scaling is not necessary for testing.

Allelic differentiation among patches

For studies of seed and pollen movement, it is useful to understand the uniqueness of each patch in terms of its composition (see Scofield et al. 2012). Here we augmented our measures of inter-patch turnover (β-diversity) with measures of inter-patch 'identity' and its translation into non-overlap measures of allelic composition. When dispersal is extensive (open patches), adjacent patches may share propagule sources and may (thus) exhibit low allelic divergence. However, for minimal dispersal distances (canopy patches), even closely neighboring patches may exhibit high allelic divergence.

We computed inter-patch identity measures as the probability that two randomly drawn individuals, one from each of the *g*th and *h*th patches, share the same allele. For a single locus:

$$r_{gh} = \sum_{k=1}^{K} \left(\frac{x_{kg}}{n_g} \cdot \frac{x_{kh}}{n_h}\right), \tag{5}$$

where x_{kg} and x_{kh} are the allelic tallies for the k-th allele within the g-th and h-th populations, and for any particular locus, and where the n_g and n_h values are to the two haploid sample sizes; we then average over the six loci, as for Eqs. (1) and (3). We next combined our within- and between-patch identity estimates (r_{gg}, r_{gh} and r_{hh}) into an average among-patch measure of compositional divergence

$$0 \leq \delta = \left(1 - \frac{2 \cdot \sum_{g \neq h}^{G} r_{gh}}{(G-1) \cdot \sum_{g=1}^{G} r_{gg}}\right) \leq 1, \tag{6}$$

for which '0' represents complete identity of allele frequencies across patches and '1' represents total divergence (no compositional overlap) among patches. Allelic overlap is readily computed as $\omega = 1 - \delta$).

Comparisons of divergence in allelic composition

We computed δ values for female and male gametes and diploid seedlings for canopy and open patches, and expect canopy patches to diverge more in their composition than open patches when the gene flow has been derived from different parental sources. To the extent that pollen is disseminated further than seed, we would also anticipate that inter-patch divergence among male gametes would be less than that among female gametes.

The hypothesis that $\delta = 0$ (no divergence among patches) is tantamount to ($\beta' = 1$), or to ($\alpha_1 = \cdots = \alpha_G$) or ($\alpha = \gamma$), when all patches have identical allele frequencies. To construct a null distribution for no compositional divergence among patches ($\delta = 0$), we repeatedly permute the N gametes or diploid genotypes among the G patches, holding the array of sample sizes constant, empirically determining the probability that randomly permuted membership of newly recruited seedlings among the patch types yields an estimated δ-value that exceeds the observed value.

Spatial genetic structure

For analysis of fine scale allelic spatial structure associated with the movement of paternal and maternal gametes, we deployed well-described procedures developed by Smouse and Peakall (1999) and Smouse et al. (2008), available in GenAlEx 6.5 (Peakall and Smouse 2006, 2012). We analyzed patterns of spatial autocorrelation for maternal and paternal gametes associated with canopy and open seedling patches, using separate inter-paternal and inter-maternal gametic distance matrices, both extracted via TwoGener routines of Smouse et al. (2001), embedded in GenAlEx. For the diploid seedling test, we used an inter-seedling genetic distance matrix, calculated directly from seedling genotypes.

Because the dispersal landscape at Figueroa Creek is two-dimensional (Austerlitz and Smouse 2002; Dutech et al. 2005; Grivet et al. 2005, 2009; Pluess et al. 2009), we spaced our distance classes out logarithmically (1–31 m, 32–62 m, 63–125 m, 126–250 m, 251–500 m), as recommended by Rousset (2004) and Vekemans and Hardy (2004). The site extends for 3000 m along the long axis of the valley, but the numbers of pairs for distance classes greater than 500 m are too small to provide enough precision to support meaningful analysis. In any event, the essential patterns are evident within the first 500 m, so we truncated the treatment beyond that point.

Results

Seed dispersal distances

The dispersal distances for seedlings within each patch type, based on maternity analysis, document our classification of canopy and open seedling patches. Within each of the 14 canopy patches, the seedlings were from a single maternal source, so the effective number of seed parents (N_{em}) was 1.0 (Table 1). All seed dispersal was restricted to short dispersal distances (Fig. 2b), but all acorns within canopy patch 963 came from an adjacent tree (844, at 27 m distance). The open patches, by contrast, included frequent long distance dispersal events (Fig. 2a), and 19 % of its seedlings were derived from seed trees more than 1 km from the patch itself, even though most seedlings represent fairly local dispersal (Fig. 2b). For open-patch seedlings, dispersal distance was 12–2776 m, averaging 457 ± 50.5 m). Average dispersal distances for seedlings found in open patches were: patch-1, 581 ± 129 m; patch-2, 644 ± 119 m; patch-3, 235 ± 57 m; and patch-4,

Table 1 Raw and effective numbers of seed sources and α diversity of female and male gametes contributing to seedlings sampled from low-dispersal canopy patches and high-dispersal open patches at Figueroa Creek valley, Sedgwick Reserve, Santa Barbara Co., CA, USA

Patch type and ID	Sample size of seedlings	Contributing seed sources		α (within patch) diversity		
		Number	Effective number (N_{em})	Female gametes	Male gametes	Seedlings (diploid)
Canopy patches						
Canopy-032	13	1	1	1.73	4.98	3.65
Canopy-151	8	1	1	2.53	3.29	2.89
Canopy-152	18	1	1	1.58	4.88	3.20
Canopy-159	13	1	1	1.49	5.77	3.19
Canopy-642	10	1	1	1.42	5.63	2.90
Canopy-675	5	1	1	1.36	4.83[†]	3.43
Canopy-774	15	1	1	1.51	3.83	2.84
Canopy-776	11	1	1	1.47	3.48	2.58
Canopy-844	12	1	1	1.50	2.53	2.39
Canopy-889	16	1	1	1.84	4.60	4.43
Canopy-931	9	1	1	1.80	3.78	3.49
Canopy-957	13	1	1	1.56	2.60	2.57
Canopy-963	18*	1	1	1.52	3.52	2.85
Canopy-964	13	1	1	1.47	3.73	2.97
Open patches						
Open-001	37	22	12.81	2.78	3.46	3.43
Open-002	40	20	11.14	1.83	2.56	2.17
Open-003	77	15	1.82	2.22	3.62	3.28
Open-004	46	21	4.29	2.11	3.40	2.69

* All from neighboring seed tree (844)

† α_g for two loci infinite (all alleles singletons), mean reported is of other four loci

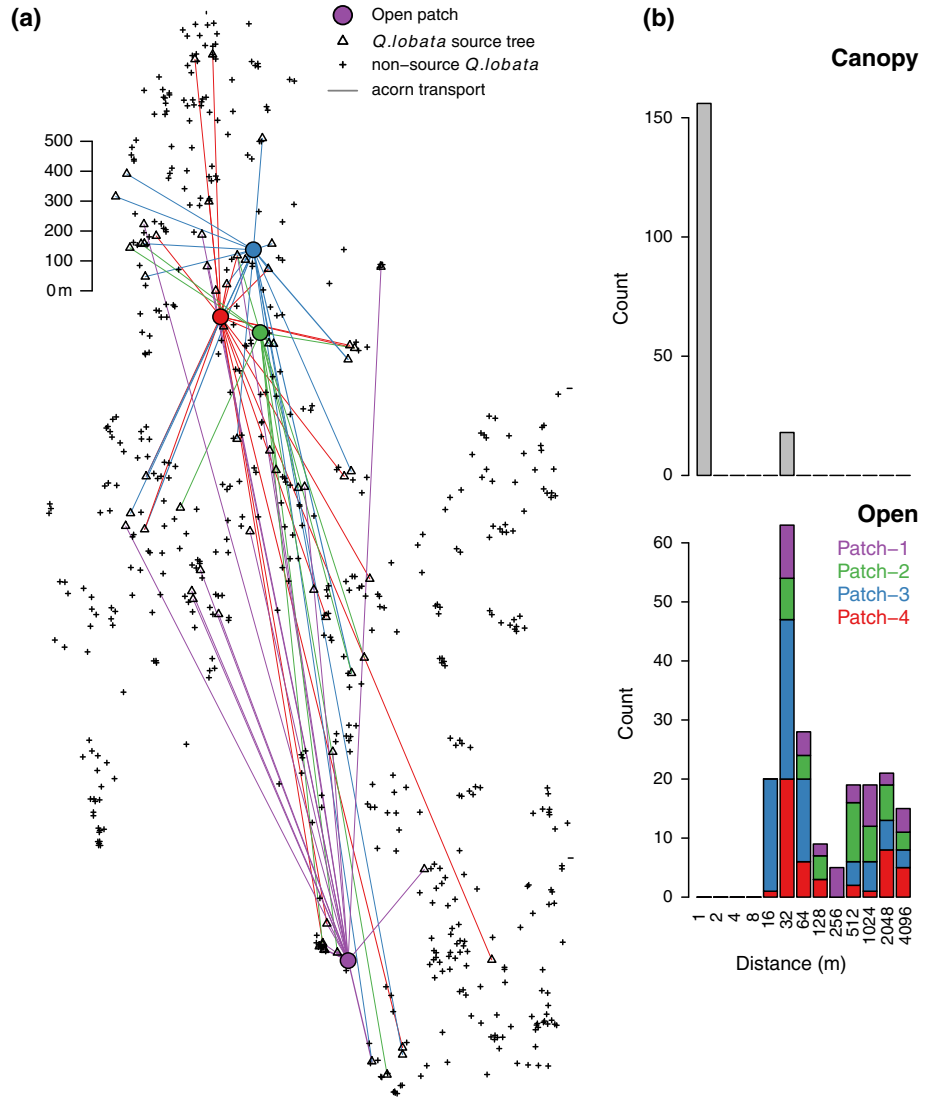

Fig. 2 Summary of acorn movement for canopy and open patches. **a** Map of dispersal events in open patches, color-coded by patch; mean dispersal distance is 457 ± 50.5 m (s.e.m.) and maximum distance is 2776 m. **b** Histograms of frequencies of dispersal events across distance classes for canopy and open patches. Dispersal events into open patches are color-coded by patch

568 ± 124 m. The number of maternal parents varied between 15 and 22 across the four open patches (Table 2), for a total of 65 maternal parents contributing to open patches.

Genetic diversity metrics

The effective number of alleles per locus per patch for male gametes, female gametes, and seedlings is measured by the α-diversity values. The α-diversity of female gametes is

Table 2 Diversity components for valley oak seedlings sampled from fourteen low-dispersal canopy patches and four high-dispersal open patches, separately for male and female gametes and for diploid seedlings including: diversity measures for within-patch (α) and total across patch (γ) and respective scaled measures (α' and γ'); and among patch measures for patch turnover (β and β'), and average pairwise divergence (δ)

Sample sizes	Male gametes		Female gametes		Diploid seedlings	
	Canopy 174	Open 200	Canopy 174	Open 200	Canopy 174	Open 200
Within-patch and total diversity components						
α	2.87	3.04	1.44	2.01	2.49	2.87
α'	0.66	0.68	0.31	0.51	0.60	0.66
γ	3.19	3.13	2.50	2.52	3.21	3.33
γ'	0.69	0.68	0.60	0.61	0.69	0.70
Among patch turnover, overlap and divergence measures						
β	1.11	1.03	1.74	1.25	1.29	1.16
β'	0.12	0.03	0.51	0.24	0.27	0.17
δ	0.12	0.04	0.45	0.25	0.26	0.18

See text for statistical tests

always lowest and that of male gametes always highest, with that of seedlings intermediate, whether in canopy patches or open patches (Table 2), consistent with the fact that observed seed dispersal is more restricted than pollen dispersal. Note also that all α-diversities were lower for canopy than for open patches (female gametes, $P = 0.0002$; seedlings, $P = 0.0013$; but male gametes, $P = 0.37$), consistent with expectations for gravity versus animal-vectored seeds. Similar patterns emerge with α' scaled metrics (Table 2).

The values of γ-diversity measure the cumulative diversity across patches. By contrast with the α-diversity patterns, values of γ-diversity were highest for seedlings, but were not significantly different from male gametes for either canopy patches ($\gamma_{S\text{-}CA} \approx \gamma_{M\text{-}CA}$) or open patches ($\gamma_{M\text{-}OP} \approx \gamma_{S\text{-}OP}$). Female gametes showed lowest γ-diversity in both patch types ($\gamma_{F\text{-}CA} < \gamma_{M\text{-}CA}$) and ($\gamma_{F\text{-}OP} < \gamma_{M\text{-}OP}$). In contrast to these sexually asymmetric patterns within patch type, γ-diversity differences between patch types are small between female gametes, male gametes and seedlings (Table 2). The contrast of γ between patch types for male gametes is not significant ($\gamma_{M\text{-}OP} \approx \gamma_{M\text{-}OP}$) (Table 2), but seemingly small magnitude differences of γ (Table 2), between patch type for female gametes and seedlings are statistically significant ($\gamma_{F\text{-}CA}$ vs. $\gamma_{F\text{-}OP}$, $P = 0.0045$; $\gamma_{S\text{-}CA}$ vs. $\gamma_{S\text{-}OP}$, $P = 0.0117$). The significance of the test can be understood by recalling that diversity estimates are averaged across loci, but the contrast tests aggregate strength of differences at each of the six loci. Among the six loci, two are not significantly different in γ-diversity between patch types, three exhibit higher γ-diversity for open patches, and one shows higher γ-diversity for canopy-patches. For male gametes, there is almost no γ-diversity difference between patch types for any of the six loci (Table 2; $\gamma_{M\text{-}CA}$ vs. $\gamma_{M\text{-}OP}$, $P = 0.48$ overall, $P > 0.2$ for each locus). The same patterns of relative magnitude of γ-diversity emerge from γ'-values (Table 2).

Female gametic β diversity is higher in the canopy than open patches, while the male gametic β diversity is more similar but slightly higher (Table 2). The β-diversity for diploid seedlings is again intermediate between those for male and female gametes for both

patch types (Table 2). The same patterns holds for scaled β' values (Table 2). No tests were conducted for these β parameters, but we did test our estimates of the divergence between allele pools (δ), which is scaled [0, 1]. We find that the hypothesis of $\delta = 0$ (tantamount to $\beta = 1$) was rejected with divergence greatest for female gametes, intermediate for seedlings, and lowest for male gametes, and in both patch types ($\delta_{F\text{-}CA} > \delta_{S\text{-}CA} > \delta_{M\text{-}CA}$) and ($\delta_{F\text{-}OP} > \delta_{S\text{-}OP} > \delta_{M\text{-}OP}$) ($P < 0.01$ vs. no divergence in all cases). Notably, divergence between patches is consistently greater for canopy than for open patches (Table 2).

In broad overview, the within patch pattern shows α_F lowest and α_M highest with α_S in between, in both patch types. The site-wide pattern is slightly different, with γ_F still lowest but γ_S highest and γ_M slightly lower than γ_S but not statistically different, again for both patch types. Turnover in allelic diversity reverses the pattern in α-diversity, with β_F highest and β_M lowest with β_S intermediate. This ranking of turnover is mirrored in pairwise divergence (δ), which is also greatest for female gametes and weakest for male gametes, and strongest for all divergence measures in canopy versus open patches. Evidently, the difference in patch type is not consequential for male gametes, as pollen moves relatively freely across the entire site before the seed dispersal phase (Table 2).

Spatial autocorrelation

Canopy patch seedlings have female gametes that show a very striking 'isolation by distance' (IBD) pattern; affinity is high ($r = +0.45$) at short distance, approaching the maximum of ($r = +0.50$) expected of half-sibs, but by 500 m, it has declined to ($r = -0.04$) (Fig. 3a). open patches also exhibit SGS, but the IBD pattern is less striking, ranging from ($r = +0.27$) at short distance to ($r = -0.07$) at 500 m (Fig. 3b). The female gametic patterns are a consequence of differences in seed dispersal distances for canopy vs open patches. Male gametes, by contrast, evince very subtle IBD pattern for both types of recruiting patches. For canopy patches, male gametes have positive but small affinity ($r = +0.03$) at short distance, which decays by 500 m to ($r = -0.01$) (Fig. 3a). For open patches, the affinity patterns are almost identical, ranging from ($r = +0.03$) at short distance to ($r = -0.02$) by 500 m (Fig. 3b). Wind-vectored male gametes have virtually the same degree of dispersal for both types of patches, and evidently move considerably

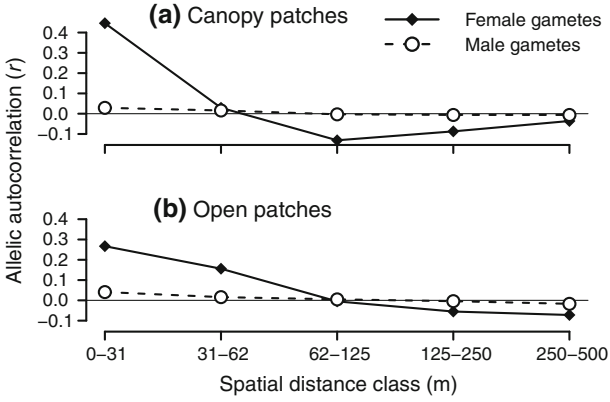

Fig. 3 Spatial autocorrelograms of male and female gametes: **a** low dispersal canopy patches; **b** high-dispersal open patches

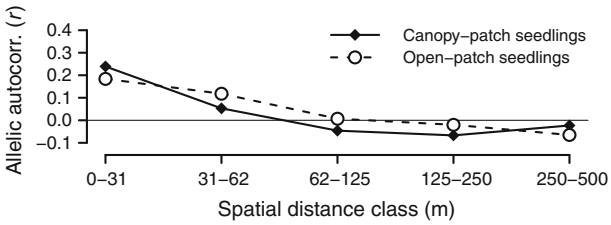

Fig. 4 Spatial autocorrelograms of diploid seedlings, comparing patterns for low-dispersal canopy and high-dispersal open patches

further than either type of subsequent seed dispersal, generating only very subtle SGS pattern for male gametes.

For the diploid seedlings and for canopy patches, IBD structure ranges from ($r = +0.24$) at short distances to ($r = -0.02$) at 500 m, but for open patches, IBD structure is reduced, ranging from ($r = +0.18$) at short distances to ($r = -0.07$) at 500 m (Fig. 4). In short, genetic structure for diploid seedlings is intermediate between those of female and male gametes; and since there is virtually no meaningful IBD structure for male gametes, that among newly recruited seedlings is roughly half of that for female gametes.

Discussion

As with other study systems that compare haploid pollen dispersal and diploid seed dispersal (e.g., Chybicki and Burczyk 2010; Garcia et al. 2007; Grivet et al. 2009), we find that pollen contributes more to gene flow than does seed dispersal. Previously, the extent to which asymmetric dispersal translated into asymmetrical impact on allelic diversity and spatial patterns of that diversity was not clear. By utilizing new statistical techniques, we assess male and female gametic contributions directly, rather than contrasting haploid pollen with diploid seedling genotypes; basically, we contrast their gametic contributions to succeeding generations, through the lens of gametophytic diversity and spatial structure, demonstrating very different impacts of the two dispersal processes. Pollen dispersal is so extensive that it has almost no differential effect on subsequent diversity or spatial genetic structure for either canopy versus open patch seedlings. For either patch type, within-patch male gametic diversity closely matches the total male gametic diversity across the site; to a first approximation, ($\alpha_{M\text{-}CA} \approx \gamma_{M\text{-}CA}$) and ($\alpha_{M\text{-}OP} \approx \gamma_{M\text{-}OP}$). Because seed dispersal always comes after pollen movement, however, the resulting balance between α (within-patch) and β (among-patch) allelic diversity in newly recruited seedlings is determined more by restricted seed dispersal than by extensive pollen dispersal.

Canopy versus open seedling patches

As shown by Grivet et al. (2009), one of the best ways to understand the impact of seed dispersal is to compare recruiting patches beneath the canopies of maternal acorn sources (zero distance dispersal) and those in the open, away from adults. In this study, the open patches that require transport away from the tree were comprised of, on average, 19 trees per patch patch (range 15–22; Table 1), while the seedling patches beneath an adult canopy contained essentially one maternal tree per canopy patch. In the open seedling patches, we observed 19 % of the seedlings came from adult trees located 1–4 km from the seedling patch (Fig. 2c). The bimodal distribution of dispersal events above and below the 256 m class suggests the possibility of two types of dispersal agents—rodents for local dispersal

and jays for long distance dispersal. Jays are the most likely long distant disperser given our own observations at our study site and the fact that jays are well known as long distant dispersal agents (Darley-Hill and Johnson 1981; Gomez 2003). It is particularly noteworthy that the seedlings in open patches came from oak adults located at multiple compass directions around the patches (Fig. 2a). Unlike the foraging patterns of acorn woodpeckers, which resulted an effective number of seed sources in their granaries that is less than two trees (Thompson et al. 2014), here we find that the effective number of seed sources in the seedling patches ranged from 1.8 to 12.8 acorn trees (Table 1). These seedling patches (along with one other in the valley) were the only places that we found significant seedling recruitment in 2002, and they contained seedlings derived from acorns dispersed into that patch from all directions. This result suggests that the dispersal may represent a case of directed dispersal. Other studies have described cases of seed dispersal by vertebrates where the destination of the seeds is directed to specific destinations (Garcia et al. 2007; Gomez 2003; Karubian et al. 2010; Schupp et al. 2010; Wenny 2001). This type of dispersal can lead to long distance dispersal into a nonrandom distribution of sites, but it also creates the opportunity for higher levels of the genetic diversity within seedling patch than a patch with local dispersal only.

Allelic diversity of male and female gametic contribution to seedlings

Our finding that male gametes disseminate more allelic diversity than do female gametes is not unexpected for a wind-pollinated, animal-dispersed tree species. Both the contribution of maternal and paternal gametes to within-patch α-diversity and the accumulated γ-diversity are asymmetric, with male gametes contributing more diversity than female gametes and spreading it farther. Because of long distance seed dispersal, our a priori expectation was that wind dispersal would enhance the contribution of male gametes, such that the within-patch α-diversity of open patches would be larger than in canopy patches, by virtue of the fact that the male gametes are moved twice for recruiting seedlings—first through pollen dispersal and then through seed dispersal. Our results demonstrate, however, that the difference in α-diversity of male gametes in the two patch types was negligible. In contrast, differential female gametic dispersal into canopy and open patches results in lower within-patch α-diversity within canopy patches, but no difference in accumulated γ-diversity across the valley. Canopy versus open seed dispersal per se does not affect site-wide allelic (γ) diversity, just its distribution within and among patches of the two types. However, the fact that the female gametes contribute less allelic diversity than male gametes, across the valley as a whole, suggests that long distance seed dispersal is not as effective as the even more extensive dispersal of pollen.

Grivet et al. (2009) also demonstrated the asymmetric contribution of pollen and seed dispersal for this same study system, but using a different approach. Using their data (Grivet et al. 2009, Table 2), the ratio of effective number of pollen donors to seed donors is $\sim$7 in canopy patches and 5.6 or 8.3 in open patches, depending on whether one uses kinship-based or F_{ST}-based estimates. The spatial scale of these estimates would be equivalent to that of our α-diversity estimates. Yet, our (α_M/α_F) ratios of male to female gamete contributions are 2.0 and 1.5, for canopy and open patches, respectively (Table 2). Comparison of the two studies, which effectively use the same seedlings, reveals again that estimating the effective number of pollen and seed donors can be more strongly asymmetric than are the resulting genetic contributions of the male and female gametes to the resulting seedling progeny.

Spatial genetic structure of male and female gametes

The autocorrelograms offer a spatial view of allelic diversity across the landscape. Male gametes yield essentially flat (and indistinguishable) correlograms for both open and canopy patches. By contrast, female gametic correlograms decline sharply with increasing distance, and more steeply so for canopy than open patch types. Female gametes are highly correlated within a canopy patch for the 1st distance class, then drop to zero for the 2nd distance class, representing a neighboring patch. In contrast, for open patches—away from any fruiting adults, we see modest correlation for both the 1st and 2nd distance classes, because many of the seedlings were derived the same source trees. To a first approximation, the 1st distance class represents the outcomes of gravity dispersal, the 2nd distance class the outcomes of small mammal dispersal, with avian dispersal contributing to subsequent distance classes.

The asymmetry in male and female gamete dispersal has implications for the degree of fine scale genetic structure of seedling allelic diversity, with female gametes shaping micro-spatial genetic structure, in spite of the homogenizing flow of male gametes across the site. We also see that extensive animal-vectored seed dispersal attenuates the correlogram, but does not erase spatial structure entirely. Dutech et al. (2005), examining autocorrelation among the adults, found minimal spatial structure for this same population, but just for the first distance class (1–31 m), with a value of (r_1 (Adults) $\approx$ 0.04). While micro-scale genetic structure is low among adults, it is impressive that demographic sampling (random attrition processes) and considerable levels of mortality (and thinning) between seedling and adult stages does not completely erode the micro-scale structure, shaped by seed dispersal (in excess of a century earlier). Residual SGS might serve to concentrate (locally adaptive) genetic kinship on a micro-ecological scale, even as pollen dispersal ensures continuing evolutionary opportunity for the wider population.

Conclusions

1. Despite long-distance seed dispersal in valley oak, female gametes do not contribute as much to seedling genetic diversity as do wind-dispersed male gametes, and the difference is substantial, probably reflecting the fact that the seed dispersing jays move acorns from a limited number of trees.
2. Seed dispersal also shapes the α, β, and γ decomposition of diversity and spatial genetic structure patterns, despite the fact that even longer distance pollen dispersal tends to distribute allelic diversity uniformly across the site and results in genetic diversity of male gametes where $\alpha \approx \gamma$. For valley oak, at least, the dispersal of male gametes maintains both the internal diversity and connectedness of the regional gene pool, but does not eliminate fine scale genetic structure.
3. The examination of γ-diversity adds an important element to the assessment of the genetic consequences of dispersal, because it provides an effective way of summarizing accumulated genetic diversity across an extended site. The measurement of γ-diversity showed that the seed dispersal per se did not impact the overall genetic contribution of female gametes on a site-wide scale, but it was abundantly clear that female gametes contributed less genetic diversity (overall) than did male gametes to recruiting populations.

4. Plant species exhibit sexual asymmetry in gametic dispersal, typically involving different anatomical structures, temporal separation, and dispersal vectors. Here, we have dissected the separate contributions of male and female gametes from the seed and pollen phases, and have illustrated their separate contributions to local (micro) and site-wide (meso) patterns of genetic diversity. Given that female gametes move after male gametes, they have a disproportionate impact on local diversity and fine scale genetic structure. Clearly, sexually asymmetric dispersal syndromes have a large impact on SGS patterns across micro and meso scales. Comparative work in systems with contrasting dispersal syndromes should clarify the ways that pollen and seed dispersal shape the ecology and evolutionary dynamics of plant populations, especially as anthropogenic disturbances alter these processes.

Acknowledgments The authors thank F. Davis (UCSB) for our early collaboration. The fieldwork was performed at the University of California Natural Reserve System Sedgwick Reserve administered by the UC Santa Barbara. We thank M. Williams, K. McCurdy, A. Lentz, and the staff at the Sedgwick Reserve for logistical support over the years. We thank F. Austerlitz and J. J. Arnuncio for intellectual stimulation. For technical assistance in genotyping and scoring genotypes of difficult tissue, we are grateful to C. Winder of the Sork lab and J. Papp and U. Dandekar of the UCLA Genotyping Core facility. We thank members of the Sork lab for comments on earlier versions of this manuscript. The research and V.L.S, D.G., D.G.S. were supported by NSF-DEB-0514956 and NSF-DEB-0089445; P.E.S. was supported by NSF-DEB-0514956 and USDA/NJAES-17111 and -17160.

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