

# Causes and consequences of unequal seedling production in forest trees: a case study in red oaks

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**Abstract.** Inequality in reproductive success has important implications for ecological and evolutionary dynamics, but lifetime reproductive success is challenging to measure in long-lived species such as forest trees. While seed production is often used as a proxy for overall reproductive success, high mortality of seeds and the potential for trade-offs between seed number and quality draw this assumption into question. Parentage analyses of established seedlings can bring us one step closer to understanding the causes and consequences of variation in reproductive success. In this paper we demonstrate a new method for estimating individual seedling production and average percentage germination, using data from two mixed-species populations of red oaks (*Quercus rubra*, *Q. velutina*, *Q. falcata*, and *Q. coccinea*). We use these estimates to examine the distribution of female reproductive success and to test the relationship between seedling number and individual seed production, age, and growth rate. We show that both seed and seedling production are highly skewed, roughly conforming to zero-inflated lognormal distributions, rather than to the Poisson or negative-binomial distributions often assumed by population genetics analyses. While the number of established offspring is positively associated with mean annual seed production, a lower proportion of seeds from highly fecund individuals become seedlings. Our red oak populations also show evidence of trade-offs between growth rate and reproductive success. The high degree of inequality in seedling production shown here for red oaks, and by previous studies in other species, suggests that many trees may be more vulnerable to genetic drift than previously thought, if immigration is limited by fragmentation or other environmental changes.

**Key words:** Coweeta LTER, North Carolina, USA; Duke Forest, North Carolina, USA; effective population size; fecundity; lognormal distribution; negative binomial distribution; parentage; Poisson distribution; *Quercus*; reproductive success.

## INTRODUCTION

The distribution of reproductive success has important implications for ecological and evolutionary dynamics. When offspring production is highly unequal, both the fixation of favorable alleles and the loss of genetic variation to random drift are accelerated (Wilson and Levin 1986, Gillespie 2004). Loss of standing genetic variation can in turn reduce population viability (Ellstrand and Elam 1993, Nunney and Elam 1994, Newman and Pilson 1997). Variation in reproductive success also affects ecological processes such as population spread (Clark et al. 2001). While estimates of reproductive success in trees are usually based on seed production (for example, Fuchs et al. 2003, Schoen and Stewart 1986, Herrera and Jovani 2010), from an evolutionary or population-dynamics perspective an individual has not successfully reproduced until its offspring are themselves of reproductive age (Howard 1979, Primack and Kang 1989). Because most tree

species are long lived and produce annually variable numbers of seeds that may take decades to reach maturity, it is currently impossible to count how many adults a particular tree contributes to the population. However, with modern genetic methods, it is possible to identify the parents of tree seedlings, bringing us one step closer to understanding true reproductive success (Dow and Ashley 1996, Schnabel et al. 1998, Asuka et al. 2005, Burczyk et al. 2006, Hardesty et al. 2006, Moran and Clark 2011).

Many early population-genetics analyses assumed that reproductive success follows a Poisson distribution, in which the variance in offspring number is equal to the mean (Karlin and McGregor 1968, Wilson and Levin 1986). Some later analyses, recognizing that factors such as competition for mates may lead to a much higher variance, have used distributions such as the negative binomial, though female reproductive success is still often assumed to be Poisson distributed (Wood 1987, Nunney and Elam 1994). However, most natural populations of plants and animals studied to date exhibit highly skewed distributions of offspring production for both males and females (e.g., Meagher and Thompson 1987, Clutton-Brock 1988, Schnabel et al.

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1998, Clark et al. 2001, Gonzalez-Martinez et al. 2006, Sezen et al. 2007, Jacquemyn et al. 2009, Nakanishi et al. 2009, Gaino et al. 2010, Hampe et al. 2010, Koelewijn et al. 2010, Herrera and Jovani 2010). It has been proposed that reproductive success in plants should follow a lognormal distribution due to the multiplicative effect of interacting environmental factors on individual size (Herrera and Jovani 2010). Size distributions in plants do tend to be skewed, and in most species size is closely linked with fecundity (Heywood 1986, Wilson and Levin 1986). However, if a large fraction of individuals produce no seed or established offspring, as has been observed in many populations (Clutton-Brock 1988, Schnabel et al. 1998, Jacquemyn et al. 2009, Nakanishi et al. 2009, Gaino et al. 2010), this may result in an excess of zeroes relative to a lognormal distribution.

The stage at which reproductive success is measured (e.g., number of matings, number of seeds/eggs, number of established offspring) can strongly affect conclusions about the variation in reproductive success (Howard 1979, Clutton-Brock 1988). Earlier stages are generally easier to measure. We conducted a literature search and found that of hundreds of published studies examining reproductive success in woody plants 75% defined reproductive success in terms of seed production or percentage seed set, while less than 8% considered germination probabilities or numbers of established offspring. However, because mortality at the seed-to-seedling transition is high in most plant species (Harper 1977), and because there is potential for trade-offs between seed number and seed quality (Primack and Kang 1989) as well as for density-dependent mortality beneath maternal crowns (Janzen 1970), seed number is not necessarily a good proxy for lifetime reproductive success. Genetic markers have made it possible to identify the parents of established seedlings and saplings (e.g., Dow and Ashley 1996, Schnabel et al. 1998, Asuka et al. 2005, Burczyk et al. 2006, Hardesty et al. 2006, Moran and Clark 2011), but very few studies have examined individual reproductive success in woody plants in terms of the production of established offspring. Several parentage-analysis studies (Aldrich and Hamrick 1998, Schnabel et al. 1998, Sezen et al. 2007, Nakanishi et al. 2009, Gaino et al. 2010, Hampe et al. 2010) have found that the number of sampled seedlings assigned to different mother trees was highly unequal. Gonzalez-Martinez et al. (2006), applying Burczyk et al. (2006)'s "seedling neighborhood model," found that female relative reproductive success was highly skewed in *Pinus pinaster*. However, to our knowledge, no previous study has used pedigree and dispersal data to calculate the distribution of total seedling production by individual trees.

Here, we develop a simple method for estimating total seedling production, suitable in any case where dispersal kernels and parentage have been previously estimated. We apply this method to data from two mixed-species populations of hybridizing red oaks (*Quercus rubra*, *Q.*

*velutina*, *Q. falcata*, and *Q. coccinea*) (Moran and Clark 2011; Moran et al. 2012), in order to address two questions: (1) What is the distribution of seedling production by mother trees? and (2) What traits are associated with high seedling production? First, we test the fit of seed and seedling production in these populations to the lognormal, Poisson, and negative-binomial distributions proposed by other authors (Karlín and McGregor 1968, Wilson and Levin 1986, Wood 1987, Nunney and Elam 1994, Herrera and Jovani 2010). We then discuss the consequences of the observed variation in offspring number for effective population size. In order to better understand what distinguishes individuals with high reproductive success from less successful individuals, we also examine predictions regarding three frequently measured individual-level traits:

**Seed production.** (1) Seedling production will be positively associated with average annual seed production (Venable 1992, Gonzalez-Martinez et al. 2006). (2) Highly fecund trees will exhibit a lower percentage of seeds that survive to become seedlings (Venable 1992), due to density-dependent mortality, number-quality trade-offs, or other processes that uncouple seed production and seedling establishment (Jordano and Herrera 1995).

**Age.** (3a) Age of the mother will be positively associated with seedling number because old individuals have experienced more opportunities for seedling establishment (Schnabel et al. 1998). (3b) Age of the mother may not be positively associated with seedling number if trees senesce and old individuals produce fewer seeds or seedlings annually (Silvertown et al. 2001).

**Growth rate.** (4a) If fast-growing, vigorous trees have more resources available for provisioning seed (Venable 1992, Gonzalez-Martinez et al. 2006), they will also produce more seedlings. (4b) If there are tradeoffs between growth and reproduction, growth rate will be negatively correlated with seedling number (Charlesworth and Morgan 1991).

## METHODS

### *Study sites and focal species*

This study makes use of data collected for a study of parentage, seed dispersal, and hybridization in two mixed-species populations of red oak in North Carolina (Moran and Clark 2011, Moran et al. 2012; E. V. Moran and J. S. Clark, *unpublished manuscript*). The study sites are located in the Blackwood Division of the Duke Forest (35°58'N, 79°5'W, elevation 155m) and at Coweeta LTER in the Southern Appalachians (35°03' N, 83 °27' W, elevation 1030 m). The focal species are northern red oak (*Quercus rubra*), black oak (*Q. velutina*), and southern red oak (*Q. falcata*) at Duke Forest, and *Q. rubra*, *Q. velutina*, and scarlet oak (*Q. coccinea*) at Coweeta.

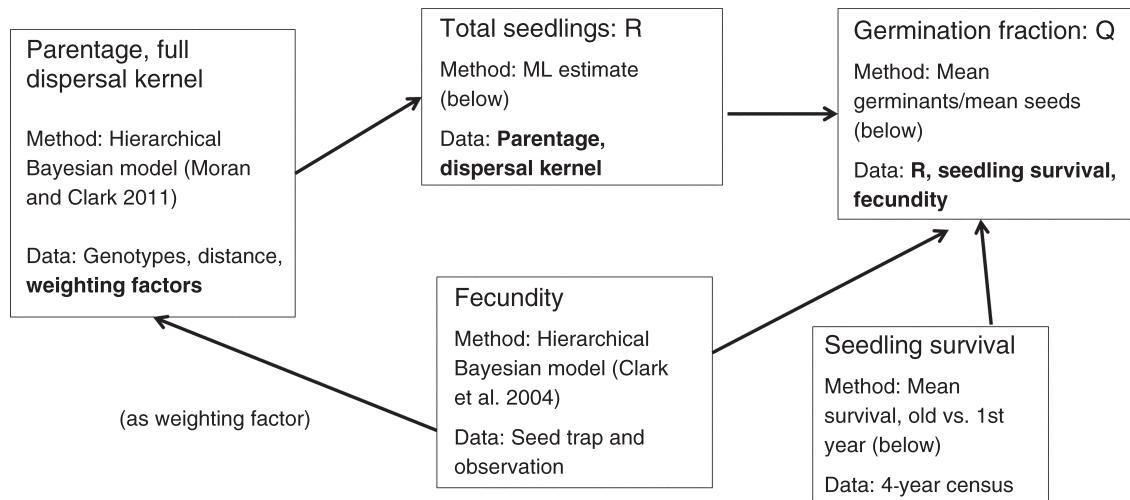


FIG. 1. Flow chart of steps involved in calculating  $R$  and  $Q$  and data needed.  $R_i$  is the total number of seedlings from tree  $i$  and alive at the time of the parentage analyses;  $Q_i$  is the average annual germination fraction (the fraction of seeds that become first-year seedlings). Arrows indicate where the results of one calculation were the basis for another calculation. Boldface type indicates that input comes from other analyses (as opposed to raw data). Fecundity was used as a weighting factor in the parentage analysis; genotype and distance were the deciding factor when determining if a tree could be the parent of a seedling, but more-fecund trees have a higher probability of dispersing seed a given distance. Weighting factors could also include adult size (dbh) or other factors likely to affect the probability of parentage. Fecundity and dispersal kernels were estimated in previous analyses. Methods for estimating survival, reproductive success, and germination fraction are described in the text (*Methods*).

At both sites, an irregularly shaped area had been mapped for earlier forest dynamics studies (Beckage and Clark 2003, Clark et al. 2003, 2004, 2010a, Ibanez et al. 2007). Within this area, adult diameter, seed-trap, and seedling census data have been collected since 2000. In order to regularize plot shape and reduce the proportion of “immigrant” seed and pollen by expanding the number of potential parents, all red oaks within a 30–60 m border area were mapped and genotyped in 2006, bringing the total plot area to 12 ha at Duke Forest and 7.5 ha at Coweeta. All seedling sampling plots were >30 m from the edges of the expanded plot. Further description of the study sites can be found in Moran et al. (2012) or Ibanez et al. (2008). Seedlings in permanent seedling census plots ( $N = 217$  seedlings at Duke Forest;  $N = 179$  at Coweeta) and all trees >10 cm dbh ( $N = 118$  at Duke Forest;  $N = 199$  at Coweeta) were genotyped at six microsatellite loci (Moran and Clark 2011).

There was little differentiation in allele frequencies between co-occurring species, as measured by Bayesian STRUCTURE analysis (Pritchard et al. 2000),  $F_{st}$ , or other population structure statistics, suggesting past inter-specific gene flow; furthermore, parentage analyses suggest that >30% of seedlings have parents belonging to two different species (Moran et al. 2012). Hybridization between these species has been inferred from morphology, and cryptic introgression in other red oaks has previously been reported (Jensen 1977, Guttman and Weigt 1989, Tomlinson et al. 2000, Dodd and Afzal-Rafii 2004). Therefore, as in previous analyses, we treat all red oaks at each site as members of one potentially interbreeding population. Acorns do not persist in the

soil for >1 year (Hille Ris Lambers et al. 2005), but seedlings have high survival in the understory. In a previous planting experiment conducted at these two sites, over 50% of first-year *Q. falcata* and *Q. rubra* seedlings survived until the end of the 4-year study (Ibanez et al. 2008).

We will refer to the total number of seedlings originating from tree  $i$ , and existing in the seedling pool at the time of the parentage analysis, as  $R_i$ , and the average annual germination fraction (the fraction of seeds that become first-year seedlings) as  $Q_i$ . We estimate these quantities based on the previously estimated dispersal kernel and parentage of sampled seedlings, seed production by individual adults, and seedling survival (Fig. 1). Next, we describe how we assessed the distribution of  $R_i$ , and how we tested hypotheses regarding tree-level traits and offspring number.

#### *Estimating parentage and the dispersal kernel*

At each site, we previously estimated parentage of sampled seedlings and seed and pollen dispersal kernels using a hierarchical Bayesian model that incorporates genetic and ecological data and accounts for uncertainty in genotype and seed production (Moran and Clark 2011). In this model, the posterior probability for the pedigree and the seed and pollen dispersal parameters given the data is proportional to the relative probability that pollen disperses from tree  $i'$  to tree  $i$  and seed disperses from tree  $i$  to the location of seedling  $k$  (given the distances between individuals and individual fecundity) times the relative probability that trees  $i$  and  $i'$

could produce a seedling with the observed genotype (given genotyping error rates, Mendelian inheritance, and the observed genotypes of  $i$  and  $i'$ ) times prior distributions for the dispersal parameters. Because red oaks are monoecious and self-incompatible, any tree could be both a mother and a father, but could not be both mother and father to a single seedling. We allowed for dispersal from outside the mapped stand, assuming that the density of trees and the frequency of alleles were similar inside and outside of the plot. We did not assume that the closest parent must be the mother, but the means of the prior distributions were chosen to indicate that seed dispersal was likely to be more limited than pollen dispersal; however, priors were broad and overlapping. Genotyping error rates for the six microsatellite loci were estimated by re-genotyping many individuals and loci. The model was implemented in R (R Development Core Team 2008) using a Gibbs sampler/MCMC approach. For a detailed description of the model, see Moran and Clark (2011).

In this analysis of seedling production, we use posterior means (“best estimates”) for the seed-dispersal parameter and seedling maternity at both study sites (E. V. Moran and J. S. Clark, *unpublished manuscript*). It should be kept in mind that there is uncertainty associated with the parentage estimate, but as many parentage-analysis methods do not generate a distribution for probability of parentage we will not deal with that issue here. Male reproductive success is not considered because the high levels of out-of-plot paternity (>50%) and long pollen-dispersal distances (mean >145 m) estimated for both sites (E. V. Moran and J. S. Clark, *unpublished manuscript*) would make the uncertainty associated with total number of seedlings fathered so high that the estimates would not be informative.

*Total current number of seedlings,  $R_i$*

We assume that seedling recruitment in each census plot is conditionally Poisson, so that the likelihood of observing  $s_{ij}$  seedlings from mother  $i$  in seedling census plot  $j$  is

$$L = \prod_j \frac{e^{-r_{ij}} r_{ij}^{s_{ij}}}{s_{ij}!} = K_{ij} A_j R_i$$

where  $K_{ij}$  is the probability of a seed dispersing from mother  $i$  to plot  $j$  (expressed per square meter),  $A_j$  is plot area, and  $R_i$  is the number of seedlings produced by  $i$ . The Poisson distribution is generally considered appropriate for situations in which there is a count in a given length of time or spatial area, including seedling number (Clark 2007). For a 2D-t dispersal kernel, the distribution used in our previous analyses, the calculation is

$$K_{ij} = \frac{1}{\pi u \left(1 + \frac{d_{ij}^2}{u}\right)^2}$$

where  $d_{ij}$  is the distance between tree  $i$  and plot  $j$ , and  $u$  is the seed-dispersal parameter (Clark et al. 1999). Other functional forms for the dispersal kernel could also be used, where appropriate. At Coweeta, posterior mean  $u = 92$  for red oaks, corresponding to an expected dispersal distance of 15 m, while at Duke Forest posterior mean  $u = 6300$ , corresponding to an expected dispersal distance of 125 m (E. V. Moran and J. S. Clark, *unpublished manuscript*).

If, as described above, the dispersal parameter and the parentage of each seedling are assumed to be known, the maximum-likelihood estimate of  $R_i$  is

$$\hat{R}_i = \frac{\bar{s}_{ij}}{K_{ij} A_j}$$

This distribution is degenerate (i.e., does not work) for parents with no observed offspring. Therefore, in the analyses that follow, we focus on individuals previously estimated to be the parent of at least one sampled seedling. The standard error of the estimate can be approximated from Fisher information:

$$\hat{\sigma}_{R_i} = \frac{\hat{R}_i}{\sqrt{\sum_j s_{ij}}}$$

*Average annual germination fraction,  $Q_i$*

In many mid-to-late-successional tree species, such as oaks, seedlings may remain in the seedling pool for years. The seedling pool at any given time therefore contains an accumulation of cohorts.  $R_i$  at time  $t$  is equal to the number of new recruits plus surviving seedlings. We provide an approximation of annual seedling production from which  $Q_i$  can be calculated, recognizing that it is only a rough index for a mean value.

First-year seedlings often experience higher mortality, so assuming constant annual mortality after the first year,

$$R_i = \sum_{t=1}^{\infty} Y_i S_{\text{new}} S_{\text{old}}^{t-1}$$

where  $Y_i$  is the average number of new seedlings produced by tree  $i$ ,  $S_{\text{new}}$  is the probability of surviving the year following germination,  $S_{\text{old}}$  is the probability of surviving each subsequent year, and  $t = 1$  is the current year. Note that assuming a constant annual probability of mortality for older seedlings is a pragmatic choice, because while individual seedlings were tracked over the four years of our study (2006–2009), oak seedlings can persist in the understory for over 10 years. The exact age of many seedlings was unknown, though budscar numbers suggested that more than 50% germinated between 2001 and 2005. At Duke Forest,  $S_{\text{new}} = 0.85$  and  $S_{\text{old}} = 0.959$ , while at Coweeta,  $S_{\text{new}} = 0.667$  and  $S_{\text{old}} = 0.982$ . Where exact ages are known, further divisions

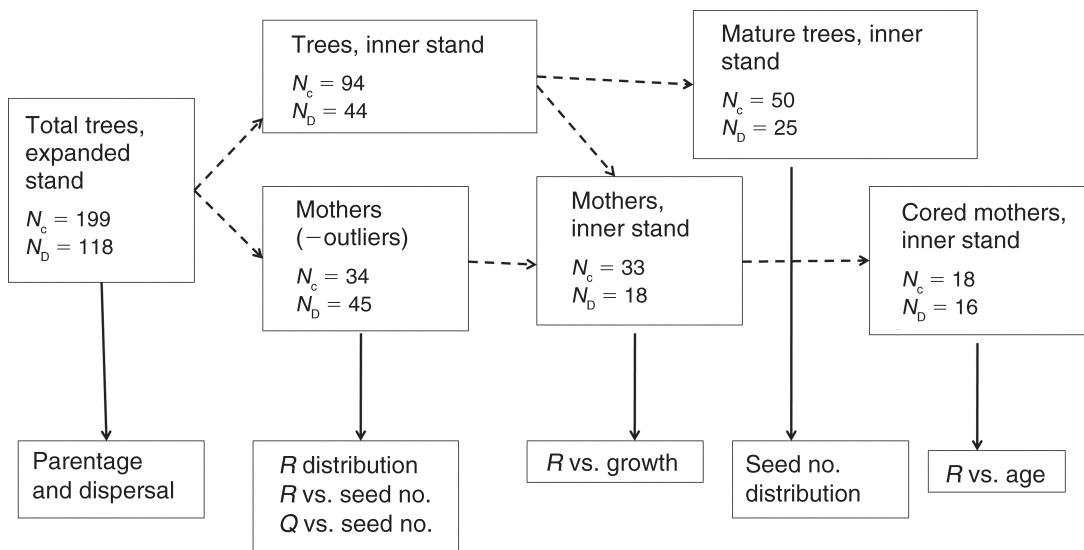


FIG. 2. Sample sizes of adult trees for the analyses discussed in this paper. “ $N_c$ ” indicates sample size at Coweeta; “ $N_D$ ” is the sample size at Duke Forest. The original parentage and dispersal analysis included all trees >10 cm dbh within the expanded plot area (12 ha at Duke Forest, 7.5 ha at Coweeta) as potential parents. Subsets of these individuals (dashed lines) were used for subsequent analyses. “Mothers” refers to trees that were the mother of at least one sampled seedling, “Mature trees” refers to individuals with a >50% probability of being reproductively mature, and “Cored” refers to trees with increment core data available.  $R$  is the total number of seedlings, and  $Q$  is the annual seed germination fraction.

between mortality of different age classes can be made as necessary.

We can solve for  $Y_i$  using a geometric series:

$$Y_i = \frac{R_i}{S_{\text{new}} \sum_{t=1}^{\infty} S_{\text{old}}^{t-1}} = \frac{R_i(S_{\text{old}} - 1)}{S_{\text{new}}(S_{\text{old}}^t - 1)}$$

and, as  $t$  grows large, this tends to

$$Y_i = \frac{R_i(1 - S_{\text{old}})}{S_{\text{new}}}$$

If  $F_i$  is the average annual seed production, estimated in a previous study for these sites (Clark et al. 2004, 2010a), then  $Q_i = Y_i/F_i$ .

Confidence intervals were created based on uncertainty in  $R_i$  and  $F_i$ . We drew 200 samples from

$$R_i^* \sim \mathcal{N}\left(\frac{\bar{s}_{ij}}{K_{ij}A_j}, \frac{\hat{R}_i}{\sqrt{\sum_j s_{ij}}}\right)$$

and 200 samples from  $\ln F_i^* \sim \mathcal{N}(\text{mean}[\ln F_i], \text{SE}[\ln F_i])$  in order to calculate the 95% confidence intervals of the  $Q_i$ 's.

*Distribution of seedling production*

To assess the inequality of seedling production, we estimated  $R_i$  for all individuals estimated to be the mother of one or more sampled seedlings. We then assessed the fit of  $R$  to the Poisson and negative-binomial distributions using a chi-squared test, and to

the lognormal distribution using the Anderson-Darling normality test for log-transformed values. We did the same for average annual seed production in trees estimated to have a >50% probability of being mature (see *Seed production*, below). Unlike the analysis of  $R$ , in the analysis of seed production we focused only on trees within the original mapped stand because, as long-term records of growth and seed-trap data are available for these trees, we have more confidence in their seed production estimates.

*Traits associated with seedling production*

*Seed production.*—Annual seed production has been estimated for all trees within the original mapped stands (Fig. 2). Annual seed production given maturity ( $F_i$ ) is estimated based on seed-trap and growth data (Clark et al. 2010a). Theta, the probability that a tree is sexually mature, equals 1 if reproductive structures (flowers, fruit) have been observed; otherwise,  $\theta$  depends on tree size. Parameter estimates derived from this analysis allow us to estimate the probability of maturity and annual seed production given maturity for the border trees as well:

$$\theta = \text{inverse logit}(\alpha_0 + \alpha_1 D + \alpha_2 C)$$

$$\ln(F_i | \theta = 1) = \beta_0 + \ln(D_i)\beta_1 + \ln(D_i^2)\beta_2 + \ln(C_i)\beta_3 + \ln(I_{t-1})\beta_4 + \varepsilon$$

where  $D$  is diameter,  $C$  is canopy area,  $I$  is diameter growth increment, and  $\varepsilon$  is an error term based on individual-, year-, and site-level variability.

TABLE 1. Fit of seed and seedling production to Poisson, negative-binomial, and lognormal distributions.

Distribution	Annual seed production, <i>F</i>		Number of seedlings, <i>R</i>	
	Coweeta ( <i>N</i> = 50)	Duke Forest ( <i>N</i> = 25)	Coweeta ( <i>N</i> = 34)	Duke Forest ( <i>N</i> = 45)
Poisson	$\chi^2 = \infty$ <i>P</i> = 0	$\chi^2 = \infty$ <i>P</i> = 0	$\chi^2 = \infty$ <i>P</i> = 0	$\chi^2 = \infty$ <i>P</i> = 0
Negative binomial	$\chi^2 = 354.3$ <i>P</i> = $1 \times 10^{-49}$	$\chi^2 = 223.3$ <i>P</i> = $1 \times 3^{-35}$	$\chi^2 = 306.3$ <i>P</i> = $1 \times 5^{-47}$	$\chi^2 = 256.2$ <i>P</i> = $1 \times 2^{-33}$
Lognormal	AD = 1.19 <i>P</i> = 0.0042	AD = <b>0.56</b> <i>P</i> = <b>0.1438</b>	AD = <b>0.23</b> <i>P</i> = <b>0.7999</b>	AD = <i>0.78</i> <i>P</i> = <i>0.0432</i>

Notes: Sample sizes (*N*) for seed production refer to trees with multi-year estimates and >50% probability of maturity. “AD” indicates the test statistic for the Anderson-Darling test of normality when variance is unknown. The best fits are shown in boldface type, and marginal fits in italic type.

Thus the comparisons of *R* and *Q* to average seed production use data from all trees with maternal offspring among sampled seedlings: 45 trees at Duke Forest, 40 trees at Coweeta.

*Age.*—Diameter is sometimes used as a proxy for age, though this should be approached with caution due to individual- and site-level differences in growth (McMahon et al. 2009). We therefore test our predictions using ring counts from increment cores. Exact ages are only known for individuals that have been cored (Fig. 2).

*Growth rate.*—Annual diameter-growth increment has been estimated for all trees within the original mapped stands (Fig. 2), based on periodic diameter measurements and increment cores (Clark et al. 2010a).

RESULTS

*Reproductive inequality*

Seedling production in red oaks was highly unequal at both sites. At Duke Forest (North Carolina, USA), 38.1% of potential parents were estimated to be the mother of at least one seedling, while 50% were either a mother or a father. At Coweeta LTER (North Carolina, USA), seedling production was even more skewed: 20.1% of potential parents were mothers of at least one seedling, while 32.7% were the mother or father of at least one seedling. One tree at this site was estimated to be the mother of 14% of all sampled seedlings. At Coweeta, some trees located far from the sampling plots were assigned very high values of *R<sub>i</sub>* (>4000 seedlings; *R<sub>i</sub>* is the total number of seedlings from tree *i* at the time of the parentage analysis) with very high standard errors (>3000 seedlings) by the maximum-likelihood approach. The 2D-t kernel, like most dispersal kernels, suggests that if one seedling is found far from a parent tree, many must be found close to the parent, but when there are no seedling plots close to the parent the uncertainty associated with seedling number is high. These individuals were removed from subsequent analyses. This effect was not seen at Duke Forest, where seedling sampling plots were more widely distributed.

The distributions of *R<sub>i</sub>* for trees with identified offspring were highly skewed. The fits of seed production (given maturity) and seedling number (given at least one observed offspring) to Poisson, negative-binomial,

and lognormal distributions are shown in Table 1. If reproductive success follows a Poisson distribution, then the ratio of the variance in offspring number to the mean is ~1. However, this ratio ranged from 180 for *R<sub>i</sub>* at Duke Forest to 1540 for *R<sub>i</sub>* at Coweeta. The negative binomial distribution accommodates a greater degree of inequality, but was still a poor fit. In Fig. 3A and B, the distribution *R<sub>i</sub>* for trees with at least one observed offspring is shown with fitted lognormal distributions. In Fig. 3C and D, the distribution of average annual seed production for mature trees is shown in dark bars with fitted lognormal distributions, while light bars indicate estimated annual seed production for the large fraction of trees with <50% probability of being mature. Seed production given maturity at Duke Forest and offspring number given at least one offspring at Coweeta were both well described by lognormal distributions (Table 1). Seedling number at Duke Forest is only a marginally good fit to a lognormal distribution, due to a relatively large number of extreme values of *R*.

*Traits associated with seedling production*

As predicted, seedling production was moderately to strongly correlated with average annual seed production (Fig. 4: Duke Forest, *r* = 0.296; *P* = 0.1, Coweeta, *r* = 0.413, *P* = 0.03). In Fig. 4A and B, as in the subsequent figure, vertical bars represent the 95% confidence interval around the estimate. On average, <2% of the seeds produced a first-year seedling, but for some individuals at Coweeta this fraction was as high as 20% (Fig. 4C and D). Consistent with our prediction that highly fecund trees would exhibit lower seed survival, germination fraction *Q<sub>i</sub>* for individual trees was negatively correlated with seed production. This effect was stronger at Duke Forest (*r* = -0.38, *P* = 0.01) compared to Coweeta, where there was only a nonsignificant trend (*r* = -0.21, *P* = 0.3), consistent with the stronger correlation between seed production and seedling production at the latter site. There was no relationship between *Q<sub>i</sub>* and any other variable measured.

*R<sub>i</sub>* did not exhibit a positive linear relationship with age, but rather a hump-shaped pattern consistent with our alternative hypothesis of a senescence-related decline

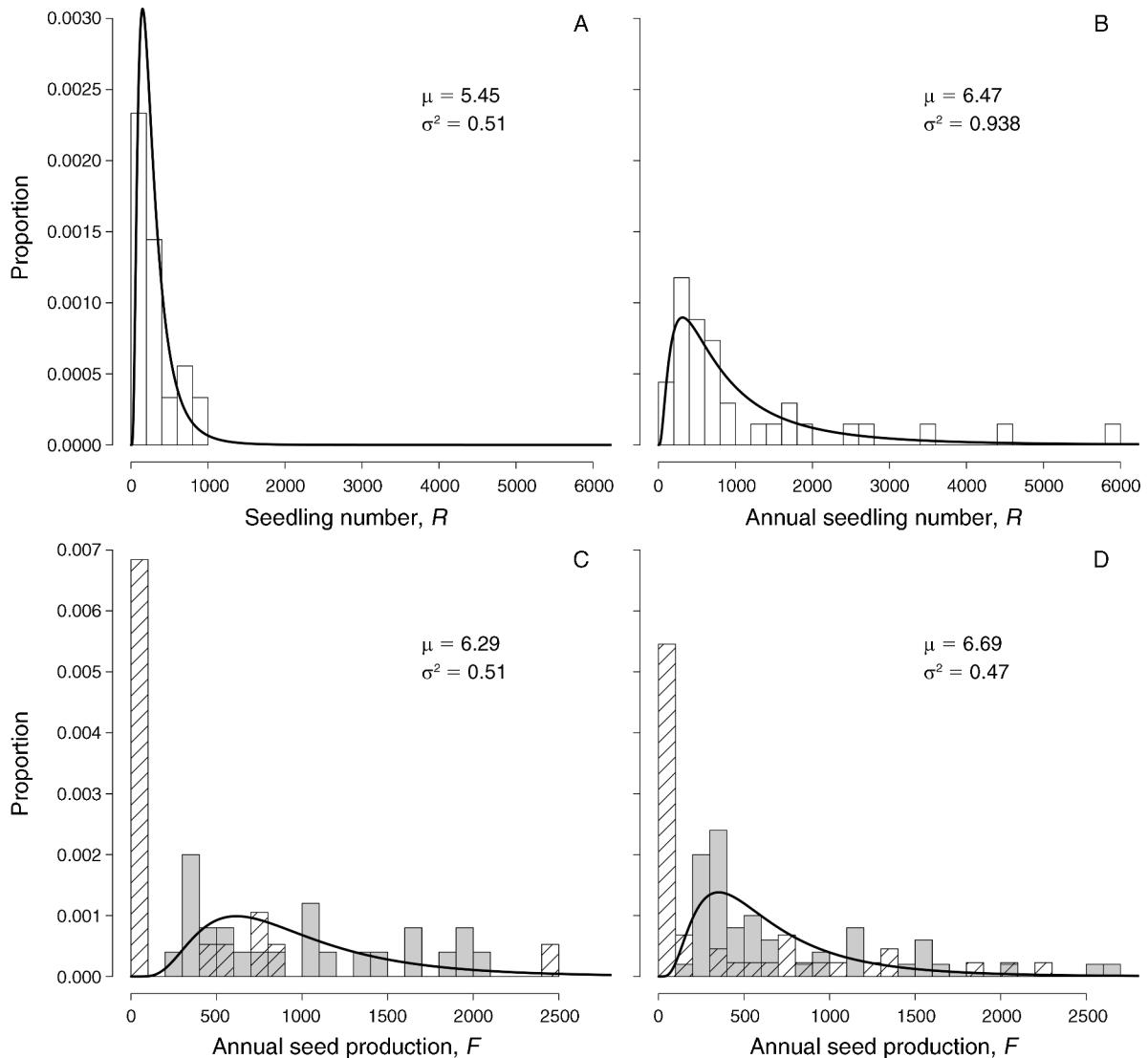


FIG. 3. (A, B)  $R_i$  given at least one observed offspring (bars), with fitted lognormal distributions (curves) for (A) Duke Forest and (B) Coweeta. (C, D) Mean annual seed production for trees with  $>50\%$  probability of maturity (gray bars), with fitted lognormal distributions, and for trees with  $<50\%$  probability of maturity (hatched bars) for (C) Duke Forest and (D) Coweeta.

in seedling production. However, sample sizes were small and quadratic regressions were not a very good fit (the parameter for the quadratic term had a  $P$  value of 0.17 at Duke Forest and 0.23 at Coweeta). We therefore fit a smoothing spline function to simply illustrate the trend (Fig. 5A and B). However, it should be noted that this pattern depends on one or two trees of advanced age at each site, and a small number of young trees with established offspring. Seedling production also exhibited a hump-shaped relationship to annual growth increment (Fig. 5C and D). As in the case of age, we fitted a smoothing spline. The quadratic regression was a very poor fit at Duke Forest ( $P$  value for quadratic term = 0.6), but marginally significant for Coweeta ( $R = -1839 + 15\,131(\text{inc}) - 18\,249(\text{inc}^2)$  [where "inc" stands for "growth increment"];  $P$  value for quadratic term =

0.058). The spline curve shows an even higher intermediate peak than the quadratic. Because there was no relationship between age and growth increment, this may be driven by a trade-off between growth and reproduction at higher growth rates and a lack of resources in the slow-growing trees. The slowest-growing individuals are those that are "suppressed"; shorter than the dominant canopy trees, they receive relatively little light.

#### DISCUSSION

We find that the distribution of seedling production for red oaks at both of our study sites is highly unequal, with a few individuals contributing disproportionately to the next generation while many individuals produce few or no offspring. Among reproductive individuals,

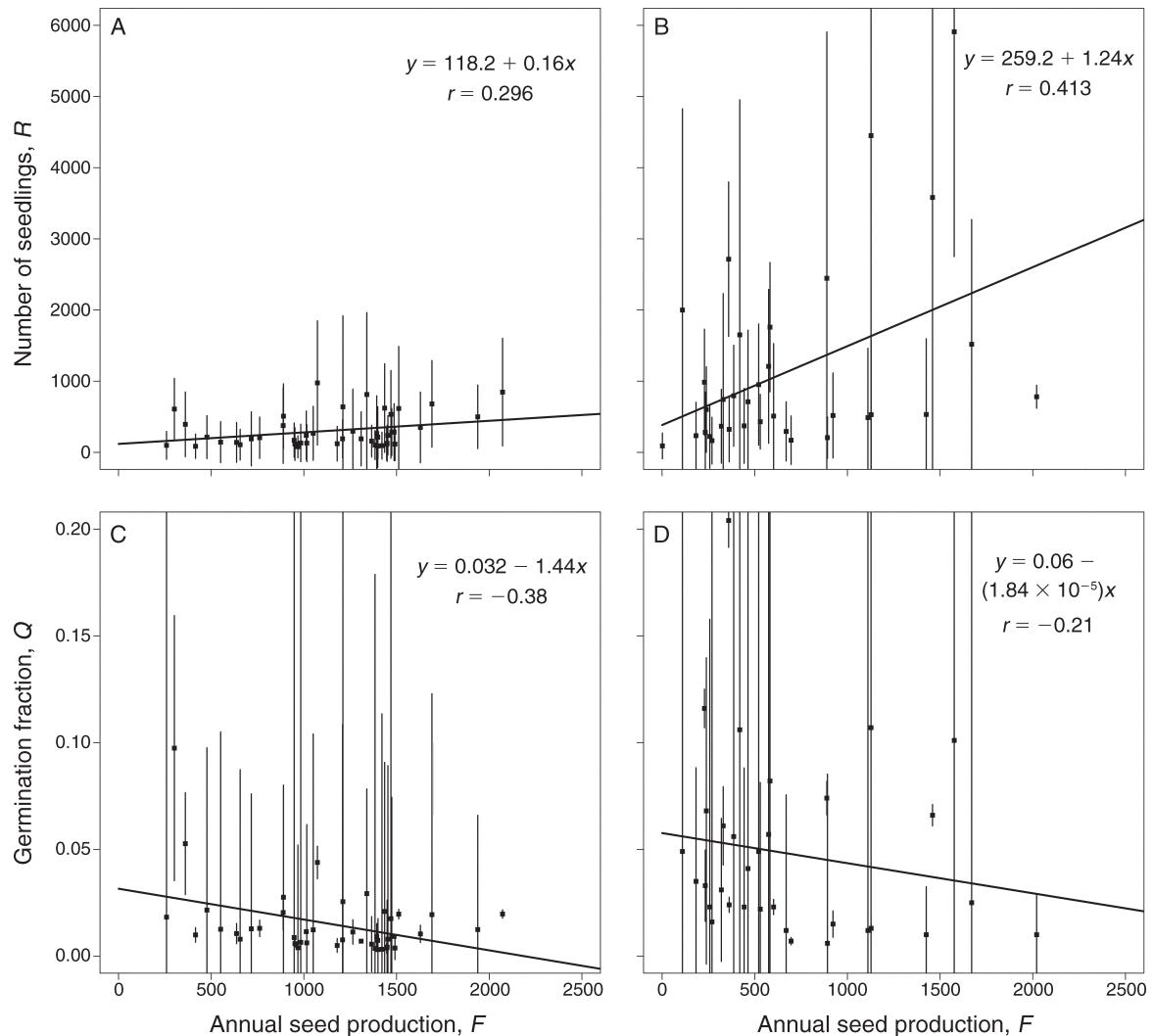


FIG. 4. (A, B) Seedling number ( $R$ ) vs. mean annual seed production for (A) Duke Forest and (B) Coweeta. (C, D) Average germination fraction vs. mean annual seed production for (C) Duke Forest and (D) Coweeta. For all panels, data point estimates are presented with vertical lines showing 95% CI.

offspring number followed a roughly lognormal distribution. Such findings have strong implications for ecological and evolutionary dynamics. It has been shown that variation in reproductive success  $R_0$  due to stochastic mortality can lower asymptotic migration rates by an order of magnitude relative to estimates based on mean  $R_0$  (Clark et al. 2001). Variation in  $R_0$  due to skewed offspring production would likely have a similar effect because most individuals, including long-distance migrants, contribute little to the next generation. However, those rare individuals with high reproductive success can make a crucial contribution to local population establishment and growth. Reproductive inequality also leads to a high degree of heterogeneity in seed and seedling density across the landscape, which may affect competition both within and between species (Aguilar and Sala 1997, Clark et al. 1998, Levine and

Murrell 2003, Boyden et al. 2008, Milla et al. 2009). The distribution of reproductive success also affects the potential strength of selection and genetic drift, which in turn can affect population viability, as is discussed further below.

Our results are consistent with previous studies of reproductive success in forest trees that examined seedling production. For instance, 46–58% of sampled *Gleditsia* seedlings were produced by just three female trees (8.6–8.8% of all mature females), while 47–51% of females each contributed less than 1% of seedlings (Schnabel et al. 1998), and 10% of censused *Pinus pinaster* trees could have produced 50% of all saplings (Gonzalez-Martinez et al. 2006). In tropical systems, it was observed that 46% of *Simarouba* females had no offspring among sampled seedlings (Hardesty et al. 2006), that isolated *Symphonia globulifera* in pastures

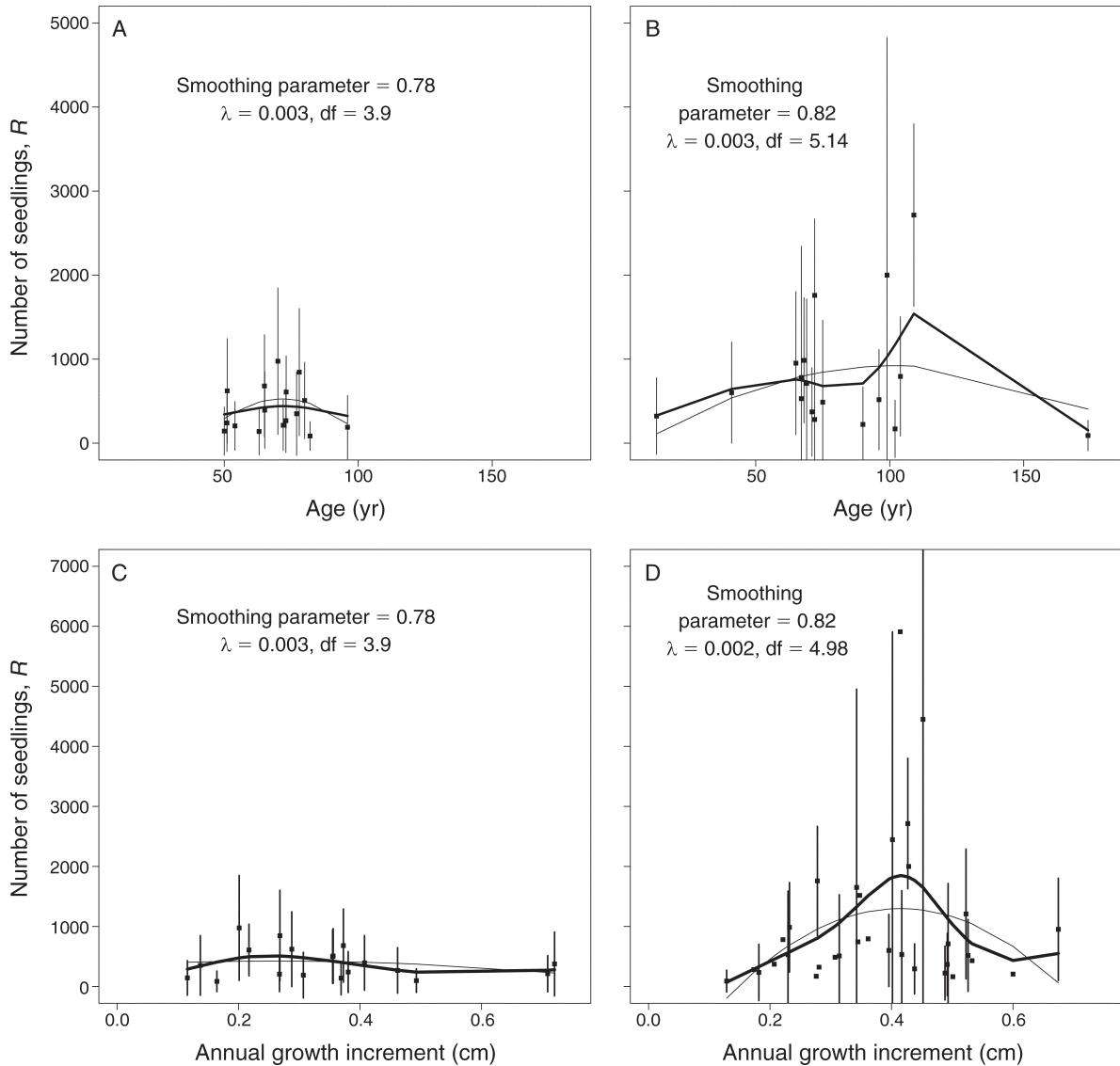


FIG. 5. (A, B) Current number of seedlings ( $R$ ) vs. Age for (A) Duke Forest and (B) Coweeta. (C, D) Number of seedlings ( $R$ ) vs. average annual diameter growth increment for (C) Duke Forest and (D) Coweeta. The spline fit indicating the trend is shown by the thick dark line. The thin light line shows the quadratic regression, which was a poor fit in all four cases.

contributed disproportionately to recruitment in nearby forest fragments (Aldrich and Hamrick 1998); and that in a plot undergoing secondary succession two old-growth *Iriarte* palms contributed almost 50% of offspring while the remainder of parents contributed <6% each (Sezen et al. 2007). Highly skewed distributions of offspring production have also been observed in herbaceous plants (e.g., Meagher and Thompson 1987, Wright and Meagher 2004) and in many animals (Clutton-Brock 1988, Koelewijn et al. 2010). Moreover, many of these previous studies also observed a large zero class: individuals that are of adult size but have no offspring. This is generally not due to year-to-year variation but rather to individual differences that persist over multiple years (Schnabel et al. 1998, Gonzalez-

Martinez et al. 2006, Clark et al. 2010a, Herrera and Jovani 2010).

Many studies have focused on seed production as a proxy for overall reproductive success in plants. Primack and Kang (1989) questioned this assumption, pointing out that plants with fewer seeds may produce seeds of higher quality. Patterns of dispersal and survival could also disrupt the connection between seed number and seedling number (Janzen 1970, Jordano and Herrera 1995). We found that trees with high annual seed production did tend to exhibit high seedling production ( $R_i$ ), especially at Coweeta, but the average fraction of seeds that become seedlings ( $Q_i$ ) tended to be lower for highly fecund trees, especially at Duke Forest. This second result supports Venable's hypothesis (1992) that

density dependence may lead to diminishing returns in offspring number for increasing levels of seed production. The ratio of the variance in offspring number to the mean is smaller for seedlings than for seeds at Duke Forest (180 vs. 362), indicating that mortality at the establishment stage had an equalizing effect, but was higher for seedlings than seeds at Coweeta (1540 vs. 503), indicating that seedling production is less even than seed production. At the stand level, the proportion of acorns produced in the previous fall that become new seedlings is 0.011 at Duke Forest (range, 0.001–0.017) and 0.047 at Coweeta (range, 0–0.154). These stand-level estimates of germination fraction fall comfortably within the range of individual-level germination fractions (Fig. 4). As in most plants, seed production in oaks is positively associated with size, as measured by diameter and canopy dominance (see Clark et al. 2010b, and *Methods: Seed production*). We also examined the relationships between age and growth rate and seedling number. Some, but not all, woody plants exhibit reproductive senescence (Silvertown et al. 2001, Clark et al. 2010a, Herrera and Jovani 2010). For older trees, reduced seed production plus the advancement of previously established offspring out of the seedling class may reduce the standing number of seedlings, leading to the hump-shaped pattern we observed. Because both the Duke Forest and Coweeta sites are secondary forests, few oaks >100 years old exist at either location (E. V. Moran and J. S. Clark, *unpublished manuscript*). It would be instructive to examine the relationship between age and offspring number in old-growth forests or for shorter-lived tree species. A hump-shaped relationship was also observed between average growth rate and seedling production, suggesting that under some conditions there is a positive relationship between growth and reproduction, whereas under others there is a trade-off. That is, while some individuals may lack the resources (e.g., carbon, due to low light levels) to invest much in reproduction or growth, and other individuals allocate to both, very fast growth may only be possible when resources are diverted away from reproduction. However, it should be noted that at both sites one to two fast-growing trees did exhibit relatively high reproductive success (Fig. 5). There was no relationship between germination fraction and growth rate, and therefore no evidence that the offspring of fast-growing trees have a competitive advantage (Venable 1992). Both relationships were weaker at Duke Forest than at Coweeta, and there was no relationship between age and growth rate.

Results were based on a new technique for estimating total seedling production for individual mother trees, applicable to any case where dispersal kernels and parentage for a subset of seedlings have previously been estimated. It should be noted, however, that because estimates of seedling production were based on posterior mean estimates of parentage and dispersal parameters rather than the full posterior distribution, the confidence intervals shown in Figs. 4 and 5 do not reflect the full

uncertainty in offspring number. Uncertainty in dispersal parameters (Moran and Clark 2011) had only a minor effect on estimates of offspring number; uncertainty in parentage assignment may be a more important factor. Because microsatellites are bi-parentally inherited, if the best estimate of parentage for seedling  $k$  was  $P_k(i,j)$ , where  $i$  is the mother and  $j$  is the father, then  $P_k(j,i)$  also had a positive probability; due to the potential for genotyping error, other parent pairs might also be assigned a positive probability (Moran and Clark 2011). While in many cases repeated draws from the posterior distribution can be used to incorporate uncertainty in a parameter into subsequent calculations, in this case that was not possible because if the “observed” number of offspring in a given iteration is 0 then  $R$  cannot be meaningfully calculated (see *Methods: Total current number of seedlings,  $R_i$* ). We found that when such an iterative approach was employed, the distribution of  $R$  in each iteration for individuals with >0 observed offspring continued to roughly follow a lognormal distribution, but the identity of those individuals shifted slightly between iterations. It would therefore be desirable to develop parentage and dispersal models that also estimate total seedling number for individual adults. Although larger models may require larger data sets, and can be computationally expensive (Moran and Clark 2011), this would allow reproductive success to be estimated as part of a full probability framework. The neighborhood model of Burczyk et al. is the best attempt to date to integrate reproductive success into a full probability model, although it focuses on “relative reproductive success” within the neighborhood of a seedling rather than total number of offspring per adult (Burczyk et al. 2006, Gonzalez-Martinez et al. 2006). Another method for simultaneously estimating seedling number and parentage might be to adapt the genetic inverse modeling approach that has been applied to seed (Ribbens et al. 1994, Jones and Muller-Landau 2008), allowing for bi-parental inheritance.

It has been suggested that lifetime reproductive success in both plants and animals follows a lognormal distribution resulting from interacting random environmental effects (Herrera and Jovani 2010). Our data suggest that this is roughly true for those individuals that are reproductively active, but not for the population as a whole. The large numbers of trees that do not produce seed or that have no established offspring create a large zero class. However, for reproductive individuals the lognormal distribution was a much better fit than the Poisson or negative-binomial distributions. Wright’s binomial sampling model, which has been widely used in calculations of the influence of drift and selection in finite populations, implicitly assumes a Poisson progeny distribution (Karlin and McGregor 1968). While not all population genetic models require this assumption (Wood 1987, Crow and Denniston 1988), some do, including models developed specifically for use in conservation biology (e.g., Nunney and Elam 1994).

This has important implications, because skewed distributions of reproductive success (such as the lognormal or negative binomial) can lead to both more rapid spread of favorable alleles and an increased influence of drift on overall genetic diversity than in the Poisson case (Wilson and Levin 1986). Thus, models assuming a Poisson progeny distribution may overestimate effective population size and underestimate the rate of loss of genetic diversity to drift in many populations.

Although inequality in offspring production among reproductive individuals lowers effective population size, increasing the probability that alleles will be lost to genetic drift, many tree populations exhibit high genetic diversity and a low degree of between-population genetic differentiation, indicating that gene flow across large areas keeps effective population size high (Hamrick 2004). In oaks and other wind-pollinated trees, for instance, it is not unusual for >50% of offspring to have fathers located outside the focal stand (Dow and Ashley 1996, Streiff et al. 1999, Nakanishi et al. 2009, Chybicki and Burczyk 2010). However, certain environmental changes could reduce levels of between-stand gene flow. Habitat fragmentation and reduction in adult densities have been shown to result in pollen limitation and/or reduced seedling allelic diversity even in wind-pollinated species (Knapp et al. 2001, Sork et al. 2002, Fernandez and Sork 2007, Gaiino et al. 2010). While some animal dispersers are undeterred by habitat fragmentation, and may even carry seed or pollen longer distances in fragmented landscapes (e.g., Aldrich and Hamrick 1998, Gomez 2003), in other cases fragmentation can greatly impede disperser movement and effectiveness (e.g., Cramer et al. 2007, Kirika et al. 2008, Cordeiro et al. 2009). The loss of dispersers' human-impacted areas due to hunting or habitat loss can also substantially reduce gene flow (McConkey and Drake 2006, Forget and Jansen 2007, Terborgh et al. 2008, Brodie et al. 2009).

We illustrate the impact of reproductive inequality in the absence of immigration using the following calculation. The inbreeding effective population size ( $N_{ei}$ ) is equal to the inverse of the probability that two alleles in the zygote came from the same grandparent (Crow and Denniston 1988):

$$\frac{1}{N_{ei}} = \frac{\mu_k - 1 + (\sigma_k^2/\mu_k)}{N_{t-2}\mu_k - 2}$$

where  $N_{t-2}$  and  $\mu_k$  and  $\sigma_k^2$  are the mean and variance of offspring number. If we assume that the size of the grandparental generation was similar to the number of trees observed to have offspring in the parental generation (59 trees at Duke Forest, 66 trees at Coweeta), then (disregarding overlapping generations)  $N_{ei} = 37$  trees at Duke Forest and  $N_{ei} = 28$  trees at Coweeta. The decline in heterozygosity over time can be approximated by  $H_t/H_0 = e^{-t/2N_e}$ , where  $H_t$  is the heterozygosity in generation  $t$  and  $H_0$  is the initial heterozygosity. If the effective population size were equal to the observed population size ( $N = 199$  trees at

Coweeta, 118 trees at Duke Forest), then heterozygosity would decline by just 0.3–0.4% per generation, even in the absence of immigration or mutation. If reproductive success were Poisson distributed for reproductively active individuals,  $N_{ei}$  would be between 59 and 65, heterozygosity would decline by 0.8% per generation. For  $N_{ei} = 28$ –37, however, heterozygosity would decline by 1.3–1.8% per generation—three to six times faster than if  $N_{ei} = N$ . In addition, taking into account overlapping generations as well as the effect of distance-dependent seed and pollen dispersal would further decrease effective population size (Gillespie 2004).

Based on the results of this analysis and previous studies, we make three recommendations:

- 1) Whenever possible, reproductive success should be assessed in terms of established offspring (seedlings or saplings), as a range of factors may weaken the relationship between seed number and lifetime reproductive success.
- 2) Reproductive success in most species is highly unequal; this has consequences for both population genetics and population dynamics. Wherever possible, conservation genetics analyses and models of population dynamics should use skewed distributions of reproductive success based on parentage data, rather than simply using the mean number of offspring or assuming that offspring number is Poisson distributed.
- 3) Most trees exhibit high gene flow relative to other plant species, which should make them resistant to the erosion of genetic diversity. However, in cases where landscape-level gene flow is reduced relative to historic levels, conservationists should keep in mind that variation in reproductive success may effectively make populations much smaller than they appear.

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