Patterns of Mating in an Insect-Pollinated Tree Species in the Missouri Ozark Forest Ecosystem Project

Victoria J. Apsit[1], Rodney J. Dyer[2], and Victoria L. Sork[3]

Abstract.—Contemporary gene flow is a major mechanism for the maintenance of genetic diversity. One component of gene flow is the mating system, which is a composite measure of selfing, mating with relatives, and outcrossing. Although both gene flow and mating patterns contribute to the ecological sustainability of populations, a focus of many forest management plans, these processes are often overlooked in forest management studies. As part of the Missouri Ozark Forest Ecosystem Project (MOFEP) we conducted a study of mating patterns in flowering dogwood (*Cornus florida* L), an insect-pollinated tree that is abundant and ubiquitous under story tree of upland Missouri Ozark forests. In 1998 and 1999, we collected fruit from over 200 *Cornus florida* individuals located in six compartments (MOFEP sites 1-6; ~250-500 ha each), which were subjected to one of three management treatments: even-aged, uneven-aged, and no harvest. To see whether the management treatments influenced tree density surrounding the study trees, we measured and compared tree density across treatments. Because differential germination could reflect either genetic or environmental factors affecting the mating system, we measured germination success on a per maternal tree basis. We then measured the outcrossing rate, the rate of consanguineous mating (mating with relatives), and the effective number of pollen donors for each of the six sites and tested the hypotheses that both treatment and local tree density have no influence on these aspects of mating. Furthermore, the percent germination among mothers was not significantly influenced by the application of forest treatments. Multilocus outcrossing, t_m (range 0.981-1.000), single locus outcrossing, t_s (range 0.976-0.996), and the genetic effective number of pollen donors (range 4-11) did not differ among management treatments. For 1998, mating with relatives tended to increase with local density (df=1,28, F=4.07, P=0.053, 1998 only), suggesting local familial structure at the site level. No trend in consanguineous mating was observed in the data collected in 1999. The overall results show that the first cycle of timber harvesting had little effect on insect-mediated pollen movement in *C. florida*. This lack of impact could be due to the fact that the treatments did not alter pollinator behavior. Thus, to evaluate the general impact of forest management on gene flow and mating in woody plants, we recommend ongoing monitoring as management treatments are continued and further studies on additional plant species.

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[1] Post-doctoral Associate, University of Missouri-St. Louis, St. Louis, MO 63121-4499.

[2] Doctoral Candidate, University of Missouri-St. Louis, St. Louis, MO 63121-4499; e-mail: rodney@jinx.umsl.edu.

[3] Professor of Biology, University of Missouri-St. Louis, St. Louis, MO 63121-4499; current address: Department of Organismic Biology, Ecology, and Evolution and Institute of the Environment, UCLA, Los Angeles, CA 90095-1786; e-mail: vlsork@ucla.edu.

Pollen-mediated gene movement that occurs through mating patterns is crucial to the viability of plant populations in at least two important ways. First, outcrossing can promote or at least maintain genetic diversity, which is critical to the ability of populations to adapt to environmental change (Avise 1995, Falk and Holsinger 1991, Hedrick and Miller 1992, Lande 1995, Riggs 1990). Disruption or impediments to gene movement by anthropogenic landscape change may restrict the amount of genetic variation available to succeeding generations. Second, pollen-mediated gene movement can affect the fitness of progeny through its impact on the extent of outcrossing and inbreeding. For populations with an evolutionary history of outcrossing, inbred matings often lead to inbreeding depression and lowered population fitness (Charlesworth and Charlesworth 1987) and eventually a decrease in the likelihood of local persistence (e.g., Ellstrand and Elam 1993, Gilpin and Soule 1986, Ledig 1992, Soule 1980). Thus, the mating patterns of plants are critical to the long-term sustainability of plant populations although their genetic impact may be unseen until some time in the future.

Ecological sustainability is a focus of many forest management plans (Christensen *et al.* 1996, Franklin 1996, Grumbine 1994, Kohm and Franklin 1997, United Nations 1992) and often sustainability relies on biological diversity (Lindenmayer *et al.* 2000). Ecosystem sustainability is defined in terms that identify "desired future trajectories" for a specific ecosystem (Christensen *et al.* 1996). To determine whether defined goals are being achieved, management plans must include short-term and long-term monitoring (Gram *et al.* 2001). These monitoring efforts often focus on individual species (e.g., birds, Clawson *et al.* 1997; invertebrates, Harper and Guynn 1999; leaf-chewing insects, Marquis and LeCorff 1997; toads, Johnson 1997), species diversity (e.g., Hansen *et al.* 1991, Hunter 1990, Margules *et al.* 1988, Noss and Cooperrider 1994, Pickett *et al.* 1997, Scott *et al.* 1987), as well as the maintenance of ecosystem integrity (e.g., Grumbine 1994, Likens 1992, Pickett *et al.* 1997). In the Missouri Ozark Forest Ecosystem Project (MOFEP), which is monitoring the impact of ecosystem management collectively as well as separately, some species in animal communities are increasing while others are decreasing (Gram *et al.* 2001).

Landscape change may influence mating patterns (Sork *et al.* 1999). For example, Mitton (1992) found that outcrossing rates in low-density stands were lower than those in high-density stands. He postulated that a tree's probability of receiving its own pollen is increased with fewer individuals contributing to the local pollen pool. Furthermore, Dyer and Sork (2001) found that the local forest structure, including con- and hetero-specific individuals can significantly influence pollen pool diversity in shortleaf pine, *Pinus echinata*, in the Missouri Ozarks. These results suggest that pollen movement can be impeded by increased local stand density. In terms of outcrossing rates, if timber management has created large clearings in a manner that promotes pollen movement, we predict that outcrossing will increase because each mother is sampling a larger population of pollen donors. Both Young *et al.* (1993) and Fore *et al.* (1992) analyzed fragmented populations of *Acer saccharum* and found that fragmentation may actually increase pollen-mediated gene flow. They concluded that landscape fragmentation promotes long-distance gene flow by changing wind patterns. Similarly, in a study of an animal-pollinated Sri Lankan tropical tree, *Shorea megistophylla*, Murawski *et al.* (1994) observed lower outcrossing rates in disturbed than in undisturbed populations. In contrast, in the insect-pollinated canopy tree *Spondias mombin*, Nason and Hamrick (1997) found rates of pollen immigration into small, insular forest fragments (1 to 4 adults each) to be 100 percent. Yet, both fruit set and germination rates were significantly lower in small fragments than in continuous forest populations. Their study illustrates the benefits of measuring germination rates as additional information about mating.

Less is known about the impact of landscape change on pollen pool composition. One method of gauging the influence of landscape alteration on pollen pool composition is to examine the genetic effective number of pollen donors, N_{ep}. The effective number of pollen donors is an excellent indicator of the genetic diversity of a seed crop. If the number of pollen donors is small, the progeny may be less genetically diverse than when the number of pollen donors is larger. The literature in conservation and population genetics is just starting to accumulate estimates of N_{ep} for forest tree populations. Previously, we found that the effective number for *Quercus alba* is about eight individuals, and the average pollen movement is only about 11 m (Smouse *et al.* 2001). In a study of shortleaf pine (*Pinus echinata*) within all MOFEP sites, the estimated pollen pool structure (ϕ_{ft}=0.095) can be translated into a value of N_{ep}=10.5 individuals (Dyer and Sork 2001). In contrast, a considerably smaller number of pollen donors have been reported for both sugar pine in California (*Pinus lambertiana*, N_{ep}=1, Westfall, in prep.) and the insect-pollinated mimosa in Georgia (*Albizia julibrissin*, N_{ep}=1-2, Hamrick *et al.*, in prep.). In general, pollen donor neighborhood size seems small across many of these species. If landscape alteration influences the dispersal of pollen in natural populations, then we expect to see those changes reflected in the genetic composition of sampled pollen pools.

Here, we present a case study of the impact of forest management in MOFEP on mating patterns in an insect-pollinated tree species, *Cornus florida*. MOFEP is designed to monitor the ecosystem effects of three management treatments: even-aged, uneven-aged, and no-harvest management (Brookshire and Hauser 1993, Sheriff 2001, Sheriff and He 1997). We had three specific objectives. First, we tested whether the density of con-specific adults surrounding our study trees differed across forest management treatment. Because local tree density has been shown to influence pollinator behavior, it is essential to determine whether treatments altered the density of flowering *Cornus* individuals. Our second objective was to test whether germination success differed across management treatments. Differential germination could reflect genetic processes associated with pollen movement, and it could reveal the environmental impact of management on seed quality that could influence the outcome of mating patterns. Third, we tested whether the mating system was influenced by landscape alteration. Specifically, we measured the single- and multi-locus outcrossing rates, rate of consanguineous mating (i.e., mating with relatives), and genetic effective number of pollen donors.

METHODS

Study Species

Cornus florida, flowering dogwood, is an understory, insect-pollinated, self-incompatible woody plant, ubiquitous throughout MOFEP sites. It flowers from late March through April (Radford *et al.* 1968). Numerous insect visitors have been documented for *C. florida*, primarily andrenid and halictid bees (J. Grant, personal communication), as well as beetles, flies, and butterflies (Eyde 1988). The inflorescence consists of four white or cream colored bracts subtending 15 to 35 individual, perfect flowers, each with a single ovule. A single *C. florida* inflorescence matures up to eight drupes (Apsit and Sork, personal observation) that turn bright red as they ripen during late September and October. The seeds are dispersed by birds, mammals, and gravity (McLemore 1990).

The Study Site

MOFEP is a long-term large-scale, landscape-level experiment administered by the Missouri Department of Conservation (MDC) to examine the effects of forest management practices on multiple ecosystem components, both biotic and abiotic (Brookshire *et al.* 1997). MOFEP includes study sites located across Carter, Reynolds, and Shannon Counties in southeastern Missouri. The study area has a history of anthropogenic-mediated disturbance through intensive harvesting and then burning and grazing. Since 1880, this disturbance has transformed the local forest structure from predominantly shortleaf pine (*Pinus echinata*) stands to a mixture of oak (*Quercus alba, Q. coccinea, Q. stellata, Q. velutina*) and hickory (*Carya tomentosa, C. glabra*; Cunningham and Hauser 1989). At the onset of this experiment, these counties were 84 percent forested with agricultural activity limited to bottomland streams (Xu *et al.* 1997).

The MOFEP experiment has three treatment types (no-harvest, uneven-aged management, and even-aged management) over nine experimental sites divided into three blocks (Sheriff and He 1997). The nine sites, which range in size from 266 to 527 ha, were divided among three blocks based on spatial proximity: sites 1-3 to block 1, sites 4-6 to block 2, and sites 7-9 to block 3 (see map in Sheriff 2001). Treatments were assigned randomly to each site within a block. In this analysis, we examined only the northern sites 1-6.

The uneven-aged and even-aged treatments were initially implemented in 1991-1992 according to MDC "Forest Land Management Guidelines" (1986). These guidelines call for even-aged areas to be managed for regeneration, poletimber, and sawtimber tree size classes, while uneven-aged managed areas are to be for oak-hickory-pine regeneration and a balance of tree size classes equivalent to even-aged sites. Treatments were applied through regulated harvest of approximately 10 percent of the standing biomass per site. Ten percent per site was left as old growth forest with no timber harvest. Harvesting occurred over different spatial configurations in each treatment type. Under uneven-aged management, 5 percent of the timber harvest was single-tree selection to balance tree size classes and 5 percent was harvested as group openings (21 to 43 m in diameter depending on slope aspect) to promote regeneration. Even-aged harvesting occurred over six to nine 3- to 12-ha clearcut areas per treatment site. No timber was harvested on the no-harvest (control) sites.

Field Sampling

We sampled 252 trees across 57 locations within MOFEP sites 1-6. At each location we sampled a cluster of two to five trees, resulting in 57 clusters total. Trees within a cluster were 20-100 m apart and distance between cluster perimeters was a minimum of 75-100 m. Within every site we selected five clusters at each of two ecological landtypes (ELT): ridgetop (ELT 19) and south to southwest (SSW or ELT 17; see Meinert *et al.* 1997 for more details on ecological landtypes). Cluster location varied according to treatment. Clusters within even-aged treatments (sites 3 and 5) were located within a 50-m border of the clearcut areas at the proper ELT or aspect. Clusters within the uneven-aged treatment (sites 2 and 4) were situated within a 50-m border surrounding group cuts, as well as within the group cuts themselves. Clusters in no-harvest sites 1 and 6 were established only with respect to ELT.

In fall 1998 and 1999, we sampled sufficient fruit from the 252 study trees to ensure 25 germinants for each maternal tree. During spring 1998, we collected fresh leaf material from all adults for identification of maternal genotypes. During our field sampling, we also measured the density of neighboring adult trees by counting all con-specific individuals (d.b.h. ≥2.54 cm) within a 25-m radius about each tree. Local density estimates were converted into the number of flowering individuals per hectare (~0.405 acres).

Germination Studies

Sampled fruit was transported to the laboratory where we removed seeds from fruit and surface sterilized in 10 percent bleach solution for 10 to 15 minutes. The seeds were then planted in 96-well flats, four seeds per well. Seeds from each maternal tree were planted in consecutive wells, in columns starting with the upper left well and finishing at the lower right well for each flat. A plastic stake with the maternal tree identification number marked the beginning of each family. Seeds were cold stratified at 5°C for 120 days. Flats were moved to the University of Missouri - St. Louis Biology Department greenhouse in early spring of both years and kept at 18°C. Germination rates were calculated for each maternal tree for both 1998 and 1999 as the proportion of seeds germinated out of the total number of seeds planted per individual. We then calculated the average proportion germinated per family per cluster.

Laboratory Analysis

After the seeds germinated, we collected freshly harvested leaf material from approximately 12 to 18 germinants per maternal tree (table 1). We extracted enzymes by grinding the leaf material in 1 ml of a modified phosphate buffer (Alvarez-Buylla and Garay 1994) with mortar and pestle, absorbing the exudate onto chromatography paper wicks, and storing the wicks at –70°C. We identified four polymorphic allozyme loci (Kephart 1990, Soltis *et al.* 1983, Sork *et al.* 1993) on two gel/electrode buffer systems (table 2): fluorescent esterase (*Fe*, 3.1.1.1, 3) and triosephosphate isomerase (*Tpi*, 5.3.1.1) on a modified system 8 (Soltis *et al.* 1983); isocitrate dehydrogenase (*Idh*, 1.1.1.42) and phosphoglucomutase (*Pgm*, 2.7.5.1) on morpholine citrate pH 8.0 (Soltis *et al.* 1983).

Table 1.—*Number of* C. florida *seeds analyzed in 1998 and 1999*

Treatment	Site	1998 # Trees	 # Seeds	 per Tree	1999 # Trees	 # Seeds	 per Tree
No harvest	1	18	215	12-21	115	289	7-50
No harvest	6	14	211	7-36	16	313	12-32
Uneven-aged	2	28	337	12-14	15	287	8-24
Uneven-aged	4	28	324	7-12	22	433	7-51
Even-aged	3	33	386	8-12	24	386	8-28
Even-aged	5	30	337	8-12	22	396	7-36
Totals		151	1,810		114	2,104	

Table 2.—C. florida *adult allele frequencies by sites within each treatment type. Allozyme name is followed by the locus number. Locus number is given when more than one locus is present for an enzyme.*

Locus	Allele #	No harvest Site 1	 Site 6	Uneven-aged Site 2	 Site 4	Even-aged Site 3	 Site 5
Fe-3	1	0.000	0.000	0.012	0.000	0.000	0.000
	3	0.396	0.422	0.202	0.315	0.305	0.375
	5	0.604	0.578	0.786	0.684	0.683	0.625
	7	0.000	0.000	0.000	0.000	0.012	0.000
Idh	2	0.000	0.000	0.000	0.011	0.012	0.000
	3	1.000	0.988	1.000	0.978	0.988	0.938
	5	0.000	0.012	0.000	0.011	0.000	0.062
Pgm-1	1	0.017	0.000	0.012	0.011	0.037	0.000
	2	0.103	0.088	0.060	0.022	0.024	0.050
	3	0.880	0.900	0.928	0.967	0.939	0.950
	5	0.000	0.012	0.000	0.000	0.000	0.000
Tpi-1	3	0.362	0.566	0.500	0.554	0.439	0.563
	5	0.638	0.422	0.489	0.446	0.524	0.425
	7	0.000	0.012	0.011	0.000	0.037	0.012

Data Analysis

To assess whether management treatments influenced density of adult *C. florida* trees surrounding the study trees, we used a mixed-model ANOVA (Proc GLM, SAS) with three main effects—block, treatment, and ELT. In this model, ELT and treatment were fixed effects, and block was treated as a random effect. Adult density was log transformed to achieve normality. The analyses were done using average density per cluster. We calculated germination rates for each maternal tree as the proportion of seeds germinated out of the total number of seeds planted per individual. We analyzed the effects of treatment on germination separately each year with block as a random effect (Proc GLM, SAS). The dependent variable was mean germination per cluster, which was arc sine square root transformed for the analysis to achieve normality.

Mating system parameters, which were estimated for each site using MLTR (Ritland and Jain 1981, Ritland 1990), include the following: the average adult inbreeding, F; the average multilocus outcrossing rate, t_m; the average single locus outcrossing rate, t_s; the consanguineous mating rate, t_m-t_s; and the probability that a random pair of individuals within a progeny array share a father, r_p. The average effective pollen donor number per site (N_{ep}) was calculated as the reciprocal of r_p ($N_{ep}=1/r_p$). The multilocus outcrossing rate, t_m, is often considered a better estimate of the "true" selfing rate, while the average single locus outcrossing rate, t_s, includes inbreeding through selfing and mating with relatives. Estimates of the mating system parameters used in hypothesis testing were generated from 100 bootstrapped values of the grouping procedure of the MLTR mating system program (Ritland 1990, Ritland and Jain 1981).

To test whether the mating system differed among treatments or ELT, we estimated the mating system parameters separately for each cluster. Then, using two of those parameters, mating between related individuals (t_m–t_s) and N_{ep}, we conducted a mixed-model ANOVA with the same model that we used for adult tree density. The estimate of (t_m–t_s) was arc sine square root transformed to achieve normality. In addition to the ANOVA, we performed two separate regression analyses (Proc REG, SAS Institute) for 1998 and 1999 to examine the relationship between adult tree density and mating among relatives (t_m–t_s). Both variables were transformed as before.

RESULTS

For the locations that we sampled, adult densities of *Cornus florida* individuals averaged over clusters among sites tended to be lowest in uneven-aged treatments (127 to 129 per ha), intermediate in no-harvest sites (135 to 151 per ha), and highest in even-aged treatments (148 to 175 per ha; fig. 1). The effect of treatment was significant although the overall model was not (table 3). Adult densities for our samples were somewhat greater in block 2 (sites 4-6) than in block 1 (sites 1-3, see fig. 1). In spite of these trends, results of the mixed-model ANOVA on adult density indicated that none of the main effects or their interactions were significant (table 3).

Germination rates were analyzed for every tree with fruit in both 1998 and 1999, regardless of whether that tree was included in the mating system analyses. Overall, there was no significant treatment effect on the germination rate in either 1998 or 1999 (table 4) although the trend in germination success increased with the degree of canopy removal adjacent to the cluster (fig. 2). With an alternate statistical design, this trend might be significant. However, with the current design, we run the risk of a type II error.

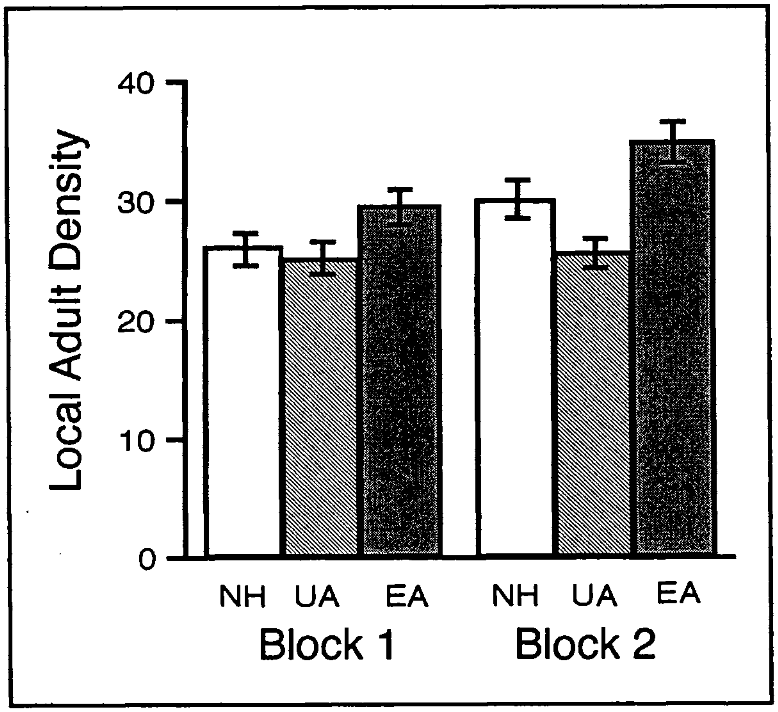

Figure 1.—*Mean density of* Cornus florida *adults at sample locations of this study by management type. Block 1 consists of sites 1, 2, and 3. Block 2 consists of sites 6, 4, and 5. Vertical lines indicate 95 percent confidence intervals.*

Populations at all six sites for both years showed essentially 100 percent outcrossing based on the multilocus outcrossing rate. The rates of single locus outcrossing, which includes both mating with relatives and selfing, were also quite high but always significantly less than 1.0 (table 5). Estimates of mating with relatives (t_m–t_s) varied between 0 and 2 percent. Values for consanguineous mating were quite low in all sites both in 1998 (t_m-t_s ranged from 0.000 to 0.019) and 1999 (t_m-t_s ranged from 0.004 to 0.019). Estimates of (t_m–t_s) were not significantly different from zero in site 4 in 1998 and in site 6 in 1999. The outcrossing rate estimates (tm) had very similar ranges for all sites in both 1998 (t_m ranged from 0.981 to 1.0) and 1999 (t_m ranged from 0.995 to 1.000; table 5). Estimates of t_m were not significantly different from 1.0 for one site in 1998 (site 2) and for three sites in 1999 (sites 2, 4, and 6; table 5).

The most variable mating system parameter across sites is the correlation of paternity (r_p; table 5). Converting r_p into the effective number

Table 3.—*ANOVA results for* C. florida *adult density, averaged by cluster, using a 3-way mixed model with block as a random effect*

Source	df	MS	F	P
Model	11	2.294	0.91	0.549
Block	1	0.016		
Treatment	2	0.339	22.40	0.04
Block*Treatment	2	0.015		
ELT	1	0.262	0.55	0.59
ELT*Block	1	0.479		
ELT*Treatment	2	0.999	9.89	0.09
ELT*Treatment*Block	2	0.101		
Error	23	5.287		

Table 4.—*Results of mixed model ANOVA of* C. florida *germination rates in 1998 and 1999*

Source	df	MS	F	P
1998				
Model	11	0.014	0.70	0.721
Block	1	0.008		
Treatment	2	0.066	5.08	0.16
Block*Treatment	2	0.013		
ELT	1	0.001	1.00	0.50
ELT*Block	1	0.001		
ELT*Treatment	2	0.002	0.04	0.96
ELT*Treatment*Block	2	0.057		
Error	19	0.383		
1999				
Model	11	0.021	0.66	0.759
Block	1	0.009		
Treatment	2	0.038	2.11	0.32
Block*Treatment	2	0.018		
ELT	1	0.056	56.00	0.08
ELT*Block	1	0.001		
ELT*Treatment	2	0.004	0.10	0.91
ELT*Treatment*Block	2	0.039		
Error	19	0.032		

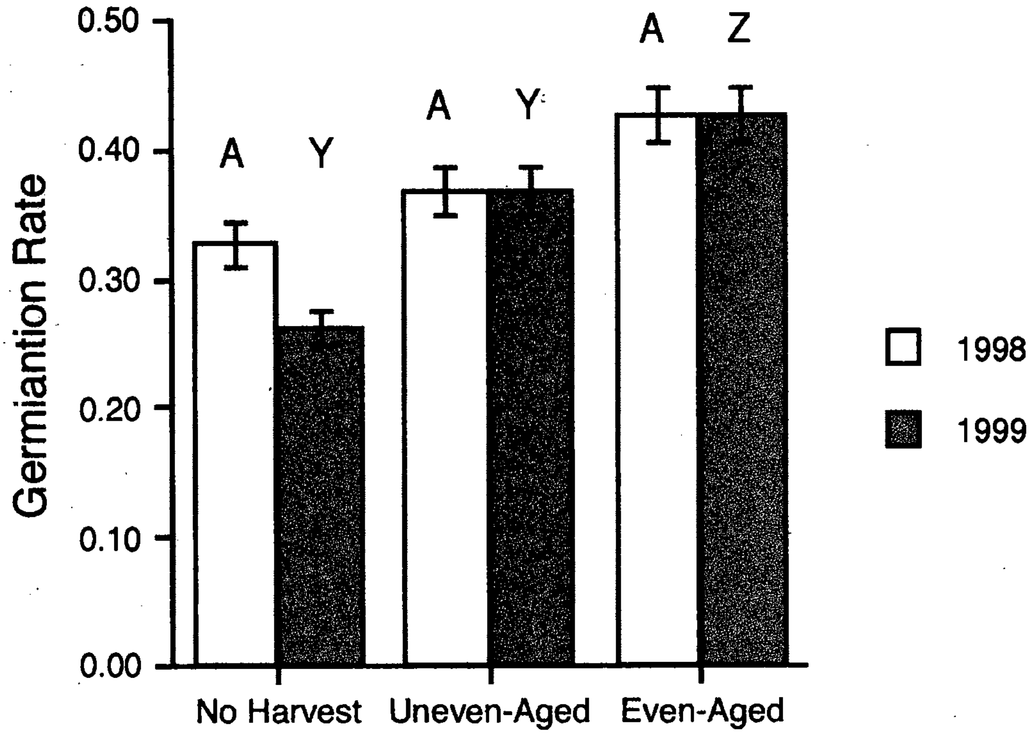

Figure 2.—*Germination rates for* Cornus florida *in 1998 and 1999 by treatment type. Vertical lines indicate +/- 1 standard error.*

Table 5.—*Mating system parameter estimates for* C. florida *in 1998 and 1999. Numbers in parentheses are 95 percent confidenc intervals based on 100 bootstrapped values of the data set.*

Year	Site	Treatment	F[a]	t_m	t_s	t_m-t_s	r_p
1998	1	No harvest	0.019 (0.010, 0.028)	0.997 (0.996, 0.998)	0.978 (0.972, 0.984)	0.019 (0.013, 0.025)	0.137 (0.111, 0.163)
	6	No harvest	0.084 (0.023, 0.145)	0.999 (0.998, 1.000)	0.984 (0.983, 0.985)	0.015 (0.014, 0.016)	0.091 (0.076, 0.106)
	2	Uneven-aged	0.118 (0.060, 0.176)	0.981 (0.978, 0.985)	0.979 (0.972, 0.986)	0.002 (0.000, 0.004)	0.088 (0.083, 0.093)
	4	Uneven-aged	0.015 (0.012, 0.018)	0.996 (0.995, 0.997)	0.996 (0.995, 0.997)	0.000 (-0.001, 0.001)	0.127 (0.112, 0.142)
	3	Even-aged	0.033 (0.024, 0.042)	0.997 (0.996, 0.997)	0.989 (0.988, 0.990)	0.008 (0.007, 0.009)	0.230 (0.170, 0.236)
	5	Even-aged	0.048 (0.038, 0.058)	0.996 (0.995, 0.997)	0.990 (0.989, 0.991)	0.006 (0.005, 0.007)	0.197 (0.194, 0.200)
1999	1	No harvest	0.165 (0.077, 0.253)	0.998 (0.997, 0.999)	0.979 (0.969, 0.989)	0.019 (0.009, 0.029)	0.157 (0.140, 0.174)
	6	No harvest	0.060 (0.026, 0.094)	0.981 (0.958, 1.004)	0.981 (0.979, 0.983)	0.000 (-0.020, 0.020)	0.165 (0.145, 0.185)
	2	Uneven-aged	0.032 (0.026, 0.038)	1.000 (0.999. 1.001)	0.990 (0.989, 0.991)	0.010 (0.009, 0.011)	0.243 (0.213, 0.283)
	4	Uneven-aged	0.024 (0.021, 0.027)	0.999 (0.998, 1.000)	0.987 (0.986, 0.988)	0.012 (0.011, 0.013)	0.200 (0.170, 0.230)
	3	Even-aged	0.145 (0.101, 0.189)	0.995 (0.994, 0.996)	0.976 (0.975, 0.977)	0.019 (0.018, 0.020)	0.132 (0.080, 0.184)
	5	Even-aged	0.569 (0.511, 0.627)	0.988 (0.982, 0.994)	0.984 (0.982, 0.986)	0.004 (0.000, 0.004)	0.137 (0.113, 0.161)

[a] Mean adult inbreeding rate, not to be confused with the F-statistic reported in other tables.

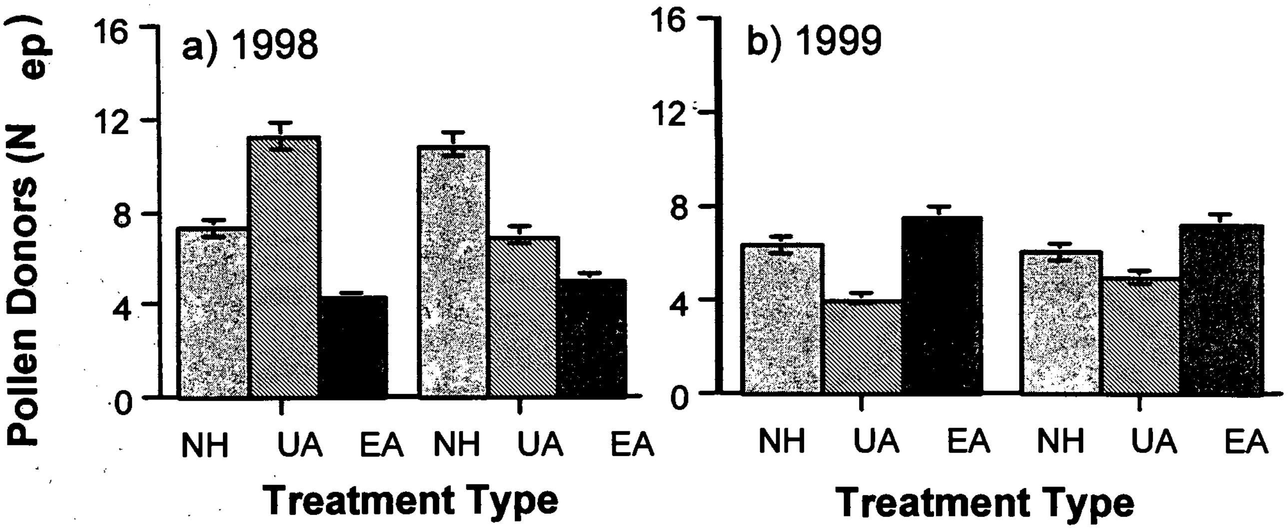

Figure 3.—*Effective pollen donor number* (N_{ep}) *of* Cornus florida *per site by treatment type in 1998 (a) and 1999 (b). Vertical lines indicate 95 percent confidence intervals.*

of pollen donors ($N_{ep}=1/r_p$), we see that the 1998 pollen donor number (N_{ep} ranged from 4.3 to 11.4) was greater than that for 1999 (N_{ep} ranged from 4.1 to 7.6; fig. 3). These estimates are heterogeneous across treatments, blocks, and years. Site 3 (block 1) had the lowest N_{ep} (4.3) in 1998 but the highest in 1999 (N_{ep}=7.6 donors). Site 2 (block 1) had the highest N_{ep} in 1998 (11.4) but the lowest in 1999 (4.1).

Our examination of mating system parameters estimated for each cluster revealed no significant pattern in consanguineous mating by treatments, blocks, or ELT (table 6). The current sampling design with blocks, treatments, and ELT, and associated interactions, caused some problems with the analysis of consanguineous mating in 1999 (table 6). In this mixed-model design, the error terms are estimated by equating the observed Mean Square values (MS) to the expected (E[MS]) to provide the test statistic. Our data show that there are no significant effects in this model. We then examined the association between adult density surrounding study trees and t_m - t_s in separate regressions for the 2 years. In 1998, clusters with higher adult density had higher consanguineous mating (df=1,28; F=4.07; P=0.053; R^2=0.131; fig. 4). The scatter plot demonstrates that adult densities vary a great deal within and among management treatments (fig. 4). In 1999, we found no trend toward significance for an effect of adult density on t_m-t_s (df=1,29; F=0.9; P=0.332; R^2=0.032).

Table 6.—*Mixed-model ANOVA results of related mating* (t_m-t_s) *in* C. florida *in 1998 and 1999*

	1998				1999			
Source	**df**	**MS**	**F**	**P**	**df**	**MS**	**F**	**P**
Model		0.0058	0.88	0.57	1	0.0009	1.42	0.21
Block	1	0.0010			1	0.0019		
Treatment	2	0.0003	0.30	0.77	2	0.0006	2.00	0.33
Block*Treatment	2	0.0010			2	0.0003		
ELT	1	0.0000	0.00	0.99	1	0.0028	9.33	0.20
ELT*Block	1	0.0013			1	0.0003		
ELT*Treatment	2	0.0001	0.14	0.88	2	0.0005	0.41	0.71
ELT *Treatment*Block	2	0.0007			2	0.0012		
Error	23	0.0137			34	0.0006		

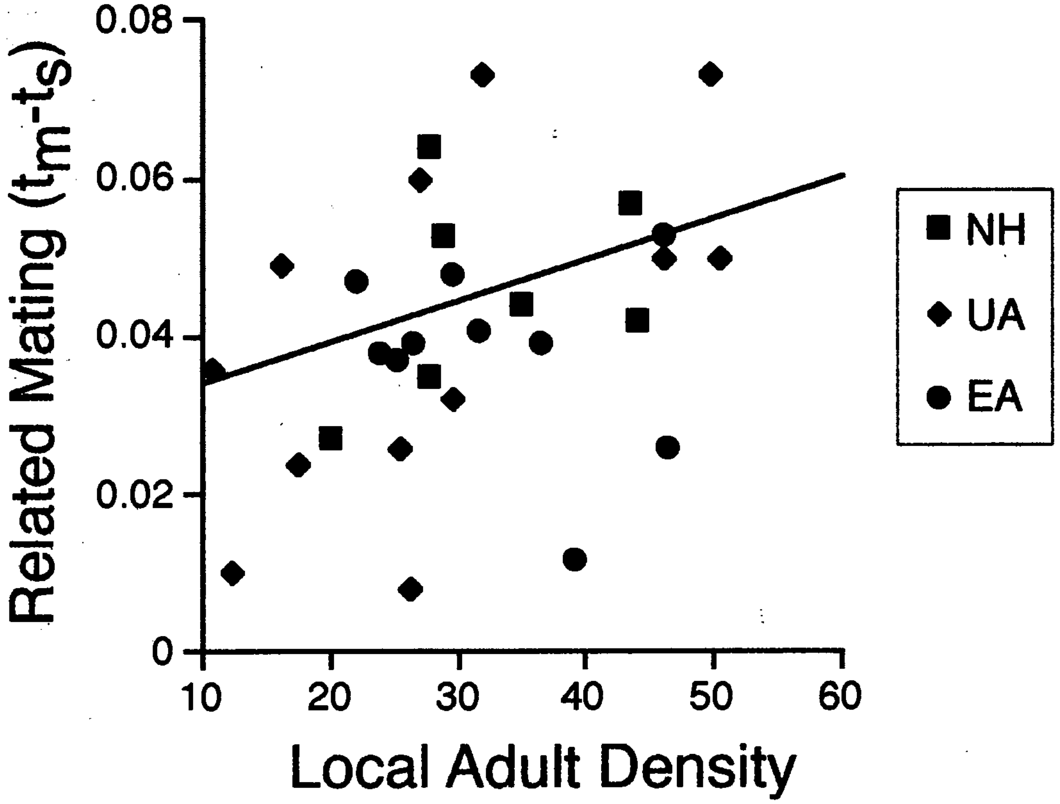

Figure 4.—*Mating between related individuals* (t_m-t_s) *of* Cornus florida *per cluster and average local density of adult trees within 25 m of each adult within each cluster in 1998. (Least squares regression: df=1,28; F=4.07; P=0.053;* R^2 *=0.131).*

DISCUSSION

The foremost finding of the study is the lack of differences in mating patterns of *Cornus florida* across three types of forest management. This finding is noteworthy because this study is the first to test a hypothesis concerning the impact of landscape change on a component of gene movement. The question is whether this finding will be true for other species as well. Dogwood may have been unaffected by the first phase of MOFEP management treatments for several reasons. Because dogwood is highly abundant throughout the MOFEP area, a change in landscape may not affect the availability of trees as pollen sources or hamper the behavior of its pollinators. It is also self-incompatible, which may account for essentially 100 percent multilocus outcrossing rate and the extremely high but not especially variable single-locus outcrossing rate, which includes mating with relatives.

Having acknowledged that the abundance of *C. florida* may have buffered the mating patterns against the impact of landscape change, we should point out that the way we sampled study trees may have reduced our sensitivity in detecting an impact. One might expect that the clearcuts, group cuts, and intermediate tree thinning associated with uneven-aged and even-aged treatments could cause loss of available mates for some species in the MOFEP landscape. Instead, we observed that the local densities of *Cornus florida* adults surrounding the study trees did not differ significantly among treatments. Relative to the no-harvest treatment, the uneven-aged treatment showed slightly lower local densities and the even-aged treatments had slightly higher local densities, but these trends were not strong enough to produce an overall significant result. The lowered densities in the uneven-aged treatment are expected due to the thinning that took place throughout the sites. The slightly higher densities in the even-aged treatment are counterintuitive except that our study trees were sampled adjacent to, not within, the forest clearings. Nonetheless, these two treatments may not have created sufficient landscape or population density changes to shape mating patterns in *C. florida*.

The effective number of pollen donors (N_{ep}) is an aspect of mating system that one might expect to be influenced by landscape change, especially if that landscape change influenced availability of mates. Although we observed a great deal of heterogeneity in N_{ep} across years and treatments, this parameter did not differ according to management treatment. The genetic effective number of pollen donors is a measure of the genetic diversity in the pollen pool and a good indicator of pollen movement (Smouse *et al.* 2001). Our estimates of N_{ep} in *C. florida* (4 to 11 individuals) are similar to those observed in MOFEP populations of white oak, *Quercus alba* (N_{ep}~8 individuals, Smouse *et al.* 2001) and shortleaf pine, *Pinus echinata* (N_{ep}~10 individuals, estimated from Dyer and Sork 2001). These values are much higher than that found for a savanna population of California valley oak, *Quercus lobata* (N_{ep}~4 individuals, Sork *et al.*, in press). Other studies report N_{ep} in the one to two individual range (wind-pollinated *Pinus lambertiana*, Westfall, in prep., and insect-pollinated *Albizia julibrissin*, Hamrick *et al.*, in prep.). The high variation in estimates across studies demonstrates the need for further work on the relationship between landscape and pollen donor numbers in range of species and pollen vectors. As we suggested for the outcrossing rate result, the first cycle of landscape change may not be sufficient to influence this component of mating. So, in spite of the observation that our estimates of N_{ep} ranged from 4 to 11, management treatments do not show a consistent effect.

To support our suggestion that local tree density can be expected to influence the patterns of mating, we examined its relationship between mating system of tree clusters sampled throughout MOFEP. In general, the amount of consanguineous mating is relatively small, ranging from 1 to 9 percent across clusters. During one of the years, we found that sites with higher density showed higher levels of consanguineous mating or more inbred mating. One explanation for this trend is that in denser locations, trees are more likely to be pollinated by neighboring plants, which tend to be related in many plant populations (Bradshaw 1972). One implication for MOFEP of the positive relationship between mating with relatives and local density is that a reduction in density should lead to decreased levels of inbreeding in *C. florida* populations and perhaps decreased inbreeding depression. If true, then as the continuation of tree thinning reduces local densities of *C. florida*, we might observe reduced inbreeding.

The first cycle of management treatment appeared to have no strong influence on germination rates. This finding is consistent with the observations that removal of canopy individuals has no influence on the probability of producing inbred offspring. If there are no differences in inbreeding in terms of multilocus selfing (table 5), consanguineous mating (table 6) or the density of local pollen donors (table 3) caused by the treatments, then the only other possible factor influencing germination would be local environmental factors. Local factors that may influence germination include light, water, and nutrient availability, which may be particularly important for an understory tree. Our results suggest that timber removal did not alter local environmental factors to such a degree that germination in *C. florida* was changed.

It is important to discuss the general applicability of our results to other woody plant species and the future of MOFEP. First, we have studied an insect-pollinated tree species in the MOFEP study sites. Wind-pollinated species may be more influenced by landscape architecture than insect-pollinated species. In the latter, the pollinators can fly to the next tree, even when forest treatment has increased the inter-tree distance. In wind-pollinated species, pollen movement can be affected by stand density. For example, Dyer and Sork (2001) found that genetic diversity in *Pinus echinata* was lower in locations with high overall tree density. In fact, Dyer and Sork (unpublished data) have found significant differences across treatments, including lower consanguineous mating in even-aged treatments and higher number of pollen donors in the uneven-aged and even-aged treatments. Thus, we know of at least one other species whose mating patterns were changed by the MOFEP experiment, and the difference may be that wind-pollinated species are more affected by changes in vegetative structure. Second, we have studied an abundant understory tree that was generally harvested only when it fell within a clearcut or group selection opening. A less abundant species or one whose density was more affected by thinning between openings may be more sensitive to management. Third, this study was conducted after a single phase of stand treatments. We did not predict how the mating patterns of *C. florida* and other species might respond to long-term change.

In summary, the pattern of pollen movement in *Cornus florida* after the first phase of timber harvest seems to be unaffected by the MOFEP management treatments. Because it is generally feared that the consequences of landscape change are always negative, the results of our study are encouraging in that landscape change can occur without necessarily harming the genetic diversity or fitness of a plant population. It is also encouraging that the direction of results favors retention of genetic diversity and reduction of inbreeding. We cannot resolve whether the results will remain the same as timber harvest continues for another 90 years when overall adult densities are reduced. Thus, to truly understand the long-term consequence of forest management on gene flow and future genetic diversity, it will be necessary to continue monitoring pollen movement in this and other species.

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