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Founder Placement and Gene Dispersal Affect Population Growth and Genetic Diversity in Restoration Plantings of American Chestnut

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1. Introduction

The American chestnut, *Castanea dentata* [Marsh.] Borkh (Fagaceae), was an abundant canopy tree inhabiting the mixed mesophytic forests of eastern North America. The species was struck by a fungal pathogen (*Cryphonectria parasitica* [Murrill] Barr*)* introduced from East Asia in the late 1800's on imported Asian chestnut material with the consequence that billions of trees have been destroyed (Barakat *et al.,* 2009; Pierson *et al.,* 2007; Elliot & Swank 2008; Jacobs 2007; Stilwell *et al.,*2003; Paillet, 2002; Huang *et al.,* 1998; Russel, 1987). The near elimination of this once important species has had widespread effects on the ecological functioning of eastern North American forests, and has also had a severe impact on economic forest extraction practices (e.g., strong workable lumber; chestnuts as food and forage). *Castanea dentata* has escaped complete elimination from its native range by persisting as occasional sprouts from the root collar of trees damaged by the blight; these sprouts rarely reach full sexual maturity (Jacobs, 2007; Stilwell *et al.,*2003; Paillet, 2002). Efforts are underway to restore this former keystone species and prevent extinction, reestablishing its ecological and economic roles in its natural habitat. Breeding of blight-resistant strains is being attempted (e.g., by the American Chestnut Foundation, TACF) through a series of initial hybridizations between *C. dentata* and the Chinese chestnut *(C. mollisima* Blume), followed by a series of backcrosses with the American chestnut always selecting for blight-resistance, to develop strains that are predominantly American chestnut in genotypic constitution but which retain Chinese blight-resistance genes. For example, some of the most recent blight-resistant strains ready for re-introduction are calculated to be genetically 94% American chestnut and 6% Chinese chestnut (Jacbos, 2007; Diskin *et al.,* 2006).

The conservation of endangered plant species often involves restoring these species back to their natural habitats and/or *ex situ* rescue plantings (Merritt & Dixon, 2011), and the American chestnut is no exception. Considerable resources are being expended in generating blight-resistant strains of *C. dentata*, thus necessitating optimization of restoration programs which are usually labor-intensive and expensive. Costs of such restoration efforts

include propagule generation and collection, storage, treatment, site preparation, planting, protecting, provisioning, travelling to and from the introduction site, monitoring, and future manipulations of individuals (Rogstad & Pelikan, 2011).

One approach to optimizing restoration of the American chestnut is to use computer programs to model the population growth and genetic effects of restoring plant populations in different ways. While restoration programs have been widely undertaken for a number of plant species, we lack the tools to analyze how factors like founder number and geometry of placement within a restoration habitat interact with varying founder or species life history characteristics, and whether these factors impact resultant population growth rates and preservation of genetic diversity. While ecological edge effects have been documented as being evident at the borders and edges of restoration preserves due to altered micro-environments in terms of wind-speeds, light availability and organismal composition among other factors (Primack, 2010), less is known about whether placement of founders at varying distances from the preserve edge impacts the population dynamics and genetic diversity measures of establishing populations. Further, can differing founder placement patterns interact with other life-history characteristics such as pollen and offspring dispersal distances to bring about different population growth rates and genetic diversity levels? Exploring these potential demographic and genetic edge effects in the field with *C. dentata* would not be feasible due to the costs associated with carrying out such experiments on a wide-scale to ensure statistical reliability of data, especially since blight-resistant individuals are expensive and time-consuming to produce, and thus must be used judiciously. In this case modeling virtual populations through computer simulations represents a more tractable alternative to field experiments, potentially providing valuable insight for restoration managers on how best to re-introduce the American chestnut into preserves.

In this study, the computer program NEWGARDEN (Rogstad & Pelikan, 2011) was used to model blight-resistant American chestnut population restoration in a virtual preserve to explore the population growth and genetic effects of placing founders at different distances from preserve borders under differing patterns of gene dispersal. Our null hypothesis is: Varying American chestnut founder placement at various diagonal distances from the preserve border, while altering offspring and pollen dispersal distances, will have no effect on population growth rates or retention of founding genetic diversity. We used comparative trials to examine the degree to which some patterns of introduction might be preferable over others.

2. Methods

We used NEWGARDEN to model the population growth and genetic diversity of newly establishing chestnut populations. This program simulates natural population development based on a set of user-specified initial input conditions (Rogstad & Pelikan, 2011). One set of input conditions constitutes a "trial" and input between trials may vary as to founder number and geometric patterning, preserve characteristics, and with regard to various life-history characteristics (see below). For each age (bout of mating with mates chosen randomly as conditioned by the input) of the developing population, NEWGARDEN provides output statistics (for each new cohort and for the entire population; only the latter are given here) concerning the population size, the number of founding alleles retained, heterozygosity (observed and expected), and F_{it} (a measure reflecting deviation from Hardy-Weinberg expectations due to subdivision and/or inbreeding; hereafter referred to as F

value). For each set of input trial conditions, the user can specify the number of replicate runs of those conditions to be used to calculate a mean and standard deviation for each of the listed output statistics. The user can thus compare whether means of statistics differ for populations of contrasting trials that differ in one or more input conditions.

2.1 Input parameters held constant

The input parameters common to all experimental runs are described following their order in the NEWGARDEN input file. These constant input parameters are based on population development data obtained from the only known chestnut restoration stand which is naturally developing at West Salem, Wisconsin (for details, see Pierson *et al.*, 2007; Rogstad & Pelikan, 2011).

2.1.1 The preserve grid system

Populations for all trials develop on a Cartesian grid system defined by the user. Individuals can only establish on grid points, the spacing of which represents the average minimum distance that can exist between reproductive trees. In our simulations, the grid system represents a restoration preserve (a 5 km x 5 km square), comprising a 1000 x 1000 grid point system with 5 m between grid points. This simple model represents an approximate average minimum distance spacing needed between two reproductive trees based on a mature chestnut community at the carrying capacity.

2.1.2 Loci and allelic variation

The ideal, non-inbred source population for the founders was set to have 30 loci per founder, each with 100 alleles of equal frequency (frequency = 0.01 per allele). NEWGARDEN randomly draws two alleles for each locus from the source population when creating a founder's genotype. In each new generation, every individual was censused for its allelic status at each of the 30 loci to generate the genetic diversity output statistics.

2.1.3 Mating system

All individuals are bisexual with 100% outcrossing.

2.1.4 Offspring production

The age-specific reproduction rate (r) specified in all input files (based on population development at West Salem) was held constant as shown in Table 1. In the intermediate years not defined, the rate of offspring production is linearly interpolated between the bounding age values. An established offspring does not reach reproductive age until its eighth year (Table 1). Offspring production is distributed across eligible reproducing individuals according to a Poisson distribution. As in natural settings, reproductive individuals may create multiple offspring, but all of these may not establish into saplings. Offspring counted in a generation's reproduction rate are potential recruits for establishment and growth at a grid point. The number of such potential recruits does not indicate the exact size of the newly established cohort for any particular age in one bout of mating. See mortality for ways in which potential offspring "die" or fail to establish in NEWGARDEN.

2.1.5 Age-specific pollen rate

For established individuals, the relative rate of serving as an eligible pollen donor that contributes pollen to a given mating is conditioned by its age according to Table 1. Pollen production is proportional relative to the highest value in the input. For the ages that are not specified by the input values, the pollen rate is linearly interpolated. Once NEWGARDEN selects an age-class and distance class (see below) for the pollen donor, one donor is chosen at random for a particular mating from the pool of eligible potential donors.

2.1.6 Mortality

Individuals can "die" in a number of different ways during a trial run. Death means that the individual is removed from the grid system and from further population processes and analyses. If the offspring is distributed outside of the defined preserve grid system, it automatically dies. An offspring will die in the event that it lands on a grid point that is already occupied by an individual that will survive to the next generation. When an ovule isn't pollinated since an eligible pollen donor is not within the range of the ovule producer, this counts as a reproductive event followed by immediate death of the potential offspring. If two or more offspring land at the same grid point, one is randomly chosen as the survivor with others deleted. Death of individuals is also age-dependent as specifiable by the user. For all trials here, age-specific probabilities of dying are given in Table 1. Ages without a specified risk of death are linearly interpolated between bounding values. In our trials, founders reach age 114, so there is a probability that several founders are still alive by the end of the trial run.

Age	Relative rate of reproduction	Relative rate of pollen provisioning	Percent mortality
0	0	0	0.3
1	0	0	0.2
4	0	0	0.1
5	0	0	
6	0	0.2	
7	0		0.05
8	0.02		
10	0.04	0.5	0.02
12	0.08		
17	0.2		
25		0.95	
70	1.3		
75	1.3	1.2	
115	1.3	1.16	0.02

Table 1. Input Parameters Held Constant. User specified age-specific input conditions for reproductive rate, pollen provisioning, and mortality used in all trials. Values not given were interpolated between the bounding values. See text for more details.

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2.1.7 Initial population

Aging of the population begins with the founders and it will continue to age until the specified number of generations is completed. 169 founders, this being approximately the minimum number of founders needed to capture > 95% of the source population alleles (Lawrence *et al.*, 1995; Chakraborty, 1993), of initial age 13 were used with founders located every other grid point in a 13 x 13 individual square (26 x 26 grid points). This simulates a 10 m distance between founders in a planting square 130 m on each side. This square of founders remained constant across all trials, although it was moved to different distances from the preserve borders.

2.1.8 Generations

Beginning with the founders, 100 bouts of reproduction (101 generations or ages including the founding generation) were conducted for each set of trial conditions. Output results in Figures 1 to 3 are reported for the entire population at each age. For the pollen and offspring dispersal distance comparison trials (Figures 4 to 6) only the results at the terminal age 100 are given.

2.1.9 Replicate runs

The output values reported are mean values calculated from 40 replicate runs for each set of trial input conditions. When trials are said to differ, we mean that reported generation mean values differ significantly (p value $\leq$ 0.05) unless otherwise stated. This convention is used rather than reporting each standard deviation and t-test results for all trial comparisons.

2.2 Variable input parameters

2.2.1 Region and founder placement

In the first series of comparative trials, the square of 169 founders was placed at increasing diagonal distances from the preserve border beginning with the founders at the lower left corner (trial a). Seed and pollen dispersal distances were held constant at 25% to or from each distance frame (see below) in this initial series. In a subsequent series of trials, the constant-sized founder square was likewise moved diagonally toward the center of the preserve while offspring and pollen dispersal distances differed in various combinations (Table 2).

2.2.2 Offspring dispersal distribution

Offspring dispersal on the grid system is based on a nested series of limiting frames called "distance frames". When an offspring is dispersed to a particular distance frame based on given probabilities, the lower and upper values of each frame define the limits of dispersal. For a given dispersal event, one point within the selected distance frame is chosen at random. The limits of the four frames used in our trials and their varying respective dispersal probabilities across trials are described in Table 2. In the "Basic Conditions" trials, offspring establishment was evenly divided to the four distance frames with 25% probability of dispersal to each frame. Modifications to the "basic" trial conditions to create alternate comparative trials are detailed in Table 2. We use the summary phrase "Offspring

less distant" to indicate restricted offspring dispersal (compared to the "Basic Conditions" trials) within 65 m of the parent (13 grid points), whereas in "Offspring least distant" trials, the majority of offspring dispersal was within 30 m (6 grid points) of the parent plant. The summary phrase "Offspring more distant" is used for the trials in which the greatest percentage of offspring were dispersed between distances 110 m to 1500m (22 to 300 grid points) from the parent plant (Nathan *et al.*, 2008; Jansen *et al.*, 2008).

2.2.3 Pollen transport distances

The "Basic Conditions" and "Offspring less/least/more distant" trials had equal probability of pollen dispersal from within each of the four distance frames (Table 2). Trial E has 90% of pollen dispersal limited to from within a 30 m frame of the producing individual. Trial F has 90% of pollen dispersed from 110 m to 1500 m (22 to 300 grid points) from the parent plant.

2.3 Output

Based on population characteristics developing from the initial input specifications, NEWGARDEN provides means for four statistical measures reported here: population size, mean number of founding alleles retained, observed heterozygosity, and F_{it} (or F value) calculated as:

$$F_{it} = 1 - H_{ob} / H_{ex} \qquad (1)$$

where H_{ob} equals observed heterozygosity (based on actual counts of heterozygous loci across all loci for all the individuals in the population) and H_{ex} equals the Hardy-Weinberg expected heterozygosity based on the allele frequencies across all loci in the entire population. In general, F_{it} increases as inbreeding and/or subdivision increase in the population and $F_{it} = 0$ in the absence of inbreeding. For the first series of trials (Figures 1 through 3) mean output values are reported for the total number of individuals in the population at the end of each age. For the second series of trials (Figures 4 through 6), values are given only for the total population after 100 bouts of mating.

3. Results

Under the "basic" conditions of offspring and pollen dispersal (25% to or from each frame respectively; see Table 2), mean population size increased with increasing diagonal distance of the standard square of 169 founders from the preserve corner (Figure 1). At age 100, founders situated at the corner (trial a) had the lowest mean population size (2,018 individuals), while the equally highest mean population sizes (approximately 7,000) were attained by populations with founders inset by 300, 400 and 500 grid points from the corner (trials d, e, and f, respectively). Even an inset distance of 100 grid points (ca. 500 m; trial b) increased the mean population size by 148%, compared to founders placed at the corner. The percent gain in population increase per unit inset distance declines as the inset distances increases beyond 100 grid points, only increasing by approximately 21% when inset distances increases from 100 to 200 grid points, and approximately 13% when inset distances increase from 200 to 300 grid points. Beyond 300 grid points the rise in mean population size was not statistically different.

		Frame dimensions (in grid points)							
		0-5		6-12		13-22		22-301	
		%Pollen	% Offspring	%Pollen	% Offspring	%Pollen	% Offspring	%Pollen	% Offspring
Trial Description	Trial	from	to	from	to	from	to	from	to
Basic conditions	A	25	25	25	25	25	25	25	25
Offspring less distant	B	25	60	25	30	25	4	25	6
Offspring least distant	C	25	90	25	5	25	3	25	2
Offspring more distant	D	25	2	25	3	25	15	25	80
Pollen less distant, Offspring more distant	E	90	2	5	3	3	15	2	80
Pollen more distant, Offspring least distant	F	2	90	3	5	15	3	80	2

Table 2. Percent offspring and pollen dispersed to or from each distance frame for NEWGARDEN trials described further in the text. Trials were otherwise identical.
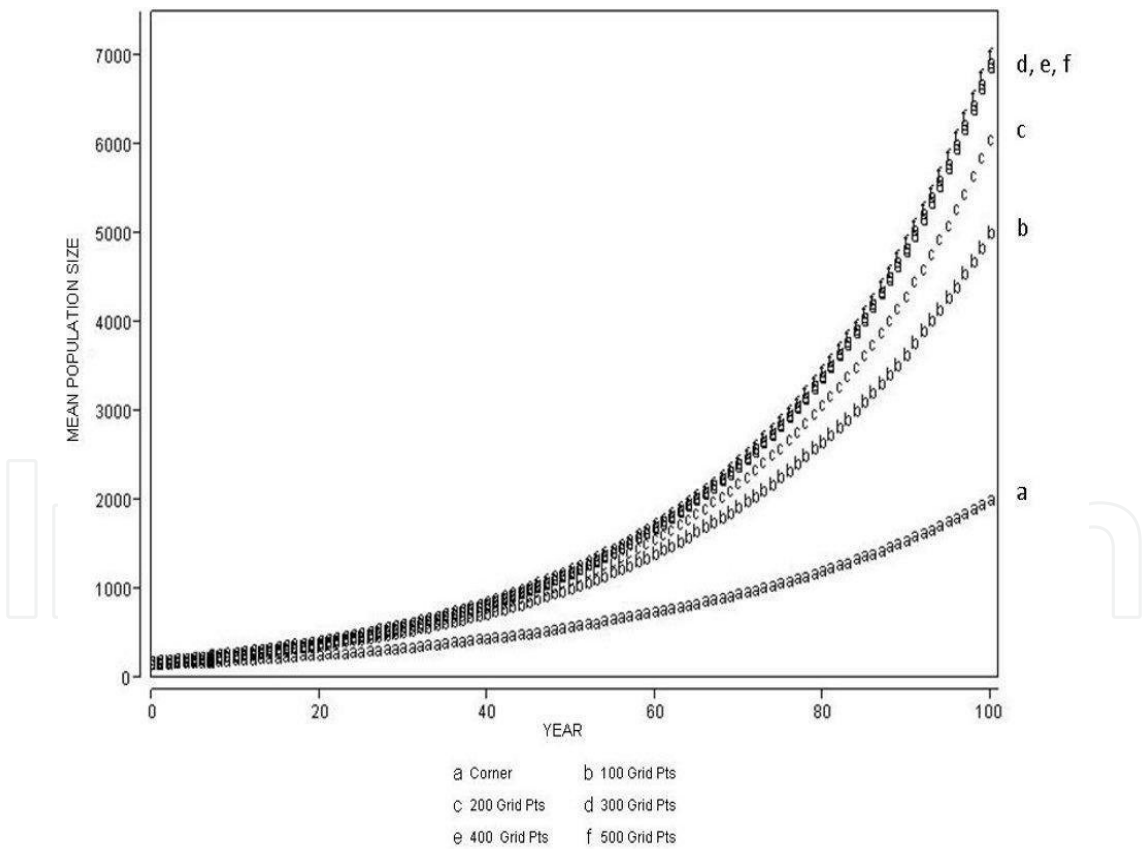
Fig. 1. Mean population sizes for each age of American chestnut populations founded at differing diagonal inset distances. These comparative trials span 101 generations at the basic offspring and pollen dispersal conditions (25% to and from each frame respectively). See text for more details.

Figure 2 shows the mean number of founding alleles retained across 101 generations for the trials depicted in Figure 1. In the source population, 3000 alleles each at frequency of 0.01, were available for the founding population. Drawing 169 founders, approximately 2900 alleles were present at founding (97% of the source population alleles; Figure 2). For example, imagine a restoration project where 1,690 trees are planted with 90% attrition prior to reproduction (e.g., Primack & Miao, 1992). On average such a population would have approximately 97% of the alleles in the original source population. NEWGARDEN can be used to estimate founding population sizes needed given the effects of attrition, to provide target numbers of individuals for establishing new populations or supplemention as needed.

For all populations, the number of alleles retained declined through generations, with populations founded at greater inset distances retaining higher numbers of alleles (Figure 2). The 169 founders were all aged 13 at the beginning of the trials, and given the mortality rate of 2% per generation (Table 1), approximately 22 founders should remain in populations after 100 bouts of mating. This suggests that a significant proportion of the total founding alleles remaining in the population at age 100 are carried by the descendents of founders that have died.

After 100 bouts of mating, there was approximately a 6% decline in number of founding alleles retained for populations inset at least 100 grid points or more (trials b, c, d, e and f), compared to the 9.6% decline seen for populations situated at the corner (trial a). At year 100, placing the founders 100 or more grid units inward from the corner produced a 3.8% (at the least; trials b through e) increase in alleles retained compared to placing the founders at the corner (trial a). The differences between various inset distances from 100 to 500 grid points (trials b through f) were not statistically different (although notice the trend). Variations of inset distances under basic dispersal conditions did not have significant or biologically meaningful effects on observed heterozygosity levels (ranging from 0.97 to 0.99) across generations, at basic dispersal conditions (data not shown).

There was little population subdivision and inbreeding observed across generations under basic dispersal conditions as founders were placed at greater inset distances (Figure 3). At year 100, F values increased slightly across generations, with the highest F values (almost 0.02) being reached by founders inset the furthest (by 500 grid points; trial f). F values tended to be lower for decreasing inset distances (e.g., trials a and b) at year 100. Although all trials are increasing in F, only by increasing the number of generations could it be determined the degree to which F values might become important (e.g., approach 0.05) in future generations.

Next, we ran a series of comparative trials varying not only in the inset distance of the square of 169 founders, but also altering the offspring and pollen dispersal conditions relative to the basic conditions (25% to or from each frame respectively) used in the trials just reviewed in Figures 1 through 3. We conducted this next trial series to investigate how differing types of gene dispersal might interact with founder distance from a border to affect population growth and genetic diversity.

Figure 4 shows population growth results (at population age 100 only) from these trials when both inset distances and dispersal conditions were varied. Trends observed here included increasing mean population sizes as inset distances increased from the corner to
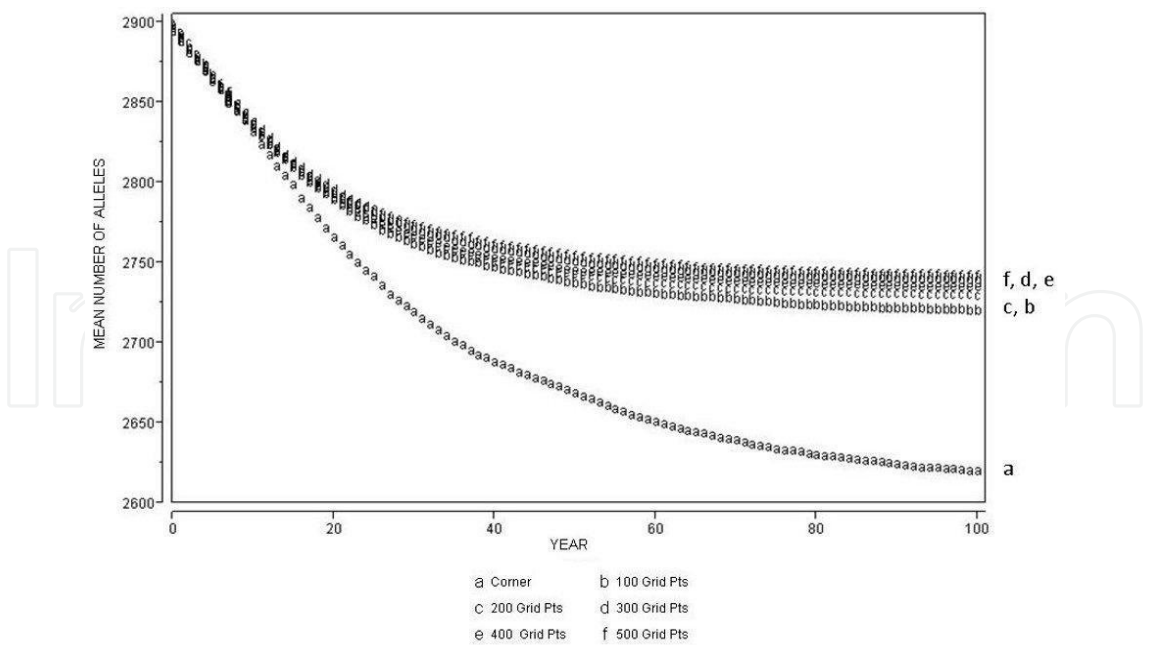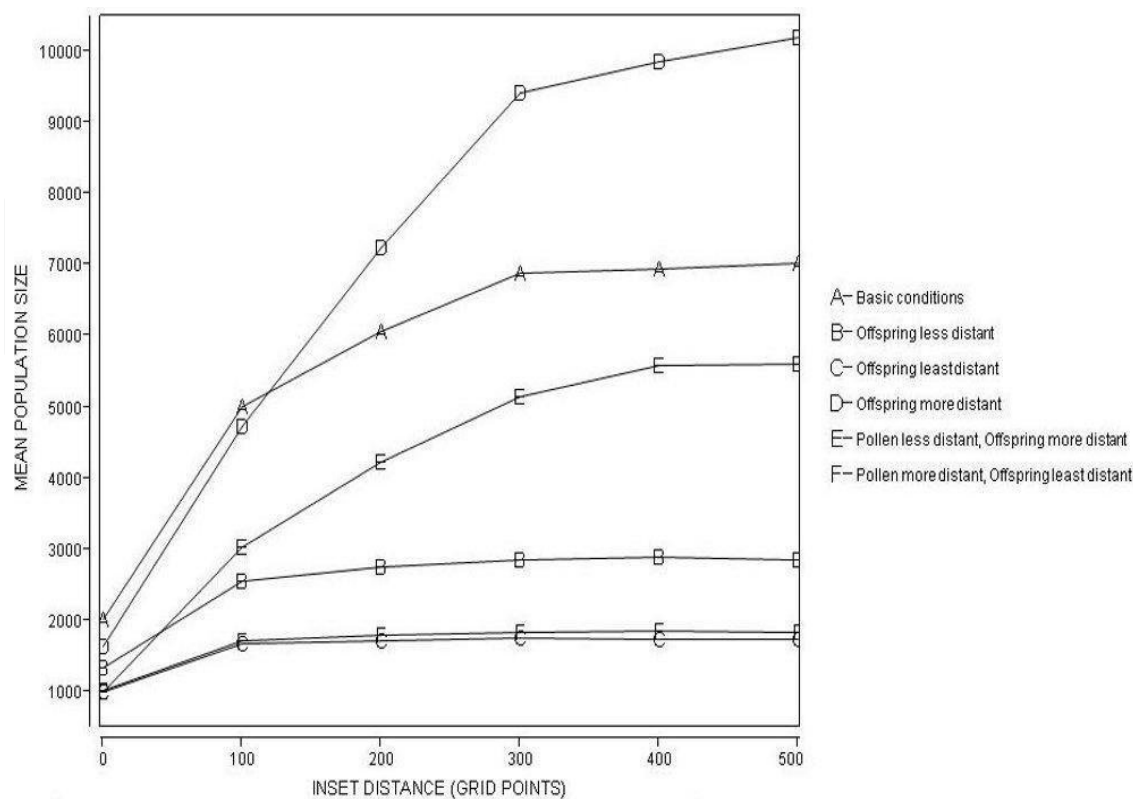
Fig. 4. Mean population size differences for comparative trial populations differing as to both founder inset distances (x-axis) and with greater or lower offspring and/or pollen dispersal distances (indicated by different letters A through F) relative to the "basic" dispersal conditions (see Table 2). Data points depict population size for each trial at age 100 only. In the trial condition summaries to the right of the graph, if a dispersule type (i.e., offspring versus pollen) is not mentioned, that dispersule disperses according to the basic conditions.

500 grid points for population D, up to 400 grid points (E), up to 300 grid points (A), and up to 100 grid points (B, C, and F). For populations B, C and F, increasing founder inset distance to 100 grid points from the corner raised mean population size significantly. However beyond 100 grid points, population sizes remained more or less constant across further increase in inset distances. If actual dispersal patterns match those in trials B, C, or F, a restoration manager will not gain higher rates of population growth by planting founders beyond 100 m into the preserve. Relative to the "basic" dispersal conditions trials just discussed in Figures 1 through 3 (trials marked A in Figure 4), altering offspring and pollen dispersal distances caused various but pronounced differences in rates of population growth. Trial D, with only the offspring dispersing to greater distances, was the only trial that exceeded trial A ("basic" conditions) at founder inset distances greater than 100 grid points. Trial D showed the greatest overall population growth compared to all trials at those inset distances.

For each set of trial conditions (A through F) the greatest allele loss occurred when founders were placed at the preserve corner (Figure 5). More alleles were retained under otherwise

constant trial conditions when founders were inset only 100 grid points although even further inset distances caused no further major increases in allele retention for trial conditions A, B, C, and F, while inset distances of 300 grid points were needed to maximize allele retention for trial conditions D and E. Considering all of these trial conditions, the greatest difference in the mean number of founding alleles retained is between trial E at the corner and trial D at 400 grid points (a 10.9% difference).
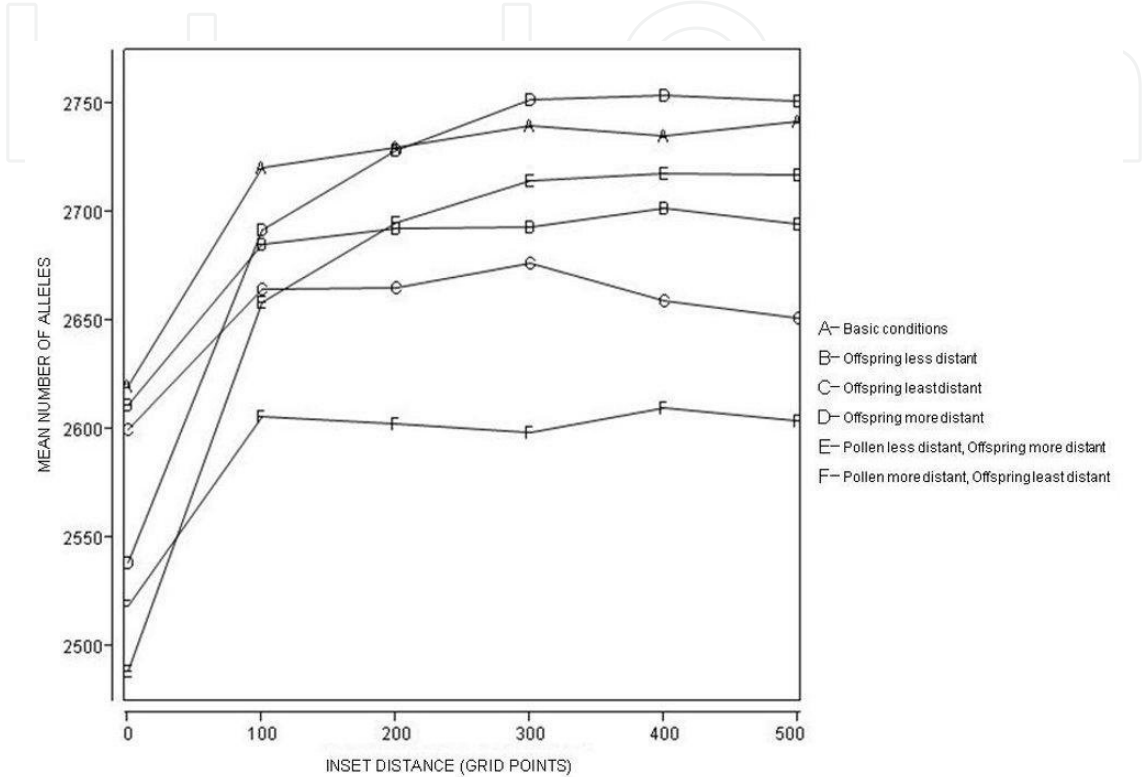

Fig. 5. Change in mean number of founding alleles retained in NEWGARDEN populations after 100 bouts of mating for trials depicted in Figure 4. Trial conditions differed with regard to both founder inset distance and offspring and pollen dispersal distances as indicated (see summaries for A through F to the right of the graph). Connected data points show alleles retained under one set of trial dispersal conditions when founders were placed at diagonally increasing distances from the preserve corner (x-axis). See text for more details.

Observed heterozygosity values for all trials after 100 mating bouts did not vary by a large amount (ranging from 0.967 to 0.980), showing only a 1.3% difference between the highest and lowest values. At generation 100 there was little population subdivision and inbreeding seen across trials with differing founder inset distances and various dispersal conditions (Figure 6). The highest F values were seen for populations under basic dispersal conditions (trial conditions A), followed by populations with offspring being dispersed less distantly (trial conditions B and C). Populations tended to have slightly greater F values at inset distances beyond 100 grid points, except for trial D, where offspring were more distantly dispersed (80% to the last frame) and trial F, where pollen was more distantly dispersed and offspring least distantly dispersed (80% from the last frame and 90% to the first frame, respectively).
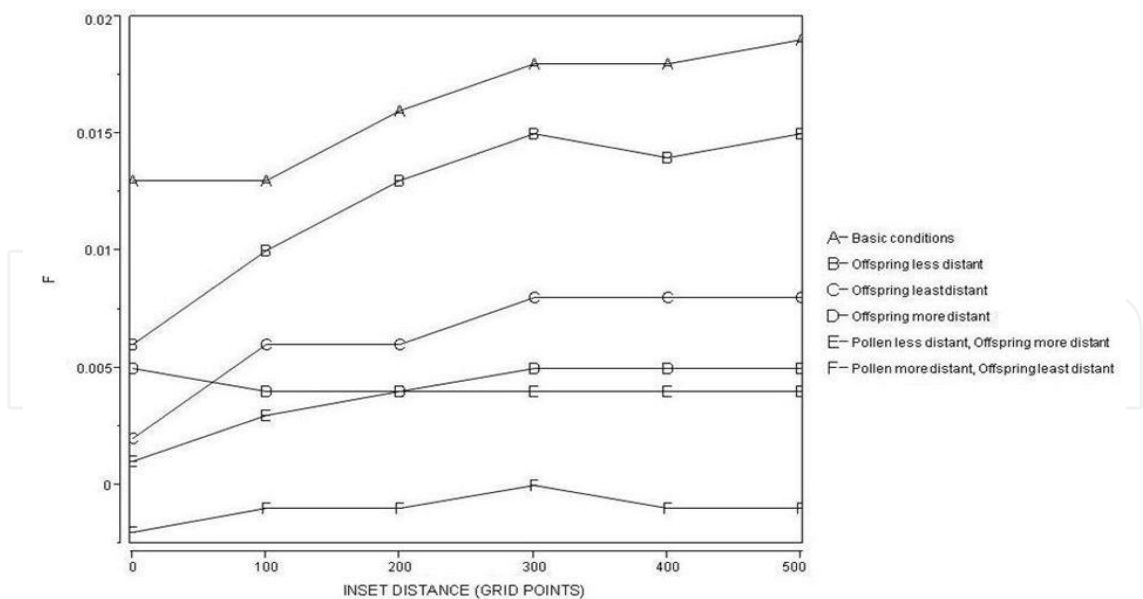
Fig. 6. Changes in F values in populations after 100 bouts of mating (the same populations shown in Figures 4 and 5). Trial conditions differed with regard to both founder inset distance and offspring and pollen dispersal distances as indicated (see summaries for A through F to the right of the graph). Connected data points show F values under one set of trial dispersal conditions when founders were placed at diagonally increasing distances from the preserve corner (x-axis). See text for more details.

4. Discussion

4.1 Practical applications

The null hypothesis that placing founders at differing distances from the edge of a restoration preserve will have no effect on subsequent population growth or genetic diversity was falsified according to results involving the first series trials with the basic dispersal conditions only (Figures 1 through 3). These results confirm that populations can manifest different degrees of population growth and genetic edge effects (Rogstad & Pelikan, 2011) depending on the distance of founders from preserve borders. In terms of population development, increases in growth rates were correlated with increasing distances of founder placement from a border up to a point: with the "basic" gene dispersal distances, planting founders 300 grid points (1500 m) into the preserve is as good as planting them 500 grid points (2500 m) into a 5 km x 5 km or larger preserve. Increasing founder placement up to 300 grid points increasingly allows founders a greater number of viable grid points to establish their offspring thereby reducing mortality levels. As for genetic diversity, the greatest loss of alleles occurred when founders were placed less than 100 grid units from the border (trial a, Figure 2). However, even at the corner, losses were not considerably greater than placing the founders 100 grid points into the preserve (corner trial a retained 90.4% while trial b retained 93.9% of the founding alleles). A preserve manager not interested in maximizing population growth but who only wants to maximize genetic diversity retention could thus plant the founders 100 grid points (500 m) into a 5 km x 5 km or larger preserve. Beyond that, planting further into the preserve does not significantly increase the number of founding alleles conserved. Differences in losses of

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genetic diversity as indicated by changes in observed heterozygosity or F values were not pronounced at age 100 among these trials, and thus are not of major concern to a restoration manager through the initial establishment period modeled.

The second series of trials in which offspring and pollen movement distances were varied in populations with founders placed at increasing distances from the border (Figures 4 through 6) demonstrate that population and genetic edge effects are further affected by variations in gene dispersal distances. Compared to the basic conditions used in Figures 1 through 3, population growth was increasingly reduced (Figure 4) when pollen dispersal was more restricted and offspring dispersal was more distant (trial E), when offspring dispersal was less distant but pollen dispersal matched the basic conditions (trial B), when pollen dispersal was more distant and offspring dispersal less distant (trial F), and when offspring dispersal was most restricted but pollen dispersal matched the basic conditions (trial C). Only when offspring establishment was more distant but pollen dispersal matched the basic conditions (trial D) did population growth exceed that exhibited when the basic dispersal condition applied (trial A). These results suggest that in restoration projects with conditions similar to those simulated here, large gains in population growth might be promoted by ensuring that more offspring establish at greater distances than are occurring naturally.

Differences in founding allele retention among this second series of trials were also evident (Figure 5), with the greatest retention in alleles being under the basic and offspring more distant dispersal conditions (trials A and D respectively). For trial conditions A, B, C, and F, there was a sharp increase in allele retention by moving founders from the corner inwards 100 m, after which further gains were not as pronounced to various degrees for different trial conditions at increasing distances. Under trial conditions E and D, placing founders at 300 grid points would be preferable since significant gains in allele retention were not had beyond that distance. Across all of these trials, the greatest difference in allele retention was 9.6% (between trial E founders at the corner and trial D founders inset by 400 grid points). Inbreeding and subdivision appear to attain the highest values under the basic dispersal conditions with founders inset into the preserve (Figure 6), although none of the values are yet approaching pronounced levels. Causes driving the minor differences seen in F values among trials are not always readily interpretable (e.g., note trials E versus F versus C).

Overall, the relationships among trial conditions, inset distance, population growth, genetic diversity retention, and inbreeding/subdivision can be complex and are not necessarily intuitive. Given this complexity, NEWGARDEN modeling can be used to suggest restoration management strategies. As noted earlier, restoration programs and management need to be as cost-efficient as possible. By understanding interactions between life-history characteristics of *C. dentata* and inset distance for founder establishment, program managers can estimate the best methods to minimize such costs. For example, results of this study suggest that planting and stewarding a limited number of founders (thousands at one location are not needed) at least 1500 m into a preserve and promoting successful offspring establishment beyond that which is occurring naturally, rather than expending that effort promoting establishment within the developing stand, is less costly and potentially more successful in terms of ease of population establishment and growth, maintenance, as well as retention of genetic diversity and avoidance of inbreeding and subdivision compared to other options. Managers may have to make cost-benefit decisions such as which is more important: saving funds by planting near a border, maintaining genetic diversity at the

sacrifice of maximizing population growth, or planting further into a preserve at greater expense. The results here stress the need for accurate knowledge of realized gene dispersal attributes (and of other life history attributes) in any modeling-derived restoration management planning. Lacking such information, restoration managers should preferably take the most conservative approach to restoration using as accurate estimations of life history characteristics as possible, in this case, planting the founders at least 1500 m from a border.

4.2 Evolutionary implications

Natural populations establish with varying numbers of founders (often low numbers), degrees of isolation, and geometry of founding. Interpopulation and interspecific life history variation compound the complexity of establishment events as indicated in trials here. The results above suggest that these factors can interact differentially among newly founded populations, and that even seemingly slight differences in initial conditions (e.g., just 500 m difference in founder placement) may have significant effects on the future trajectories of population growth and genetic diversity measures. NEWGARDEN can be used to explore this variation in theoretical and existing situations.

4.3 Further considerations

We emphasize that the results reported here were generated with a subset of the potential input conditions including constant input parameter values designed to simulate population development in the only known restoration population of chestnuts, the West Salem stand (Rogstad & Pelikan, 2011). However, conditions at other restoration sites will surely differ (e.g., density of competitors and rates-distances of establishment, age-specific offspring and pollen production, age-specific mortality rates, gene dispersal distances, etc.). Further, other species will often have drastically different conditions from those modeled here (e.g., short lived perennials or annuals, different densities, different gene dispersal patterns). Finally, the ecological niche will vary across species in ways that might affect geometric patterning (e.g., the section of a forest the species naturally inhabits: one species that would typically be found living on the outer regions of a forest would have different life history characteristics than a species that would inhabit the center part of that forest). NEWGARDEN can be used to explore such intra- and interspecific differences in the conditions of population establishment and development.

Previous studies (Rogstad & Pelikan, 2011) have indicated that differences in the geometric placement of founders (e.g., spacing between individuals; arranged in lines versus squares; founder subdivision into a series of smaller squares) can affect rates of population growth and genetic diversity maintenance. When planting a founding population, the simplest pattern is to plant trees in straight lines to make rectangular or square founder areas. In our experiments, the founders were established in a 13 x 13 square of individuals to be easily manipulated for each trial of varying inset distances. This square shape only allowed for one offspring to establish within the founding square between founding parents, which may not allow for higher rates of population growth in the first few years of reproduction if the offspring have limited dispersal. One question not addressed in our trials was whether or not varying geometry of founder establishment patterns (e.g., completely random founder locations, X-shaped lines, various straight lines, circles, or hollow squares) would affect

population growth and genetic diversity. Different establishment patterns may allow for a greater number of offspring to land in unoccupied grid points than in the square pattern used in the above trials, and possibly reduce the loss of genetic diversity. It is also possible that the geometric pattern of the founder establishment interacting with the inset distance would affect the overall population growth and maintenance of genetic diversity. Trial comparisons where geometry is varied in combination with distance from edges and dispersal distances are underway.

For the above trials, 169 founders were used based on previous studies (Lawrence *et al.*, 1995; Chakraborty, 1993) that suggest a minimum of approximately 172 founders is needed to capture the greatest majority of alleles from the source population while also minimizing reintroduction costs in restoration projects. NEWGARDEN could be used to further investigate what would be the minimal number of founders needed to minimize allele loss over generations under a range of conditions.

Since it is not possible to investigate differences in all input conditions *a priori*, NEWGARDEN modeling can also be used *a posteriori* to generate simulated populations reflecting conditions and population growth outcomes for stands that have already been established. Such simulations can then be used to evaluate the degree to which population growth and genetic diversity preservation could be improved by supplementations or manipulations of actual populations (e.g., planting more individuals, altering gene exchange distances via increased seed distribution, reducing mortality rates at certain life stages, etc.).

If the restoration program includes harvesting offspring to redistribute within the preserve or at new locations, where should the offspring be collected from? Samples could be taken in the immediate area surrounding the entire founding population. However, this might not be optimal due to travel distance into the preserve. It would be better to collect offspring closer to one edge of the preserve, minimizing travel distance. However, perhaps the farther in one direction the offspring are from the founders, the greater the risk of loss of genetic diversity and increased offspring subdivision. One area for further study would be to analyze cohort (not population) growth, heterozygosity and F values, and loss of genetic diversity in subregions that are at varying distances from the founders. This would allow restoration managers to determine how close to an edge they could collect offspring that would still retain the greatest genetic diversity for new plantings. The results of such experiments would also provide information on the erosion of genetic diversity over space and time in entire populations and the degree to which erosion might be localized.

5. Acknowledgements

6. References

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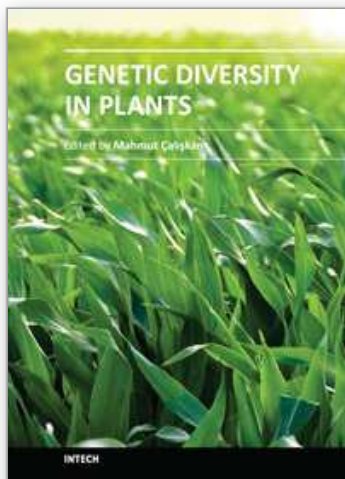
Genetic Diversity in Plants

Edited by Prof. Mahmut Caliskan

Genetic diversity is of fundamental importance in the continuity of a species as it provides the necessary adaptation to the prevailing biotic and abiotic environmental conditions, and enables change in the genetic composition to cope with changes in the environment. Genetic Diversity in Plants presents chapters revealing the magnitude of genetic variation existing in plant populations. The increasing availability of PCR-based molecular markers allows the detailed analyses and evaluation of genetic diversity in plants and also, the detection of genes influencing economically important traits. The purpose of the book is to provide a glimpse into the dynamic process of genetic variation by presenting the thoughts of scientists who are engaged in the generation of new ideas and techniques employed for the assessment of genetic diversity, often from very different perspectives. The book should prove useful to students, researchers, and experts in the area of conservation biology, genetic diversity, and molecular biology.

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