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TOWARD GUIDELINES FOR HARVEST INTENSITIES AND REGENERATION TARGETS WITH MINIMAL IMPACT UPON RETAINED GENETIC DIVERSITY IN CENTRAL HARDWOOD TREE SPECIES

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ABSTRACT.—There is an urgent need for a coordinated and systematic approach to the *in situ* conservation of the genetic resources of commercially important forest tree species in the Central Hardwoods. Effective *in situ* management of genetic resources would benefit from clear guidelines for how many adult trees can be harvested with minimal impact on allelic diversity. We are constructing a computer model for this purpose, and present preliminary results based upon replicate harvests of a virtual forest stand consisting of 200 adult trees. Our model explores how much regeneration is needed so that there is no more than a 10 percent risk of retaining less than 90 percent of the original allelic diversity. In the absence of regeneration, up to 55 percent of the adult trees can be harvested without exceeding the 10 percent risk level. At higher harvest intensities, locally-derived regeneration is needed to replace the alleles removed from the adult population. When all 200 adult trees are harvested, the 10 percent risk level is not exceeded if there are at least 116 regenerants, provided that these are derived from pre-harvest random mating among the adults. In the presence of substantial pollen flow from a genetically differentiated outside pollen source (*e.g.*, 10-20 percent pollen flow), the minimum amount of regeneration needed is reduced. This indicates that outside pollen can be more efficient, relative to pollen from within the stand, at replacing alleles lost from the adult population.

Genetic diversity of commercially important timber species is a critical resource that, in addition to providing a basis for tree improvement programs, is essential to tree species' future adaptive potential (Ledig 1988, 1992, Young and others 2000). However, in the Central Hardwood forest region, beyond the selection and breeding of elite trees for commercial purposes, it seems that scant attention has been paid to gene conservation in economically important forest tree species such as black walnut (*Juglans nigra* L.), northern red oak (*Quercus rubra* L.), or black cherry (*Prunus serotina* Ehrh.). Such tree species in the Central Hardwood region face a triple threat in regard to their genetic diversity. First, since European settlement, much of the formerly continuous forest in this region has been cleared for agriculture resulting in today's highly fragmented landscape (Hicks 1998). Second, in many of the remaining stands, the most valuable species have been subjected to repeated high grading, the targeted logging of phenotypically superior individuals (McGuire and others 1999). And third, shade intolerant species, such as those mentioned above, are exhibiting widespread recruitment failure, largely as a result of current management practices under which creation of large gaps is often avoided and fires are suppressed (Lorimer 1993). In the face of these mounting pressures on the genetic resources of Central Hardwood tree species, it would seem that the time is ripe for a coordinated and systematic approach to gene conservation in this region.

Gene conservation in trees is generally accomplished by a combination of *ex situ* and *in situ* approaches (Ledig 1988). *Ex situ* programs utilize seed stores, seed orchards, clone banks, and/or progeny or provenance tests (Lipow *et al.* 2002). *In situ* programs attempt to conserve genetic resources in their natural surroundings through management of native stands (Ledig 1988). *In situ* gene conservation is

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not necessarily incompatible with economic exploitation; it should be possible to adapt management practices to limit the potential deleterious impact of timber harvest upon local gene pools (Ledig 1988, Millar and Libby 1991). This could be achieved by ensuring that the regeneration of the tree species of interest is derived from local seed sources, preferably from pre-harvest matings (Glaubitz and others 2003b). Toward this end, guidelines for the amount of regeneration needed to minimize genetic diversity loss, depending on the intensity of harvest, are sorely needed (Jennings and others 2001). We are developing a computer simulation model to help provide such guidelines for Central Hardwood tree species, beginning with black walnut as a model. The key role that computer simulation models will play in forest tree conservation genetics has recently been emphasized by Boshier and Young (2000).

In this paper, we present results from our preliminary model, exploring the amount of regeneration needed in a forest stand to minimize the loss of genetic diversity caused by harvest, under the assumption that the regeneration was produced by pre-harvest random mating among the original adults. We also explore the modulating effect of pollen flow from a genetically differentiated outside pollen source, on either the allelic richness (the average number of alleles per locus; A_R) of the stand after harvest, or on the proportion of the alleles present in the original adult population that are retained (proportional allelic retention; PAR). We demonstrate that, in the presence of pollen flow, PAR is superior to A_R as a gauge of the immediate impact of harvest upon local genetic diversity.

Methods

General Scenario

We have modeled a genetically diverse forest tree population, consisting of 200 adult individuals of a single species, in which numerous replicate, partial harvests were performed. We will refer to this population as the *focus stand* or *focus population*. We have examined the potential genetic effects of harvesting on this focus stand, depending on the amount of surviving regeneration. In our current model, the regeneration population is produced prior to harvest via random mating among the adults, with varying amounts of pollen flow from an outside pollen source. In this scenario the regeneration could derive, in theory, from any or all of the following:

1. Advance regeneration that has not reached reproductive maturity,
2. A seed-bank of dispersed seed derived from pre-harvest matings, or
3. Seedlings grown from a representative seedlot collected from the focus stand prior to harvest.

Our simulation model treats the adult and regeneration populations in the focus stand as two discrete, non-overlapping generations.

Simulation Model Details

To explore the potential impacts of various harvest intensities on genetic diversity, we simulated genotypes at ten unlinked, Mendelian loci for two populations, the focus population and the outside pollen source. We wanted the focus population to have exactly 150 alleles in total, and the outside pollen source and focus population to have a Nei's genetic identity (Nei 1972) of 0.7 to 0.8. To obtain a pair of populations with these characteristics, we first generated a 'reference population' consisting of ten thousand individuals. This reference population started out completely monomorphic at all ten of the simulated loci, and then was allowed to evolve for one hundred thousand generations at constant size, under a 'k-alleles model' of mutation (KAM; Crow and Kimura 1970), with a mutation rate of 0.001 and a maximum number of alleles (k) of 60 at each locus. Each subsequent, non-overlapping generation was formed by random mating. From this large and highly genetically diverse reference population, a smaller population of 400 randomly-chosen individuals was founded and allowed to evolve via drift and mutation, again under random mating with KAM mutation, but with a tenfold lower mutation rate of 0.0001. This mutation rate was selected because it falls within the typical range observed at microsatellite loci (Whittaker and others 2003). After 45 generations, this population was split into two, namely, the focus population and the outside pollen source. These two populations were

each held at a constant size of 200 randomly mating individuals and allowed to drift independently (with mutation at the same rate of 0.0001) until the allelic richness in the focus population fell to exactly 15.0 (this required 14 generations of independent evolution).

In this manner, both the focus population and the outside pollen source had levels of genetic diversity and allele frequency distributions similar to what we have observed with microsatellite DNA markers[1] in a sample of 40 black walnut trees from a protected stand in the Hoosier National Forest, IN (data not shown). The degree of genetic similarity between the focus population and the outside pollen source was determined by the ratio of the number of generations that they co-evolved as one population versus the number of generations that they evolved independently: the numbers that we employed (45 and 14) resulted in a Nei's genetic identity (Nei 1972) between the two populations of 0.75.

With a focus population and outside pollen source in hand, the next step in our simulation was to perform numerous replicate harvests under a range of values of the following three parameters:

1. The proportion of the adults harvested from the focus stand,
2. The number of surviving regenerants, and
3. The proportional contribution of pollen from the outside pollen source.

The regeneration population was formed by random mating among the adult population in the focus stand prior to harvest, with pollen gametes contributed via Mendelian inheritance from randomly selected individuals from the outside pollen source according to the desired rate of gene flow via pollen. There was no gene flow from outside via seed. Also, there was no mutation during the formation of the regeneration.

For each replicate, the allelic richness (total number of alleles; A_R) relative to the original focus population of 200 adult trees was calculated for the combined population of regeneration and surviving adults. In addition to the relative allelic richness, the 'proportional allelic retention' (PAR) was also calculated, again relative to the original focus population of 200 adults. PAR measures the proportion of the alleles present in the original focus population of 200 adults that, after harvest, were still present in at least one copy in the combined population of regeneration and surviving adults. Note that in a closed system, with no gene flow via pollen or seed from outside the stand, relative A_R after harvest and PAR after harvest will be identical.

Our first objective was to show the response surface of relative A_R over the full range of harvest intensities (*i.e.*, from 0 to 100 percent harvest) with varying amounts of surviving regeneration (from 0 to 200 regenerants), in the absence of gene flow from outside the focus stand (fig. 1). Here, for each unique combination of the two parameters, harvest intensity and number of regenerants, we plotted the average relative A_R based on one thousand replicate harvests. We examined intervals of harvest intensity and number of regenerants of 1 percent and one regenerant, respectively (*i.e.*, $101 \times 201 \times 1{,}000 = 20{,}301{,}000$ simulated harvests in total for Figure 1).

Our next objective was to examine the effects of pollen flow on the minimum amount of surviving regeneration needed so that there would be no more than a 10 percent risk either of reducing allelic richness by more than 10 percent, or of retaining less than 90 percent of the alleles present in the original focus population. We examined levels of pollen flow from the outside pollen source of 0, 1, 2, 5, 10 or 20 percent. The minimum amount of regeneration needed was determined for harvest intensity levels varying from 0 to 100 percent, at 5 percent intervals. For this purpose, we developed a 'contour-finding' algorithm which we ran for each level of pollen flow, and for relative A_R and PAR

[1]Microsatellite DNA markers are commonly used genetic markers consisting of tandem repeats of a simple sequence motif (*e.g.*, CACACACACA…). Such markers usually have numerous alleles differing in their repeat number (*e.g.*, CA_{10} vs. CA_{13}).

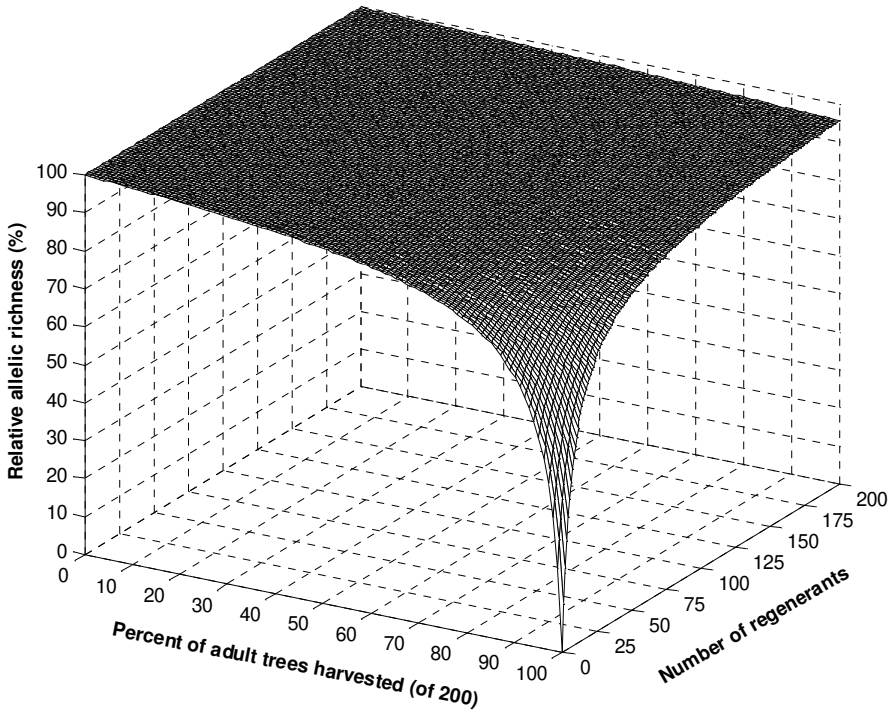

Figure 1.—Effects of harvest intensity and amount of regeneration on retained allelic diversity in a simulated, randomly mating forest tree population, in the absence of pollen flow from outside. Mean allelic richness (relative to the original adult population) is plotted based on 1000 replicate harvests.

separately. Ten thousand replicate harvests were performed for each unique combination of harvest intensity and amount of regeneration examined by our algorithm. Depending upon our purpose, either relative A_R or the PAR in the combined regeneration and surviving adult population was calculated for each replicate, and the resulting distribution of outcomes was then sorted from lowest to highest. The tenth percentile (*i.e.*, the one thousandth observation) was taken to represent the level of relative A_R (or PAR) corresponding to 10 percent risk; in other words, there was no greater than 10 percent risk that A_R (or PAR) would fall below that level, for that particular combination of harvest intensity and amount of regeneration.

Our 'contour-finding' algorithm began at 0 percent harvest and zero progeny (relative A_R or PAR of 100 percent, by definition), and then successively increased the harvest intensity by 5 percent, until the relative A_R (or the PAR) at the 10 percent risk level fell below 90 percent. At this point, the number of regenerants was successively increased by one until the relative A_R (or the PAR) at the 10 percent risk level either equaled or surpassed 90 percent. Once this occurred, the harvest intensity was again increased by 5 percent, and the number of regenerants (starting from the last value taken at the previous harvest intensity) was again successively increased by one until the relative A_R (or the PAR) at the 10 percent risk level again either equaled or surpassed 90 percent. At each level of harvest intensity, the minimum number of regenerants needed for no greater than a 10 percent risk of reducing A_R (or the PAR) by more than 10 percent was recorded. This process was repeated until, finally, the minimum number of regenerants was determined for a 100 percent harvest of all 200 adult trees in the focus stand.

Our simulation was written in the programming language C++, and carried out on PC computer running Microsoft Windows 2000.

Results

The response surface of the average (or 'expected') value of relative A_R, over the full range of harvest intensities, with varying amounts of surviving regeneration, and in the absence of gene flow from outside the focus stand, is shown in Figure 1. The 100 percent reference point for relative A_R lies at 0 percent harvest and no regeneration, and is equivalent to the A_R in the original focus stand of 200 trees

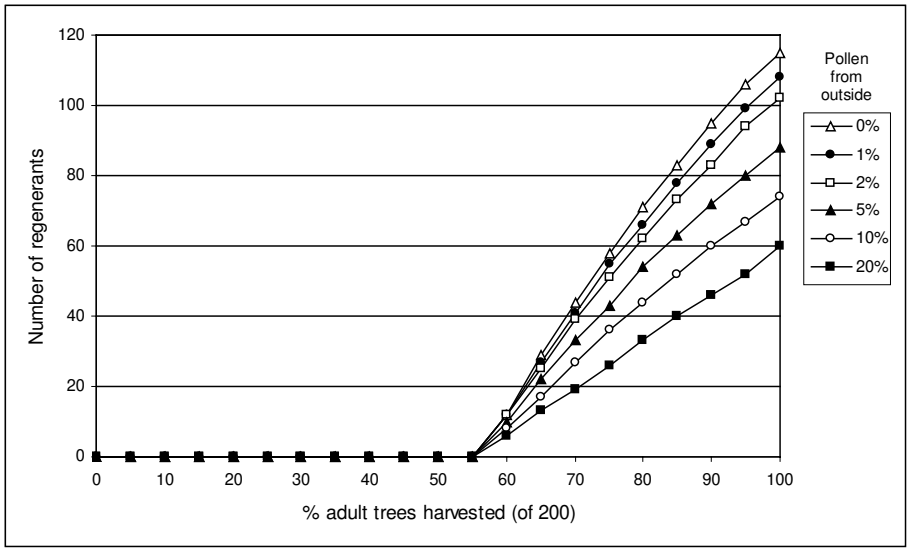

Figure 2.—The minimum number of regenerants required for no more than a 10 percent risk of reducing allelic richness by more than 10 percent. The effects of various levels of pollen flow from a genetically differentiated outside pollen source are shown.

prior to regeneration or harvest. When no adults are harvested, relative A_R does not rise with increasing numbers of regenerants, but, since there is no pollen flow from outside in this scenario, instead stays constant at 100 percent (note that, if there was pollen flow from a genetically differentiated outside pollen source, relative A_R would rise gradually with increasing numbers of regenerants). With increasing harvest intensity, A_R in the remaining trees is reduced, but this reduction does not become 'drastic' until high harvest intensities (*i.e.*, greater than 70 percent) in combination with low numbers of regenerants (*i.e.*, less than 75). Beyond this, A_R drops off dramatically. Obviously, at 100 percent harvest with no regeneration, relative A_R is zero. With 200 regenerants and 100 percent harvest, there is a slight reduction in expected A_R, in accordance with population genetic theory regarding genetic drift in finite populations (Hartl and Clark 1997). Overall, the results shown in Figure 1 suggest that there is a broad range of harvest intensities and amounts of regeneration over which there will only be a relatively mild impact upon the allelic diversity in a randomly mating forest tree population.

Each point in Figure 1 represents an *average* A_R based upon one thousand replicate harvests. However, it may be more pertinent for forest managers to consider gene conservation in a risk management context (Namkoong 1999). A forest manager or policy maker may wish to decide upon a target level of genetic diversity to conserve, and then set a maximum level of risk of falling short of this target. For the purposes of this study, we have chosen 90 percent of the allelic diversity in the original adult stand as the target level to conserve, and 10 percent as the acceptable level of risk of falling below this target.

To this effect, Figure 2 plots the minimum number of regenerants required to maintain a 10 percent or lower risk of reducing A_R by more than 10 percent, over the full range of harvest intensities (zero to 100 percent harvest). This relationship is shown for various levels of pollen flow from the genetically differentiated outside pollen source. In general, the risk level deceases as you move towards the upper left hand corner of Figure 2 (less harvest and more regeneration), and increases as you move towards the lower right (more harvest and less regeneration). The figure shows that, in the absence of regeneration, up to 55 percent of the adults can be harvested without exceeding the 10 percent risk level. Note that up to this point (55 percent harvest) the level of pollen flow from the outside stand is irrelevant.

Relative to the curve for 0 percent pollen flow in Figure 2, pollen from the genetically differentiated outside pollen source clearly has a marked effect, with as little as 1 percent pollen flow causing a discernable reduction in the amount of regeneration needed. When outside pollen flow is 20 percent,

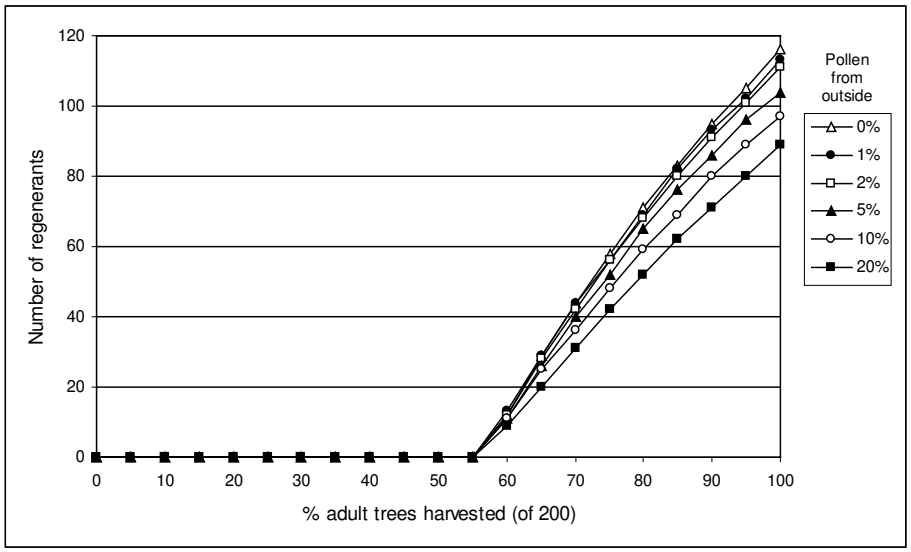

Figure 3.—The minimum number of regenerants required for no more than a 10 percent risk of retaining less than 90 percent of the alleles present in the original adult population. The effects of various levels of pollen flow from a genetically differentiated outside pollen source are shown.

the amount of regeneration needed to maintain relative A_R at 90 percent after all of the adults are harvested is nearly halved. This effect is primarily due to the novel alleles that are introduced to the focus population via pollen flow. This illustrates the limitation of using A_R as a sole measure by which to gauge the genetic effects of forest management. Allelic richness a non-discriminating measure, since it merely takes into account the number of alleles, but not their identity (Glaubitz 2003a, 2003b). If the outside pollen source was highly divergent (*e.g.*, an 'exotic' plantation) it is conceivable that, under high levels of pollen flow, relative A_R could be maintained or even substantially increased, concomitant with loss of a large proportion of the alleles present in the original adult stand.

For this reason, we also plotted the minimum number of regenerants required to maintain a 10 percent or lower risk of reducing the *proportional allelic retention* (PAR; defined above) by more than 10 percent, for various levels of pollen flow from the outside pollen source (fig. 3). With PAR, in contrast to A_R, 'novel' or 'foreign' alleles introduced via pollen flow from outside do not contribute. Since in a closed system (without outside pollen flow), A_R and PAR are identical, the lines for 0 percent outside pollen in Figures 2 and 3 are equivalent. However, when PAR is used (fig. 3), pollen flow from outside has a much weaker reducing effect on the amount of regeneration needed, as compared to using A_R (fig. 2). In Figure 3, a low level of pollen flow (*i.e.*, 1 or 2 percent) has an inconsequential effect. However, the reducing effect of 20 percent outside pollen on the amount of regeneration needed is still substantial. For example, when all of the adult trees are harvested, only 89 regenerants are needed with 20 percent pollen flow versus 116 with 0 percent pollen flow. This reduction indicates that pollen from the outside source is more efficient, relative to that from inside the stand, at replacing alleles that have been removed from the adult portion of the focus stand by harvesting.

Discussion

One purpose of this paper was to demonstrate the superiority of proportional allelic retention (PAR) over allelic richness (A_R) as a measure of the amount of allelic diversity conserved in a forest tree population after harvest. The weakness of A_R is that it does not take into consideration the identity of alleles; with this measure, alleles lost due to harvest of the adults can be compensated for by the gain of 'foreign' or 'exotic' alleles via gene flow from outside. This is not the case with PAR; here outside pollen flow can only contribute to the retention of allelic diversity via replacement of the actual alleles lost from the adults via harvest. The contrast in the two measures can be seen by comparing Figures 2 and 3.

Through the use of PAR, we have demonstrated that pollen from a genetically differentiated outside pollen source can be more efficient than pollen from within the stand at replacing alleles removed from the adult population by harvest, even when the regeneration has been derived from pre-harvest matings. In order to explain this seemingly paradoxical effect, we must first note that it is the low frequency alleles that are most likely to be lost due to partial harvest (Buchert and others 1997, Glaubitz 2003a, Glaubitz 2003b). Furthermore, if the outside pollen source is somewhat genetically differentiated from the focus population, then, among the set of alleles that are *rare in the focus population*, there will likely be a subset that are *more common in the outside pollen source*. It is these alleles that will be more efficiently replaced by pollen from outside relative to pollen from within the stand. If this is the case, then we would expect the level of outside pollen to have a 'diminishing returns' effect: once all the alleles in this class have been replaced, then additional pollen from the outside source will have no further reducing effect on the amount of regeneration required to obtain a PAR of 90 percent or more. If we allow even higher levels of pollen flow from outside (up to 100 percent) we find that this is indeed the case, with the maximum reducing effect nearly obtained at 40 percent pollen flow (results not shown).

With high levels of pollen flow from outside, a potential deleterious side effect accompanying more efficient allelic replacement might be the influx of a large number of foreign alleles into the stand. The magnitude of this effect will be reflected in the difference between relative A_R and PAR, with a large difference indicating influx of a large number of foreign alleles. It is difficult to say whether this would be detrimental or not from a conservation genetic standpoint, since preserving 90 percent of the original alleles found in the adult stand while adding additional alleles via pollen flow may actually enhance the adaptive potential of the focus population. If our goal is to preserve natural processes, then it would depend on the level of gene flow that would naturally occur in the absence of human disturbance or management. More empirical data is needed on this, particularly in the Central Hardwoods; we are currently gathering such data in our empirical studies of black walnut. Clearly, a large influx of foreign alleles from an *exotic* pollen source, such as a plantation derived from non-local germplasm, would be detrimental to gene conservation.

We will use the empirical data that we are gathering from black walnut using microsatellite DNA markers to help refine the basic computer simulation model that we have presented here, in order to make it more realistic. Refinements that we plan to incorporate include the following:

1. The influence of spatial position, wind direction, crown size and reproductive phenology on pollination success.
2. The influence of spatial proximity to gaps and gap size on female reproductive success.
3. The genetic distance to likely outside pollen sources (both 'natural' and plantation-based), and
4. The effect of alternative harvest practices and/or seed collection strategies, including consideration of the timing of harvest relative to reproduction.

It should be noted, however, that recent empirical data that we have collected from black walnut indicate that our basic assumption of random mating represents a reasonable first approximation. Based upon a sample of 89 black walnuts from two adjacent fragments in Carroll County, IN, we obtained an estimate of the panmictic index (F_{IS}) of -0.0042 across 15 microsatellite loci. This is very close to an F_{IS} value of zero, indicating random-mating genotypic proportions.

We eventually hope to use our model to project further into the future, accounting for overlapping generations, and larger spatial scales. Projection into the future may best be achieved by coupling our genetic model with succession-based models predicting future stand demography in relation to varying management practices (Porte and Bartelink 2002).

One potential application of the results of this study (and future extensions thereof) would be for the effective management of Genetic Resource Management Units (GRMU's; Ledig 1988, Millar and Libby 1991). The concept of GMRU's is to allow some level of timber extraction via partial logging, provided that this does not interfere with the overarching goal of conserving the local genetic resources

in situ. Future refinements of the basic model that we have presented here could lead to guidelines on what level of harvest would be appropriate in a GRMU, in relation to the target amount of allelic diversity to conserve and the acceptable level of risk, given the amount of regeneration expected to survive to maturity. Although GRMU's have not been adopted in the Central Hardwoods, considering the commercial value of many of our fine hardwood species, and the high levels of fragmentation, human disturbance and high-grading that have occurred in large portions of this region, the establishment of GRMU's for important timber species in the Central Hardwoods seems long overdue.

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Literature Cited

Boshier, D.H.; Young, A.G. 2000. **Forest conservation genetics: limitations and future directions.** In: Young, A.; Boshier, D.; Boyle, T. Forest conservation genetics: principles and practice. New York, NY: CABI Publishing. pp. 289-297.

Buchert, G.P.; Rajora, O.P.; Hood, J.V.; Dancik, B.P. 1997. **Effects of harvesting on genetic diversity in old-growth eastern white pine in Ontario, Canada.** Conservation Biology 11(3): 747-758.

Crow, J.F.; Kimura, M. 1970. **An introduction to population genetics theory.** New York, NY: Harper and Row. 591 p.

Glaubitz, J.C.; Murrell, J.C.; Moran, G.F. 2003a. **Effects of native forest regeneration practices on genetic diversity in *Eucalyptus consideniana*.** Theoretical and Applied Genetics 107(3): 422-431.

Glaubitz, J.C.; Wu, H.; Moran, G.F. 2003b. **Impacts of silviculture on genetic diversity in the native forest species *Eucalyptus sieberi*.** Conservation Genetics 4(3): 275-287.

Hartl, D.L.; Clark, A.G. 1997. **Principles of population genetics (third edition).** Sunderland, MA: Sinauer Associates, Inc. 542 p.

Hicks, R.R., Jr. 1998. **Ecology and Management of Central Hardwood Forests.** New York, NY: John Wiley and Sons, Inc. 412 p.

Jennings, S.B.; Brown, N.D.; Boshier, D.H.; Whitmore, T.C.; Lopes, J. do C. A. 2001. **Ecology provides a pragmatic solution to the maintenance of genetic diversity in sustainably managed tropical rain forests.** Forest Ecology and Management 154(1-2): 1-10.

Ledig, F.T. 1988. **The conservation of diversity in forest trees: why and how should genes be conserved?** BioScience 38(7): 471-479.

Ledig, F.T. 1992. **Human impacts on genetic diversity in forest ecosystems.** Oikos 63(1): 87-108.

Lipow, S.R.; St. Clair, J.B.; Johnson, G.R. 2002. ***Ex situ* gene conservation for conifers in the Pacific Northwest.** Gen. Tech. Rep. PNW-GTR-528. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station: 53 p.

Lorimer, C.G. 1993. **Causes of the oak regeneration problem.** In Loftis, D.L.; McGee, C.E., eds. Oak regeneration: serious problems, practical recommendations. Gen. Tech. Rep. SE-84. Knoxville, TN: U.S. Department of Agriculture, Forest Service, Southeastern Research Station: 14-39.

McGuire, M.; Stevens, J.; Potter-Witter, K. 1999. **Assessing scarcity of the north central veneer log resource.** Northern Journal of Applied Forestry 16(3): 160-166.

Millar, C.I.; Libby, W.J. 1991. **Strategies for conserving clinal, ecotypic, and disjunct population diversity in widespread species.** In: Falk, D.A.; Holsinger, K.E., eds. Genetics and conservation of rare plants. New York, NY: Oxford University Press. pp. 149-170.

Namkoong, G. 1999. **Genetic conservation strategies: who needs data?** In: Matyas, Cs., ed. Forest genetics and sustainability. Dordrecht, The Netherlands: Kluwer Academic Publishers, pp. 211-216.

Nei, M. 1972. **Genetic distance between populations.** American Naturalist 106(949): 283-292.

Porte, A.; Bartelink, H.H. 2002. **Modelling mixed forest growth: a review of models for forest management.** Ecological Modelling 150(1-2): 141-188.

Whittaker, J.C.; Harbord, R.M.; Boxall, N.; Mackay, I.; Dawson, G.; Sibly, R.M. 2003. **Likelihood-based estimation of microsatellite mutation rates.** Genetics 164(2): 781-787.

Young, A.; Boshier, D.; Boyle, T. 2000. **Forest conservation genetics: principles and practice.** New York, NY: CABI Publishing. 352 p.