NATGEN: AN APPLICATION OF GENETIC PRINCIPLES TO NATURAL REGENERATION

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Abstract.--The utility of PC-based computer simulation holds promise as an effective tool for answering questions about genetic diversity in forest tree species. NATGEN is a prototype educational software package that combines management objectives, silvicultural prescriptions, diameter growth projections, and genetic parameters for one quantitative trait. The targeted species during development was northern red oak (Quercus rubra L.). Preliminary results of repeated diameter limit cutting (18 inches and above) for a population of size 100, indicated changes in desirable gene frequencies from 0.5 to 0.01, by 560 years (six rotations). Changes in gene frequencies were mitigated when population size was increased to 600 and advanced regeneration was considered in the model. Cutting from below was one method that maintained desirable gene frequencies around 0.5. Once desirable gene frequencies approach zero, the prototype demonstrates that larger tree diameters cannot be attained by merely extending rotation ages and/or skipping cutting cycles.

Keywords: Ouercus rubra L., genetic diversity, natural regeneration, simulation.

INTRODUCTION

A joint effort between U.S.F.S. Eastern Region (Region 9) and N.C. Experiment Station was initiated in 1989 to address the need to understand genetic changes in naturally regenerated forest tree populations, with particular emphasis on northern red oak. This need arises from the fact that over 75 percent of harvested forest lands in Region 9 are naturally regenerated (Murphy and Kang, 1989).

Historically, silviculturists and forest managers have influenced genetic properties of naturally regenerated populations without much input from geneticists. A common precept among geneticists has been avoidance of dysgenic practices such as high grading and diameter limit cutting (Synder 1972).

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Defining an undesirable/acceptable level of loss/gain has proven to be frustrating. Limited efforts have been made to determine the changes in genetic quality of stands due to silvicultural treatments, and have generated conflicting results. Wilusz and Giertych (1974) and Yazdani et al. (1985) concluded that certain silvicultural practices significantly influenced the genetic quality of stands, while Neale (1985) and Pitcher (1982) suggested otherwise. Such conflict may be attributed to three causes: (1) local environmental conditions among experiments, (2) varying experimental designs, and (3) statistical significance was the only means of assigning the importance of the observed values.

This inability to clearly define dysgenic practices does not imply that we lack useful genetic principles and/or techniques. These difficulties primarily arise from the limited field information, which is necessary to transform currently available genetic principles into management prescriptions. Communication among researchers and land managers can be enhanced through the use of educational software and decision models.

NATGEN was developed as a visual training tool to provide an appreciation of the potential genetic changes in Lake States' northern red oak following vegetation manipulations. The attractiveness of NATGEN is that the user has fingertip access to information on genetics, regeneration, and growth and can readily "see" the results of specific management practices on a tree population via the computer screen, rather than waiting several years to see the effects of their actions on the ground.

In order for non-geneticists to benefit from this educational software, the model was developed from a silviculturist's point of view. Given what is known in the literature about the genetics of hardwoods, the trait of interest to execute prescriptions and monitor genetic response is tree diameter at breast height (DBH), as compared to modeling height growth.

NATGEN aids the user in evaluating the consequences of silvicultural prescriptions such as high-grading, thinning from below, or thinning from above, by diameter classes. Additional development is on-going to incorporate individual-tree selection into the model.

METHODS

NATGEN was developed using Borland C++ version 2.0. Version 1.0 models a second-growth stand of northern red oak. The first prototype had a population size of 100 trees. The maximum number of trees for the full model is 600, at 20-foot spacing, on six acres. Each individual phenotype is made up of three components: genotype, environmental deviate and site value. No genotype-by-environment interaction term is considered.

The genetic component is stochastically determined using a random number subroutine, characterized by an additive gene model, with one quantitative trait with five loci, and two genes (A and a) at each locus (Mahalovich 1990). Default gene frequencies are set to 0.5 ; however, the user has the flexibility of altering these frequencies. Genetic values for the following gene combinations at a locus are: AA=2, Aa=1, and aa=0. Individual genotypes are the sums of the five-locus genotypic values.

The user can either choose a default individual tree heritability of 0.2, an average value for tree diameter, or pick another value between 0 and 1. Thereafter, heritabilities change relative to the silvicultural prescriptions selected and the number of individuals following regeneration. Procedures for determining total genetic, phenotypic, and environmental variance follow Mahalovich (1990).

The site value component, is unique, in that some form of "mapping" individuals to the computer screen was needed to carry out management objectives and silvicultural prescriptions from a two-dimensional bird's eye view. Site values can be considered as a "fixed" environmental component of the phenotype.

Users may choose one of two environmental sites. The extreme site values range from 0.0 to 2.0 (no units, variance = 0.15), with a pattern resembling a mixed terrain contour map. The more uniform site values range from 0.1 to 1.0 (no units, variance = 0.04), with a pattern resembling a gentle slope. Site values were selected to serve the purpose of mapping individuals to the screen, but so as not to "wash out" heritability. In other words, an initial heritability with the site values considered as part of the total phenotypic variance had to be within 1% of an initial heritability without site values.

Phenotypic scores are translated into a normal diameter distribution based on an initial age of 80 years (Gevorkiantz and Scholz 1948 and McGill et al. 1991), characterizing a second-growth stand. Tree diameters, represented by varying circle widths, are displayed on a grid corresponding to their site value location.

Cutting/growing intervals are set at a minimum of 20-year intervals, based on Clark and Watt (1971), who reported both damage in advanced oak reproduction during logging and increased mortality following sudden sun exposure, when entry cycles were too frequent. The maximum number of intervals modeled for N=600 is 200 years (i.e., if a tree at initiation (age 80) remained uncut throughout the simulation, it would be 280 years of age upon exiting the program).

Following harvesting by three-inch diameter classes, the user may choose to regenerate trees by a seed tree method (only uncut, reproductively mature trees are parents for the progeny population) or by considering advanced regeneration (reproductively mature trees before and after harvesting are considered as parents for producing the next progeny population). Reproductive maturity in Lake States' northern red oak is defined as a mininimum DBH of 10 inches, and a range of 50 to 120 years of age (Mr. Dick Cutler, USDA Forest Service, Nicolet National Forest, Rhinelander, WI, personal communication). Comparisons of total tree number to total number of reproductively mature trees conveys the concept of effective population size.

Diameter growth projection follows the harvest and regeneration modules. Lake States' TWIGS equations (Miner et al. 1988, Brand 1981) are most reliable for individuals not exceeding 120 years of age. Diameter growth projection is constrained to a maximum age of 150 years.

Version 1.0 is a prototype educational software package, which is presently being tailored to address research objectives. Such applications require replication to determine an average response to a given silvicultural prescription. Problems arise however, when more than one factor is varied among cutting cycles, which then limits the user to the results of one replication.

RESULTS AND DISCUSSION

NATGEN as an Educational Tool

The large population model, N = 600 and five loci, is designed to give each user the flexibility of making consistent prescriptions every cycle or to make changes, after reviewing the diameter distribution and residual basal area per acre. NATGEN is constrained to 10 cycles because of the reliability of correctly projecting diameter growth beyond 120 years of age (Miner et al. 1988, Brand 1981). For genetic considerations, it would be ideal to accurately predict diameter growth beyond 200 years of age.

When N < 600, the user may choose among: 1) seed tree regeneration (only reproductively mature trees following tree removal are considered as parents), 2) advanced regeneration (i.e., number of reproductively mature parents and their gene frequencies are determined before tree removal), or 3) skipping regeneration and proceeding to grow the trees for 20 years. Option (2) provides a larger effective population size among parents. The two approaches to natural regeneration combined with the reproductive maturity constraints, conveys the concept of effective population size. Results of repeated diameter limit cutting every cycle are readily apparent by the fourth and fifth cycles, since the user has generally exhausted the number of reproductively mature trees for options (1) and (2) and has to skip regeneration and grow the remaining trees for 20 years.

Reports of total genetic, phenotypic, and diameter means and variances are available after the user elects to stop the simulation. If the scientist user level is selected, reports are provided on the change in desirable gene frequency (A gene), along with measures of heterozygosity at the locus-level.

NATGEN as a Research Tool

An extension of NATGEN was developed to permit five replicate runs of selected silvilcultural prescriptions under a management objective of optimizing volume production. Two population sizes (N=100 and N=600), with one and five loci, respectively, were used to characterize tree diameter. Default values were selected at initiation (heritability = 0.2, with equal gene frequencies per locus, A = a = 0.5). Diameter limit cutting (18+ inches) or diameter limit cutting combined with cutting from below (18+ inches and < 9 inches in DBH) were modeled for both population sizes. Regeneration was based on the seed tree method.

For the N=100 one-locus model, natural regeneration followed harvesting at rotation (80 years). Harvesting occurred every 80 years. The desirable gene frequency (A-gene) reached a frequency of 0.1 as early as six rotations under both harvesting regimes for the extreme site type (Figure 1). The A-gene frequency and total genetic variance were unable to recover under diameter limit cutting; however, slightly higher levels of genetic variance were maintained with the combined 18/9-inch harvest regime. Diameter distributions changed over time as the original population was carried for 10 rotations, with fewer trees represented in the larger diameter classes (Figure 2).

For the larger model (N=600 and five loci), natural regeneration could occur every 20-year cycle if N < 600 and at least two remaining trees had reached reproductive maturity. Desirable gene frequencies among the five loci ranged from 0.5 (± 0.01) at initiation, to 0.48 (± 0.02) at 280 years for both site types. Gene frequencies at 280 years are higher than the one-locus model at three rotations due to an increase in population size (Figure 1). Amounts of genetic variance differed between sites for diameter limit cutting (18+"E, 18+"U) (Figure 3). Total genetic variance was more stable when diameter limit cutting occurred at cycles 1, 5, and 9 and cutting from below occurred at cycles 3 and 7 (18ALT9"E and 18ALT9"U, Figure 3).

Changes in diameter distributions for the extreme site (Figure 4) yielded more trees in the lower diameter classes over time, for both harvesting regimes. Diameter limit cutting resulted in a larger number of total trees, with trees represented in the lower diameter classes (Figure 4). Fewer numbers occurred in the combination harvesting regime (18ALT9"E) at 280 years, since the number of reproductively mature trees was the limiting factor in natural regeneration.

For the uniform site, the number of reproductively mature trees was not a limiting factor, hence, there were equal numbers of trees at 280 years for both harvesting regimes (Figure 5). Changes in diameter distributions over time were noted only in the proportion of trees represented in each diameter class by harvesting regime, but not in total numbers.

Only one factor could vary among replicate runs, in order to get an average response. In some cycles however, when harvesting was scheduled to occur, residual basal area per acre was below 80 square feet. In practice, no harvesting would have occurred so as to maintain desirable stocking levels (McGill et al. 1991), and tree removal would have been delayed until residual basal area per acre exceeded 80 square feet.

CONCLUSIONS

There are genetic consequences for each management objective and combination of silvilcultural prescriptions on tree populations. Results of these simulation trials demonstrated both a reduction in genetic variance, desirable gene frequency, and changing diameter distributions, with fewer individuals in the larger diameter classes in later years. The full model

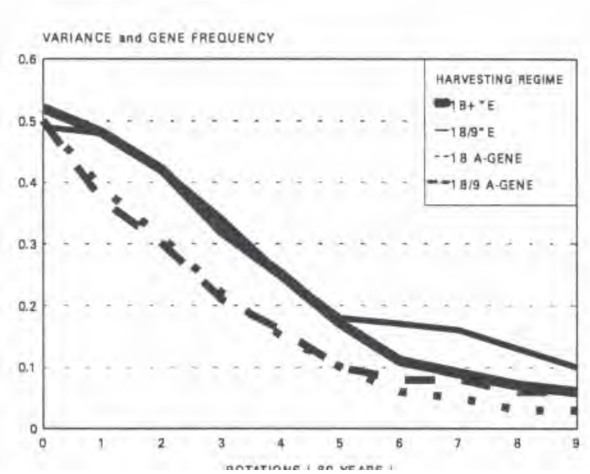

Figure 1. Total genetic variance and A-gene frequency following seed tree regeneration for one locus and N= 100 trees.

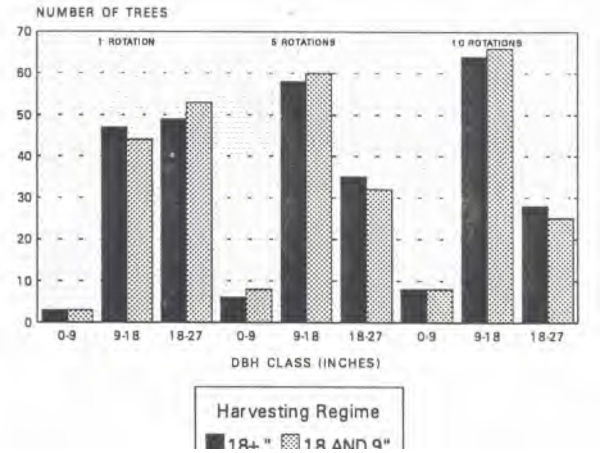

Figure 2. Diameter distributions by harvesting regime, at one, five and 10 rotations, for N= 1 00.

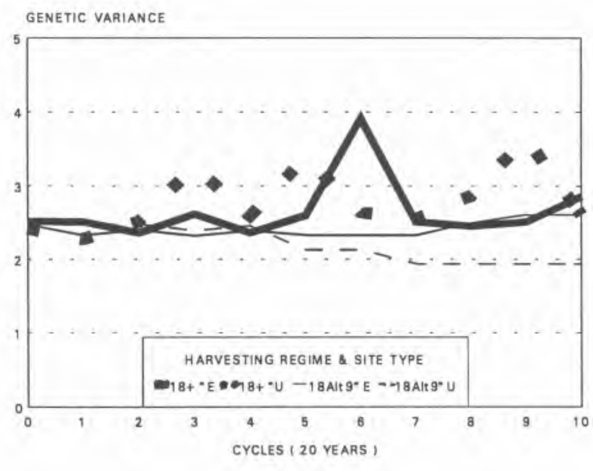

Figure 3. Total genetic variance following seed tree regeneration for five loci and N= 600 trees.

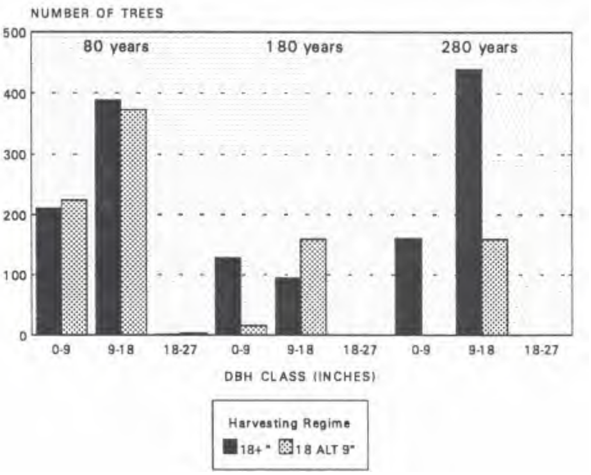

Figure 4. Extreme site (El diameter distributions by harvesting regime, at cycles 0, 5 and 10, for N = 600.

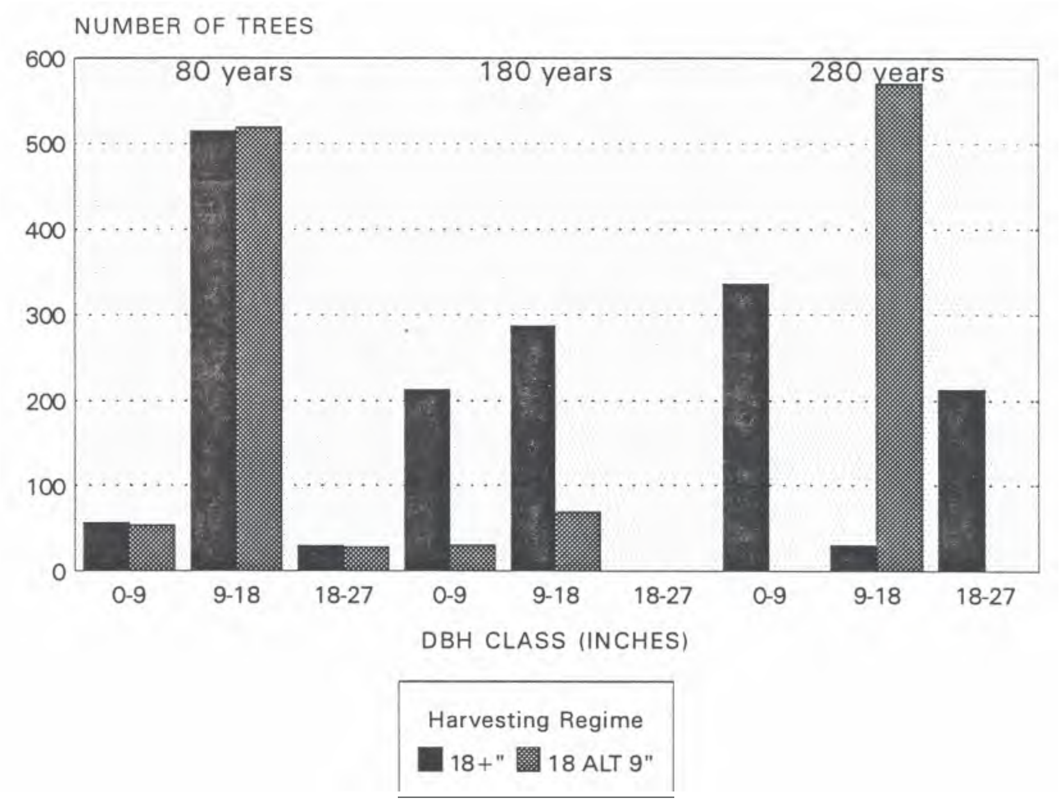

Figure 5. Uniform site (U) diameter distributions by harvesting regime, at cycles 0, 5 and 10, for N = 600.

demonstrates that with declining gene frequencies and fluctuations in the number of reproductively mature parents, large diameter trees cannot be achieved merely by skipping cuttings cycles or by extending rotation ages in an uneven-aged system. The results reported would be more conservative if mortality functions had been included or if natural regeneration patch sizes had been limited to no smaller than one-fifth of an acre (Lorimer 1983). Selection of advanced regeneration would offset the decline in gene frequencies and total genetic variance, since the effective population would be expected to be higher than with the seed tree method.

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