Sugar Pine

Status, Values, and Roles in Ecosystems

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Conservation of Biodiversity in Sugar Pine: Effects of the Blister Rust Epidemic on Genetic Diversity

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ABSTRACT. Genetic diversity in sugar pine will be severely reduced by the blister rust pandemic predicted within the next 50 to 75 years. We model effects of the epidemic on genetic diversity at the stand and landscape levels for both natural and artificial regeneration. In natural stands, because natural frequencies of the dominant gene (R) for resistance are low, the most obvious effect on sugar pine will be demographic, with a crash in population size expected following disease onset. Many stands in areas of lowest R frequency may lose the allele during the initial epidemic and go extinct. In stands that maintain the resistance allele, R will increase in frequency under strong selection in subsequent generatior.., and population sizes in these stands should recover. But a significant reduction in effective population size (Ne) is also expected following disease onset; this results in a severe and long-lasting effect on genetic diversity in sugar pine. Harvest of mature susceptible sugar pines during the initial epidemic will exacerbate declines in effective population size and greater long-term diversity losses relative to unharvested stands. In situations of artificial regeneration, planting resistant sugar pines should usually increase effective population sizes and long-term genetic diversity. High effective numbers of parents of the planting stock (over 20) and admixture of natural regeneration counter the potential of planting to reduce geographically structured genetic diversity. Allelic diversity and effective population sizes on a landscape level are kept highest when resistant trees used for artificial regeneration are scattered over the landscape rather than clustered.

Introduction

A goal for managing widespread native species is to conserve the integrity of genetically structured populations. Several features of sugar pine (*Pinus lambertiana*) make this goal unusually difficult to attain. Sugar pine occurs naturally as scattered individuals or small groups in mixed-conifer forests. High commercial value of sugar pine has led to heavy harvest throughout the last century, further reducing densities of mature trees. Most importantly, sugar pine is faced with an exotic and fatal disease, white pine blister rust (caused by *Cronartium ribicola*), that is expected to become pandemic on sugar pine throughout most of its range within the next 50 to 75 years (Kinloch and Dulitz 1990; R. S. Smith, these proceedings). Combined, these factors will significantly reduce the size of the breeding population in present and subsequent generations, leading inevitably to loss of genetic diversity. In this paper, we show the relation between population size and maintenance of genetic diversity, and we model the impacts of white pine blister rust on these factors in different situations of natural and artificial regeneration. We also consider management options to mitigate losses of diversity.

Relation of Diversity to Population Size

Biodiversity conservation seeks to counter extinction—of genes, individuals, populations, and species. For sugar pine, the goal is to maintain an adequate number of sugar pines through the rust epidemic, well-distributed in diverse community types, throughout the native range. For the species to adapt and evolve beyond the epidemic, sufficient genetic diversity must be maintained. Genetic diversity is critical to sugar pine in the short term to reduce inbreeding depression, and in the long term to provide raw material for adaptation to changing environments.

How much genetic diversity is adequate? Although we are far from being able to predict minimum genetic diversities necessary for long-term survival of sugar pine, we can begin to assess how certain events, such as the blister rust epidemic, timber harvest, or artificial regeneration, may reduce or elevate genetic diversity from current levels. If large, these effects will have implications for management.

Aside from effects of selection, mutation, and migration, we know that the amount of genetic diversity in a population over time depends on the population size (census number), N. The smaller N is, the more diversity is lost through chance events (Wright 1969). As N becomes larger, losses of diversity due to chance are negligible. Thus, anything that causes population size to crash (like blister rust) puts populations at increasingly greater risk of losing genetic diversity.

The actual number of individuals contributing to genetic diversity may be less than N. Many natural processes cause a population of size N to act like a much smaller (rarely, larger) population in regard to genetic diversity. For example, populations in which there is non-random mating, unequal sex ratios, unequal numbers of offspring per parent, or fluctuating population sizes lose genetic diversity over time faster than would be expected based on their census size (Wright 1969). This *effective number*, N_e, is equal to the census of a population only where mating is random, when all parents are equally fecund, reach sexual maturity at the same age, where sex ratios are equal, and when population sizes don't fluctuate over time (Wright 1969). An example from animal breeding of the effect of unequal sex ratios on loss of genetic diversity is the insemination of many cows by a single bull. Although there may be a large total number of cattle involved in breeding, the single male reduces the effective number of parents to approximately four and accounts for half of the genetic diversity in the next generation.

Transmission of genetic diversity takes place within a "genetic neighborhood," defined as the area within which mating is effectively random (Falconer 1989). The concept of genetic neighborhood reflects the genetic substructuring of populations that may occur because of the likelihood that matings take place more frequently among trees that are closer together than those more distant from each other. A genetic neighborhood is usually smaller than the geographic limits of the stand or local population, especially when populations are more or less continuous over large geographic areas and elevational ranges, such as those of sugar pine. Its size depends on the spatial distribution and density of trees of reproductive age, and the dispersal distances of seed and pollen. Mathematically, it is the area described by the circumference of a circle of a radius equal to the standard deviation of the dispersal distances (Wright 1976).

Effective population size significantly affects allelic and genotypic population diversity. Rare alleles have increasing probabilities of being lost when N_e falls below 50. For example, an allele at frequency of 0.01 has a 13 percent probability of being lost when N_e is 100, a 61 percent probability when N_e is 25, and a 90 percent probability when N_e is 5 (Krusche and Geburek 1991). Population heterozygosity also declines rapidly when N_e is low. For example, a population that maintained an effective size of 20 would decline 5 percent in heterozygosity in one generation, 14 percent over 5 generations, and 25 percent over 10 generations (Fig. 1).

Because large amounts of diversity are lost even in one generation when N_e is low, a single generation of low N_e can have a severe and long-lasting effect on diversity in a species. Diversity lost during a single-generation bottleneck is only slowly regained, even if census
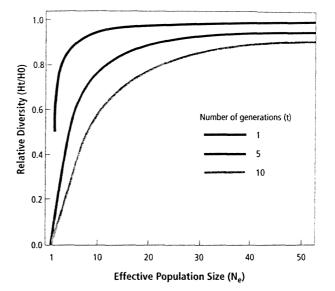

Figure 1. Relation of genetic diversity to effective population size over time. Diversity is measured as the observed population heterozygosity (H) at time t relative to expected heterozygosity at time 0.

size recovers rapidly. Loss of alleles and increases in homozygosity are potentially detrimental to a population. Inbreeding depression is common in tree species, and can trigger declines in population vigor, potentially leading to extinction of the population, especially one that is already small. Loss of allelic diversity is a concern for long-term population persistence, in that continual adaptation to changing environments depends on genetic diversity being available for selection.

Our points to emphasize for sugar pine management from this general discussion are that effective population sizes, not actual census numbers, determine the maintenance or loss of genetic diversity over time, and that effective population size may be much less than actual population size. Once a population declines in actual numbers, effective sizes may be so low as to seriously reduce diversity.

Modeling Rust Effects on Sugar Pine

Model Parameters for Sugar Pine

Formulae exist to calculate N_e from N empirically, although only recently have they been modified to account jointly for all the factors that affect N_e. Because of the difficulty of obtaining numerical values for the variables, few empirical estimates of N_e are available, but in many cases N_e has been estimated to be much smaller than N (Crawford 1984; Barrowclough and Coates 1985; Govindaraju 1988; Muona and Harju 1989; Smith and McDougal 1991; Grant and Grant 1992). Detailed develop-

ment of our model parameters is being prepared for a separate paper. For calculating N_e in sugar pine, we used formulae of Lande and Barrowclough (1987) to calculate stand-level N_e and of Ryman and Laikre (1991) to calculate regional N_e. We used data from Schubert and Adams (1976), Schoen and Stewart (1987), and Muona and Harju (1989) to calculate variances in fecundity in pollen and seed production, and assumed the range of densities of mature sugar pine in natural stands to be 3 to 20 trees per hectare (USDA Forest Service, Pacific Southwest Regional database).

For estimating genetic neighborhood, we adopted 70 m for pollen dispersal, based on Wright's (1976) mean pollen dispersal for nine conifers of 66 m, on Neale's (1983) estimate of 72 m for Douglas-fir (*Pseudotsuga menziesii*), and on Adams and Birkes's (1988) estimate of 70 m for Douglas-fir. For incoming migrant pollen we used Neale's (1983) estimate of 0.30 per neighborhood per generation. For seed dispersal we used Fowells and Schubert's (1956) estimate of 25 m. Using formulae of Wright (1969, pages 302 and 303) and assuming discrete generations, we estimate a genetic neighborhood size in sugar pine of 3.86 hectare. In this paper we use the word "stand" or "population" to refer specifically to a genetic neighborhood in sugar pine.

Model Parameters for White Pine Blister Rust

In modeling diversity, we assume blister rust will continue to spread to new areas and then intensify within those areas, according to patterns already observed (Kliejunas 1984; Kinloch and Dulitz 1990). Eventually the disease will become pandemic, chronic, and severe throughout virtually all populations. This process could take a half-century, or longer for regions where it has not yet arrived, such as the Transverse and Peninsula ranges of southern California and Mexico where increasing aridity reduces the probability of establishment and rate of spread. However, there are no intrinsic limitations to the eventual arrival of blister rust even in these populations (R. S. Smith, these proceedings).

The effect of the disease is almost certain mortality to all seedlings and young trees lacking genetic resistance. Older and larger trees may be killed in areas of severe disease hazard, either directly, or indirectly through stress that predisposes them to other damaging agents. Where infection is less intense, varying degrees of crown damage occur. Some trees develop increasing resistance with age. In any event, older trees usually survive long enough to contribute genes to the next generation through seed and pollen. The main effect of rust infection on older trees is on fecundity: mean fecundity is reduced (through branch mortality) and variance is increased, which together reduce N_e. For simplification, we have assumed tree mortality of 20 percent (Kliejunas

1984) of mature trees present at the time of disease onset, and a uniform average reduction of 50 percent in fecundity of sexually mature (defined as > 30 cm diameter at breast height), susceptible trees.

Major gene resistance (MGR) is the only kind of resistance that we consider, and we assume no sugar pine regeneration lacking this resistance will survive to maturity once the disease is pandemic. Frequencies of the R allele for resistance range from less than 0.01 in the northern part of sugar pine's distribution to 0.08 in the southern Sierra (Kinloch and Davis, these proceedings). Wind-pollinated seeds from heterozygous (Rr) parents will yield a 1:1 ratio of resistant:susceptible seedlings under epidemic conditions. Although other kinds of resistance exist (see Kinloch and Davis), their frequencies are unknown but are probably lower, so their omission does not compromise the overall integrity or robustness of the model. In calculating changes in demography, we assume a high rate of population increase, with recovery dependent only on proportions of MGR in each generation. This is an optimistic estimate of population recovery.

Effect of Rust Epidemic on Sugar Pine at the Stand Level

Natural Regeneration

The immediate and most obvious effect of the epidemic is demographic. Seedlings and young trees lacking the resistance allele (R) will die. In most parts of sugar pine's range, susceptible mature trees will survive much longer than young trees, although their crowns are likely to be damaged, thereby reducing their fecundity. Heavy damage predisposes them to other stresses, such as drought and bark beetles.

In Figure 2, we graph population dynamics for five generations, plotting in each generation the mature stand after natural selection for R. Generations are discrete. In generation 0, stands are free of rust. We assume that rust attacks stands of generation 1 after they mature, causing about 20 percent mortality. As plotted in Figure 2, generation 1 is the remaining mature stand. Since susceptible mature trees still compose most of the stand after infestation, they will be the major producers of seeds for generation 2. Because of the low frequency of R in the residual stand, however, most seedlings die, creating a significant crash of N in generation 2.

In this and subsequent generations, R is strongly selected since only resistant genotypes survive, and the frequency of R increases rapidly. Population sizes (N) recover, and most of the individuals now carry the resistant allele. Yet, the effect of the blister rust epidemic on N_e is severe and long-lasting (Fig. 2). Due to selection against susceptible genotypes (resulting in mortality and
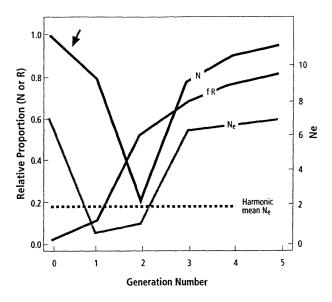
Figure 2. Effect of the blister rust epidemic on population size (N), frequency of R allele (fR), effective population size (N_e) in sugar pine populations over five generations, and harmonic mean N_e for this period; natural conditions are assumed, with no planting or harvest. Here, N and R are relative proportions. Arrow indicates onset of blister rust epidemic. Generations are assumed to be discrete, initial frequency of the R allele is 0.01, and density of mature sugar pines is 3 per hectare. For generations 1 to 5, the mature population after selection by the rust is graphed.
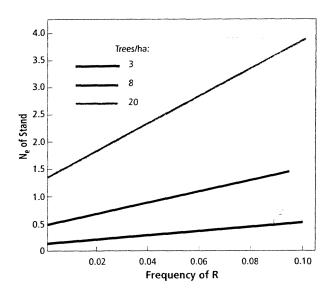

Figure 3. Relation between frequency of R allele and effective population size at different mature tree densities in a sugar pine stand infested with blister rust.
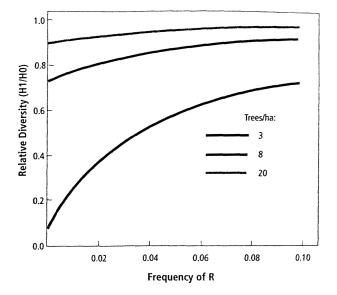

Figure 4. Relationship between frequency of R allele and genetic diversity in a sugar pine stand at generation 1 (diseased stand) relative to generation 0 (undiseased stand). Genetic diversity is measured as the expected population heterozygosity in generation 0 and observed heterozygosity in generation 1.

lower fecundity), effective population size crashes in the first generation to critically low numbers. For example, in a population with initial density of three mature trees per hectare and frequency of R = 0.01, we estimate N_e in our assumed genetic neighborhood to fall to 0.7 in the first generation (i.e., 50 to 75 years) after the onset of the disease. This compares to N_e of 7.1 in a similar stand without rust. Figure 3 shows how N_e depends on the frequency of the R allele in the healthy stand (generation 0) and how the density of mature sugar pines affects N_e: stands with low densities and low R frequencies will suffer the greatest reduction in N_e.

The crash in N_e significantly affects genetic diversity in subsequent generations, with the greatest impact in the first and second generations (Figs. 3, 4). At low frequencies of R and low densities (i.e., low N_e), loss of diversity is most severe. For example, in stands with frequency of R less than 0.02 and with only three mature trees per hectare, genetic diversity may decline 60 to 90 percent in the first generation because of low N_e. Where densities and R frequencies are higher, loss of diversity is less, even in heavily rusted stands (Fig. 4).

In subsequent generations, as the frequency of R increases and the population (N) recovers, N_e also recovers, though gradually (Fig. 2). This means that losses of diversity in subsequent generations will be relatively low as the population comes out of the bottleneck. However, the low N_e values in generations 1 and 2 have a serious and long-lasting effect on diversity. During the period of low N_e, much diversity is lost that is never regained. The

impact of low N_e in generations 1 and 2 extends over five generations, which have an average N_e of 1.99 (Wright 1969: 210). Such low N_e values put the species in jeopardy of losing large and cumulative amounts of genetic diversity (Fig. 1).

Management implications. High effective population sizes of sugar pine stands will promote the management goal of maintaining current levels of genetic diversity. How might effective numbers be enhanced? As the epidemic intensifies, two classes of sugar pines become especially important: mature trees and their seedling reproduction. The genetic contribution of susceptible mature trees from generation 1 to generation 2 (for traits other than rust resistance) is extremely important for maintaining diversity of sugar pine over the long term. The mature susceptible trees compose over 83 percent of the stand even at the highest estimates of R frequency, and represent most of the genetic diversity in the stand. Many or most would survive long enough to produce seed for some time even after becoming infected. Although they contribute only r alleles at the MGR locus and most of their offspring will die, their diversity at other loci will be carried into generation 2 in zygotes receiving R from resistant pollen donors or by contributing pollen to resistant seed parents. In this way, their essential contribution to N_e and diversity is maintained.

The significance of this contribution is illustrated in Figure 5, where conditions are assumed to be identical to Figure 2, except that mature susceptible trees do not 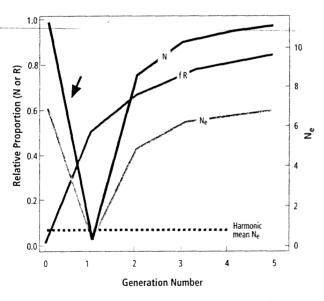contribute to generation 2 (e.g., they are harvested). The proportion of surviving individuals in generation 2 is potentially much higher than in unharvested stands, due to the higher frequency of R. However, N_e in generation 1 is much lower than in unharvested stands (0.12 vs. 0.7). This results in an even greater loss of genetic diversity to sugar pines in subsequent generations, indicated by the low average N_e for 5 generations (0.63 [Fig. 5] vs. 1.99 [Fig. 2]) These relationships indicate the detrimental effect to long-term diversity of removing any mature trees, including susceptible genotypes, especially in generation 1.

A second focus is the regeneration class. Wherever possible, natural regeneration should be encouraged, especially between generations 1 and 2. The large increment of genetic diversity contributed from the susceptible mature trees in generation 1 is captured in the stand only if those trees produce established seedlings either via seed or pollen. Since resistant seedlings are rare, large numbers of seedlings are needed. Large numbers also help to maintain rare alleles (such as R itself), thus improving the chances of population survival and promoting higher N_e values in the next generation.

Artificial Regeneration

Many government and industrial landowners plant from 10 to 25 percent sugar pine into natural forests in mixtures with other conifers. Sugar pine seeds derive from parents that range from wind-pollinated, unscreened wild parents to clones with proven genetic resistance. When planted sugar pines have higher frequencies of R than natural regeneration, the crash in N should be less than with natural regeneration alone. The frequency of R should increase more rapidly in generation 2 and subsequent generations relative to natural regeneration, with the magnitude of the increase depending on the frequency of R in the planting stock and the relative stocking of planted and wild seedlings.

What about the effect of planting on N_e and maintenance of genetic diversity in a stand? First, we assume that the plantation comprises both planted seedlings and some natural regeneration (volunteers by inseeding). We simulate current management by assuming that planted seedlings derive from wind-pollinated seeds of MGR seed parents, and that most of these parents are heterozygotes (thus, that 50 percent of the planted seedlings survive). We further assume that stocking densities are sufficient to promote stable, mature tree densities of sugar pine over generations without further planting. Plantations are assumed to equal the size of a genetic neighborhood (3.86 ha). Parents of planted seedlings are assumed to be from the same seed zone, but are not necessarily cohorts of the wild trees in the neighborhood of the plantation. The composite or overall effective size in such stands depends on the N_e of parents of the wild seedlings, N_e of parents of the

Figure 5. Effect of the blister rust epidemic on population size (N), frequency of R allele (fR), effective population size (N_e) in sugar pine stands over five generations, and harmonic mean N_e for this period. Mature susceptible trees are assumed to be removed from generation 0 after the onset of the disease. Other assumptions of Figure 2 pertain.

planted seedlings, and the relative proportion of both kinds of seedlings in the stand (Ryman and Laikre 1991).

The first of these we have discussed above; N_e of the wild mature stand is estimable given an R frequency and stand density. To calculate N_e of the nursery stock we assume that the same kind of factors that affect transmission of genetic diversity in wild populations affect nursery populations. The effective number of parents that transmit genetic diversity to the offspring generation is usually not equal to the number of clones used for breeding or the number of trees used for collection of wind-pollinated seeds. Intrinsic differences among clones in pollen, cone, and seed productivity, as well as orchard conditions that affect differential size and number of ramets, cone and pollen availability, and productivity per clone cause N_e to be much less than N. These deviations sometimes can be compensated for, for instance, by equalizing the contributions of seed from maternal clones. Other factors are difficult or impossible to control, such as the paternity of seedlings or meiotic sampling from small numbers of genotypes.

In the next generation, the overall N_e of the plantation depends on the relative proportion of surviving wild vs. planted seedlings in the stand. If most of the stand consisted of planted seedlings, the overall N_e would be closer to the N_e of the parents of the planted seedlings; if most of the stand were wildings, the overall N_e of the stand would be most like the N_e of the wild parents. The maximum attainable N_e in the stand is the weighted sum of the N_e values for both sets of seedlings.

Figure 6 illustrates the effect of planting on N_e for three stand conditions. The N_e of parents of planted seedlings varies from 2 to 20, the latter being the target number of MGR parents for the U.S. Forest Service Rust Resistant Sugar Pine Program for each of seven designated breeding zones in the California range of sugar pine (Kitzmiller 1976; U.S. Forest Service Regional Policy for Sugar Pine, October 1990). It is clear from these analyses that under most rust hazard conditions when the N_e of the parents of the planting stock is even modestly large, planting increases the overall N_e of the stand relative to the natural regeneration alone (Fig. 6a, b). This occurs over a wide range of planting stock proportions. Planting is most beneficial when frequency of R or density of mature trees in the wild stand is low. Under these conditions, the naturally occurring N_e is low, and except where very few parents contribute a large proportion to the stand, planting improves the stand N_e. By contrast, when the frequency of R is higher in the wild stand, the relative gain in N_e from planting decreases. In most instances, nevertheless, artificial regeneration will improve N_e of the resulting stand.

A second conclusion is that the maximum N_e attainable results from a mix of planted and wild seedlings, with the proportion depending on the conditions of the
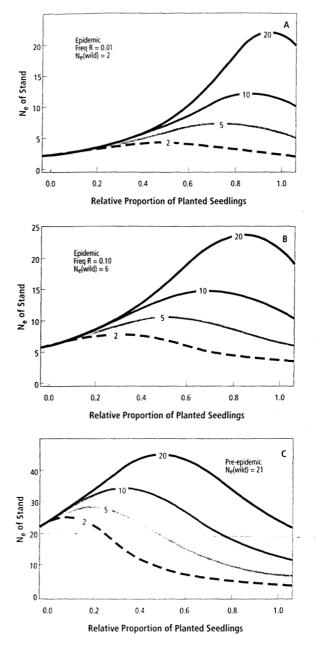

Figure 6. Effect of artificial regeneration on overall effective population size (N_e) of a sugar pine stand. Curves represent different effective population sizes of the parent population of planted trees (i.e., from seed orchards or selected trees). The new stand is assumed to comprise partly artificial regenerants (planted seedlings) and partly natural regenerants. N_e (wild) is the effective population size of parents of the natural regeneration. Density is eight mature trees/ha. Stand size approximates our assumed genetic neighborhood size (c. 4 ha). (A) rust-diseased stand where frequency of R allele in the wild stand is 0.01, N_e (wild) is 2; (B) diseased stand where frequency of R allele is 0.10, N_e (wild) is 6; (C) healthy stand, N_e (wild) is 21. Situations in A and B represent relatively low and high values of R and N_e, respectively, under epidemic conditions; C represents a "control" scenario, where rust is absent (or R = 1.0).

wild stand (frequency of R and stand density), and the N_e of the planted seedlings. Where the frequency of R is low (0.01, Fig. 6a), the stand N_e is highest when planted seedlings make up about 90 percent of the stand (where N_e of planted parents is 20). When the N_e of planted parents is only 5, however, the maximum total N_e occurs at about 75 percent relative contribution of planted seedlings. As higher frequencies of R and/or higher stand densities and/or no disease occur in wild stands, so do larger wild N_e values result (Fig.6b, c). In most of these instances, the maximum stand N_e is reached at lower proportions of planted seedlings. In general, under the high rust hazard conditions we have assumed in a plantation, we expect very few wild sugar pine seedlings to become established, except when the frequency of R in the natural stand is relatively high or established regeneration is unusually dense. Therefore, without further intervention, the relative proportions of planted seedlings usually will be very high (>95 percent), in which case maximum N_e probably cannot be attained.

Finally, there are conditions where planting reduces the stand N_e below the wild N_e. This occurs where the N_e of parents of planting stock is equal to or lower than the N_e of the wild parents, and where the planted seedlings constitute a large proportion of the stand (Fig. 6a, b). In pre-epidemic stands, the depressing effect of planting on N_e is greater (Fig. 6c). A wide range of conditions exists where total N_e is lower because of planting than it would be in natural conditions. In healthy stands, however, we expect natural regenerants to outcompete planted seedlings, resulting in a higher net survival of naturals.

Management implications. At the stand level, planting with resistant stock (e.g., control- or wind-pollinated seeds from MGR parents) helps to stabilize the population demographically. Adequate genetic diversity can be assured with N_e values of 20 or more parents, which is about the naturally occurring N_e of sugar pine in healthy, moderately dense mixed-conifer forests. Thus, in most cases, seedlots for planting should comprise at least 20 (effective number) parents. The highest overall stand N_e (and thus maintenance of greatest genetic diversity) results when there are admixtures of wild and planted seedlings in the plantation. Under epidemic conditions, in the range of expected R-allele frequencies in the wild stand, maximizing N_e requires proportions of 10 to 50 percent natural regeneration in the stand. Aggressive management would be necessary to achieve so much natural regeneration, especially in epidemic conditions.

Landscape Level

The genetic and demographic consequences of the epidemic that we have projected so far apply to stands
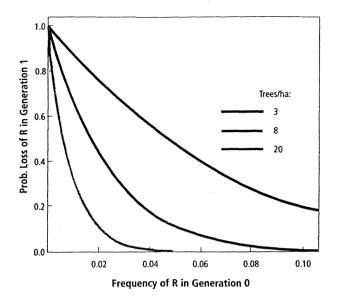

Figure 7. Probability of losing the R allele from a diseased sugar pine stand in generation 1 as a function of frequency of R allele in generation 0.

where sugar pine persists through the epidemic. It is also appropriate to ask how many entire sugar pine *stands* might be lost over the course of the pandemic, that is, what are the effects at the landscape (regional) level. Under natural conditions with no supplemental planting, we expect that a relatively large number of stands would lose the R allele in the first generation. The probability of losing R by chance events of meiotic sampling is greatest in stands with lowest R frequency and/or low densities of mature trees (Fig. 7). Assuming that stands which lose the R allele go extinct, these probabilities translate to proportions of stands over the landscape that may go extinct. In stands where R frequency is low (≤ 0.01), 31 to 86 percent of stands could go extinct (for densities of 20 and 3 trees/ha); where R frequency is high (0.10), < 1 to 16 percent of stands could lose sugar pine. Thus, surviving stands that follow the expected recovery in Figure 2 represent only 14 to 69 percent of the stands in regions of low R frequency, and 84 to 99 percent of the stands in areas of high R frequency. Worst-case situations pertain to portions of the range in Oregon, northwestern California, and Baja California where R frequency is low, and to other stands throughout sugar pine's range where densities are low.

For assessing the effects of planting at the landscape level, stand analyses can be extended to a wider geographic region. Consider the effect on overall N_e of planting sugar pines in an average Sierra Nevada seed zone with an elevation band of 150 m, the unit used for local planting by the USDA Forest Service (Kitzmiller 1976, 1990). We estimate that forests with sugar pine

cover 15,000 hectares within this area. Modeling is more complex at the landscape level, and we take several approaches to illustrate different points. We consider neighborhood size as before, but assume no population-genetic substructure within the seedzone. Similarly, we consider the N_e of the wild forest, the N_e of parents of the planting stock, and the relative proportions of planted and wild seedlings that compose each planted stand. We estimate N_e of the wild forest to be the sum of the N_e values for the individual neighborhoods in the area, assuming that a certain percent of neighborhoods go extinct because of the probability of losing the R allele. For R frequency of 0.01 and 0.10, N_e of sugar pines in the wild at this geographic scale would be 3,120 and 21,260, respectively. We assume that all seedlings planted over this area derive from the same set (or subsets) of MGR parents within the seed zone, and that N_e of parents of planted seedlings is 20. This corresponds to a Forest Service program that targets a minimum of 20 (N_e, not N) MGR female parents for regeneration at this scale (Kitzmiller 1976; USDA Forest Service, Regional Policy for Sugar Pine, October 1990).

The resulting overall N_e values at this scale depend on the proportion of land planted. Planting only 5 percent (750 ha) of available (15,000 ha) sugar pine forest within the seedzone depresses the wild N_e insignificantly at most mixes of wild and planted seedlings. The slight reduction of N_e from what it would be without planting occurs because in 5 percent of the neighborhoods, the same parents are represented (i.e., the parents of the planting stock), thus displacing the natural diversity. This planting level approximately corresponds to some current programs, such as that of the Forest Service (Samman and Kitzmiller, these proceedings), where proportionally few seedlings from identified local MGR seed parents are available for outplanting within seed zones.

Planting has such a small effect on N_e at the landscape scale because so few acres are planted. By contrast, in the extreme case where 100 percent of the available sugar pine neighborhoods within the same 150 m seed zone are planted, planting drastically depresses the overall N_e for the seed zone. Except in situations where plantations have high proportions of wild seedlings, overall N_e of the seed zone drops below 50. Increasing the N_e of the planting stock helps only somewhat. Although such an extreme planting situation is highly unlikely, it points to the importance of encouraging natural regeneration of sugar pine while planting MGR seedlings throughout seed zones from a limited number of parents.

An important issue when population substructure is introduced into landscape consideration is the geographic distribution of selected MGR parent trees. Consider two extreme situations, one where 20 MGR trees are selected from a single genetic neighborhood (e.g.,

from a single seed-production area) as opposed to one where single MGR trees are selected from 20 different neighborhoods within a seed zone. The role of pollen is important here in determining N_e of progeny, even when the number of mothers is the same. Assuming wind-pollinated seeds are collected from wild stands, in the former situation (clustered MGR trees) only the pollen diversity available around one neighborhood is captured by the select MGR trees, and the resulting N_e of the offspring is 28. In contrast, when MGR trees are scattered, each tree samples a different pollen cloud, which raises the N_e of the offspring of these trees by 20-fold (560). Although the former N_e is quite low, the latter N_e seems safe under diverse planting situations (Fig. 1). One way to capture some of this diversity if MGR trees must be clustered would be to control-pollinate with diverse pollen.

Another way to assess the genetic consequences of selecting clustered vs. scattered MGR trees is by determining the effect of sampling on the geographic distribution of alleles. Assuming that allele frequencies vary over the landscape for both stochastic and deterministic reasons, clustered MGR parent trees will result in greater losses of landscape-level allelic diversity than will scattered MGR parents. Losses in diversity are estimated by comparing heterozygosities resulting from the contrasting MGR selection schemes to heterozygosities predicted from random sampling of trees in the wild. To do this requires a geographically hierarchical model, with heterozygosities of trees in the wild determined for population-within-region and region-within-seed-zone levels. Populations are taken to be as before (c. 4 ha); regions the size of a Ranger District are each 15,000 hectares; the seed zone is here taken to be three Ranger Districts, or 45,000 hectares.

Since geographic partitioning of heterozygosity tends to vary in conifers (including sugar pine: Conkle, Jenkinson, these proceedings) depending on the type of loci, we chose two contrasting sets of heterozygosity values for random sampling of natural genetic structure. In the first case, allelic diversity was assumed to be distributed as 95 percent within populations, 3 percent among populations within regions, and 2 percent among regions (a typical isozyme pattern). For random sampling of alleles, we chose an average heterozygosity value for sugar pine of 0.180 (see Conkle, these proceedings). Selecting 20 trees from one population would result in heterozygosity of 0.171, which indicates a 5 percent loss in diversity relative to random sampling. By contrast, selecting 20 trees scattered over 20 distinct populations would give a heterozygosity of approximately 0.174, or a 3 percent loss in diversity.

In the second case, allelic diversity was assumed to be distributed as 60 percent within populations, 20 per-

cent among populations within regions, and 20 percent among regions (a typical pattern for some quantitative traits). Selecting 20 MGR trees from one population would result in heterozygosity of 0.110, representing 40 percent loss in diversity from random sampling, vs. heterozygosity of 0.140 for scattered MGR trees, representing 21 percent loss in diversity. This example points to the importance of scattering MGR parents over seed zones to capture geographically diverse alleles, especially in adaptive trait loci.

Conclusion: The Fate of Sugar Pine

Although there has been concern that blister rust, in conjunction with heavy timber harvest, might trigger extinction of sugar pine, species extinction does not appear from our analysis to be a likely consequence. Population extirpation, however, and widespread loss of genetic diversity are real threats. Our MGR analyses indicate a high likelihood that many sugar pine populations, if unassisted, may go extinct as blister rust becomes pandemic, especially in regions where the R frequency is low or in stands where density of mature sugar pines is low. In stands that retain sugar pine, populations are expected to crash in the first generation after onset of the disease, but subsequent generations should recover rapidly from natural selection and increase of MGR, even where R is in relatively low frequency. Enough of these populations should persist that sugar pine will remain represented throughout its current range, although northern populations are at high risk and Baja populations at greatest risk, if and when rust arrives. Planting will be especially important for population stabilization and recovery in these areas.

Even after recovery in population numbers, the bottlenecks imposed by the rust will have long-lasting detrimental genetic consequences on sugar pine. Effective population sizes of diseased stands are about one-eighth that of healthy stands, imposing drastic reductions in diversity. Diversity lost, especially of rare alleles, will not be regained. We can think of no more compelling example of the value of rare alleles than MGR itself. Almost literally, MGR was a genetic solution waiting for a problem. It would never have been detected in the absence of blister rust, and we have to ask ourselves how many other such problems, biotic or abiotic, are latent in our rapidly changing environments. Diversity retained in sugar pine

populations through the bottleneck will keep opportunities open for future adaptation. Our modeling suggests that diseased stands where densities of mature trees are below 20 trees per hectare are in jeopardy of serious loss of diversity. Retaining mature resistant and susceptible sugar pines and encouraging natural regeneration from them is the best prescription for maintaining diversity in natural forests through the bottleneck.

Development of rust resistance in operational programs can improve sugar pine's recovery if effective numbers of parents are kept high and local trees are used as seed parents. Our model suggests that effective numbers of parents of planting stock should be kept at least at the level of the original, pre-epidemic stands. By our calculations, effective population sizes of pre-epidemic sugar pine stands are roughly half the census number of mature trees in the stand.

At the landscape level, N_e of planting stock optimally would mimic total wild N_e values in the landscape, which are very large. In practice, it is exceedingly difficult to incorporate large numbers of MGR parents into breeding programs. A paradoxical situation occurs in that widespread planting of resistant sugar pine may help to stabilize sugar pine populations demographically, yet if progeny from low effective numbers of parents replace wild parents across the landscape, N_e drops and genetic diversity in the long term declines. Planting programs could compromise by expanding the hectares planted only as increased numbers of local resistant parents become available.

Finally, we reiterate that our analyses and conclusions are tentative. Estimation of N_e is highly sensitive to the size of genetic neighborhoods, which depends on pollen dispersal distance and pollen immigration, both difficult parameters to estimate. Our estimates of the extent and timing of pandemic conditions also affect our predictions about N_e and diversity. Other resistance mechanisms have not been included in this model; when their inheritance and frequencies are known, these should be added. Despite the potential for mis-estimating exact numbers with simplified models, we feel that the relative implications suggested are robust. Since timing is critical for sugar pine, we report these preliminary conclusions now in the hope that they will help in making critical management decisions that affect the gene pool of future sugar pine populations.

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