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Genetic strategies for reforestation in the face of global climate change

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ABSTRACT

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If global warming materializes as projected, natural or artificial regeneration of forests with local seed sources will become increasingly difficult. However, global warming is far from a certainty and predictions of its magnitude and timing vary at least twofold. In the face of such uncertainty, reforestation strategies should emphasize conservation, diversification, and broader deployment of species, seed sources, and families. Planting programs may have to deploy non-local seed sources, imported from further south or from lower elevations, which necessitates a system for conserving native gene pools in seed banks or clone banks. Planting a diverse array of species or seed sources is a hedge against the uncertainty inherent in current projections of warming. Most tree improvement programs already stress genetic diversity and deployment of multi-progeny mixes, but may better prepare for climate change by testing selections in an even wider set of environments than is now the case.

INTRODUCTION

Numerous stresses threaten forests in the next century. Chlorofluorocarbons will probably deplete the earth's protective ozone layer by 7%, perhaps, reducing yield in some crop plants and forest trees (Caldwell et al., 1989). Other atmospheric pollutants are already destroying forests or changing forest composition in some areas, such as the Los Angeles Basin (Miller, 1973) and the Valley of Mexico. Acid deposition is leaching soils, which may in time affect forest growth even in areas remote from sources of pollution (Schulze, 1989). And finally, mean annual temperatures are projected to increase 2.5°C by the year 2050 as a result of the release of 'greenhouse gases', i.e. methane,

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chlorofluorocarbons and carbon dioxide produced by the burning of fossil fuels and tropical forests (Schneider, 1989).

Warming will be most pronounced at high latitudes, an increase of 5–10°C at the latitude of Vancouver (see Harrington, 1987, for a review of climatic change). Higher temperatures will mean higher evapotranspiration in many areas, increased moisture stress, and closure of stomata earlier in the day or dry season. Increased atmospheric carbon dioxide concentrations may somewhat compensate for stomatal closure and help to maintain normal rates of photosynthesis; nevertheless, global warming will displace many plants and animals near the southern margins of their ranges, reducing forest cover in the US, and eventually timber harvest, without an offsetting increase in Canada (Peters, 1990; Davis and Zabinski, 1991).

A great deal of uncertainty surrounds these projections. Not everyone agrees that the climate will warm. However, most meteorologists predict a global warming and the real uncertainty seems to be the amount of warming and how it will affect the amount and distribution of precipitation. We do not wish to argue the merits of the various projections of global warming, but instead ask what forestry's response should be, assuming rapid climate change. Uncertainty must be the guiding factor for planning reforestation efforts over the next several decades.

In this paper we consider the genetic strategies for reforestation in an uncertain future. The discussion is organized around three levels of forest management: (1) native, naturally regenerated forest; (2) plantation forestry where the seed source is controlled; (3) highly intensive forestry in which plantations are established from seeds produced on superior selections grown in seed orchards. Throughout, we refer to three tactics — conservation, diversification, and deployment — how they apply to reforestation and what changes, if any, foresters should consider in regeneration practices and tree breeding. We use our experiences in the western US as a model, but the paradigms are easily extrapolated to other temperate climates.

NATIVE FOREST

Native forest may change in composition and some species may be entirely eliminated over large areas of the US as a result of climatic change. In the eastern half of the country, major components of the forest, such as paper birch (*Betula papyrifera* Marsh.), sugar maple (*Acer saccharum* Marsh.), beech (*Fagus grandifolia* Ehrh.), and eastern hemlock (*Tsuga canadensis* [L.] Carr.) may virtually disappear (Davis and Zabinski, 1991) (Fig. 1). Some species displacement may occur in as little time as 30 years, depending on which model of global warming is used (Botkin and Nisbet, 1991). In the West, steep elevational gradients provide an escape route up which tree spe-

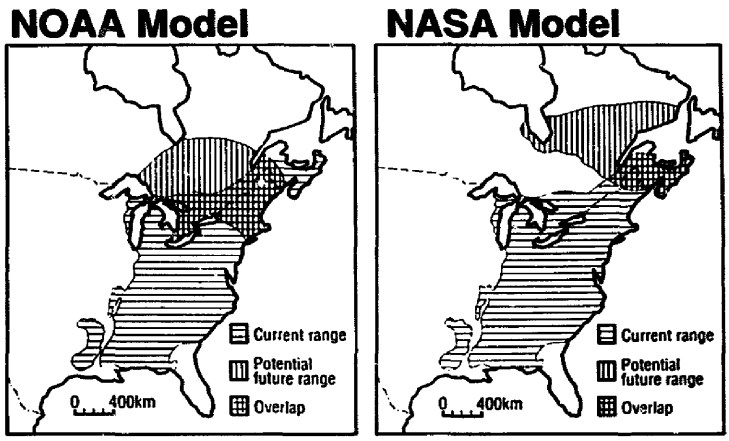

Fig. 1. Current and projected range of American beech under two models of global warming, the National Oceanic and Atmospheric Agency (NOAA) model and the National Aeronautics and Space Agency (NASA) model. (After projections by Davis and Zabinski, 1991.)

cies can migrate for refuge. Montane areas provide a diversity of climate over short distances, so displacement will be largely vertical. Nevertheless, many western species will suffer major reductions in range. Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) will be largely eliminated from California and coastal Oregon where it is now the most important timber species (Fig. 2).

The reductions in range are predicted as a direct effect of higher temperatures and drought stress on growth, and perhaps as the result of failure to meet winter chilling requirements (Kimmins and Lavender, 1987; McCreary et al., 1990). However, higher temperatures may also affect flowering and seed formation (Cannell, 1987), reducing the ability of some species to regenerate at their southern margin and at low elevations, even though vegetative growth is not reduced. In addition to direct effects of global warming, higher temperatures will favor insect pests because they will suffer less overwinter mortality and may be able to complete more generations during the longer growing seasons that result from global warming. High temperature and drought stress will weaken trees and make them more vulnerable to insect attacks, as evidenced by the increased mortality from bark beetles during the recent drought years in California.

Douglas-fir, for example, will decline even on those sites that remain suitable for the species in general. This decline will occur because populations are genetically adapted to the conditions under which they are now growing, not conditions 2.5°C warmer, as documented by an extensive literature on seed source variation (e.g. Ching and Hinz, 1978). To maintain Douglas-fir on sites in Oregon's Cascades may require active intervention; for example, in-

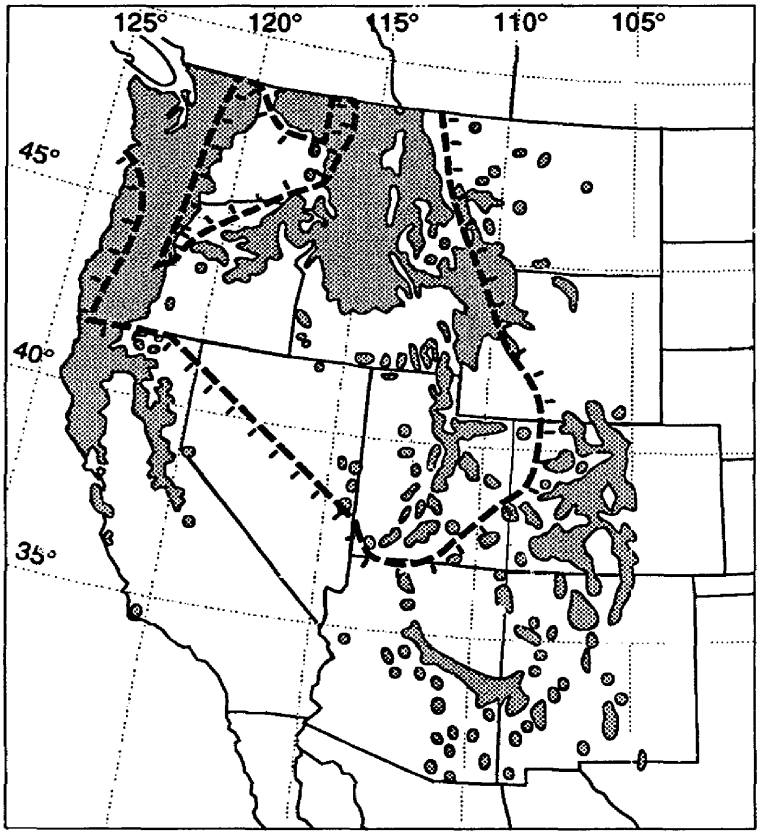

Fig. 2. Current range of Douglas-fir in the western US and potential changes under projections of global warming. Hatch marks point toward areas where Douglas-fir may suffer range reductions. (After Leverenz and Lev, 1987.)

troducing seed from areas further south in the Sierras, where the Douglas-fir are adapted to a warmer, dryer climate.

To intervene and counter possible destructive changes to native forests, foresters must know a lot more about the range of adaptation within tree species. At present, they can make intelligent guesses, but an intensified program of provenance or seed source testing is needed to fill the gaps in knowledge and give precise information for guiding seed transfer and forest restoration.

Conservation of genetic resources will be necessary to restore declining forests. Seed banks must be capable of providing suitable planting stock. Regional seed banks, such as the one operated by the Forest Service nursery at Placerville, California, should be expanded. Stocks were not sufficient for ca-

tastrophes such as the fire siege of 1987, much less global changes. Furthermore, the Forest Service's seed banks store samples from the National Forests and may not adequately cover non-federal lands. If the climate warms, low-elevation races from private lands may be better adapted for some federal lands than the races that now grow there.

PLANTATION FORESTS — SEED SOURCE CONTROLLED

We began with a consideration of natural regeneration and finished by concluding that we may have to resort to planting merely to ensure survival of the forest. That brings us to plantation forestry. Plantation forestry bypasses two problems that natural regeneration must contend with. First, trees pass their most vulnerable, seedling stage in the nursery where conditions can be managed to give them the best start possible. Second, it does not matter whether conditions are suitable for flowering and seed production since the plantation will be replanted after harvest. Nevertheless, even in plantation culture, stresses may be great enough to threaten survival and reduce growth and yield.

Genetic diversity is the best tool to counter environmental change and to hedge against uncertainty. Genetic diversity among populations and among trees within populations are both useful. Tree species have a higher level of genic diversity than animals or herbaceous plants (Hamrick et al., 1979). Even in a seed source that is not adapted to the plantation site, some seedlings will survive and grow remarkably well. For example, in Munger and Morris' (1936) classic 1925 Douglas-fir seed source study, planted at several sites in Washington and Oregon, all seed sources produced at least one tree whose height after 35 years was 90% greater than the average for the seed source, even when the seed source per se was a failure (Pacific Northwest Forest and Range Experiment Station, 1964).

Most tree improvement programs attempt to maintain high levels of genetic diversity. The goal of the US Forest Service's 'base-level' program in California (Kitzmiller, 1976), is to collect seed for reforestation from at least 20 trees, widely distributed throughout a seed zone, an area that covers about 50 miles north and south and an elevational span of ± 500 ft (152 m). Such a broad genetic base provides for a wide range of variation among trees, and it is hoped that at least some of these will be adapted to the new conditions.

However, to achieve commercial stocking it may be necessary to plant at higher density than is now customary. Campbell (1975) presented a useful model for this several years ago. The idea is simple. Assume, for example, that 80% of the planted seedlings are adapted to present conditions (i.e. 20% non-adapted). If conditions change so that only 40% are expected to be adapted (60% non-adapted), planting density should be increased threefold according to Campbell's model (Table 1 and Fig. 3). Increasing the density of plant-

TABLE I

Number of seedlings to plant per acre under various levels of random planting mortality and various proportions of non-adapted seedlings. The numbers are calculated to ensure that 95% of each 20 ft × 20 ft quadrat is stocked with at least one crop tree. Random planting failures of 0, 20, and 40% are used, corresponding to plantation survival rates of 100, 80, and 60% when using a seed source appropriate to the site. Results are calculated for proportions of non-adapted seedlings ranging from 10 to 90%.

Proportion non-adapted seedlings (%)	Planting mortality (%)		
	0	20	40
10	142	177	236
20	203	253	338
30	271	339	452
40	356	445	593
50	471	588	784
60	639	798	1064
70	915	1143	1524
80	1462	1827	2437
90	3096	3870	5161

ing is not a perfect solution to climate change, but it assures reasonable forest cover and reduces the risk of near-complete failure. Obviously, nursery costs and planting costs will increase. What may not be immediately obvious is that foresters must also invest more in seed collection and seed storage to accommodate the higher planting rate. Seed and gene conservation is important whether for artificial regeneration in plantation culture or for the restoration of native forest.

Deployment is another tool to counter environmental change. Instead of following the general rule of thumb that says local seed sources are best, foresters may find that transfers across seed-zone boundaries are a better counter to climatic change. Faced with global warming, they can either move seed northward from warmer climates or upward from lower elevations. Using seed from a seed zone lower in elevation should be safest. The seasonal change in photoperiod will be identical to the one in which the seed parents evolved and, if temperature changes are predicted correctly, the thermoperiod will match as well. According to Hopkins' Law (Hopkins, 1938), temperature decreases 1.4°C for each 1000 ft (305 m) increase in elevation in the US. Therefore, under projections of a 2.5°C change in temperature by 2050, seed should be imported from 1800 ft (about 550 m) lower in elevation. The actual adiabatic lapse rate may deviate from Hopkins' Law, and transfers should be adjusted accordingly. It is premature to prescribe transfers now, but forest managers should begin preparing the necessary infrastructure, and be ready to act in the event that the signal for global warming becomes clearer in the next 10 years.

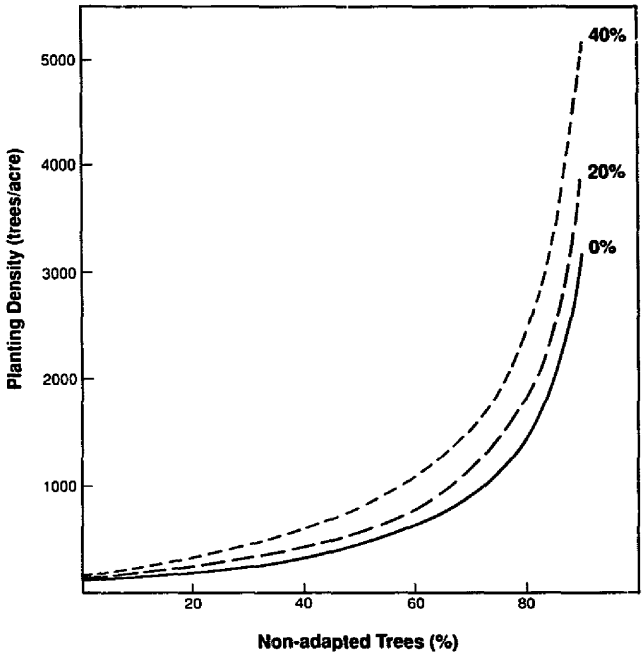

Fig. 3. Planting density required to achieve at least one crop tree on each 20 ft×20 ft quadrat (with 95% probability) as a function of the percent non-adapted seedlings. That is, of the 109 20 ft×20 ft quadrats acre^{-1}, between 103 and 104 will have at least one crop tree, given the proportion of non-adapted seedlings planted (the abscissa) at various levels of non-selective (random) planting mortality (the curves for 0, 20, and 40%) that result from poor planting technique or other, non-genetic causes.

The Institute of Forest Genetics' classic, ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.), elevational-transect study (Conkle, 1973) provided a model for seed transfer. Volume production by the local seed source at the high elevation test site (5650 ft or 1722 m above sea level) is 98% of the maximum at 50 years (Fig. 4). With a projected temperature increase of 2.5°C, the high-elevation site will become climatically much like the plantation site at 2730 ft above sea level (832 m) is now. Under those conditions, the seed source from 5650 ft will produce volume yields that are only 68% of the volume of the source from 2730 ft above sea level. Likewise, at 2730 ft above sea level, the use of the local seed source may result in a reduction in yield of 10%, and the best seed source then will be from lower elevation. In fact, should projections of global warming materialize, 2730 ft above sea level may well be the local, low-elevational limit for ponderosa pine in the next century, unless seed sources are imported from further south or inland.

Moving seed up in elevation or north in latitude may result in increased

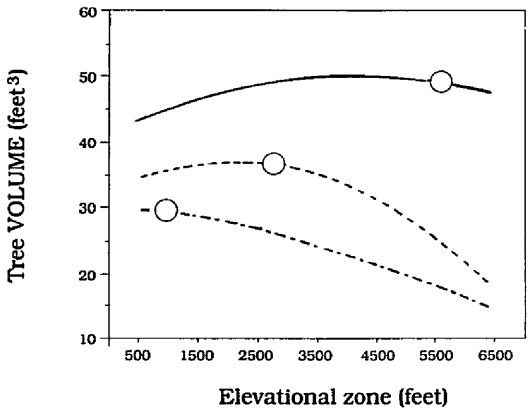

Fig. 4. Response curves for 50-year volume of ponderosa pine seed sources in relation to elevation of origin at three planting sites: high- (——), mid- (– –), and low-elevations (— — —). (M.T. Conkle, unpublished data, 1988.)

yields under present climatic conditions (Namkoong, 1969; Wells, 1969; Mangold and Libby, 1978) (Fig. 4), but not without risk. Selection has probably resulted in local populations that are adapted to survive extreme conditions, such as infrequent late spring or early fall frosts. Thus, they fail to take full advantage of the growing season in average years. Transfer from a milder climate may result in increased yields, but also entail some risk of occasional losses to frost (e.g. Squillace and Silen, 1962). The risk may be reduced in a period of global warming. In the Pacific Southwest Tree Improvement Program, mean 7-year height of ponderosa pine progenies increased with decreasing elevation of origin at all planting sites (Fig. 5), although the same relationship may not apply to all species. The low- and mid-elevation sources also outgrew the high-elevation sources at all plantations in the early years of the ponderosa pine elevational-transect study (Mirov et al., 1952), but were overtopped by the local-elevational sources by about 25 years. Warming temperatures over the next several decades should mean that low-elevation sources will maintain their lead in future plantings. Under the global warming scenario, the chances of cold damage to low-elevation sources will decrease with time.

Since meteorologists are uncertain about the actual amount of warming, foresters should employ the diversity principle. The best way to use diversity might be to mix seed sources. Forest managers could at least mix the local seed source and one they expect to be adapted under a worst-case scenario. The relative amounts of each would depend on how confident they felt about projected changes.

When seed sources are moved northward, the results are not as straightfor-

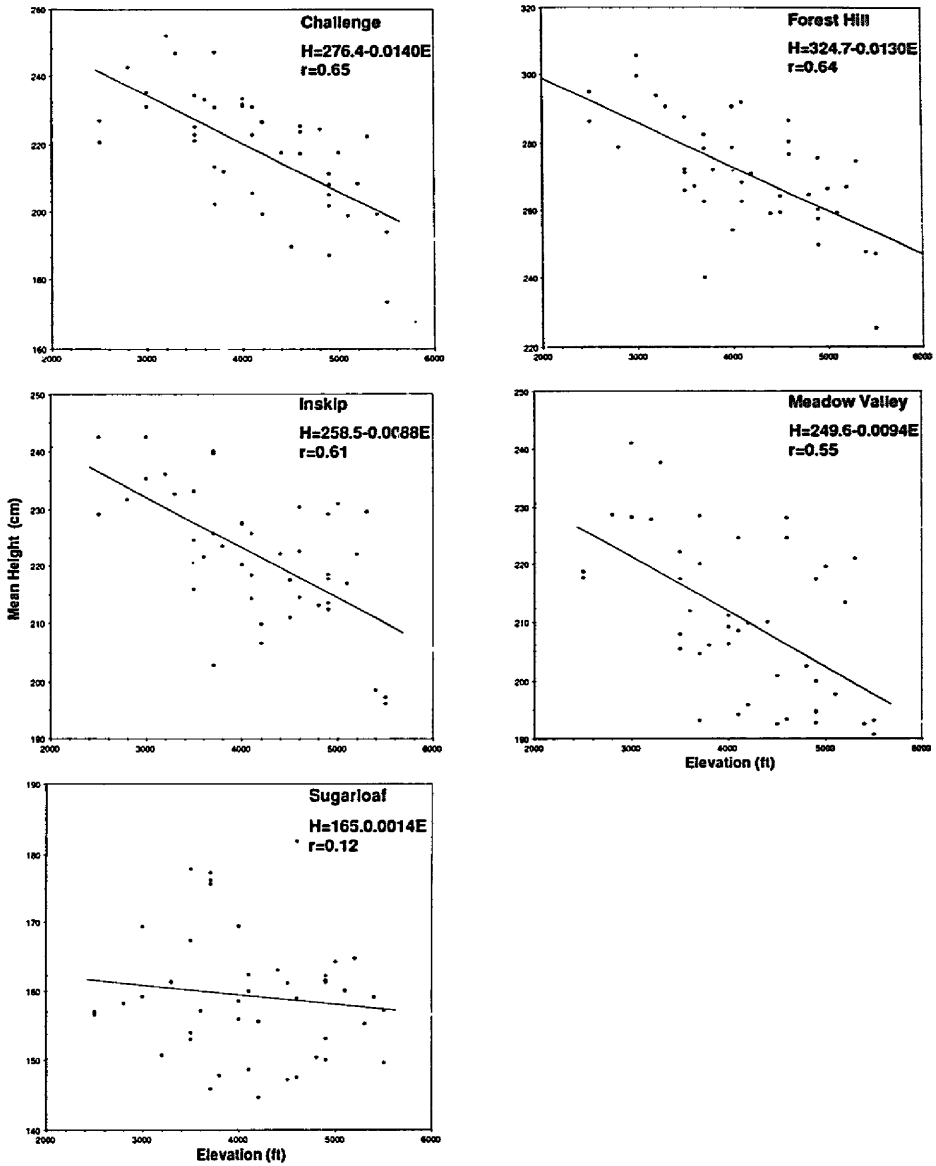

Fig. 5. Relation of 7-year height to elevation of origin for 44 open-pollinated families of ponderosa pine grown in five different locations. Note that height scale differs among graphs. (J.H. Kitzmiller, unpublished data, 1986.)

ward as when they are moved to a higher elevational zone. If a southern seed source is moved to a northern site, climate change may result in a thermoperiod similar to the one the seed came from, but the photoperiod will be different (Fig. 6). Photoperiods during the growing season are longer in northern latitudes than in southern. Seed sources moved north are often 'tricked' into remaining active too late in the autumn and, therefore, suffer frost damage. Moving seed great distances northward is an uncertain solution. One- or two-hundred miles, however, is not unreasonable.

The two tactics (i.e. maximize diversity and deploy seed to new zones), are not mutually exclusive. But of the two, maintaining or maximizing diversity is absolutely essential because climatic change will not stabilize for a long time. Conditions today are not the conditions that will exist 25 years from now and conditions 25 years from now will not be the same as in the year 2050. Furthermore, most projections use 2050 only for convenience; 2050 is the year when atmospheric carbon dioxide will have doubled. Climatic change would continue on after 2050 even if society were to entirely halt the production of greenhouse gases right now (Harrington, 1987) because it will be some time before the oceans and the atmosphere equilibrate. And nothing suggests that the production of greenhouse gases will be halted anytime soon, so atmospheric conditions will continue to change. Therefore, neither diversity

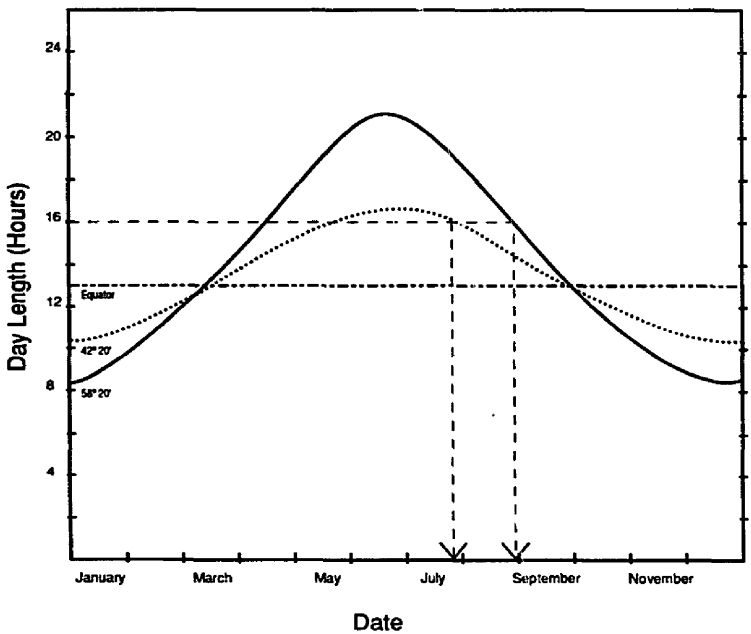

Fig. 6. The annual cycle of photoperiod at latitudes 42°20′ (....) and 58°20′ (——).

nor deployment can completely cope with rapid warming; the trees that survived in the establishment phase might no longer be adapted in the second half of the rotation.

PLANTATION FORESTS — IMPROVED SEED

Tree breeding offers the opportunity to reduce uncertainty and to make maximum use of the tools of conservation, diversification, and deployment. The degree of testing is the most important distinction between using seed collected in native stands versus using improved seed produced by selection and breeding (Fig. 7). Progeny, or family, tests are conducted over a range of sites in most tree improvement programs. Because the same families are grown in different environments, the tree breeder has the opportunity to measure their range of adaptation and then deploy them to maximum advantage. Two strategies are possible: (1) select and breed for specialists, varieties that perform exceptionally well in specific, defined conditions, and then deploy them to the appropriate site type; (2) select and breed for generalists, varieties that do at least moderately well in a broad range of environments.

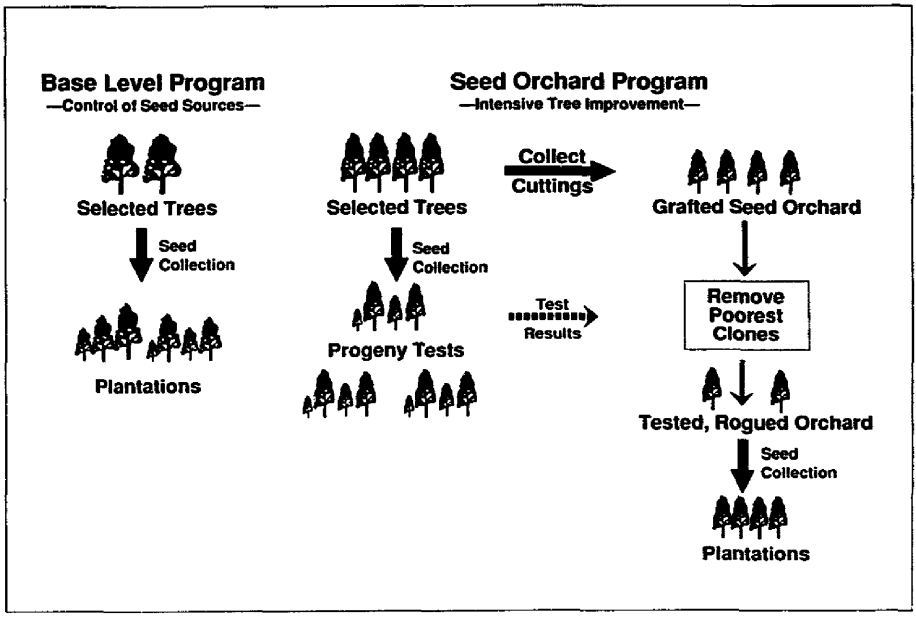

Fig. 7. At present, most reforestation efforts in the western US (left) use source-identified seed from parents of better-than-average appearance, but untested. In seed orchard programs (right), progeny are tested and only trees that produce superior progeny are retained for further seed production and reforestation.

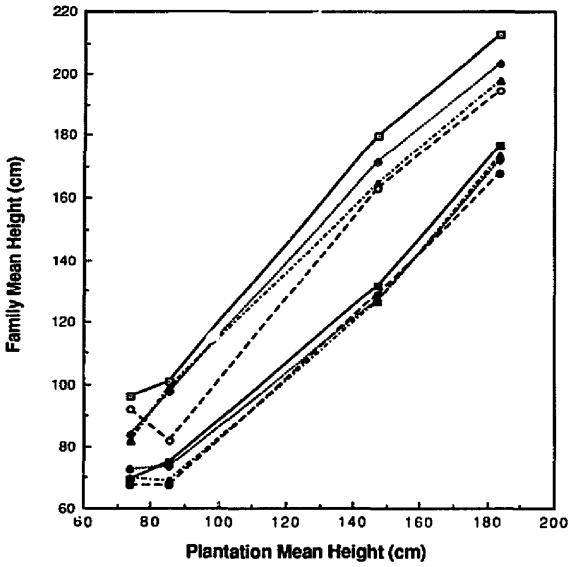

Fig. 8. Fifth-year height of the four best open-pollinated families and the four worst out of 32 families of ponderosa pine, plotted over plantation mean for four contrasting sites. The best families tend to be tallest and the worst families shortest on all sites, from the poorest to the most favorable. (J.H. Kitzmiller, unpublished data, 1984.)

If specialists are selected, a different subline or subgroup must be bred for each distinct site type. If predictions of future environmental conditions were accurate, the sublines could easily be deployed to appropriate sites. However, the future is not certain, so sublines must be deployed in mixtures and planted at high density. The breeder can bring different sublines together in a seed orchard and allow them to interbreed, generating a diverse progeny that will consist of crosses between sublines and within sublines. Crosses among sublines may show hybrid vigor, or heterosis, and perform well on a wide range of sites. Unfortunately, crossing sublines will require longer than simpler breeding procedures and may be impractical if climatic change occurs as quickly as some models project.

Because current climate models cannot accurately predict the magnitude of changes nor predict when they will stabilize, it is risky to select and deploy specialists. Of the two options, it is logistically simpler to select and breed for generalists, if they exist. In fact, they do exist. Progeny tests of ponderosa pine and Douglas-fir show that some families do well at virtually every site on which they are tested (Fig. 8). The effects due to differences among families are two to three times larger than the variation due to interactions between the families and the planting sites. Similar results are found in loblolly pine

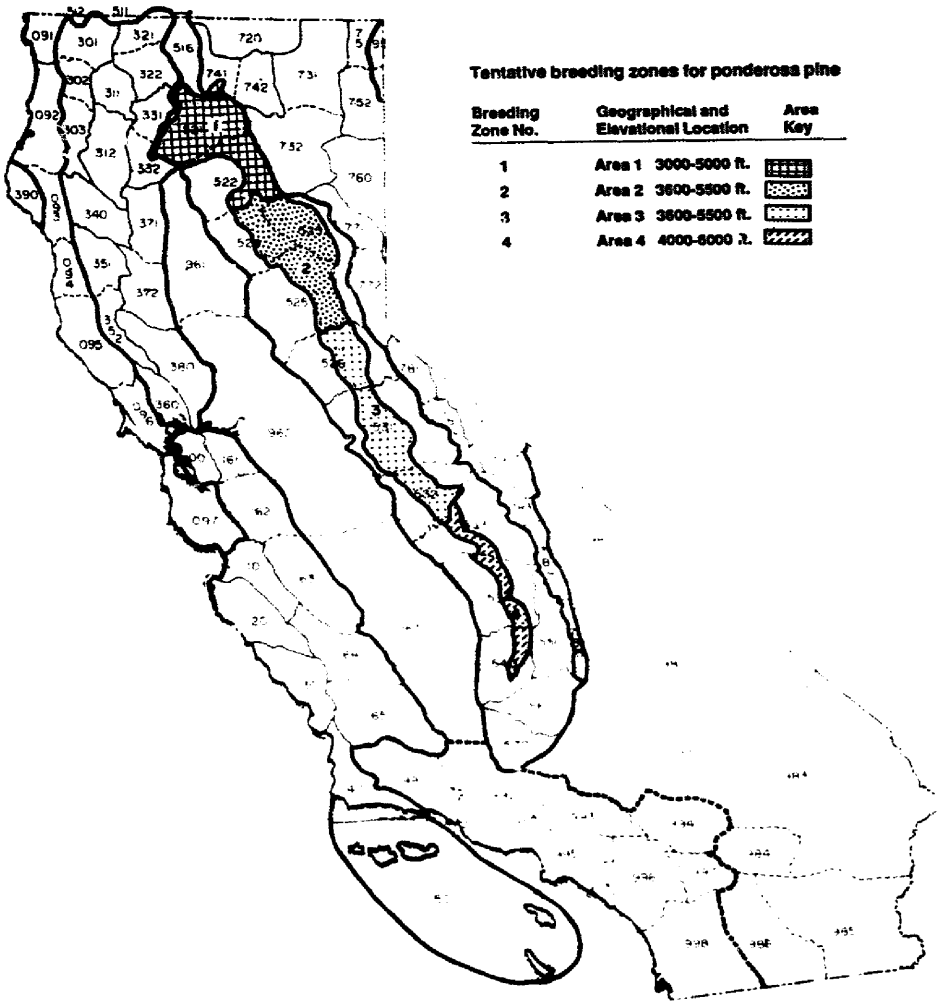

Fig. 9. Current breeding zones for ponderosa pine in the Sierra Nevada of California, superimposed on a seed collection zone map. (From Kitzmiller, 1976.)

(Li and McKeand, 1989) and many other species. Starting with a broad genetic base, the breeder should be able to uncover several good 'generalists' and maintain high levels of diversity.

Tree breeders establish breeding zones, areas in which their improved lines, the product of their seed orchards, will be used in reforestation. The breeding

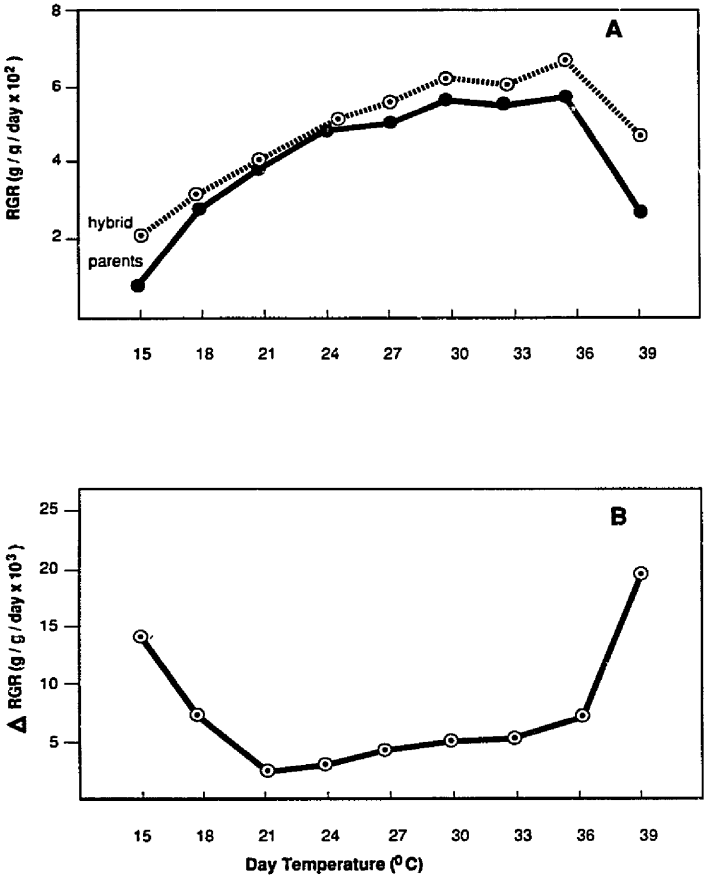

Fig. 10. (A) Relative growth rate (RGR) of a maize hybrid and mean RGR of its inbred parents as a function of temperature under controlled conditions. (B) The difference between RGRs of the hybrid and its parents. (After McWilliam and Griffing, 1965.)

zone is the area in which the line is tested (e.g. Fig. 9). Each breeding zone is served by a different seed orchard and a different breeding population. Given the possibility of climatic change, tree improvement programs should expand their testing programs to include a range of sites beyond current breeding-zone boundaries — beyond what was anticipated 10–15 years ago. If the range of tolerance is identified for the progeny of each clone in the seed orchard, appropriate mixtures of seed could be developed for every planting site, to take advantage of differences among families and to maximize diversity, buffering against uncertainty.

A second way to use genetic diversity as a hedge against uncertainty is to

maximize individual diversity. Most commercial conifers have two copies of each gene, one from their mother and one from their father (coast redwood is a notable exception). These copies may differ slightly, in which case the tree is called a heterozygote for that gene. Alternatively, both copies may be identical and the tree is a homozygote. Individuals heterozygous for several genes exhibit hybrid vigor, as in hybrid maize. Heterozygotes seem to perform well under extreme or stressful conditions and can tolerate a broader range of environmental conditions than homozygotes (Fig. 10).

Techniques for increasing heterozygosity can be complex, but some simple techniques are also available. One way in which many tree improvement programs attempt to increase diversity is by selecting only one tree per stand and then bringing these wide-ranging selections together in a seed orchard. In the seed orchard they interbreed, generating high levels of heterozygosity, and hybrid vigor, in their progeny. Many of the improvements in growth reported from early stages of tree improvement in the southeastern US are probably a result of this hybrid vigor, not solely the breeders' skills in selection.

CONCLUSIONS

Uncertainty is the major factor with which reforestation must contend, at least until better climate models are built. Worse than uncertainty, perhaps, is the assurance that whatever the conditions at the start of a rotation, they will change before the end. The buildup of greenhouse gases that result in global warming, whatever the degree, will not culminate by 2050 or even within the next century. We cannot specify an appropriate seed source or breed for specific conditions because that implies stability.

Therefore, the best plantation strategy is to maintain diversity, breed for generalists, and deploy intimate mixtures of seed sources or progeny-tested families. Foresters should not be too hasty in deploying seed among zones, but must be ready to act if the signal for global warming becomes clearer. To prepare, national governments should launch major programs of conservation to save native gene pools in seed banks, clone banks, or ex situ plantations. Seed of many conifers can probably be stored for at least a century under optimum conditions (F.T. Bonner, personal communications, 1989), and trees of clonal or seedling-origin can be maintained for just as long, although the risks of loss may be higher for plantations than for seed banks. The more conditions change and the more uncertain the future, the more these genetic resources will be needed in breeding and restoration. Unfortunately, neither the US nor other countries with which we are familiar have any national system or provisions for ex situ conservation of forest tree species. They are urgently needed.

Most of the conclusions we have drawn with regard to maintaining diversity and breeding for generalists involve little change in the tree improvement

programs that we know about. Certainly, these practices are the norm in the PSW Regional Tree Improvement Program (Kitzmiller, 1976). The main changes might be to accelerate research on adaptation, expand the present program of progeny testing to a wider range of sites, and enlarge seed banks for gene conservation.

Although it is nice to close on a positive note, it would be even better if we could say that global change posed no threat. That depends less on forest practices than it does on social and policy changes that affect consumption and procreation. To prevent major global destruction, society must curb the wasteful use of resources and control population growth.

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