ROOTED CUTTINGS IN PRODUCTION FORESTS

W.J. Libby[1]

Abstract.--This paper presents a case for using rooted cuttings in forestry. It briefly discusses their advantages and disadvantages with respect to genetics and breeding, forest ecology, and management. Hedging and other techniques are discussed as ways to control the maturation state of the clones. A major effort will be needed to adapt nursery technology to rooted cuttings.

Additional Competition, clonal selection, diversity, hedging, juvenility, specific combining ability.

INTRODUCTION

In order to take the first parts of this paper seriously, you must (at least provisionally) accept two assumptions: (1) Rooted cuttings survive and grow as well as or better than seedlings. (2) Rooted cuttings can be produced and planted at costs similar to those for seedlings. These assumptions will be discussed near the end of this paper.

GENETIC ADVANTAGES OF ROOTED CUTTINGS

There are impressive genetic advantages associated with the use of rooted cuttings. The first usually thought of concerns non-additive genetic variability, or specific combining ability. For many characteristics in many species, much of the genetic variation appears to be additive. This is fortunate, as most of our present breeding schemes and production seed-orchards are based on the general combining ability associated with additive genetic variation. But in some cases, a significant component of the genetic variation is non-additive. While some schemes have been proposed to utilize this kind of variation (such as 2-clone orchards), few are now operational. Clonal testing of rooted cuttings will allow us to identify those occasional individual genotypes that are outstanding due to a particular non-additive combination of genes. This outstanding performance will not be consistently repeated by either the sibs of such outstanding trees (the pure lines necessary for such sib consistency are not yet generally available in forestry) or by their offspring. This outstanding performance will be consistently repeated by rooted cuttings of these specific outstanding genotypes.

Inbreeding depression is another manifestation of non-additive genetic variation. It affects the offspring when relatives mate or are mated. Reductions in growth and vigor have been reported for most of the forest-tree species that have been subjected to controlled inbreeding. Inbreeding depression may be common among seedlings collected from those wild stands with a population structure that makes pollination by relatives likely. It will

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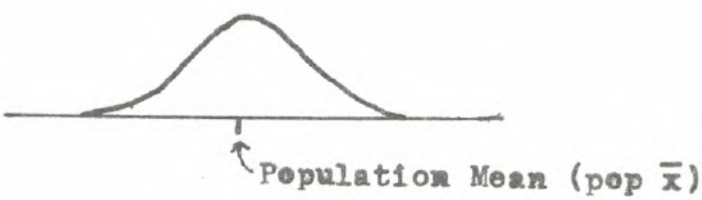
[1] Departments of Genetics and of Forestry & Conservation, University of California, Berkeley, 94720

also occur in seed-orchards that incorporate relatives. It is particularly likely in seed-orchards where more than one sib of each selected family is used to produce seed. If the normal reforestation propagule is a rooted cutting, those genotypes (seedlings or clones) exhibiting inbreeding depression can be excluded, and the production plantations can thus be free of inbreeding depression.

There is an important advantage to rooted cuttings associated with additive genetic variation, or general combining ability. Pick your favorite characteristic or index, and please consider the following:

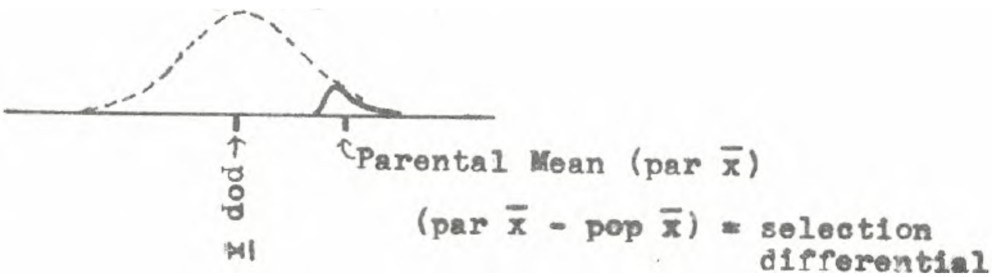
Phenotypic variability of the original seedling-origin population may be distributed something like:

A.



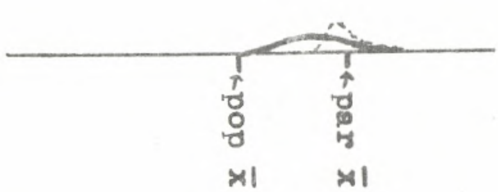
From this population, we select the following phenotypes as parents:

B.



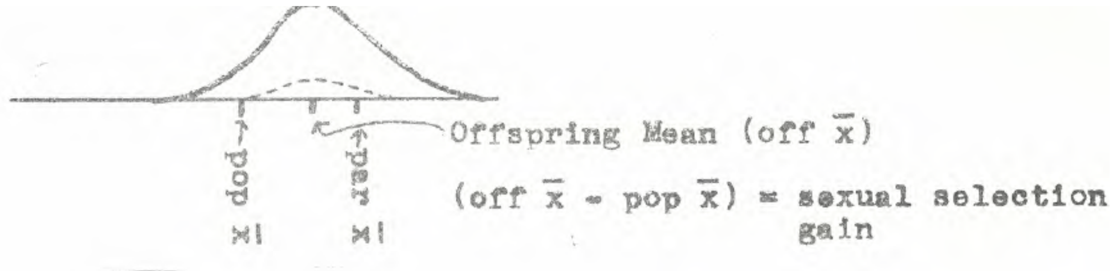
The phenotypes of these selected parents are partly the result of favorable enviroments and favorable non-additive genetic combinations. The "additive-genetic" genotypes of the selected parents may be distributed something like:

C.



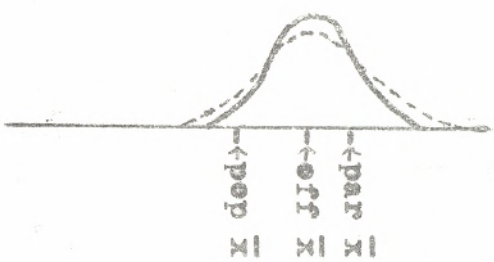
The phenotypes of their offspring will be distributed something like:

D.



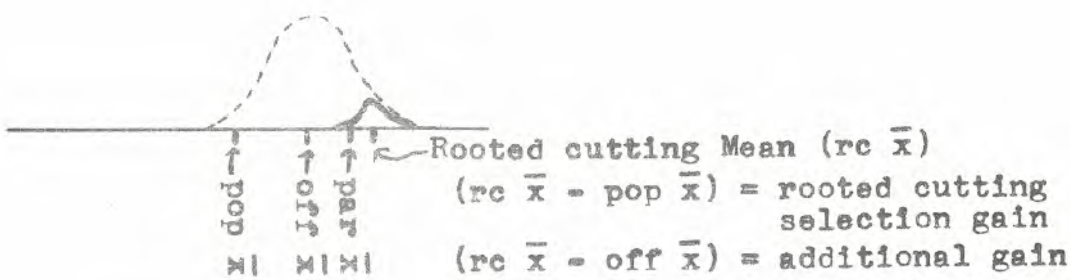
Because of sexual recombination of the parental genes, the offspring genotypes will exceed the range of the parental genotypes, and, with environmental contributions to variation averaged out, will be distributed something like:

E.



If we **use rooted cuttings** of only the best of these offspring, depending on how effective our clonal selection is, the genotypes of the selected clones will be distributed something like:

F.



This substantial additional gain is possible because half or more of the additive genetic variance occurs within families, and a tree-improvement program relying on sexually produced seedlings can only take advantage of the average performance of its selected families. By applying clonal selection and using rooted cuttings of the very best individuals in selected families, we can take advantage of the remaining half (or more) of the genetic variation thus available to us. This may require some cost in time for the additional selection. However, it can and should be done incrementally, by first eliminating those clones which are deformed or are runts, or otherwise disqualify themselves, and then periodically eliminating other clones that develop characteristics that don't measure up. Thus, within-family clonal selection can begin in the very first year that pedigreed seedlings and cloning techniques are available, and it should continue to refine the donor population as information on the clones accumulates through rotation age and beyond. Even in the first year, the average performance of the rooted cuttings should equal or exceed that of seedlings from a seed-orchard (Figure D, above), and as the number of clones under test and in use is selectively reduced from (say) 10,000 to 500, the additional gain of the rooted cuttings will approach that shown in Figure F.

In some species, many of the very best-growing trees produce few seeds and/or little pollen in seed-orchards. On the other hand, the offspring of the unusually prolific pollen- and seed-producers in the seed-orchards could repeat this sexual performance in production forests, thereby reducing average stand growth. The principle in both cases is that photosynthate devoted to sex is usually at the expense of wood production, and there is some evidence that sexiness in heritable in trees. With rooted cuttings, those genotypes that devote little energy to sex can be encouraged to produce modest numbers of offspring in at least an occasional favorable year, and some of these can be added to the set of cutting donors and put under test. Thus, while the genetic contribution of genotypes that concentrate on making wood (not love) may be small or even absent in some years in a sexually-reproducing seed-orchard, they can contribute their appropriate share of rooted cuttings every year.

Gene conservation is a genetic consideration of some importance. Clonally maintaining an appropriate sample of unselected populations may be an effective way to conserve a safe supply of future variability, without contamination by pollen from our increasingly-domesticated production forests.

GENETIC DISADVANTAGES OF ROOTED CUTTINGS

We have found that clones age, and that later cuttings are different from earlier cuttings of the same clone in such properties as growth-vigor and form. Knowing this, it has been considered futile to try to identify good clones if the clones continue to mature and thus change their properties during the test period.

In a breeding program, some selection differential is sacrificed in applying clonal selection (where each genotype is replicated over the test environments), compared to selection in a system using strictly seedlings (where each genotype appears only once). We need more theoretical work and more practical experience to help us assess the various trade-offs (such as selection accuracy, and assessment of genotype-environment interaction) against this loss of selection differential.

ECOLOGICAL ADVANTAGES OF ROOTED CUTTINGS

I now think that the most attractive feature of using rooted cuttings is the possibility of maintaining high genetic diversity within production forests. This results from two kinds of control available with clonal propagation. The first is pedigree control on each clone, so that one can avoid having related clones in the same production plantation. The second is that each clone is a separate biotype. Thus, although an insect or pathogen may be -˜osely adapted to one clone in a plantation, there will be a genetic gap between clones. By contrast, seedlings from a seed-orchard are a continuum of biotypes, with a greater possibility of incremental adaptation of the insect or disease across the entire population being used in plantations. Furthermore, since it appears economically feasible to genetically improve more species with rocted cuttings than with seedlings (see below), improved mixed-species plantings are also more feasible using rooted cuttings.

Along this same line, it is possible to manage rooted-cutting reforestation so that it is unlikely that any two plantations will have exactly the same set of clones. As an example, the project computer might have information on the known performance of (say) 2,000 good clones appropriate to a particular region. A forester would request planting stock for a plantation, and provide information on such things as latitude, longitude, elevation, soil, aspect, pest history, etc. The computer would print out the identity of the 50 best clones for such a site. These would then be planted in mixture. A request for another plantation site in that region would produce another list of 50 clones, 15 of which might be the same as for the first site, but 35 different. By contrast, if the same regional seed-orchard were serving both sites, each plantation would receive seedlings that were very similar samples of the same general seed-orchard production.

As we learn a great deal about these clones, it may be possible to prescribe not only favorable planting mixtures, but favorable planting sequences. In particular, clones making complementary (rather than competing) demands on the site would be planted next to each other.

ECOLOGICAL DISADVANTAGES OF ROOTED CUTTINGS

There is a danger of selecting too few clones per plantation, the extreme being a monoclonal planting. Then if some event occurs, such as a cold snap or a disease, an unacceptable proportion of the plantation may be damaged or lost. Note that this is not an intrinsic disadvantage of rooted cuttings, but rather, is a potential for management error.

MANAGEMENT ADVANTAGES OF ROOTED CUTTINGS

There are many problems associated with seed-orchards that can be avoided by using rooted cuttings. These include graft incompatibilities, pollen contamination, cone and seed pests, and a short cone-collection season. Economies of scale can be achieved by growing cutting-donors serving many different kinds of sites together. This should not be done with seed-orchards if there is a possibility of cross-pollination between trees from the different kinds of sites. Similarly, cutting-donors may be grown on land surrounded by forests of the same species, but pollen contamination can force the location of seed-orchards to areas far removed from other management activities.

With clones, the single-family pedigree is the unit of selection, and each cutting-donor is essentially independent of all others. Because of the flexibility this provides, relatively minor species and unusual sites can be served by a modest number of selected, known, and appropriate clones. By contrast, a special seed-orchard is unlikely to be economically justified for each specialized relatively minor demand.

Finally, known clones will have more predictable performance than will seedlings, each of which is brand new on the face of Earth. Aggressive management should be able to use this greater predicability in many ways.

MANAGEMENT DISADVANTAGES OF ROOTED CUTTINGS

Producing a healthy, plantable rooted cutting is not the same as producing a seedling. It will be necessary to develop many new nursery techniques, and this will take both time and money.

THE COMPARABILITY ASSUMPTION

In most species, cuttings taken from late-adolescent or mature trees do not grow with the same form and vigor as do seedlings. While some aspects of form are better in such rooted cuttings, the cuttings are almost always distinctly inferior to seedlings in both early survival and volume growth. However, cuttings taken from young seedlings are very similar to seedlings in survival, development, and growth. In other words, the growth and development of a rooted cutting is very much dependent on its maturation state.

The trick, then, is to keep some members of each clone in a juvenile stage of maturation, not only until other members of the clone can be evaluated, but for a much longer time so that identified superior clones can be extensively employed. There now appear to be several ways to accomplish this trick. My current favorite is called "hedging", which means that a seedling or rooted cutting is repeatedly clipped back, thus forming it into a hedge. Cuttings taken from such repeatedly hedged donors are juvenile, even though the chronological age of the hedge is well beyond a juvenile age. We have done this for several years with Monterey pine (Pinus radiata), and are now engaged in parallel studies with about a dozen species. Several other research centers are also engaged in such studies with many other species. The early results are encouraging, but for most species we won't know how long clones can be held in a juvenile state until we've actually done the experiments for those periods of time.

Another method being used to arrest maturation is serial propagation--i.e., cuttings are taken from recently-rooted cuttings, which were taken from recently-rooted cuttings, etc. And, several research centers are investigating ways of reversing maturation, so that tissue from an outstanding mature tree can be returned to a juvenile state, and a juvenile clonal line of that genotype can thus be established. However, there are as yet no reliable techniques for doing this.

It is possible that we may not want completely comparable maturation states of cuttings and seedlings. For instance, early-adolescent cuttings of radiata pine have attractive advantages with respect to resistance to two important diseases, and have better stem-form than seedlings (or more juvenile cuttings), with little or no difference in relative growth rates. Thus, the preferred propagules for radiata pine reforestation may be rooted cuttings at maturation state of about 4-8 years, rather than either seedlings or juvenile cuttings. It appears that we may be able to use hedging to set and hold any maturation level we desire. Indeed, we have held over 200 clones of radiata pine at about a 4-year-old maturation state for 7 years, from 1965 to 1971, by hedging at a height of about one meter.

THE PRODUCTION ASSUMPTION

With exceptions in a few species, a plantable rooted cutting is more expensive than a plantable seedling. For some species, this may always be true. For others, it may just require creating a new technology of rooted-cutting nursery practice. When rooted-cutting research and experience is similar to that for seedlings, so may be its relative costs. If the advantages of rooted cuttings over seedlings are sufficient, absolute equality of production costs need not be achieved in order to decide to use cuttings. For example, the additional cost of vegetatively-propagated fruit trees (compared to seedlings) is easily justified. In the tree-fruit industry, seedlings are essentially limited to use in breeding programs, with selected new genotypes clonally propagated to production plantings.

A PREDICTION

Within the next 10-15 years, in a substantial number of forest-tree species now planted exclusively as seedlings, the majority of production plantations will routinely include rooted cuttings of selected clones in their planting stock.

INFORMATION ON RECENT WORK

Much recent thinking and information on rooted cuttings of forest trees is available in the proceedings of 2 symposia: the 1973 meeting on vegetative propagation of forest trees; and the 1975 meetings on juvenility in woody plants (both cited below).

LITERATURE

1974. Special Issue on Vegetative Propagation. New Zealand Jour. of Forestry Science 4(2):119-458.

1976. Symposium on Juvenility in Woody Perennials. Acta Horticulturae 56 (May):1-317.