VEGETATIVE PROPAGATION AND THE GENETIC IMPROVEMENT OF NORTH AMERICAN HARDWOODS

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ABSTRACT
Progress and problems in vegetative propagation of important North American hardwoods are reviewed with emphasis on rooting cuttings and the application of propagation techniques in breeding research. Some problems in rooting physiology are discussed.

INTRODUCTION

Vegetative propagation research with deciduous forest tree species in North America has been closely associated with genetic improvement efforts. During the last two decades these improvement programmes have expanded to include most of the region's major hardwoods. For most species, vegetative propagation is being used to establish clone banks or seed orchards of selected breeding stock. In a few hardwoods, which are especially easy to propagate by means of cuttings, commercial production of clonal stock is an objective; breeding programmes are designed to take advantage of this propagation capability.

Recent advances in hardwood propagation can be attributed to the application of now well-known physiological information and to the general use of mist propagation techniques. Propagation of difficult species may require better knowledge of the physiology of root initiation. In this paper I will review the current status of research with some major species now in breeding programmes, delineate some of the major problems facing propagators of the species, and pinpoint potentially fruitful areas for future research. Major emphasis will be placed on rooting cuttings.

VEGETATIVE PROPAGATION

Poplars

Dormant stem cuttings of juvenile eastern cottonwood (*Populus deltoides* Bartr.) and hybrid poplar root easily and are used to establish plantations (e.g., McKnight, 1970). Breeding programmes are therefore usually aimed at producing clones for commercial use. Mist propagation of greenwood cuttings has been used to rapidly expand clones of interest (Randall and Miller, 1971). In this group of species, root initials are formed during shoot development (Shapiro, 1958), and most rooting represents elongation of these primordia. While light (Shapiro, 1958) and moisture (Bloomberg, 1963; Allen and McComb, 1956) have major effects on rooting, the problem of root initiation *per se* is not an obstacle to propagation. However, appreciable genetic variance in rooting characteristics has been reported (Cunningham, 1953; Wilcox and Farmer, 1968), and establishment success also appears to be strongly related to the physiological quality of cutting stock. Research on the genetics of rootability and on stock quality will therefore be particularly valuable in the immediate future.

Physiologically mature dormant cuttings taken directly from older trees can be rooted under greenhouse conditions after treatment with indole-butyric acid (IBA) (Farmer, 1966). This material is not usually suitable for field propagation, though more easily rooted cuttings can be obtained by rejuvenating material from older trees.

Aspens

Aspen root suckers taken while still succulent will develop roots under suitable environmental conditions. Stem cuttings from more physiologically mature material are difficult to root (Afanasiev, 1939; Snow, 1938). Propagation techniques developed in Europe for *Populus tremula* L. (Muhle Larsen, 1943) have been adopted successfully for *P. tremuloides* Michx. Variable results have been obtained with *P. grandidentata* Michx. Farmer (1963) found that suckers taken from cultured root segments or from natural sucker stands would root under mist or in small polyethylene tents after IBA treatment. Rooting percentage was lower for *P. grandidentata* than for *P. tremuloides,* and survival after rooting was also lower. Benson and Schwalbach (1970) reported 70 to 90% rooting for *P. tremuloides* under polyethylene and noted that control of pathogens is important to success. Suckers of *P. grandidentata,* on the other hand, were slow to root and especially susceptible to pathogens. Wide clonal variation in rooting success with *P. tremuloides* was experienced by Barry and Sachs (1968) using mist propagation. Zufa (1971) has developed a propagation system for aspens and their hybrids in which suckers are rooted in slit polystyrene tubes placed in a polyethylene tent. While he observed considerable variation in rooting within and between species, rooting of large-tooth espen was not much inferior to that of trembling aspen. Given continued development, a commercially feasible vegetative propagation system for the aspens should be available by the time genetically improved clones are produced by breeding programmes. However, improved seedling stock may be the logical breeding product rather than clonal stock, and vegetative propagation may find use mostly in research and development.

Triploid and tetraploid aspens have been regenerated from callus tissue cultures (Winton, 1968, 1971). If the culture technique can be extended to diploid plants and developed to compete cost-wise with simpler mist propagation methods, tissue culture could have a place in breeding research or commercial production. At present, however, its most useful function appears to be as a vehicle for studying the physiology of root and shoot initiation and development.

Black Walnut

Black walnut (*Juglans nigra* L.) propagation has been recently reviewed by Farmer (1973). Most present difficulties with grafting and budding probably stem from failure to apply known principles rather than from lack of effective methods. Environmental stress inherent in field grafting and the problem of stock "bleeding" due to root pressure can be avoided with the bench grafting method of Cerny (1965), which is done while buds are physiologically dormant. While there is some evidence of clonal variation in compatibility which may affect success, both grafting and budding are suitable enough for breeding research, though relatively expensive.

Recent results of rooting research (Shreve and Miles, 1972; Farmer and Hall, 1973) indicate that black walnut is amenable to mist propagation. Both etiolated and normal shoots from juvenile material have been rooted after several types of auxin treatment. The most successful rooting results are those of Shreve and Miles, who report average rooting of 80%. They also note the successful propagation of "adventitious" shoots from at least one physiologically mature genotype and stress the necessity of using material from "adventitious" shoots. The next step in this research will be refinement of (1) procedures for producing suitable cutting material (2) chemical treatments, and (3) propagation environment. When this is done a propagation system for black walnut may consist of grafting followed by pollarding of grafted stock to produce adventitious shoots. Shreve and Miles (1972) suggest that this stock might be managed as stool beds. In a high value species such as black walnut, considerable investment in vegetative propagation is warranted if broad-sense heritability estimates for growth and other important characters indicate that clonal testing and selection is a profitable breeding approach.

Oaks

While oak grafting is considered difficult, success has been high enough to encourage its use in breeding research (Hatmaker and Taft, 1966) and some shade tree propagation (Flemmer, 1962; Skinner, 1953). Hatmaker and Taft reported 50 to 60% successful unions in experimental field grafting of northern red (*Quercus rubra* L.), white (*Q. alba* L.), and chestnut (*Q. prinus* L.) oaks. In the Tennessee Valley Authority's (TVA) more recent production grafting, approximately 30 to 40% success has been achieved with these species. Nurse-seed grafting as described by Goggans and Moore (1967) may also be useful. The bench grafting method of Cerny (1965) shows promise of greatly increasing success.

In early work Thimann and DeLisle (1939) observed up to 82% rooting of dormant *Q. rubra* cuttings taken from juvenile trees. While there are no recent reports of successfully rooting hardwood cuttings, mist propagation of juvenile material from several southern oaks has been moderately successful (Farmer, 1965; Duncan and Matthews, 1969). Duncan and Matthews have also rooted cuttings from 18 to 32-year-old trees of *Q. falcata* Michx. and *Q. nigra L.* and noted some evidence of synergistic effect between rooting hormone (IBA) and fungicide (Folpet). Lack of rooting techniques for physiologically mature trees of the major eastern deciduous oaks is probably more the result of insufficient research than an inherent species difficulty. Use of modern mist propagation with rejuvenated material (obtained as for black walnut above) should readily lead to extension of results of Duncan and Matthews to other species.

Maples

All the native American maples and a number of exotics used ornamentally in North America have been propagated by cuttings (Enright, 1958). Only sugar maple (*Acer saccharum* Marsh.), however, has been subjected to major breeding efforts. Snow (1941), using juvenile material, reported the first successful rooting of greenwood sugar maple cuttings before mist propagation was generally adopted. Continuous mist was used with limited success by Dunn and Townsend (1954) in work with physiologically mature trees, which varied in their rootability. Enright (1958) then obtained up to 90% rooting of mature material using intermittent mist and IBA. A review of recent problems and progress in maple propagation has been prepared by Donnelly and Yawney (1973). Mist propagation of cuttings taken directly from mature trees is now practical, with average rooting of approximately 70 to 80% if conditions are optimised. The best rooting is obtained with large (20 cm-long) cuttings taken in late June when shoot elongation has stopped and leaves have matured. Treatment with commercial auxin preparations or IBA enhances rooting. Considerable genotypic variation in rooting response to auxin has been noted.

The major obstacle to sugar maple propagation at present is high winter mortality of newly-rooted cuttings. In New England, where most propagation is conducted, even supplementary autumn nutrition and over-wintering at 1°C has resulted in less than 50% average survival of rooted cuttings. It is now believed that the generally low vigour of propagated plants is responsible for the overwintering problems. Strong correlation between rooting vigour of cuttings and subsequent survival tends to support this hypothesis. It is possible that renewed apical growth following rooting will be essential to enhance the nutritional status of plants before overwintering. In successfully propagating *A. palmatum,* van Klavern (1969) has noted that it is important for plants to be propagated early enough to allow new growth after rooting. This can be done with the aid of modern greenhouse facilities. A second approach might involve propagating material at latitudes considerably south of its geographical source to take advantage of longer growing seasons and milder winters.

Until problems of overwintering are solved, budding and grafting, which are now routine procedures (Kriebel and Gabriel, 1969), will remain the major propagation techniques used in breeding programmes. These programmes have as their objective improved genetic potential for timber production, maple syrup production, and shade tree characteristics. Data on variation and inheritance in maple sap yields and sugar content (Kriebel and Gabriel, 1969) indicate that testing and production of individual high-producing clones may be a rapid and effective breeding approach once rooting techniques are refined. Similarly, considerable horticultural experience in selecting for autumn colouration and form suggest that heritability for these characters is high enough to warrant reliance on vegetative propagation in producing desirable genotypes.

Yellow-Poplar

While some success with late summer budding has been reported (Funk, 1962), most yellow-poplar (*Liriodendron tulipifera* L.) selections in the several existing breeding programmes are being propagated by grafting. Late spring field grafting of dormant scions to growing root stocks has been used successfully in Tennessee by Churchwell (1965) and Evans and Thor (1971). Bench grafting, as used by TVA (Hatmaker and Taft, 1966), has been resulting in 50 to 80% successful unions when used on a production basis.

Enright (1957) was able to root 50 to 78% of cuttings taken directly from 30-year-old trees; the successful treatment was a 10-second dip in a 20 000 ppm IBA solution followed by greenhouse mist propagation in a sand medium. Though Enright's work has not been repeated, McAlpine (1964) subsequently rooted 68% of cuttings from stump sprouts in an outdoor mist bed. Kormanik and Porterfield (1966) partially girdled mature trees to obtain epicormic shoots with juvenile rooting capability; about 75% of these shoots rooted in outdoor mist beds after treatment with 0.8% IBA in talc. In a more extensive test of this procedure, 20 to 24% of cuttings taken from 30 girdled trees rooted (McAlpine and Kormanik, 1972). About 20% of rejuvenated shoots from grafted scions were rooted by McAlpine (1966). McAlpine and Kormanik (1971) have also suggested pruning crowns of mature trees to obtain rejuvenated material.

The value of individual yellow-poplar trees is not enough to justify commercial use of vegetative propagules, given current propagation problems. Thus, present objectives of vegetative propagation will include establishment of clonal breeding arboreta and production of genetically uniform material for research. Most of the recent rooting research has been done in outdoor mist beds where environmental control is difficult; greenhouse propagation may result in consistently better rooting. Further investigation of the chemical stimulation of rooting and of genetic variation in rooting response should also quickly result in higher rooting percentages.

Sweetgum

While little grafting of sweetgum (*Liquidambar styraciflua* L.) has been reported, the good success of Steinbeck (1970) with spring bench grafting suggests that it presents few problems. Sweetgum has the capability of producing root suckers (Kormanik and Brown, 1967), mostly from suppressed buds imbedded in the periderm. These suckers exhibit juvenile rooting capability, and Farmer (1966) rooted greenwood cuttings taken from both suckers on cultivated root segments and naturally occurring suckers in clear cuttings. In a sand : peat medium, up to 100% of cuttings developed roots within 6 weeks in a mist chamber; IBA was unnecessary for good rooting. Brown and McAlpine (1964) used root cuttings directly and reported that a high percentage produced both shoots and roots. Their work also pointed to the existence of some clonal variation in propagation capability.

The above propagation efforts, though successful, represent preliminary work which must be expanded to develop propagation systems. Of particular importance will be studies of root suckering and its relationship to the dormancy and carbohydrate status of roots. The relative merits of (1) directly propagating root cuttings and (2) rooting stem cuttings taken from suckers need assessment. In order to do this adequately, more routine trials under various conditions must be conducted to get a better understanding of propagation problems. As noted by Kormanik and Brown (1967), root suckering is responsible for considerable natural sweetgum regeneration, and the species can exhibit a clonal habit similar to aspens. This capability for natural vegetative propagation has implications for genetic improvement efforts since single genotypes can be expected to survive over a number of rotations.

Black Cherry

Bench grafting of black cherry (*Prunus serotina* Ehrh.) following procedures described by Hatmaker and Taft (1966) is now being routinely used in TVA's breeding programme with 40 to 60% successful unions. Methods of rooting greenwood cuttings reported by Farmer and Hall (1969) have now been used to develop a population of 33 juvenile clones which are under test. Average rooting of this material after treatment with 0.8% IBA in talc was 80 to 90% during the April-May propagation season. Only a small percentage of these clones exhibit rooting less than 50%.

Material from mature trees has been grafted, rejuvenated by drastic pruning, then rooted under mist. In preliminary work with rejuvenated material, we have observed wide clonal variation in rooting percentages; cuttings from several clones in TVA's breeding collection typically exhibit 70 to 80% rooting. Others are essentially unrootable (less than 5%) with our present techniques. The major research job at hand is to develop successful methods for these difficult rooters. While improvement of misting environments (e.g., supplemental light and carbon dioxide) should help, a better knowledge of the physiology of root initiation is probably a prerequisite to real success.

Sycamore

American sycamore (*Platanus occidentalis* L.), which is receiving increased attention in development of short rotation fibre production systems (Steinbeck *et al.,* 1972), can be propagated from dormant stem cuttings. In the early studies of Nelson and Martindale (1957) juvenile 50-cm-long cuttings planted in sandy loam exhibited up to 65% survival under nursery conditions. In southern Louisiana, Briscoe (1963) subsequently observed that similar cuttings taken throughout the year rooted in the nursery; only from May through August did rooting fall below 50%, and 100% of the March-collected cuttings rooted. Recently, McAlpine *et al.* (1972) regenerated sycamore by laying cuttings horizontally in furrows. While establishment success has been relatively easy with cuttings, we still know little about the physiology and morphology of root initiation, and nothing of the rooting potential of physiologically mature material. Some routine work with dormant cuttings under greenhouse propagation conditions should quickly lead to information and techniques needed in the development of genetically improved clones.

Elms

In contrast to the above species, elm breeding is aimed at producing trees having ornamental value and resistance to diseases, mainly the Dutch elm disease (*Ceratocystis ulmi* (Buisman) C. Moreau). While a number of breeding approaches are being used involving several species (*Ulmus americana* L., *U. rubra* Mühl, *U. pumila, U. japonica*), the final products will probably be desirable clones propagated by cuttings. Fortunately, the elms are reasonably easy to propagate. Auxin-treated softwood stem cuttings from several species were rooted successfully by Doran and McKenzie (1949) without the aid of mist. Bretz (1949) successfully rooted leaf bud cuttings in an early attempt with mist propagation. Later reports by Onellet (1962) and Pridham (1964) outline rooting systems for softwood cuttings from mature trees. Root cuttings have been used directly from *U. americana* (Shreiber. 1963) and *U. carpinifolia* (Doran and McKenzie, 1949; Bretz and Swingle, 1950). Suckers developing from root callus have also been rooted (Tchernoff, 1963; Girouard, 1971).

ROOTING PHYSIOLOGY

Recent applied research using information on juvenility, auxin effects, and environmental factors has resulted in at least moderate success with hardwood species considered very difficult to root a few decades ago. Refinement of standard techniques should improve this success, especially with some species which have not been subjected to much investigation. However, real progress beyond this point will hinge upon a much better knowledge of the physiology and biochemistry of root initiation and its relationship to environmental influences. Some investigative steps in this direction have been reviewed by Hess (1968) who concludes that root initiation is regulated by a number of components, any one of which may be limiting. Nutritional and auxin components of root initiation systems are familiar to propagators. In horticulturally orientated research considerable recent attention has been given to new components, called rooting cofactors, which may act in conjunction with auxin. For the most part these cofactors have been assayed by the Mung bean test in which they were first detected (Hess, 1962). Some root-promoting cofactors have been found in practically all material sampled, either by diffusion (Kawase, 1971) or by the more common extraction techniques; but cofactors have usually been more abundant in easily rooted material; e.g., Fadl and Hartmann (1967); Lee *et al.* (1969); Ashiru and Carlson (1968). In other work (e.g., Lipecki and Dennis, 1972) no correlation between rooting potential and cofactor level has been observed.

The cofactors have been generally identified as phenolics, and part of their synergistic effect with indole-acetic acid (IAA) (noted in bioassays) is probably due to prevention of auxin destruction. Phenolics, such as catechol, chlorogenic acid, and pyrogallol, have been shown to have properties similar to extracted cofactors in the Mung bean test. Some recent work with phenolics and extracted cofactors has been done in other systems (Hackett, 1970; Lee and Tukey, 1971), but as yet their effectiveness in a bioassay using difficult-to-root material has not been demonstrated. Lee and Tukey (1971), however, have noted that IBA and flavonol and rutin used together did increase rooting of *Euonymous.* Correlation studies (Bachelard and Stowe, 1962; Lee and Tukey, 1971) also add support to the hypothesis of an active role for naturally occurring phenolics and flavonoids.

In hardwoods, physiological and morphological comparisons of easy- and difficult-to-root material, a logical experimental approach, needs to be broader than a search for rooting cofactors as defined by Mung bean rooting. More work with bioassays involving both easy- and difficult-to-root material of the same species or clone, such as that of Hackett (1970), is needed. Work with forest species should incorporate more directly applicable bioassays; the aspen test of Hicks (1972) is a beginning. Techniques for *in vitro* culture of tissues and organs are being developed for tree species and may ultimately be useful in studying the interaction of various rooting factors. Further assays of synthetic phenolics and flavonoids using difficult material may be of practical value also.

Some grafting experiments suggest that cofactor effects may vary qualitatively. Ashiru and Carlson (1968) and Lee *et al.* (1969) demonstrated that difficult-to-root scion material on easy-to-root stock lowered the rooting potential of the stock; reciprocal grafts had the opposite effect. Reciprocal bark grafts reported by Hess (1969), on the other hand, gave evidence of a non-mobile rooting factor.

Lee and Tukey (1971) have observed that growing cutting stocks of *Euonymous* under intermittent mist results in an accumulation of natural root-inducing phenolic and flavonoid compounds in leaf tissue. Cuttings taken from these plants rooted better than those from unmisted stock. This work suggests new possibilities for preconditioning cutting material of difficult-to-root hardwoods and it gives new insight into the reasons for the success of mist propagation.

In other recent work, R. C. Hare (pers. comm.) has used combinations of auxins, fungicides, growth retardants, and sugar in talc as rooting compounds, and has rooted some difficult species of *Pinus* with them. He also has used growth chambers to obtain optimum combinations of environmental factors (light, temperature, relative humidity, carbon dioxide) resulting in increased rooting percentages relative to those observed under standard greenhouse misting systems. The enhancing effect of carbon dioxide has been previously observed by Molnar and Cumming (1968) with several woody species.

Results from the above areas of rooting research indicate that considerable progress in propagation capability with difficult species should come about within the next decade. Propagation research with improved hardwoods should, during this period, move from routine application of known information to use of these species as experimental material in more basic studies of rooting. The moderate difficulty of some hardwood species and the apparent high degree of intraspecies variation in rooting capability make them good experimental material for this stage of work. Of particular importance, once basic rooting techniques are developed, will be the genetics of rootability in species suitable for commercial clonal production.

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