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Review paper

Rootstock effects in grafted conifers: A review

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Application. Grafting is widely used to propagate conifers. Selected rootstocks can be used to improve graft success, reduce incompatibility, alter scion vigor and increase seed production. It may also be possible to alter crown characters and scion physiology.

Abstract. The literature on rootstock effects (on scions) in conifers was reviewed, specifically: graft success, compatibility, size, reproduction, phenology, crown and needle characters, mineral content, organic compounds, water relations, disease resistance and wood properties. Scions usually had higher graft success and less incompatibility on more closely related rootstocks although there were exceptions. Even intergeneric grafts have succeeded on occasion. Although there were marked rootstock effects on growth and reproduction, the effects did not follow a pattern with increasing relationship. It is also likely that some crown characters and the nutrient content of scions can be manipulated by the use of rootstocks. For many characters, a specific rootstock may give a desired result only for a limited number of scion types (species, cultivars or clones). With some exceptions, the review shows that the subject has not been comprehensively studied. Many of the studies were either short-term, inadequately replicated, or poorly designed to allow firm conclusions about rootstock effects. The physiological and biochemical mechanisms, which cause the changes seen in morphology, are not well understood. Further research and more comprehensive study of rootstock effects on scion biology are recommended.

Introduction

Large-scale grafting to produce conifer seed was done as long ago as 1820 with Corsican pine (*Pinus nigra* Arnold var. corsicana) grafted in situ on Scots pine (*P. sylvestris* L.). By 1843, 100,000 grafted pines were growing in the forest of Fontainebleau (Bouvarel 1960). More recently thousands of acres of seed orchards and clone banks have been planted and grafted for tree improvement programs. In the southeastern USA alone almost 10,000 acres of seed orchards have been established (Jett 1988). Grafting is important in propagating conifers mainly because many species are hard to root, especially when using cuttings from mature trees (Hackett 1987). Grafting will probably be widely used for years to come in forest tree improvement. For example, a third generation of seed orchards will be initiated in the southeastern USA in the mid-1990s. As this work is expensive, the potential of speciality rootstocks should not be neglected.

Fruit tree rootstocks have been developed for uses such as size control, precocity, fruit yield and quality, cold hardiness, disease resistance and adaptation to sites. Although there are several reviews on rootstock use in fruit tree species, (e.g. Tukey 1964; Lockard and Schneider 1981; Rom and Carlson 1987), such summaries are not available for conifers. However, reports on conifer rootstocks date back to Poiteau (1826).

We present here some current knowledge on the effects of rootstocks in coniferous species, divided into sections on effects on graft success, compatibility, scion size, reproduction, phenology, crown and needle characters, mineral content, organic compounds, water relations, disease resistance and wood properties. This report is limited to the effect of different genetic groups (species, cultivars and clones) used as rootstocks. Scientific and common names of conifers are as in Dallimore and Jackson (1966) while taxonomy of pines is according to Mirov (1967). The term rootstock here usually refers to a group of plants considered relatively homogeneous (e.g. full-sib or half-sib family, or population) rather than an individual.

Graft success

The terms graft survival, graft success and graft incompatibility are sometimes used interchangeably. In this paper we define a graft as successful where a graft union forms between scion and rootstock. It has long been claimed that grafts between closely related species are more successful than between distantly related combinations (Poiteau 1826; DeLamarre 1831; Loudon 1854; Carriere 1855; Laurie and Chadwick 1931). In a study with 22 species grafted on Atlas cedar [*Cedrus atlantica* (Endl.) Carr.] rootstocks, only scions from other members of the family Pinaceae grafted successfully (Yakovleva and Kuznetsov 1974). A similar result was obtained in a study with 5580 grafts using cuttings from six conifer families (Yakovleva 1974). There have been exceptions to this trend, such as higher success for slash pine (*P. elliottii* Englm.) on stocks of loblolly pine [*P. taeda* L.] than on *P. elliottii* (Sniezko 1986). Lists and recommendations are available for species and cultivars used successfully as rootstocks for different scion types (Bogdanov 1972; Dolgolikov 1975; MacDonald and Lane 1980; Alkemade 1981; Luo and Chen 1981; Hatch 1982; Blomme and Vanwezer 1982, 1984a, b).

A. *Intraspecific grafting*

Within a species, grafting on stocks more closely related to the scion may improve graft success (Kedharnath and Kapoor 1967; Popov et al. 1981), may not have a significant effect (Schmidtling 1986) or may reduce success (Silva and Romanelli 1986).

B. *Interspecific Grafting*

Sometimes a species grafts more successfully on stocks of the same species, when compared to grafts on other species within the genus. In a study with five pine species and a hybrid used as scions, the best success of a species was on its own stocks (Kim 1969). Similar results were obtained for several pine species (Magini 1965; Ahlgren 1972; Rojas and Garcia 1980; Sniezko 1986).

In other studies this trend was not clear. Three southern pines [loblolly, slash and shortleaf (*P. echinata* Mill.)] were intergrafted in all combinations (Allen 1967). Both slash and shortleaf pine had less success on their own stocks than on the other two species. Other cases with similar or better success on stocks different from the scion have been reported (Zak 1955; Slee 1967; Schmidtling and Scarbrough 1970; Brinar 1973; Gansel 1973; Schmidtling 1973, 1983, 1988; Sniezko 1986). Other interspecific pine grafts have been studied (Mirov 1940; Mergen 1954; Bouvarel 1955; Zak 1955; Singh and Mahajan 1967; Bogdanov 1972). Some successful grafts were between taxonomically distant species (Mirov 1940; Severova 1975).

Higher graft success on stocks of the same species has occurred in *Abies* (Pitcher 1959; Gathy 1961; Karlsson and Carson 1985) and *Picea* (Pitcher 1959), although other studies for these genera did not show this (Van den Driessche 1974; Meneve and Istas 1975). Other successful interspecific grafts have been reported in *Abies* (Popnikola 1964; Kolev 1967), *Chamaecyparis* (Hunt and O'Reilly 1984) *Cupressus* (Dyson 1967; Yakovleva and Kuznetsov 1972) and *Taxodium* (Elk 1967). Extensive studies on interspecific *Larix* grafts were reported by Avrov (1977).

C. *Intergeneric grafting*

Intergeneric grafts are rarely used in conifers. The wide differences in anatomy, physiology and morphology between some genera often prevent successful grafting (Magini 1965; Corti et al. 1968; Avrov 1971; Ahlgren 1972; Blomme and Vanwezer 1985). However, there have been successes, with up to 94 % success for Nootka cypress [*Chamaecyparis nootkatensis* (D.Don) Spach] cultivars on Chinese arbor-vitae (*Thuja orientalis* L.)

stocks (Blomme and Vanwezer 1982). Other successful intergeneric grafts have been made (Mergen 1954; Prozakin 1962; Popnikola 1964; Luo and Chen 1981; Drori et al. 1983). White cedar (*Thuja occidentalis* L.) rootstocks are used commercially for grafting Lawson cypress scions (Hunt and O'Reilly 1984).

Compatibility

A compatible graft has a mechanically strong union and grows healthily and normally (Lantz 1970). In this paper incompatibility is said to occur where a union forms but the plant later develops physiological and developmental malfunctions; it may be expressed soon or after several years. Compatibility is vitally important in grafting (Slee and Spidy 1970). Incompatibility between stock and scion can weaken or kill the grafted tree. If incompatibility develops after a few years, orchard composition can be unbalanced. If severe, incompatibility can cause a clone to be dropped completely from a tree improvement program. The pattern of incompatibility is similar to that of graft success, with more closely related individuals more likely to be compatible.

A. *Intraspecific grafting*

A good example of using special rootstocks is the work by Copes to overcome the serious incompatibility problems in grafting Oregon Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco]. Rootstocks from different provenances did not differ in compatibility (Copes 1971). When unrelated rootstocks were compared with stocks related as half-sibs to the scions, compatibility on half-sib stocks was 19 % higher (Copes 1973). Compatibility was also tested on two other types of stocks: (1) a stock found compatible with both parents in the cross which generated the scion family (type a) and (2) a stock found compatible with one parent of the scion family (type b). (This indirect method was used because the trees were highly self-sterile; it was therefore difficult to get seed from selfing a parent tree). Type (a) stocks were much more compatible. It was also shown that graft incompatibility was strongly inherited, with a heritability of 0.81 in one study (Copes 1974). A further study was planted on six sites from British Columbia to northern California using about 6000 grafts. Three highly compatible clones were used to generate six rootstocks: namely, three wind-pollinated families (one from each parent tree) and the three control-pollinated crosses between the clones. Five standard clones were grafted on all families at all sites. Compatibility averaged

78.6 % for the wind pollinated families (only one parent selected for good compatibility) and 91.5 % for the control pollinated families (both parents selected). In another series of experiments, the wind pollinated and control pollinated families were shown to be more graft compatible as rootstocks than unselected stocks used locally at the six sites (Copes 1982). A strategy to select for compatibility was outlined for this species: in two stages, 16 trees (of the 303 originally screened) were finally released for large-scale production of cuttings for rootstocks (Copes 1981). Another study on Douglas-fir also showed the best way to overcome incompatibility was using selected rootstocks (Slodicak 1980).

Similarly, two Virginia pine (*P. virginiana* Mill.) clones (with a tendency towards incompatibility) survived better on related stocks (Manchester 1973). The same pattern has emerged for other pine species (Slee and Spidy 1970; Van der Sijde 1974).

B. *Interspecific grafting*

Interspecific pine grafts are compatible in some instances. Dwarf mountain pine (*P. mugo* Turra) was compatible as a rootstock with five other pine species used as scions; *P. strobus* L. (white pine) with three species (Ahlgren 1972). Other compatible combinations between pine species have been reported (Matthews et al. 1963; Corti et al. 1968; Veresin and Uljukina 1970). However, some combinations were incompatible (Holst 1962; Holzer 1962; Corti et al. 1968; Ahlgren 1972; Brendemuehl 1974). Japanese larch [(*Larix kaemferi* (Lamb.) Carr.] was compatible as a rootstock for three *Larix* species (Matthews et al. 1963).

C. *Intergeneric Grafting*

Two *Cedrus* species finally became incompatible on *P. pinea* L. (Stone pine) though several grafts survived for two years (Corti et al. 1968).

Scion growth rate

Control of scion growth by specialized rootstocks is standard in some species such as apple (*Malus* spp.) (Ferree and Carlson 1987). There is evidence that rootstocks can alter scion growth rate in conifers as well. Research on conifers dates back to 1954 when Mergen reported on height growth of slash pine grafted on eight pine species. It appears that some stocks cause fast growth while others reduce growth, with some others intermediate. Rapid scion growth is not always desired; in fact, slow growth could help seed collection in seed orchards.

One hypothesis tested has been that slow growing individuals or groups (used as stocks) would slow scion growth. There is some evidence for this (Allen 1967; Krusche and Melchior 1977). However, in other studies the slow-growing stocks caused rapid growth. This occurred with Norway spruce (*Picea abies* L. Karst) grafted on dwarf rootstocks (Melchior 1984), loblolly pine grafted on the slow growing species table-mountain pine,[1] and dwarf slash pine clones used as interstocks (Schmidtling 1983b). If different degrees of incompatibility develop, studying height growth can become complicated since incompatibility reduces scion growth. A stock which often caused incompatibility would be avoided even if it had other desired qualities.

A. *Intraspecific grafting*

There were significant differences, between rootstocks, in scion elongation in intraspecific grafts in *P. taeda* (McKinley 1975; Bower 1981) and Norway spruce (Bryndum 1965). Slash pine clones grafted on related rootstocks grew faster than on unrelated stocks (Schmidtling 1986). On the other hand, there was no significant difference in growth of loblolly pine scions between 25 full-sib families used as rootstocks. Another approach in height control has been the use of witch's brooms as rootstocks; in Scots pine these inhibited the growth of grafts, but also caused the death of the grafts (Khirov 1973).

B. *Interspecific grafting*

There have been contradictory results on whether growth is reduced on stocks of other species. Scion growth of loblolly pine was compared on six rootstock types (three half-sib families of loblolly pine, two half-sib families of slash pine and a spruce pine (*Pinus glabra* Walt.) bulk population) (Schmidtling 1983a). The scions were significantly shorter at five years on the spruce pine stocks than on the other types; the most growth was on loblolly stocks. Slower scion growth, when grafted on other species, was reported in several studies (Dyson 1975; Karlsson and Carson 1985). On the other hand, loblolly pine scions were shorter on loblolly than on shortleaf stocks four years after grafting (Schmidtling 1973) although this difference cancelled out at age 11 (Schmidtling 1983a). Faster scion growth on species different from the scion were reported in other studies as well (Allen 1969; Holzer 1969, 1970).

The level of vigor is sometimes specific to the stock-scion combination.

Growth of Norway spruce was faster on Norway spruce seedlings than on Servian spruce [*Picea omorika* (Pancic) Purkyne], but slower than on Oriental spruce [*P. orientalis* (L) Link] (Bryndum 1965). Similar results were seen for *Pinus* species (Ahlgren 1972).

Some species may induce slower growth overall. Red pine (*P. resinosa* Ait.) caused slow scion growth of four pine species, about half the rate on *P. strobus* (Ahlgren 1972). Finally, there were cases where the species used as rootstock caused little difference in scion growth (Van den Driessche 1974; Sniezko 1986).

Reproduction

As grafting is widely used in seed orchards, rootstock effects on reproduction are important. The desired outcome is earlier and heavier production of seed. Available literature, mainly on strobilus formation, dates back to the 1950s with reports on pine grafts (Hermann 1951; Mirov 1951; Mergen 1954).

The ideal for seed orchard management are stocks which reduce scion vigor and increase seed production. Some dwarfing rootstocks used in fruit crops in fact increase fruit yield and induce precocity (Lombard and Westwood 1987). This may occur among conifers as well; red pine of Japan (*P. densiflora* Sieb. and Zucc.) rootstocks caused early strobilus formation in loblolly pine while reducing height growth (Schmidtling 1983). Incompatibility may stimulate pollen and cone production on occasion (Ahlgren 1972; Zobel and Talbert 1984).

A. *Intraspecific grafting*

The merit of dwarf rootstocks for promoting strobilus formation remains uncertain. More ramets developed female strobili when grafted on dwarf Norway spruce stocks (compared to normal-growing stocks) in one study (Krusche and Melchior 1977). However, there was no significant effect in two other studies (Melchior 1984, 1987).

Strobilus formation in pine scions differed between rootstocks, two years after grafting (Byram et al. 1987, authors unpub. data). However, the difference was not significant by age four in one case (Byram et al. 1988). Little is known how closer relationship within a species affects reproduction. Formation of male strobili was consistently higher on related rootstocks, compared to unrelated stocks, in slash pine; on the other hand, more female strobili were formed on unrelated rootstocks (Schmidtling, 1986).

B. *Interspecific grafting*

Interspecific grafts sometimes produce more strobili than grafts on stocks of the same species (Schmidtling 1969, 1983), and it has even been said that interspecific grafts are generally more fruitful than intraspecific (Schmidtling 1973). In other instances grafting a species on its own rootstocks has given more strobili (Ahlgren 1972; Sniezko 1986). One reason for the contradictory results may be that the rootstock has less effect during a year with a heavy cone crop (Schmidtling 1973). Spruce pine appeared useful in reducing vigor in loblolly pine scions but not in stimulating strobilus formation (Schmidtling 1973). However, *P. sylvestris* stocks appeared to stimulate both growth and strobilus production in other pine species (Nikitin 1963; Severova 1968). The effect of interspecific grafts in genera other than *Pinus* has been studied little.

Other studies with both intra- and interspecific grafts showed no significant rootstock effects, such as on:

- cone size and seed properties (Johnsson et al. 1954);
- cone and seed yield (Johnsson 1961);
- time of pollen shedding (Schmidtling 1971);
- seed yield (Dyson 1975);
- cone survival and seed yield (Schmidtling 1983); and
- strobilus production (Grabovskaja 1966; Guldager 1972; Sniezko 1986).

Other traits

In addition to graft success, compatibility, scion size and reproduction, other aspects of scion behavior have been studied. In most cases there is insufficient information to generalize, but reported effects on physiological characters may give clues as to how morphology, size, reproduction, or other traits are affected. It has been claimed, for example, that auxin levels may be altered in certain graft combinations (Yakovleva 1977), and that chlorophyll and photosynthesis can be affected (Kamaltinov 1964).

A. *Phenology*

Rootstocks did not significantly affect scion phenology in intraspecific grafts of two species: in the flushing of *Picea abies* (Melchior 1984), and the cessation of scion elongation in loblolly pine (Jayawickrama et al. 1990). Further, no difference in the vegetative phenology of loblolly pine was observed between grafts on five pine species (Schmidtling 1973).

B. *Crown and needle characters*

Rootstocks can affect crown characters: the number of branches (Holzer 1970; Van den Driessche 1974), branch characters (Schrock 1966) and crown form (Hoffmann 1965). However, there was little difference between provenances (used as rootstocks) on the number of branches per whorl, branch angle and branch diameter in inter- provenance grafting of *P. kesiya* Royle ex Gord. (Guldager 1972). Scion needle length differed by rootstock in interspecific pine graft combinations (Ahlgren 1972), but there was no consistent relationship between needle length and either rate of growth or compatibility. Needle length in Arolla pine (*P. cembra* L.) differed according to the species used as rootstock (Holzer 1970).

C. *Mineral content*

Significant rootstock effects on scion mineral content have been observed in the following: foliar Ca in spruce species (Van den Driessche 1974), eight elements in pines (Tomchuk 1969) and P, K, Ca and Mg in loblolly pine. Levels of N and K were unaffected in spruces (Van den Driessche 1974) and N in loblolly pine; Mg, S, P, K, Mn and Fe were not affected by rootstock in slash pine (Schmidtling 1988).

D. *Organic compounds*

In general, different rootstocks have had little effect on the concentrations of the organic compounds studied. This was found with monoterpenes (Schmidtling 1974; Kossuth and Barnard 1983), terpenes (Chudnyi and Dokuchaeva 1979), resins (Santamour 1977), oleoresins (Mirov 1940) and starch and sucrose (Jayawickrama et al. 1990). However, there were significant differences between rootstocks (in loblolly pine) for the content of hexoses (Jayawickrama et al. 1990) and total sugars in scion needles.

E. *Water relations*

The rootstock family did not significantly affect predawn needle water potential in loblolly pine (Jayawickrama et al. 1990).

F. *Disease resistance*

Few studies linking rootstocks and disease resistance have been reported although grafting on stocks of a rust-suceptible family significantly increased fusiform rust incidence in slash pine (Hollis et al. 1979). The authors suggested that some susceptibility factor in the root system was transported to the shoot.

G. *Wood properties*

Specific gravity of scions in grafted slash pine was independent of the specific gravity of the rootstock; this was also the case for tracheid length (Anonymous 1963).

Conclusions

Of the rootstock effects discussed above, the clearest trends are in graft success and compatibility, where scions are usually more successfully grafted on more closely related stocks. Grafts between taxonomically distant species can succeed on occasion. Although clear differences in growth and reproduction are caused by different rootstocks, it is difficult to predict a rootstock's influence. There is insufficient reported research to see trends in other aspects of scion behavior, although it is likely that some crown characters and scion contents of some minerals can be manipulated by the use of selected rootstocks. For many characters, it appears that a specific rootstock will only give a desired effect in a limited range of scions. Regrettably, many reports did not give reasons for using the rootstocks employed in the research. Without this information, the reader can only assume that these rootstocks were commonly used or expected to have a desired effect. Further, several studies had too few grafts of some or all combinations; some others used too limited a range of scion types (e.g. one or two clones) to safely characterize the effect of the stocks. The lack of an effect in some of the studies could be due to their short duration, especially if only monitored over one or two years.

Based on the research reviewed, priorities for future research are suggested. These studies should include enough genotypes and replications, and be maintained for long enough, to draw reliable conclusions.

1. More comprehensive coverage of rootstock effects (on variables such as size, strobilus production, phenology, adaptability, disease resistance, and crown characters) is needed.
2. Resolving the reported contradictions, such as faster growth on stocks of the same species in some studies, and faster growth on other species in other studies.

3. Further research on effects of different stocks on the physiology and biochemistry of grafted conifers. It may then be possible to identify mechanisms that cause the observed changes in morphology, as have been suggested for other tree species (Lockard and Schneider 1981; Jones 1984).
4. More research on genera other than *Pinus*, to get a more balanced understanding of rootstock influences for conifers.

How much available information on rootstock effects is actually used operational forestry and horticulture is unknown, since little is reported on this. Sixteen very compatible rootstocks were developed and widely used in clonal seed orchards of Oregon Douglas fir (Copes 1981). Pond pine has been routinely used for incompatible clones of loblolly pine.[1] In areas of the southeastern USA with a high incidence of fusiform rust, rust resistant families of loblolly pine are used for grafting the same species. Scots pine has many good features for use as rootstocks in the USSR (Nikitin 1963; Severova 1968; Veresin and Uljukina 1970).

Despite these examples, there is room for better use of rootstocks to solve problems and improve efficiency. Procedures to screen and test plants for use as rootstocks are similar to procedures used to identify plants for other desired features. Broad-based programs are needed to select plants to fulfill the perceived needs. Information on rootstocks is too valuable to leave unused.

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1. Personal communication, Dr. B. J. Zobel, Zobel Forestry Associates, 106 Fountain Brook Circle, Cary, NC USA.

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