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INHERITANCE OF GRAFT COMPATIBILITY IN DOUGLAS-FIR

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ABSTRACT

Graft compatibility of genetically related and unrelated rootstock-scion combinations was compared. Scion clones were 75% compatible when grafted on half-related rootstocks but only 56% compatible when grafted on unrelated rootstocks. Most variance associated with graft incompatibility in Douglas-fir appears to be caused by multiple genes.

Introduction

The role of genetic relationship in graft compatibility has been well demonstrated in antigen-antibody reactions of animals. Studies with man (Billingham 1966), mice (Schultz 1959), and frogs (Volpe and McKinnell 1966) have all shown that grafts between genetically related donors and hosts have a higher compatibility than those between unrelated donors and hosts. It is widely accepted that in plants, grafts made within species are more likely to be successful than those between species, genera, or families (Hartmann and Kester 1968). A correlation between genetic relationship and graft compatibility has been suggested for grafts of peach-plum (Grasselly 1968), almond-plum (Kester, Hansen, and Panetsos 1965), apricot-peach (Lapins 1959), and peach-peach (Bregger 1948). Indirect evidence of inheritance of graft compatibility was demonstrated in apple trees by correlating likenesses of protein

spectra of rootstock and scion with biological data for graft compatibility. Stocks and scions with similar protein spectra were more likely to form compatible unions than were those with unlike spectra (SAFONOV and VEIDENBERG 1969). Little else is known of gene control of compatibility response in plant grafts. This preliminary study was started to explore the nature of gene control over graft compatibility in the conifer Douglas-fir (*Pseudotsuga menziesii*).

Material and methods

Genetic effect on graft compatibility in Douglas-fir was investigated in two different experiments. The objective of experiment 1 was to determine whether more compatible grafts resulted when the scion and rootstock were genetically related than when the scion and rootstock were unrelated. The objective of experiment 2 was to determine the compatibility of seedlings grafted on rootstocks which were compatible with either one or both parents of the seedlings.

In experiment 1, scion clones were grafted on related and unrelated rootstocks. Related rootstocks were obtained by growing seedlings from crossed and wind-pollinated seed collected from the scion clones. The rootstocks received half their genes from the scion clones; thus, they are termed "half-related" throughout this report. Unrelated rootstocks were random nursery stock from hundreds of different parents. Some scion clones served as male and female parents of the rootstocks, so that maternal and paternal influence on compatibility could be tested. The parents were approximately 50- to 80-year-old trees. Seedlings from each cross were grafted with scions from each parent when they were 1 year old. A cleft graft was made on the terminal of each tree. Unrelated rootstocks were grafted with the same clones when the rootstocks were 2 years old. All grafting was done in a greenhouse on potted trees. Compatibility was determined by anatomical test 18 months after grafting (COPES 1967). The test involves the presence (incompatible) or absence (compatible) of characteristic wound areas in the xylem tissues connecting the stock and scion. No autoplastic grafts were made because a past study had already demonstrated complete compatibility of such grafts (COPES 1968).

The next step for experiment 2 should have been testing the parental clones on rootstocks grown from self-pollinated seeds. Such seedlings would have all genes in common with the scion clone and could have been termed "whole-related." Unfortunately, the Douglas-fir trees studied were highly self-sterile and few self-pollinated seedlings were available for grafting; therefore, in experiment 2, whole-related rootstocks were simulated through judicious selection. Unrelated rootstocks that were tested and found compatible with both parents of the seedlings were selected as simulated whole-related rootstocks. It was hoped that they had compatibility factors analogous to those found in actual whole-related offspring. The rootstocks were 10- to 12-year-old trees growing in a field plantation. Terminals from 1-year-old seedlings (experiment 1 rootstocks) were collected for scions and were grafted upon the selected rootstocks. Cleft grafts were made on the tips of the lateral branches. As a control, scions from seedlings of each parentage were grafted upon rootstocks which were compatible with only one of the seedling's two parents. Compatibility was determined by anatomical test 18 months after grafting (COPES 1967).

Results and discussion

Except for the highly aberrant parentage clone 14, experiments 1 and 2 showed that increased compatibility resulted from grafting genetically related rootstocks and scions. In experiment 1, scion clones grafted upon half-related rootstocks averaged 19% (75% vs. 56%) more compatible grafts than the same clones grafted upon unrelated rootstocks (table 1). The 19% gain probably occurred because the scion clones had more genes in common with half-related rootstocks than with unrelated rootstocks.

In experiment 2, an even higher compatibility resulted with simulated whole-related rootstocks than was found in experiment 1 with half-related rootstocks. In experiment 2, 91% of the grafts were compatible when seedling families were grafted upon rootstocks which were compatible with both parents, while only 50% were compatible when grafted on rootstocks which were compatible with only one parent (table 2).

Clone 14 probably deserved special genetic study because of its obvious atypical behavior in rejecting related rootstocks. In both studies it consistently rejected a high percentage of grafts in which its genes were present in both scion and rootstock. It was distinctly more compatible when either the rootstock or the scion contained no clone 14 genes. Treatment differences were highly significant in both experiments when clone 14 seedlings were excluded from an unweighted analysis of variance ($F = 20.94^{**}$ for experiment 1 and 17.66^{**} for experiment 2). Inclusion of clone 14 seedlings in the analysis still resulted in highly significant dif-

TABLE 1

AVERAGE COMPATIBILITY OF 12 CLONES GRAFTED ON RELATED AND UNRELATED ROOTSTOCKS (RELATED ROOTSTOCKS HAD HALF THEIR GENES IN COMMON WITH THE SCION CLONES)

SCION CLONE	PARENTAGE OF RELATED SEEDLING ROOTSTOCKS	% GRAFTS COMPATIBLE WHEN SCION CLONE IS GRAFTED ON: Related rootstock %	Related rootstock Range	Related rootstock N^a	Unrelated rootstock %	Unrelated rootstock N
6	6 × 5, 6 × 24, 6 × 165	68	50–100	37	67	9
8	8 × 5, 8 × 165, 8 × 16	92	80–100	39	75	15
24	24 × 6, 24 × 165	65	37–89	17	67	33
5	5 × 6, 5 × 8, 5 × 16, 5 × 165, 5 × wind[b]	56	22–68	104	47	66
165	165 × 6, 165 × 8, 165 × 24, 165 × 60, 165 × 9, 165 × 14, 165 × wind	97	86–100	224	86	34
14	14 × 16, 165 × 14, 14 × wind	12	8–19	66	67	39
16	16 × 5, 16 × 8, 16 × 14	67	50–100	46	50	6
60	60 × 165, 60 × wind	77	66–88	117	34	53
9	9 × 165	100	100	10	49	65
34	34 × wind	53	53	15	27	11
160	160 × wind	84	84	19	54	24
175	175 × wind	95	95	43	55	22
Weighted average	...	75	...	...	56	...

[a] N = number of grafts examined.
[b] Wind = wind-pollinated.

ferences in experiment 2 ($F = 12.45^{**}$) but fell somewhat below the 95% level in experiment 1 ($F = 3.82$, NS).

Scion clones grafted upon half-related rootstocks from reciprocal crosses showed identical compatibilities and therefore indicated no evidence of cytoplasmic inheritance.

Variance associated with graft compatibility in Douglas-fir may be due to a number of genes. With multiple-gene effect, parental clone grafts made upon whole-related rootstocks should have exhibited twice the 19% gain obtained from half-related rootstocks in experiment 1. Results from experiment 2 closely fit this assumption. The 91% com-

TABLE 2

AVERAGE COMPATIBILITY OF SEEDLINGS GRAFTED AS SCIONS ONTO ROOTSTOCKS COMPATIBLE WITH ONE OR BOTH PARENTS OF THE SEEDLINGS

PARENTAGE OF SEEDLINGS TESTED AS SCIONS	% SEEDLING GRAFTS COMPATIBLE WHEN ROOTSTOCKS WERE COMPATIBLE WITH: Both parents %	Both parents Range	Both parents N^a	One parent %	One parent Range	One parent N
6 × 5, 6 × 24, 6 × 165	93	78–96	57	45	0–72	38
8 × 5, 8 × 165, 8 × 16	97	91–100	101	58	50–62	12
24 × 6, 24 × 165	78	78	8	64	40–89	19
5 × 6, 5 × 8, 5 × 16, 5 × 165, 5 × wind[b]	94	92–100	50	69	62–72	26
165 × 6, 165 × 8, 165 × 24, 165 × 60, 165 × 9, 165 × 14, 165 × wind	93	38–100	204	40	0–89	162
14 × 16, 14 × 165, 14 × wind	30	14–38	20	58	30–70	33
16 × 5, 16 × 8, 16 × 14	100	100	5	57	30–70	37
60 × 165, 60 × wind	87	73–100	31	50	35–60	71
9 × 165	100	100	6	71	71	7
Weighted average	91	...	...	50	...	...

[a] N = number of grafts examined.
[b] Wind = wind-pollinated.

patibility achieved with simulated whole-related rootstocks was very near the expected whole-related value of 94% [56 + (2 × 19)].

Why some clones or seedlings are more prone to form incompatible combinations than others is not known, and we do not know which substances interact to trigger the tissue rejection mechanism. It is highly unlikely that natural selection has directly favored the more compatible or incompatible trees in the forest. Graft rejection in Douglas-fir, as in earthworms (COOPER 1969), simply illustrates biological specificity.

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