Vegetative Propagation of Mature and Juvenile Northern Red Oak

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Abstract: Rooting trials were established to evaluate rooting success of cuttings from mature and juvenile, grafted and ungrafted northern red oak (NRO). Buds from 4 mature NRO ortets and juvenile seedlings were grafted onto juvenile and mature rootstock. Cuttings were collected from the grafts and from juvenile and mature shoots developed *in situ* and subjected to a rooting trial. Of all treatments, cuttings from juvenile material rooted best. However, the rooting of cuttings from mature trees was also relatively successful. Rooting success of cuttings was significantly related to ortet genotype and ontogeny and was not directly influenced by grafting. The number of roots per cutting and post-rooting flushing behavior was significantly related to ortet ontogeny. Juvenile rootstock had little effect on the rooting, number of roots per cutting, flushing behavior, and overwintering success of meristems from mature NRO. Mature rootstock negatively influenced the number of roots per cutting, flushing behavior, and overwintering success of shoots from grafted juvenile buds.

INTRODUCTION

Northern red oak (*Quercus rubra* L.) is a wide-spread and abundant species important in both traditional and urban forestry. It is a genetically diverse species (Houston 1987, Kolb and Steiner 1989, Kriebel et al. 1988, Schlarbaum and Bagley 1981) and therefore offers great potential for tree improvement. Vegetative propagation, especially from mature individuals, is difficult and a severe hinderance to research and to the full utilization of the genetic variation within this species. The objective of this research was to identify techniques for the successful vegetative propagation of ontogenetically mature northern red oak (NRO).

In many woody species, including NRO, juvenile plant materials can be vegetatively propagated more successfully than mature (Burger and Lee 1987, Morgan 1986, Teclaw and Isebrands 1987, Vieitez et al. 1987). Successful rooting of cuttings has been demonstrated for juvenile NRO (Maynard and Bassuk 1987, Teclaw and Isebrands 1987) but success drops off precipitously as early as the second flush from a germinated acorn. The same propagation techniques have not been successful with ontogenetically mature oaks and multiplication of unproven juvenile genotypes has limited applications. Other propagation methods, such as tissue culturing and somatic embryogenesis, are difficult in woody plants and, almost without exception, not possible for explants that are beyond the juvenile phase (Bajaj 1986). Although many factors such as plant nutrition, timing, wounding, etiolation, light status, and hormones affect the rooting of cuttings, ontogenetic maturity may be the most important (Dirr and Heuser 1987).

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In some cases, grafting scions from mature plants to juvenile rootstock has resulted in scion growth that was more juvenile-like in character. Doorenboos (1954) demonstrated increased rooting ability of cuttings from mature *Hedera helix* that had been grafted onto juvenile plants. An increase in rooting was also found by Pliego-Alfaro (1981) who grafted buds from a mature avocado tree onto 1-month-old seedlings. The generated stem explants rooted readily. In oak, Moon et al. (1988) reported that two successive graftings (serial grafting) of mature *Q. acutissima* onto 2-year-old understock increased the rooting to 100%. Pliego-Alfaro (1981) and Moon (1988) concluded that grafting of adult tissue to juvenile rootstock apparently caused a phase reversal or rejuvenation of the mature tissues and restored rooting competence.

Rooting success may be increased by grafting but it may not be due to actual ontogenetic rejuvenation of mature tissues. The phases of ontogenetical aging and subsequent maturity are relatively stable and difficult to reverse (Fortanier and Jonkers 1976). In addition, various characteristics differentiating juvenile from mature may be under independent controls (Borchert 1976).

The morphological characteristic most commonly regarded as signaling phase change from juvenility to maturity is the ability to flower or "ripeness to flower" (Waring and Fryman 1976, Morgan 1986). However, mature plants differ from juvenile plants in many characteristics which may appear either before or after flowering competence is achieved. These include growth behavior, bark characteristics, seasonal leaf retention, leaf shape, rooting behavior and cold resistance (Cordero et al. 1985, Greenwood 1984, Hood and Libby 1980, Kramer and Kozlowski 1979). Thus, even if graft-induced "rejuvenation" enhances rooting success of meristems from mature trees, the propagules may have limited applications if they continue to exhibit other mature characteristics. This paper summarizes a two-year study of the effects of grafting on the rooting success and the maturation state of NRO.

MATERIALS AND METHODS

Shoot cuttings were subjected to rooting trials in 1989, 1990, and 1991. For the 1989 trial, cuttings came from mature NRO trees and juvenile seedlings. In 1990, cuttings for the rooting trial came from mature trees. In 1990 and 1991, buds from the same mature genotypes and from juvenile seedlings were grafted on juvenile and mature rootstock. For the 1991 rooting trial, cuttings were collected from the grafts, the same mature ortets, and from juvenile seedlings of different ages.

Mature and Juvenile Plant Material

Four seed-producing NRO ortets provided sources of mature plant material for grafting and cuttings. In June 1991, the trees were 12, 13, 19, and 22 meters tall and 29, 39, 68, 73 centimeters in dbh for ortets 1, 2, 3, and 4, respectively. Cuttings from shoots developed *in situ* on the mature ortets were designated M1, M2, M3, and M4.

For the 1989 rooting trial, cuttings were collected in bulk (JUV) from juvenile seedlings grown from pre-stratified acorns that were sown in pots in April and May of 1989. For the 1991 rooting trial, pre-stratified acorns were sown in pots during April 1991 in a greenhouse and grown to provide 2nd-flush cuttings (J2) for use in the rooting trial. In May 1991, acorns from the same seedlot were similarly sown in pots in a greenhouse to provide 1st-flush cuttings (J1) for use in the rooting trial. Additionally, cuttings were collected from shoots that arose from along the 1st flush of decapitated 1-year-old seedlings (JD's).

Grafting Treatments

In April of 1990, dormant scion wood was collected from the lower 1/3 of the crown of the mature trees. One hundred dormant buds from each ortet were bud-grafted onto 1-year-old potted NRO rootstock. These 1990 grafts are referred to as 90X's (X = genotypes 1, 2, 3, 4). Spring T-budding (Hartmann and Kester 1983) was used, instead of several other grafting methods for the following reasons. It allows for grafting the smallest transferable unit (a meristem) and therefore makes more economical use of propagating scions. This consideration is of particular importance in the rebudding phase where scion wood is limiting. Perhaps most importantly, spring T-budding provides in-phase development of shoots from grafted and *in situ* buds for the rooting trial. The successful 1990 grafts (47%) were maintained throughout the growing season and overwintered in an unheated greenhouse. In 1991, these grafts were used as a source of dormant buds for grafting and as a source of cuttings for the 1991 rooting trial.

In April 1991, approximately 100 dormant buds representing each mature genotype were collected from the 1990 grafts and re-grafted onto one-year-old potted NRO rootstock. Cuttings from these twice-grafted plants are referred to as 9190X's, (X = genotype number 1, 2, 3, or 4). The rootstock population consisted of 4 open-pollinated families of NRO. Seed for two of the rootstock families was collected from mature ortets #2 and #3 in 1989. Identities of the rootstock families were maintained for use in later analyses. The one-year-old rootstocks had been grown in 6.5 cm square by 23 cm tall pots. In addition, approximately 100 dormant buds collected directly from each of the 4 mature ortets (genotypes 1, 2, 3, 4) and from 1-year-old potted seedlings (J) were grafted onto the same 4 families of one-year-old potted NRO rootstock. Cuttings from these once-grafted plants are referred to as 91X's (X = 1, 2, 3, 4 and J). Buds from the mature trees were also grafted on 2-year-old NRO rootstock of unknown parentage. The 2-year-old rootstock were originally bareroot 1-0 nursery grown seedlings which were potted into 10 cm square by 25 cm tall pots in 1990 and grown for 1 year in the greenhouse prior to grafting. Cuttings taken from these grafts are referred to as 291X's (X = genotypes 1, 2, 3, 4).

In April and May 1991, additional grafts using approximately 100 buds from each of 1-year-old seedlings and mature ortet #2 were made onto the lower 1/3 of the crown of mature ortet #1 at this time. Cuttings for these treatments are referred to as J-M1 and M2-M1, respectively.

In May 1991, grafted rootstocks were decapitated just above the grafts to stimulate the grafted buds to break dormancy. Decapitation at this time provided synchrony of budbreak for both the indoor grafts and outdoor *in situ* ortets. At the same time, the 1990 grafts (90X's) were brought into the heated greenhouse to stimulate budbreak.

Rooting Procedures

For the rooting trials, all cuttings were collected in June, after shoots had reached the LAG phase (Hanson et al. 1986). Cuttings from mature trees (MX's) were collected from the lower 1/3 of the crown. Cuttings were collected daily and kept cool and moist until processing during the same day. All leaves were removed from cuttings, except 3 at the apex. The basal end of each cutting was freshly trimmed and dipped in 1.2% w/w IBA and ethanol for 5 seconds and allowed to dry for 1 minute. While drying, the remaining leaves were trimmed perpendicular to the midvein to about 1/2 of their original size. Cuttings were inserted into pre-dibbled holes in moist media (1 perlite : 1 peat : 1 coarse white sand) in 66 cc Ray Leach Pine Cells and lightly watered prior to placement in the rooting chamber.

In 1989 and 1990, cuttings were randomly placed in a high humidity chamber. Intermittent fog was provided by 4 ultrasonic humidifiers (Sunbeam model 667). Light was provided 18 hours per day by alternating Sylvania VHO cool white and Gro-lux fluorescent bulbs placed 40 cm above the cuttings. In 1991, due to increased numbers of cuttings, a larger mist chamber was constructed using the same fogging system in a greenhouse. In both years, benomyl (Benlate at 2.4 gm/l) was sprayed on the leaves every month during the rooting period.

In 1989 and 1990, cuttings were scored for rooting success about 120 days after sticking. Rooting success was defined as the presence of at least one root at least 5 mm in length. In the 1991 test, cuttings were checked for rooting and number of roots per cutting 80 days after sticking. The number of roots per cutting reflects the number of roots >5 mm in length originating from the stem or callus of a cutting. Cuttings that had not rooted after 80 days were placed back into the high humidity chamber and checked again 40 days later. Data summaries reflect the total cuttings rooted over 120 days.

In 1991, 80 days after sticking, those cuttings that had rooted were potted into 6.5 cm square pots by 23 cm tall pots filled with Pro-Mix BX and set into a shaded acclimation tent. For the next 50 days, daylength was supplemented with 18 hours per day of artificial light from sodium vapor lamps. Humidity was initially maintained at 100% and gradually decreased over 20 days to ambient greenhouse levels, at which time the shade was removed. Late-rooting cuttings were acclimated for 10 days. On 7 November 1991, the number of post-rooting flushes on the rooted cuttings were noted and the rooted cuttings were transferred to an unheated greenhouse for overwintering.

Data Collection and Analyses

In this paper we report on the rooting success (percentage of cuttings with roots), number of roots per rooted cutting, post-rooting flushing, and overwintering survival of the various treatments. Chi-square (Roscoe 1975) and logit analysis (Fienberg 1980) were used to statistically test the categorical data (rooting success, flushing, and overwinter survival) at the P=0.05 level. In logit analysis, models are developed relating response variable and explanatory factors. The data were tested to determine fit to the specified model. P-values greater than the significance level (0.05) indicate that the data fits the model and there are relationships between the response variable and the factor(s). Analysis of variance was used to test for treatment differences in the number of roots per cutting. These data were not normally distributed, treatment standard deviations were proportional to the treatment means, and some of the values were less than 10, therefore the dependent variable (number of roots+1) was log transformed to equalize the variances prior to the analysis of variance (Fowler and Cohen 1990).

RESULTS

Rooting Success - Over Years

The rooting of cuttings from mature trees varied greatly by genotype and over years (Table 1). The rooting of genotypes #2 and #3 was consistently best and poorest, respectively. Rooting results of cuttings from mature trees in 1989 and 1990 were similar but more than doubled in 1991. Rooting of cuttings from juvenile seedlings also increased but not as dramatically. Over all years, for cuttings from mature trees, genotype or year alone were not sufficient to model rooting but a model that included both genotype and the year x genotype interaction effect adequately described the data (P=0.246).

Table 1.—Percentage rooting for cuttings from 4 mature trees and juvenile seedlings over years

Cutting type	1989 % Rooting (n)		1990 % Rooting (n)		1991 % Rooting (n)	
M1	26.5	(49)	20.8	(72)	56.0	(50)
M2			51.5	(66)	86.0	(50)
M3	0.0	(50)	2.9	(69)	20.0	(50)
M4	11.8	(51)	20.9	(67)	74.0	(50)
JUV	80.0	(100)			88.9	(99)

note: Cutting type JUV represents first- and second-flush cuttings from two- and three-month old juvenile seedlings.

Rooting - 1991 Experiment

In 1991, rooting averaged 72.2% over all treatments but there were large differences among the treatments ranging from 96% for J1 to 20% for M3 cuttings (Table 2). Significant genotypic and ontogenetic effects were present but grafting was not significantly related to rooting.

Genotypic Effects

Rooting was dependent on genotype for mature ungrafted cuttings in 1991 (chi-square, $P<0.001$). For grafted cuttings of known rootstock family, logit analysis revealed that there was no significant rootstock family effect on rooting ($P=0.003$). However, there was a significant relationship between scion genotype and rooting ($P=0.491$).

Grafting Effects

Cuttings from grafts of the mature genotypes rooted more often than their ungrafted counterparts (69% vs 59%). However, when considering genotypes, logit analysis revealed that rooting success was not significantly related to the main effects of grafting or genotype ($P<0.05$). Averaged over genotypes, percent rooting was 56, 59, 70, and 79 for 91X's, mature, 9190X's, and 90X's, respectively. Grafting did decrease the differences between genotypes but not significantly so. Only for #3, the ortet with the poorest rooting performance, did every grafting treatment increase rooting compared to ungrafted controls (from 20 to 58%). Grafting treatments variably affected the other genotypes.

Ontogenetic Effects

Chi-square analysis revealed a significant relationship between rooting success and cutting maturity when comparing all mature cuttings as a group versus all juvenile cuttings ($P<0.001$). Rooting of two-month-old J1 cuttings (96%) was considerably greater than mature cuttings (59%). Interestingly, rooting of only slightly older 3-month-old seedlings (J2) dropped significantly to 82% (chi-square, $P=0.05$) and fell behind one of the 4 mature genotypes. Therefore, chronological age of the plant was not the determining factor of rooting success. This was further evidenced by the 94% rooting success of the 1-year-old JD cuttings.

Table 2.—1991 percent rooting, roots/cutting, and flushing by treatment

Cutting type	Number of cuttings	Rooting (%)	No. roots per cutting	Overwinter surv. (%)
M1	50	56.0	2.0	40.7
M2	50	86.0	4.1	79.4
M3	50	20.0	1.4	20.0
M4	50	74.0	5.8	47.2
J1	50	96.0	14.3	95.8
J2	49	81.6	14.9	80.0
JD	51	94.1	23.4	93.6
901	28	71.4	3.8	60.0
902	76	89.5	6.8	70.3
903	35	71.4	3.2	80.0
904	38	81.6	6.8	77.4
911	39	51.3	3.0	45.0
912	41	70.7	4.9	51.7
913	15	46.7	1.6	28.6
914	37	54.1	4.6	57.9
91J	42	90.5	13.5	70.3
91901	27	81.5	2.8	50.0
91902	44	72.7	4.5	65.6
91903	30	43.3	7.3	54.5
91904	30	83.3	3.6	52.2
2911	28	67.9	2.7	31.6
2912	29	79.3	4.7	54.5
2913	14	71.4	2.7	20.0
2914	35	65.7	3.8	39.1
J-M1	15	93.3	3.0	50.0
M2-M1	11	81.8	5.7	44.4

MX's = mature trees, genotypes 1,2,3,4
J1, J2 = one- and two-flush seedlings, approximately 2 and 3 months old, respectively
JD = 1st flush of one-year-old formerly multiflush but decapitated (clipped off) seedlings
90X's = 1990 grafts, one-year-old stock, X=genotypes 1,2,3,4
91X's = 1991 grafts, one-year-old stock, X=genotypes 1,2,3,4 and J (juvenile)
9190X's = twice grafted on one-year-old stock (1991 and 1990)
291X's = 1991 grafts on two-year-old stock, genotypes 1,2,3,4
J-M1 = juvenile buds grafted on mature tree #1
M2-M1 = mature genotype #2 grafted on mature tree #1

To test if buds are influenced by the environment (either juvenile or mature rootstock) in which they are formed during the growing season prior to shoot formation, a logit model was constructed pooling 90X's and 9190X's vs 91X's and 291X's (X = mature genotypes 1, 2, 3, and 4). Considering only the 4 mature genotypes, shoot cuttings from the 90X's and 9190X's grafts came from buds formed on juvenile rootstock and shoot cuttings from the 91X's and 291X's grafts arose from buds that were formed on the mature trees. Logit analysis revealed that rooting success was not significantly related to bud formation environment prior to grafting (P=0.002).

Number of Roots Per Rooted Cutting

There were significant differences among the treatments for the number of roots per cutting (P<0.0001). Rooted cuttings from juvenile seedlings had significantly more roots per cutting than those from mature trees (Table 2). Grafting treatments using juvenile rootstock did not significantly influence the number of roots per cutting. Based on the number of roots per rooted cutting, there is no evidence of grafting-induced rejuvenation.

Cuttings from juvenile buds that were grafted onto a mature tree (J-M1) had significantly fewer roots (3.0) compared to cuttings from juvenile seedlings (23.3, 14.9, 14.3 for JD, J2 and J1, respectively) and to cuttings from juvenile buds grafted onto juvenile rootstock (13.5 for 91J). There apparently was an influence of the mature rootstock on the number of roots per rooted cutting but not on rooting success, suggesting that these measures of juvenility were independently controlled.

Flushing Behavior, Post-Rooting

Shoot flushing of NRO seedlings can consist of a series of recurrent and determinate flushes (Borchert 1975). In contrast, mature trees usually produce only one flush of vegetative growth per growing season. Flushing behavior was noted as an indicator of maturity.

After the cuttings had rooted and before overwintering, some flushed once or twice. Differences in flushing behavior were apparent among the treatments (Table 3). Flushing data were similar and combined for treatments 91X and 291X due to low numbers of genotype #3. Treatments J1 and JD flushed considerably more (83.3% and 85.4%, respectively) than other treatments and a reduction in flushing behavior was apparent as early as the second flush of a seedling (J2=50%). Rooted cuttings from buds from mature trees, whether grafted or not, flushed considerably less.

Flushing averages (%) were 5.7, 15.5, 16.1, and 20.3 for rooted cuttings from ungrafted mature, 90X's, 91X+291X's, and 9190X's treatments. Considering genotype and whether grafted or not, logit analysis revealed that the flushing behavior data were not described by models using either grafting or genotype main effects. However, a model including the grafting main effect with the grafting x genotype interaction fit the data (P=0.906). The interaction apparently arose from the increase of flushing of genotypes #3 and #4 when grafted giving some evidence for the occurrence of ontogenetic rejuvenation. Interestingly, the mature rootstock negatively influenced flushing when comparing rooted cuttings from juvenile buds grafted onto the mature tree (14.3%) and those grafted onto juvenile rootstock (47.4%).

Table 3.—Percent of rooted cuttings that flushed at least once before overwintering

Grafting treatment	BUD TYPE M1	M2	M3	M4	J1	J2	JD
not grafted (%)	10.7	9.3	0.0	2.8	83.3	50.0	85.4
(n)	(28)	(43)	(10)	(37)	(42)	(40)	(48)
90X's (%)	5.0	11.9	31.0	12.9			
(n)	(20)	(67)	(25)	(31)			
91X+291X's (%)	5.1	5.8	35.3	18.2		47.4*	
(n)	(39)	(52)	(17)	(44)		(38)	
9190X's (%)	9.1	9.4	38.5	24.0			
(n)	(22)	(32)	(13)	(25)			
grafted onto M1 (%)		0.0				14.3*	
(n)		(9)				(14)	

* = buds used for grafting were from 1-year-old multi-flush seedlings

Overwinter Survival

By June 1992, 63% of the 1991 rooted cuttings were alive. Differences in overwinter survival closely mirrored rooting success (Table 2). For the most part, those treatments that had high rooting success (J's), overwintered well (90% survival) and those that had poor rooting success (M3), had poor overwinter survival (20%).

Overwinter survival was related to rooting date. For cuttings that had rooted by 80 days, 70% survived, compared to those that rooted after 80 days, only 25% survived. Of all juvenile treatments that had rooted, 97% had done so within 80 days. Only 62% of all treatments using ortet #3 had rooted by that time. Perhaps the cuttings that were early rooters were able to store more photosynthate and harden-off more completely than the late rooters. Post-rooting flushing behavior and the number of roots per cutting did not appear to directly influence overwinter survival as within-treatment averages for dead and surviving rooted cuttings were similar. Although the actual cause(s) of overwinter mortality was not certain, the roots of many of the dead rooted cuttings were infected with *Phytophthora*.

DISCUSSION

In 1989 and 1990, rooting success for cuttings of mature NRO was generally low and consistent with the conventional wisdom that oaks are difficult to vegetatively propagate (Clark 1962, Flemer 1962, Hartman and Kester 1983, Morgan 1986). However, in 1991, rooting success of cuttings from mature NRO increased dramatically and more than doubled to 59%. At this time, we have no definitive explanation for this increase but are actively pursuing several possibilities related to environmental conditions present in the different rooting chamber used in the 1991 experiment. The high level of rooting success in 1991 does not appear to be a spurious result as an additional rooting experiment performed in the same chamber in 1992 achieved similar high rooting success. Even with relatively high rooting success, large differences in responses were apparent among

treatments. For cuttings from mature trees, significant genotypic effects were found for rooting and overwintering success. Even after grafting, which decreased the differences in rooting, significant genotypic effects persisted. Other studies have demonstrated genotypic effects when rooting cuttings of other species (Burger and Lee 1987, Larsen 1986, Morgan 1986).

Ontogenetic effects were apparent for all characteristics measured. Other studies have shown significant juvenile to mature change in vegetative propagation success (Morgan 1986, Pleigo-Alfaro 1981, Vieitez et al. 1987) and this was often related to chronological age of the ortet. We experienced a similar relationship but with some qualifications. Rooting and overwintering survival decreased significantly in a relatively short time when comparing 2-month-old (J1) and 3-month-old (J2) seedlings. This was also found by Isebrands and Crow (1985) and Teclaw and Isebrands (1987) when comparing 1- and 2-flush NRO. However, chronological age was not a good predictor of success as older (1-year-old) JD seedlings did not further decline but rooted, flushed, and survived at levels similar to J1 seedlings. Ontogenetic effects are somewhat obscured by the ease of rooting and high overwintering percentages of cuttings from the much older and much larger M2 ortet. Flushing behavior and the number of roots per rooted cutting were strongly related to donor plant ontogeny regardless of whether or not it had been grafted onto juvenile rootstock.

Juvenile rootstock had no significant main effect on rooting success, the number of roots per rooted cutting, and overwinter survival. For these responses, shoot system differences (genotypic and ontogenetic) were maintained. This agrees, in part, with a study by Anderson et al. (1991) using loblolly pine (*Pinus taeda*). He concluded that expression of morphological characteristics in shoot systems of mature tissue-cultured plantlets and juvenile seedlings grafted onto seedling and plantlet root systems is controlled almost entirely by the shoot system and is not directly related to the root systems. However, in our comparison of the reciprocal grafts (buds from juvenile seedlings grafted onto mature), we have found evidence to the contrary.

Cuttings from juvenile buds grafted onto mature rootstock rooted in percentages similar to those grafted onto juvenile rootstock but had fewer roots per cutting, decreased flushing, and lower overwintering success. Mature rootstocks were apparently inhibitory for three of the measured characteristics, but not all four. There were also differences between J1 and J2 cuttings in rooting, flushing, and overwintering success but not for the numbers of roots per rooted cutting. This suggests that the responses are under relatively independent control. Borchert (1976) also suggests relatively independent control mechanisms for various juvenile characteristics.

In this study, the relatively small influence of juvenile rootstock on mature meristems does not appear to be due to ontogenetic rejuvenation but possibly physiological invigoration of the resulting shoots. For the most part, meristems appear to have predetermined rooting responses regardless of grafting. In mature oaks, dormant buds develop during the growing season prior to dormancy into either vegetative or mixed buds (containing both leaf and flower primordia) (Kozlowski 1971, Merkle et al. 1980). Assuming the differences between juvenile and mature shoots for rooting success are pre-determined in buds, then expansion of pre-formed buds originally set on a mature tree, whether it occurs *in situ* or grafted onto juvenile rootstock, should result in shoots that perform similarly. It follows that if ontogenetic rejuvenation of a meristem were to occur as influenced by juvenile rootstock, it must happen during the time of bud formation when the primordia for the next flush are formed. In our study, the corresponding treatments would be the 90X's and the 9190X's for which cuttings came from buds that formed on juvenile rootstock. The different environment provided by the juvenile rootstock during bud formation apparently did not change the mature character of the meristems and, for the most part, the cuttings responded similarly to their grafted (91X's and 291X's) or ungrafted counterparts.

Physiological invigoration of the grafted shoots by the rootstock is also supported when comparing 291X's vs 91X's. Cuttings from all of the 4 mature genotypes that had been grafted onto the older and larger rootstock (291X's) rooted more often than cuttings from younger and smaller rootstock. The more vigorous rootstock produced cuttings that were more successful rooters.

The presence of significant interactive effects suggest that if ontogenetic rejuvenation is possible, it may be genotypically dependent. It is also possible that it may take additional grafting phases for more definitive indications of rejuvenation to be manifested. In avocado, it was found that three re-grafts of mature scion shoots did not increase rooting but there was evidence that additional regrafts might improve rooting (Pliego-Alfaro and Murashige 1987). When tissue culturing *Vitis vinifera* L., Mullins et al. (1979) found that it took from 3 to 7 subcultures for shoot tips to show juvenile characteristics.

CONCLUSIONS

Juvenile rootstock had little effect on the rooting of cuttings developed from grafted buds of mature NRO. There was little evidence of ontogenetic rejuvenation of the previously grafted propagules and they appeared to maintain mature characteristics. In spite of this, rooting of mature NRO proved to be relatively successful achieving levels potentially feasible for large scale clonal production. Though one or two series of grafts onto juvenile rootstock did not significantly increase rooting or unequivocally invoke rejuvenation, grafting can be used to multiply shoots of mature genotypes while apparently maintaining their ontogenetic state. Rooted cuttings of select NRO exhibiting mature characteristics could prove to be valuable for use in physiological studies or for tree improvement work in order to establish slow-growing and early-flowering seed orchards free from graft incompatibility problems that can occur with oak. If additional re-grafting or post-rooting treatments provides evidence of ontogenetic phase reversion, rejuvenated rooted cuttings could be used as fast-growing planting stock for reforestation.

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