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Dormant Buds and Adventitious Root Formation by *Vitis* and Other Woody Plants

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Abstract

Viticulture has historically depended upon clonal propagation of winegrape, tablegrape, and rootstock cultivars. Dependence on clonal propagation is perpetuated by consumer preference, legal regulations, a reproductive biology that is incompatible with sustaining genetic lines, and the fact that grapevine breeding is a slow process. Adventitious root formation is a key component to successful clonal propagation. In spite of this fact, grapevine has not been a centerpiece for adventitious root research. Dormant woody canes represent complex assemblages of tissues and organs. Factors that further contribute to such complexity include levels of endogenous plant growth regulators, the extent and duration of dormancy, carbohydrate storage, transport, the presence or absence of dormant buds or emergent shoots, and preconditioning treatments. For the above reasons, the mechanisms driving adventitious root formation by grapevine and other woody cuttings are poorly understood. We present results indicating that the dormant bud on cane cuttings from a non-recalcitrant to root *Vitis vinifera* cultivar, cv. Cabernet Sauvignon, slows or inhibits adventitious root emergence. In contrast to Cabernet Sauvignon, removal of the dormant bud from cane cuttings of a recalcitrant to root hybrid rootstock (*V. berlandieri* × *V. riparia* cv. 420A) and an intermediate to root hybrid rootstock (*V. riparia* × *V. rupestris* cv. 101-14) had no influence on adventitious root emergence. Reciprocal transplanting of nodes containing dormant buds among all three cultivars did not affect rooting behavior. Our results indicate that the commonly held belief that bud removal diminishes adventitious root emergence is not true.

Key words: Adventitious roots; *Vitis*; Dormant bud; Grapevine; Propagation; Ecodormancy; Endodormancy

Introduction

Adventitious roots differ from laterals of the primary root system in that they originate from shoot tissue rather than from root tissue. Adventitious roots can

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arise from a wide range of shoot tissues within woody plant stems (Lovell and White 1986). Initiation of adventitious root formation is regulated by a host of internal compounds including plant growth regulators (PGRs) such as auxins and cytokinins, nitrogenous compounds such as spermine and spermidine, and carbohydrates as well as genetic background (Haissig 1974; Kozlowski 1992; Friend and others 1994; Howard 1994). Historic interest in adventitious root formation arises from a need to propagate woody plants of commercial value. Several fine books and reviews exist concerning the chemical, environmental, and genetic controls on adventitious root formation, with the majority of this work focused on cultivated woody taxa (Jackson 1986; Davis and others 1988; Davis and Haissig 1990; Davis and Haissig 1994; Altman and Waisel 1997). This study first reviews findings concerning environmental and chemical control of adventitious root development by woody cuttings with an emphasis on semi-woody perennials in the grapevine genus *Vitis*, or hybrids thereof. We then present our results on the role of the primary dormant bud in either promoting or suppressing adventitious root formation by grapevines that greatly differ in their propensity to root. We adhere to the terminology 'adventitious root formation' throughout, recognizing that 'initiation', 'initial formation', 'primordium', 'primordium formation', and 'primordium initiation' have been used interchangeably, and without standardized anatomical terminology ever having been agreed upon (Davis and Haissig 1990; Haissig 1974; Lovell and White 1986), but see Gaspar and others (1997) and de Klerk and others (1999) for a discussion of the physiological phases of induction, initiation, and expression during adventitious root formation.

Woody plant cuttings have been the focus in most research on adventitious root formation. A large and growing body of information is available on adventitious root formation by species in several important domesticated hardwood and semi-hardwood genera including *Citrus*, *Eucalyptus*, *Hedera*, *Juglans*, *Malus*, *Populus*, *Prunus*, *Pyrus*, *Salix*, and *Vaccinium*. It is not within the scope of this manuscript to fully review this larger body of information, but we shall draw upon it where physiological processes that clearly have universal relevance warrant it, and where information on grapevine is scant. In addition, we discuss existing information regarding the influence of dormant buds or bud removal on adventitious root formation in genera other than *Vitis*.

Breeding programs for woody taxa, including grapevine, are time consuming because their species are slow growing and have long generation times (Bouquet 1988). *Vitis vinifera* cultivars are hermaphroditic and self-pollinating, but readily outcross with their dioecious and subdioecious relatives (Olmo 1976). Introgressing a targeted trait into a grapevine rootstock (for example, lime tolerance from a *V. vinifera*), while backcrossing to sustain performance and insure that other desirable traits are not diminished (for example, phylloxera resistance) can require in excess of 25 years (Ravaz 1897), and still may not be successful (see for example, Lider 1957, 1958). For winegrapes, which represent more than 80% of grape production, the vast majority of cultivars have been proliferated for many centuries through vegetative propagation (Meredith 2000). Restrictions imposed by the governing boards of wine and winegrape production, the Appellation d'Orgine Controlee in France, the Instituto Nacional de Denominaciones de Origen in Spain, the Denominazione de Origine Controllata in Italy, and parallel legislation/organizations in other European countries, rule out genetic modification of conventional winegrape varieties, whether by traditional breeding methods or by molecular genetic approaches (Mullins and others 1990). Consumer preference for traditional varieties reinforces maintaining cultivars of known character. Accordingly, clonal propagation is the most appropriate method by which grape cultivars are disseminated at both the regional and international level. Adventitious root formation is central to the success of such clonal propagation programs.

Interest in adventitious root formation by woody plants may have actually slowed progress in adventitious root research for two reasons: (1) the extraction of biochemicals, proteins, and other constituents of physiological importance from woody cuttings is challenging at best, and there is always uncertainty regarding the effectiveness of an extraction procedure; (2) the slow growing nature of woody taxa complicates efforts to achieve consistent and repeatable experiments. These limitations should be kept in mind when evaluating research progress in adventitious root formation by woody plant cuttings like those of *Vitis*. Molecular genetic approaches to adventitious root research should accelerate progress in the near future (Haissig 1994).

Investigations on adventitious rooting in grapevine were notably absent through the 20th Century. A number of factors contributed to this perplexing fact. First, *V. vinifera*, the most important commercial species of *Vitis*, is an extremely prolific adventitious root former. Grapevine species and hybrids that were recalcitrant to root did not arrive on the scene until well after the phylloxera epidemics of the late 19th century destroyed the ex-

tensive plantings of 'own-rooted' *V. vinifera* varieties throughout Europe and Western North America (Ordish 1987). Grafting onto resistant rootstocks emerged as the only viable solution (Ravaz 1897). North American grapevine species that were difficult to propagate because they rooted poorly, in particular *V. berlandieri*, did not become the subjects of research programs to improve adventitious rooting behavior. Rather, such genotypes were simply crossed with easily rooted *Vitis* species such as *V. riparia* and *V. rupestris*, and occasionally *V. vinifera* to improve propagation success (Olmo 1976). Consequently, there was little impetus for research on adventitious root formation by grapevine. Improving propagation success of *Vitis* species or rootstocks by crossing them with individuals that are easy to propagate exacerbates the problem of identifying mechanisms regulating grapevine adventitious root formation. Wide genetic variation in rooting already exists among closely related woody taxa (Barlow 1994; Haissig and others 1992; Kozlowski 1992) and this appears to hold true for the grapevine species and their hybrid complexes.

Most of the information available on adventitious root formation in *Vitis* species and their hybrids has not been widely disseminated. Investigations of rooting by grape species and rootstocks have been historically proprietary, often conducted by persons whose primary interest was commercial (Galet 1988). When published, such information is often circulated within scientific journals, conference proceedings, and brochures that assist the viticulture community at large, and/or is disseminated by word of mouth. The journals that serve this community are published in no less than 12 languages. To our knowledge, the information we bring together in this review for grapevines has not been previously assembled within a single review, book chapter, or other manuscript.

Cytological and Histological Origin of Adventitious Roots

In this paper we refer to grapevine cuttings and canes interchangeably. The distinction is important because dormant cane cuttings originated as shoots that emerged from a dormant bud during the spring, grew during the summer, became lignified to form wood during the late summer and fall, and entered a state of dormancy (Mullins and others 1992), whereas a cutting taken from green growing shoots in the spring is not lignified, has not entered a dormant state, and thus is physiologically distinct. Adding to this complexity, different environmental parameters for various grapevine species trigger dormancy. *Vitis riparia* Michx. and *V.* X. *labruscana* Baily are photoperiodic, while *V. vinifera* enters dormancy as a response to lowered temperatures (Fennell and Hoover 1991; Wake and Fennell 2000). The physiological basis of dormancy for many taxa has not yet been worked out.

The canes of *Vitis* species do not contain preformed adventitious root primordia (van der Lek 1924); L. Kocsis unpublished data), as has been reported for *Salix* (Carlson 1938; Haissig 1970), *Malus* (Swingle 1927) and other woody taxa (see Lovell and White 1986). Rather, adventitious roots of grapevine cane cuttings were first reported to arise from cell divisions around tissues of the medulary rays (van der Lek 1924). van der Lek argued that such adventitious roots were probably generated from callus tissue, although the observation was strictly correlative based on the observation that callus tissue appeared before the emergence of root primordia. Farve (Favre 1973; Favre and Médard 1969) made the first detailed histological studies of adventitious root formation in *Vitis* canes, and identified the initial step as the appearance of 'swelling', or hypertrophic nuclei within clusters of cells of the interfascicular cambium. Origin within the interfascicular cambium is consistent with van der Lek's proposal (1924) that 'rows' of adventitious roots arose along the medulary rays of *Vitis* canes. The second stage of adventitious root formation was identified as the initiation of periclinal divisions among the cambium cells, followed by the third stage identified as the organization of 'morphogenetic fields' (Favre 1973). Finally, a fourth morphological stage was associated with the appearance of organized root meristems (Favre 1973). These loosely defined stages were very similar to the report of organized root 'meristemoids' that developed directly from cambial cells of, or indirectly from callus tissues of *Juglans regia* (Falasca and others 2000). The stages identified by Favre (1973) also follow closely upon defined steps in adventitious formation observed for diverse woody perennials examined by other investigators (Blakesley and others 1991; Altamura 1996; Ballester and others 1999). More recently, the focus of morphogenetic development of adventitious roots has shifted to molecular genetic stages of 'induction', 'initiation', and 'expression' (De Klerk and others 1995; Hausman and others 1995; Gaspar and others 1997; Ballester and others 1999).

Endogenous and Exogenous Plant Growth Regulators

Following upon Sach's late 19th century hypothesis that endogenously produced, nonsubstrate com-

pounds, which were transported in a polar direction, control plant organ formation (Sachs 1887), much early adventitious root experimentation was directed towards identifying a promoting substance (see Went and Thimann 1937). The landmark discovery of auxin and its association with adventitious root formation (Thimann and Koepfli 1935; Thimann and Went 1934) fulfilled such prophecy because it was produced in leaves and buds and was transported in the phloem in a basipetal direction. The identification of auxin as a root-promoting PGR was quickly followed by a period of discovery of other adventitious rooting compounds like indole-3-butyric acid (IBA) and naphthaleneacetic acid (NAA) that offered clear commercial applications (Audus 1959; Blakesley and others 1991). Further experimentation during the latter part of the 20th century has been directed towards dose response, transport, metabolism, and a search for an assumed auxin receptor site (see Haissig (1994) for an historical perspective).

The evidence that auxin and auxin-like compounds induce adventitious root formation is largely circumstantial. Nevertheless, such an overwhelming number of reports exist linking the application of auxin, basipetal transport, concentration of endogenous auxin, and response of transgenic plants (Blakesley and others 1991), as to leave little doubt of auxin's involvement (Blakesley and Chaldecott 1993). The phenomenological and correlative nature of many investigations may help to explain why the role of auxin on adventitious root formation by woody cuttings remains ambiguous. Woody cuttings represent a highly complex system in which endogenous PGR levels, transport, dormancy, storage, and inhibitory compounds influence adventitious root growth, and all of the above are dependent upon preconditioning treatments (Andersen 1986; Howard 1994; Wilson 1994). Inconsistency in reports has been particularly true for *Vitis* cuttings (Alley 1961; Tizio 1962; Alley 1979; Alley and Peterson 1977; Alley 1980). Spiegel (1955) argued that much of the inconsistency in adventitious root research encountered for *Vitis* canes was in part due to the existence of compounds that inhibit adventitious root formation. Such inhibitory compounds are allegedly leached out of canes by water soaking (Saraswat 1973; Chapman 1976). No specific compound has been identified, although Bartolini and others (1991) documented that phenolics were the major compound diffusing into soaking waters. No definitive experiment has been reported in which the favorable influence of water soaking on water status of the cane can be separated from the occurrence of specific inhibitory compounds (see Howard and Harrison-Murray 1988). Auxin itself can inhibit adventitious root formation in some species when its endogenous concentration is high (Nahlawi and Howard 1973; Biasi 1997), or it is applied outside an apparent window of sensitivity (Blakesley and others 1991). For *Vitis* species the optimal concentration range of auxin may be related to the depth of dormancy. Blennerhassett and Considine (1978) reported that *V. champinii* cv. Ramsey, a naturally occurring hybrid of the *V. candicans* × *V. rupestris* complex (Pongrácz 1983), was more difficult to root early in the dormancy period, but rooting was less recalcitrant following longer exposures to cold temperatures. Alley (1980) also reported that *V. champinii* cv. Salt Creek (syn Ramsey), and *V. champinii* cv. Dog Ridge were more recalcitrant to rooting immediately following their entering a dormant state.

Despite apparent difficulties associated with auxin use, there are many reports that auxins (NAA, IBA, IAA) improve rooting of grapevine cuttings, as reflected by its successful use for *in vitro* rooting of non-dormant materials. NAA has been reported to improve rooting of many grape cultivars and hybrids, including *V. vinifera* × *V. labrusca* cv. Delaware (Fujii 1974), several *V. berlandieri* × *V. rupestris* hybrids (Schumann and Uhl 1975), *V. champinii* cv. Salt Creek (Goussard and Orffer 1979), and Muscat Bailey A (Kawai 1996), a hybrid cross between cv. Bailey [*V. lincecumii* × (*V. labrusca* × *V. vinifera*)] × *V. vinifera* cv. Muscat Hamburg. Reports for improved rooting of grapevine cuttings by exposure to IBA include several cultivars of *V. vinifera* (Tizio 1962; Singh and Singh 1973; Alley 1976), although in some cases no effect of IBA was reported (Alley 1980), and enough inconsistencies exist as to render these reports suspect. Finally, a number of rootstocks and their hybrids show improved rooting upon exposure to IBA, including *V. berlandieri* × *V. riparia* cv. 420A (Harmon 1942), cv. 1613C which is a *V. solonis* x [(*V. labrusca* × *V. riparia*) × *V. vinifera*)] hybrid (Harmon 1942), *V. berlandieri* × *V. riparia* cv. Kober 5BB (5BB) (Tizio 1962), Salt Creek (Goussard and Orffer 1979; Alley 1980), Dog Ridge (Peterson 1973; Alley and Peterson 1977), and Harmony–a hybrid of an open pollinated seedling of 1613C × an open pollinated seedling of Dog Ridge (Alley and Peterson 1977). It must be kept in mind that in grapevine (Epstein and Lavee 1984) and in other woody taxa (Van Der Krieken and others 1997), IBA is quickly converted to IAA. In our own breeding and research programs, we find that IAA and IBA do have substantial influence on the rooting behavior of recalcitrant to root genotypes.

The role of endogenous PGRs other than auxin as signals promoting adventitious root development has been extensively examined [see the somewhat comprehensive reviews by Davis and Haissig (1990) and Blakesley (1994)]. Nevertheless, only auxins have been clearly and unequivocally identified as signals for adventitious root formation. Indeed, giberellin (GA) (Hansen 1988) and many cytokinins (van Staden and Harty 1988) have been reported to inhibit adventitious root formation in woody cuttings. Davis and Haissig (1990) have argued that the concentrations used in such experiments may be excessive with respect to endogenous concentrations of such PGRs and that ruling out GA_3 and cytokinins may be premature. Although there is no definitive evidence that either GA_3 or cytokinins are directly involved in adventitious root formation, there is indirect evidence. For example, Leshem and Lunenfeld (1968) found that the giberellin antagonist chorionic gonadotropin promoted adventitious root formation by *V. vinifera* without having any reported influence on endogenous auxin concentration. To our knowledge, this is one of few reports either for or against an influence of GA_3 on grapevine adventitious root formation.

Abscissic acid (ABA) has been reported to promote, inhibit, or have no influence on adventitious root formation (Rajagopal and Anderson 1980). The suggestion by Davis and Haissig that ABA's effect on stomatal function, and thereby improved water relations, may enhance adventitious root formation is unfounded for grapevine cuttings. We have found that canes lose water vapor freely, and such exchange does not seem to be under stomatal control because elevated CO_2 concentration has little effect on water exchange by grapevine cuttings whereas stomata generally close under such conditions (D.R. Smart unpublished data). In fact, Kawaii (1997) found that ABA could suppress bud activity and such suppression acted to inhibit adventitious root formation by cv. Muscat Bailey A. The question of ABA's effect on adventitious root formation in woody plant species is questionable at best pending further investigation (Davis and Haissig 1990).

Ethylene has also been reported to be involved in adventitious root formation but the results are highly variable and the preponderance of evidence indicates no direct involvement of ethylene on adventitious root formation (Mudge 1988; Moncousin and others 1989). For systems requiring auxin for adventitious root development, ethylene is often produced, but ethylene application alone was ineffective in promoting adventitious root formation in the absence of auxin (Mudge 1988). For a *V. riparia* × *V. rupestris* hybrid rootstock, Moncousin and others (1989) reported that ethylene production was elevated at the time of adventitious root formation. Although the early ethylene peak they identified clearly corresponded to a wound response, it was argued that a second peak in ethylene production may have been mediated by elevated endogenous auxin.

Investigations concerning the effect of PGRs on adventitious root formation by grapevine have shifted to a large extent to support *in vitro* micropropagation techniques (Monette 1988) as greater demand for virus-free rootstocks has grown (Alley and Golino 2000). The focus of these investigations concerns non-dormant buds and meristems. Thus, although the specific tissues involved may ultimately be similar (for example, callus), the initial physiological state of these cells is quite different from those of dormant cane cuttings. Extensive literature exists concerning micro-propagation of grapevines (Hamil and Chandler 1994; Tepfer and others 1994; Nilsson and Olsson 1997). Much of it is devoted to PGRs that will achieve a balance between shoot and root formation, as well as the *Agrobacterium rhizogenes'* rol1 and rol2 open reading frames that elicit rhizogenesis and hairy root disease. It is not within the framework of this manuscript to review that literature.

Polyamines are involved in plant growth regulation but, like other plant growth regulators, the mechanisms are unclear (Galston and Kaur-Sawhney 1995; Gaspar and others 1997). Polyamines are represented by a diverse group of aliphatic, nitrogen-containing polycations (Sankhla and Upadyaya 1988), with the diamine putrescine and the polyamines spermidine and spermine being most common in plant tissues. Early reports on the influence of exogenous polyamines on adventitious root formation gave conflicting results (Rugini and others 1997; Sankhla and Upadyaya 1988). Nonetheless, several reports have shown correlative increases in endogenous polyamines in root meristems or adjacent tissues during adventitious root formation (Galston and Flores 1991; Gaspar and others 1997). Polyamine biosynthesis in those cases was apparently induced by auxin applications or, in other cases, correlated with endogenous auxin concentration (Baraldi and others 1995; Friedman and others 1983; Galston and Kaur-Sawhney 1995; Nag and others 2001). The potential involvement of polyamines in adventitious root formation by grape cuttings has been recognized (Geny and others 1998, 2002). For *V. vinifera* cv. Cabernet Sauvignon, Geny and others (2002) observed that cuttings contained only conjugated or wall-bound polyamines, but correlative increases in extractable-free

polyamines occurred with adventitious root formation. Exogenous applications of putrescine and spermidine did not promote either root or callus formation (Geny and others 2002). Thus, it was unclear whether polyamines induced adventitious root formation, or simply represented a metabolic by-product of adventitious root formation.

Inorganic Compounds and Mineral Nutrients

In addition to PGRs, which are primarily carbon-based biochemicals, early investigators found that inorganic compounds could stimulate adventitious root formation by grapevine. Following upon reports by Curtis (1918) that potassium permanganate ($KMnO_4$) stimulated root growth by various woody cuttings, Winkler (1927) examined the influence of a number of inorganic compounds that were either strong oxidants or reductants on adventitious root formation by an assortment of *V. vinifera* table grape varieties, *V. labrusca*, individual clones from the *V. candicans* × *V. rupestris* hybrid complex and *V. vinifera* × *V. berlandieri* cv. 41B. Surprisingly, there was substantial evidence that solutions of low concentrations of $KMnO_4$ along with $MnSO_4$ and $K_3Fe(CN)_6$ greatly stimulated adventitious root formation by all of these genotypes. In comparison, exposure to pure water or reducing compounds, like $K_4Fe(CN)_6$, applied at the same molar concentrations as the oxidizing agents did not reduce adventitious roots. Thus, evidence indicated that changes in transmembrane redox potential, rather than ion signaling per se or osmotic effects, seemed responsible for the observed increase in adventitious root formation. To our knowledge, this line of investigation has never been pursued beyond the investigations of Winkler (1927).

The above investigations differed from a direct nutritional effect on adventitious root formation because mineral nutrient deficiencies depend on preconditioning treatments or soil fertility. Of course, one could argue that any macro- or micronutrient required by growth may limit adventitious root formation, but mineral nutrients reported to significantly influence adventitious root formation are nitrogen, magnesium, zinc, and boron. Early studies on NPK fertility found that adventitious root formation was more sensitive to N fertility than it was to either P or K fertility (Blazich 1988). Interestingly, adventitious root formation responded positively to low N levels in some reports (Blazich 1988; Vonschaesberg and Ludders 1993) and high N levels in others (Druege and others 2000). Grapevine adventitious root formation (*V. vinifera* cv. Waltham Cross) has also been reported to respond positively to low N nutrition (Pearse 1943, as cited by Blazich 1988). These results may indicate that adventitious rooting responds to inhibitory compounds produced under nitrogen deficiency, or perhaps to C:N ratios. The latter possibility, that adventitious root initiation is sensitive to C:N ratio (Blazich 1988), is unlikely given the relatively narrow range of C:N observed for higher plants. Nonetheless, these investigations suggest that a signal induction pathway, rather than growth or nitrogen nutrition per se, probably triggers adventitious root formation in response to N content.

Carbon Allocation and Adventitious Root Formation

Mechanisms that control carbon allocation in woody plants are poorly understood, but it is widely accepted that carbon allocation patterns at the whole plant level are a function of source-sink interactions (Dickson 1991; Friend and others 1994; Haissig and others 1992; Kozlowski 1992). Carbon sources are defined as tissues or organs that are net photosynthate exporters, while sinks are defined as net consumers of photosynthetic carbon (Ho 1988; Kozlowski 1992). Carbon sinks represent a complex assortment of structural and biochemical demands, that, in addition to root growth, includes biosynthesis of plant secondary defensive compounds (Jones and Coleman 1991), carbon costs associated with nutrient and water acquisition (Bloom 1986; Comas and others 2002), rhizodeposition—C fluxes to microorganisms in the rhizosphere—(van Veen and others 1991), and storage (Chapin and others 1990). Root growth and respiration probably represent one of the largest carbon sinks for woody plants, and sink activity of roots is thought to be the primary mechanism regulating C allocation between roots and shoots (Ho 1988).

The formation of adventitious roots by grapevine cuttings, and by cuttings of other woody taxa, may represent a somewhat simplified source-sink complex. Adventitious root formation often precedes the development of a shoot system by a cutting, and thus, the major sink is root growth while the primary source is stored carbohydrate. Because such stores appear to be limited, it is widely believed that carbohydrate storage and the ability to mobilize stored C to roots plays a major role in cutting establishment (Veierskov 1988; Haissig and others 1992; Friend and others 1994). Haissig (1986) argued that C allocation to adventitious roots depended on the ability to establish vascular connections. The work of Haissig (1970), Vietiez and others (1980), and Isebrands and Crow (1985)

supported this contention. Indeed, Lovell and White (1986) surveyed the histological origin of adventitious roots in a variety of woody taxa, and concluded that anatomical variation among species may ultimately determine the functional properties that regulate adventitious root formation. Consequently, differences in adventitious root formation between species, or between recalcitrant and nonrecalcitrant root formers within the same species complex, may be a consequence of genetic anatomical variation among them (Friend and others 1994). Yet, for the genera and species that comprise the grapevines, little if any information exists concerning the developmental establishment of vascular connections for adventitious roots.

Winkler (1927) recognized the importance of stored carbon on the ability of dormant cane cuttings to produce adventitious roots. He used iodine staining of cane cross-sections as an indicator of starch stored in dormant canes and found a significant correlation between apparent starch content and adventitious root production (Winkler 1927). Nevertheless, canes with diminished starch content were also those of smaller diameter and incomplete secondary vascular development. Thus, it cannot be definitively concluded that starch content was the causative factor based on previous arguments that development of vascular connections may play a role. By contrast, Kracke and others (1982) found that Kober 5BB, a *V. berlandieri* × *V. riparia* rootstock cultivar that roots readily, had approximately 33% less starch content than 140 Ruggeri (a *V. berlandieri* × *V. rupestris* rootstock hybrid), a recalcitrant root former. During adventitious root formation, which was carried out in cold temperatures and terminated after the first root emerged, starch and sucrose contents declined whereas pools of reducing sugars remained constant and low (Kracke and others 1982). Starch, sucrose, and organic nitrogen contents declined more rapidly in 5BB and faster metabolic rates (or mobilization) may have accounted for 5BB's ability to form adventitious roots (Kracke and others 1982). More recently, Bartolini and others (1996) demonstrated that 140 Ruggeri rapidly depleted nonstructural carbohydrates by 80% after 20 days during callusing and adventitious root formation. Thus, they also argued that C storage and allocation might be the limiting factor to root formation and therefore grapevine cutting establishment.

Finally, Nanda and Anand (1970) reported that starch mobilization in *Populus nigra* cuttings was dependent on season, with poor rooting during the early stages of dormancy correlated with low hydrolyzing enzyme activity, and high rooting activity correlated with high activity. They attributed the induction of enzyme activity and mobilization of soluble sugars to endogenous auxin, because starch mobilization was realized during periods of low rooting activity through applications of IAA and IBA (Nanda and Anand 1970). More recently, Berbezy and others (1997) reported that two sets of alpha-amylase isoforms were expressed by *V. vinifera* during the winter. One group was most strongly expressed immediately post dormancy, while the other group was expressed during the later half of dormancy just prior to bud burst, when adventitious root formation reaches its maximum activity (Berbezy and others 1997). Note, however that Koussa and others (1998a, 1998b) observed that ABA inhibits alpha-amylase synthesis by *V. vinifera* cv Merlot. Observed differences in ABA concentration and alpha-amylase activity between buds, where starch contents were low and adventitious root formation high, and internodes, where starch contents were high and adventitious root formation slow, suggested that nonstructural carbohydrate mobilization mediated by auxin could explain differences in adventitious root formation between buds and internodes (Kracke and others 1981). The importance of reserve C mobilization to adventitious root formation by grapevines is reinforced by the work of Bartolini and others (1996). They observed that adventitious root formation by 140 Ruggeri was well correlated with C reserves, and that nonstructural carbohydrate content was lowered by 80% during the first 20 days of root formation, at which time root growth ceased (Bartolini and others 1996).

The Role of Buds in Adventitious Root Formation

Dormant cuttings of woody plants are composed of nodal regions that nearly always contain buds. The influence of such buds on adventitious root formation depends on their physiological state, endo- or ecodormant (Lang and others 1987), and their relative source or sink strength. Dormant buds have been found to inhibit adventitious root emergence in peach (Cahlahjan and Nekrasova 1962, 1964); whereas, Gellini (1965), Fadl and Hartman (1967), and Smith and Wareing (1972) reported that buds promote adventitious root formation. The kind of bud, flowering or vegetative, also seems to carry some importance, apparently because ecodormant flower buds represent stronger sinks than ecodormant vegetative buds, thus restricting root formation to a greater extent than emerging vegetative buds (Biran and Halevy 1973). The fact that vege-

tative buds rapidly develop into strong carbon sources surely has some influence on this observation. Grapevines contain both flower and vegetative buds in a single compound bud (Mullins and others 1992). The swelling and emergence of the grape compound bud thus represents both the emergence and beginning of accelerated physiological activity of both the shoot and flower primordia. Any difference in the effect of flower versus vegetative bud would be difficult to distinguish in grapevine.

Bud phenology, or timing, becomes an essential element to be considered when addressing the role of dormant buds on adventitious root formation. Dormant buds emerge from dormancy into a highly active physiological state (Gardea and others 1994). Duration of experiments reported in previous studies hamper our ability to separate the physiological condition of buds and its influence of adventitious root formation because buds undergo substantial physiological transition in developing into shoots. In the investigations of Van der Lek (1924), who found that bud removal diminished adventitious root formation, *Vitis* cuttings were grown in a cold-frame for more than 65 days. Under such conditions, those buds would have passed through several phenological stages (Eichorn and Lorenz 1977), and developed into shoots with several fully expanded leaves (see van der Lek (1924) his Figures 5 and 6). Thus, carbon availability and its allocation may have superseded any considerations of the effects of chemicals produced by dormant or emerging, non-photosynthetic buds in promoting or inhibiting adventitious root formation. Kawai (1996, 1997) incubated cuttings for several weeks and concluded that bud removal diminished adventitious root formation. Again the presence of expanding or fully expanded photosynthetic leaves does not allow us to distinguish between the affect of potential PGR production by the bud versus the photosynthetic source contribution of a young shoot. *Vitis vinifera* shoots that have been partially defoliated produce far fewer adventitious roots than those that have not received defoliation treatments (Fournioux 1997). The role of dormant, nonphotosynthetic buds has not been thoroughly examined for grapevine or for other woody taxa. Although the physiological activity of buds was not assessed, 'coming out of dormancy' increased the emergence of preformed roots for conifer cuttings (Lanphear and Meahl 1963) and for *Populus robusta* (Smith and Wareing 1972). The duration of the dormant period, or duration of cold exposure (Smith and Wareing 1972), may influence the physiological state of buds, which in turn may have some affect on rhizogenesis (Howard 1968; Goode Junior and others 1982). In the following, we report on the influence of the dormant bud during the initial stages of bud swell and emergence on adventitious root formation. Such buds are swelling and becoming physiologically active, but are not photosynthetic. Although, the influence of carbon competition cannot be clearly separated from the involvement of chemical promoters or inhibitors of adventitious roots, our approach precedes source activity and thus more directly evaluates the influence of ecodormant buds on adventitious root formation by grapevine.

Methods

We selected two genotypes differing greatly in their propensity to produce adventitious roots: the recalcitrant to root *V. berlandieri* × *V. riparia* cv 420A (420A), and the non-recalitrant to root, *V. vinifera* cv Cabernet Sauvignon (CS). A third genotype was included that is intermediate for adventitious root formation, *V. riparia* × *V. rupestris* cv 101-14 Mgt (101-14). Six hundred 45-cm-long dormant cane cuttings of each genotype, each with three to four dormant buds, were collected from certified stock at the University of California, Davis, Foundation Plant Materials Service (FPMS) in late November of 2001. The cuttings were held in cold storage (1°C) for 1 month.

We then removed the cuttings from cold storage and surface sterilized them using 0.1% $NaClO_3$ in distilled water. The cuttings were rinsed and then cut into one-bud sections of about 3-cm-long and approximately the same diameter (Figure 1) for grafting. The 'top' section of the graft (scion) was positioned in such a manner that it would represent a distal bud with its polarity such that a shoot would normally emerge. The basal section of the grafting (rootstock) was positioned in such a manner that it would represent a basal bud of a cutting with its polarity such that roots would emerge. We grafted a scion of each genotype onto a rootstock of each genotype in all possible reciprocal combinations. This effort resulted in nine different scion/rootstock combinations: CS/CS, CS/101-14, CS/420A, 101-14/CS, 101-14/101-14, 101-14/420A, 420A/CS, 420A/101-14, and 420A/420A.

Each of the scion/rootstock combinations described above was grafted using three separate morphological kinds of scion and rootstock sections, or treatments, in all reciprocal combinations. The treatments consisted of (1) a scion or rootstock section with a node and the dormant bud intact, (2) a scion or rootstock section with a node from which

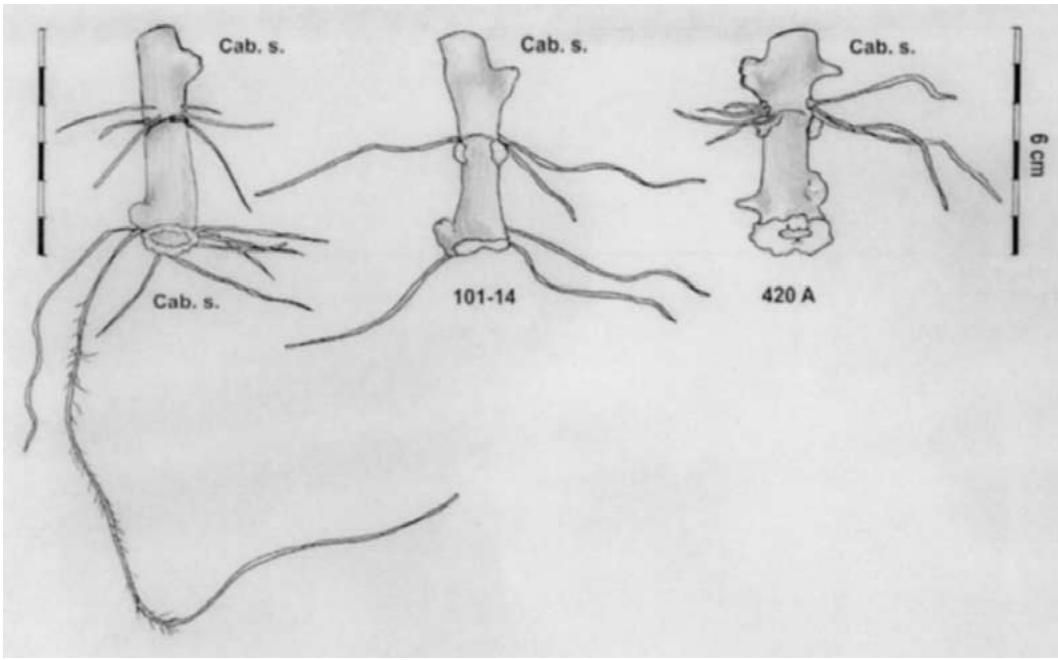

Figure 1. Diagram showing samples of the approximate configuration of the scion and rootstock cuttings used in the reciprocal transplant experiments. Each scion/rootstock combination consists of *Vitis vinifera* cv. Cabernet Sauvignon (CS) as scion, and, from left to right, CS, *V. riparia* × *V. rupestris* cv. 101-14 Mgt and *V. berlandieri* × *V. riparia* cv. 420A as rootstock.

we removed the dormant bud, and (3) a scion or rootstock internode in a section of cane without a dormant bud. There were thus nine different scion/rootstock treatment combinations (Figure 2), along with nine previously described genotypic combinations, for a total of 81 separate treatments. For each scion/rootstock combination, cane pieces were selected with nearly identical diameters and shapes so that good alignment of the vascular systems would be achieved.

The rootstock and scion sections were soaked in distilled water at 25°C for 48 hours to rehydrate them following cold storage, and remove any supposed inhibiting substances, then grafted together with an omega graft. Our research has suggested that the individual doing the actual grafting can have a significant influence on the results. For this reason, five individual scion/rootstock graftings from each of the 81 total sets were cut, soaked, and grafted by the same person (L. Kocsis) on 4 separate days for a total of 20 observations for each combination. The 5 pieces per set were tied together with cotton string, labeled, and placed in a callusing medium consisting of 2/3 peat and 1/3 perlite. Each set was then moved into a dark incubation chamber for 18 days at 30°C and a relative humidity of 98%. On the 18th day, the sets were taken out and rinsed gently, taking care not to break off any of the adventitious roots that had emerged from the cutting. The growth period corresponded to the developmental stage of bud swelling and emergence (Eichorn and Lorenz 1977); thus, it spanned a period where the bud becomes physiologically active (Alley 1980) but not photosynthetic. The callus tissue, if any, was scored on the scion at the graft union and on the rootstock according to the method outlined by Kocsis and Bakonyi (1994). Callus tissue protruding at the ends of the scion and rootstock pieces, but not at the graft union, was removed in a fresh condition and weighed. Root location was categorized according to apparent origin (scion or rootstock) and all roots were counted, removed and fresh weights recorded.

The data were analyzed by ANOVA using a completely randomized design using SPSS software, version 9.0. We employed Tukey's b-test at $P = 0.05$ for mean separation. The data were examined for homogeneity using Levene's homgeneity test. None of our data sets required transformation.

Results and Discussion

The results of our reciprocal grafting experiments are presented in a series of panels ((Figs. 3–8) that show root emergence counts from the rootstocks

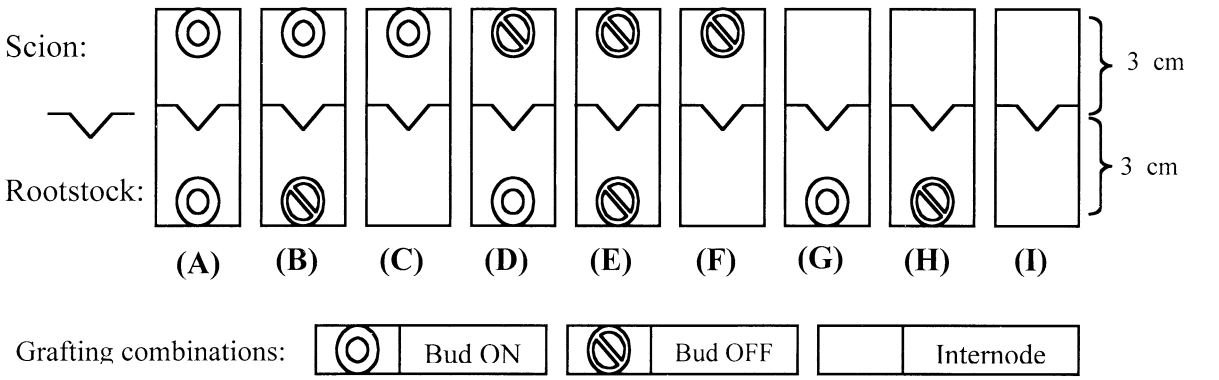

Figure 2. Shown is a schematic depicting the reciprocal grafts used to determine the influence of the dormant bud at the cane internode on adventitious root formation by a recalcitrant to root and non-recalcitrant to root grapevine rootstock. Each scion and rootstock piece was oriented with its normal polarity. In other words, the nodes of the scion pieces were towards the shoot meristem, and the nodes in rootstock pieces were distal to the shoot meristem. For **A**, **B**, and **C** the scion had the dormant bud intact. For **D**, **E**, and **F** the scion had the dormant bud dissected from the node. For **G**, **H**, and **I** the scion had no dormant bud, but was represented by an internode piece.

and scions. The columns of bars, labeled A, B, and C, in each histogram (I, II, III), show data for the rootstock when it consisted of the following: (**A**) a rootstock cutting with the bud intact; (**B**) a rootstock cutting with the bud removed; and (**C**) a rootstock cutting that was an internodal piece without a bud. The left to right rows of data in each histogram are labeled to the right of each row with the scion/rootstock combination. Counts do not necessarily document molecular induction phenomena (Ballester and others 1999). To document the total number of roots 'induced' by our reciprocal grafts, using the definition of adventitious root induction adopted by Ballester and others (1999), would require the dissection and microscopic analysis of the nearly 3,240 individual root counts required to complete this investigation. Thus, we document root emergence but acknowledge that such emergence could result from factors affecting either growth or induction processes within the cane. The purpose of our investigation was to document whether or not a bud coming out of dormancy (endodormancy) influenced root emergence. The mechanistic questions regarding why such a bud influence exists now await further experimentation.

A common belief in viticulture practice is that removing dormant buds from cuttings will diminish adventitious root formation (Hartman and others 1997). Such a belief is inconsistent with the report of Favre (1973) who stated that under certain undefined conditions disbudding promoted root emergence. Our experimental results did not support this contention. Removing dormant buds from CS rootstock sections significantly increased root emergence ($P < 0.01$). This result can be readily seen in all three histograms of Figures 3, 5, and 7 (column B first row), where disbudding the CS rootstock piece always increased the number of roots that emerged from the rootstock piece in comparison to non-disbudded rootstocks (Figures 3, 5, and 7, column A first row). Disbudding the rootstock position for 101-14 or 420A (Figures 3, 5, and 7, column B) had no statistically significant effect on adventitious root emergence from the rootstock position in comparison with non-disbudded rootstocks (same Figures, column A). It must be noted that the differences in adventitious root emergence by CS were small, with non-disbudded rootstock pieces having 4.35 ± 0.72 (mean ± SE, n = 59) and disbudded rootstock pieces having 6.6 ± 0.7 (n = 60) adventitious roots. Thus, the dormant bud check on adventitious root emergence is not absolute. Our data suggest that it is either a PGR influence that is concentration dependent or varies spatially with local tissues, or a growth limitation due to competition for limited resources.

The absence of a bud on a CS scion significantly increased adventitious root emergence from the CS rootstock regardless of whether or not the rootstock piece had a bud present ($P < 0.01$). This result can be seen by comparing the first row (CS/CS) in histogram I of Figure 3, where the dormant bud on the CS scion was left intact, with the first row (CS/CS) of histogram II of Figure 3, where the CS scion was disbudded, or histogram III, Figure 3, where the rootstock consisted of an internode. In contrast to the disbudding of the CS rootstock, removal of the dormant bud from a CS scion did not increase root emergence from the scion (compare Figure 4, I,

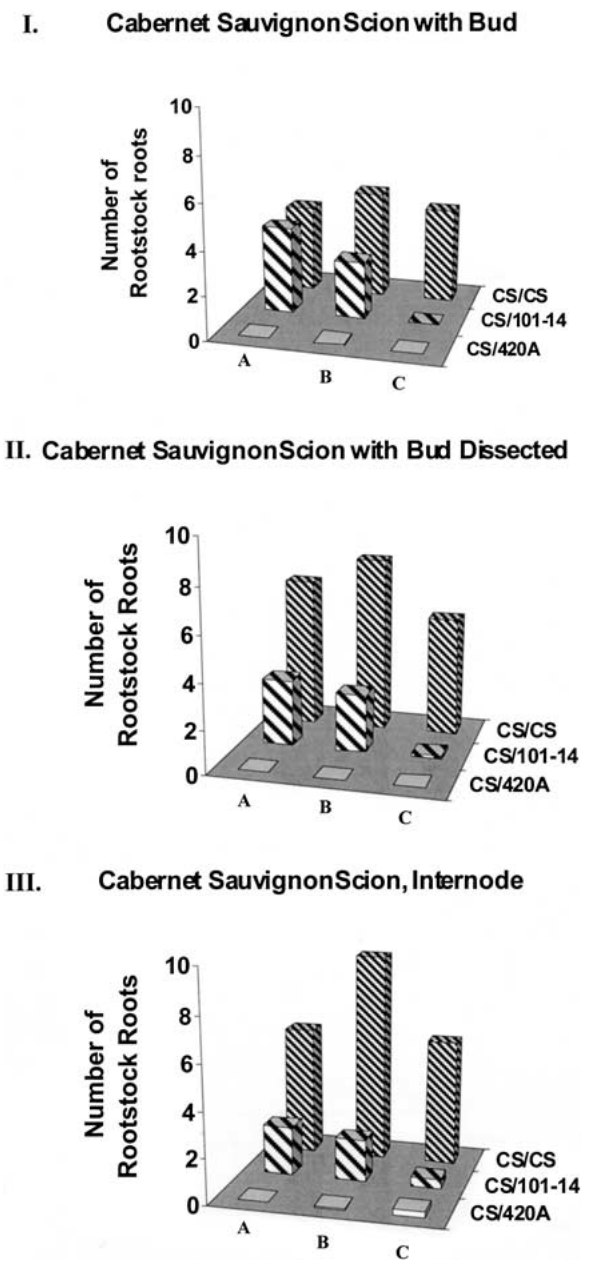

Figure 3. The number of roots that emerged from a 3.0 cm cutting in the rootstock position, when a 3.0 cm *V. vinifera* cv. Cabernet Sauvignon scion was grafted on top of it using the omega graph. Shown are the means (n ≅ 20 for each bar) when the rootstock piece consisted of (A) a node on which the dormant bud was intact, (B) a node from which the dormant bud was removed, or (C) an internode. For the first row in the back (CS/CS), the rootstock was *V. vinifera* cv. Cabernet Sauvignon. In the middle row (CS/101-14), *V. riparia* × *V. rupestris* cv. 101-14 was the rootstock. In the front row (CS/420A) *V. berlandieri* × *V. riparia* cv. 420A was the rootstock. Standard deviations were generally less than 20% of the mean.

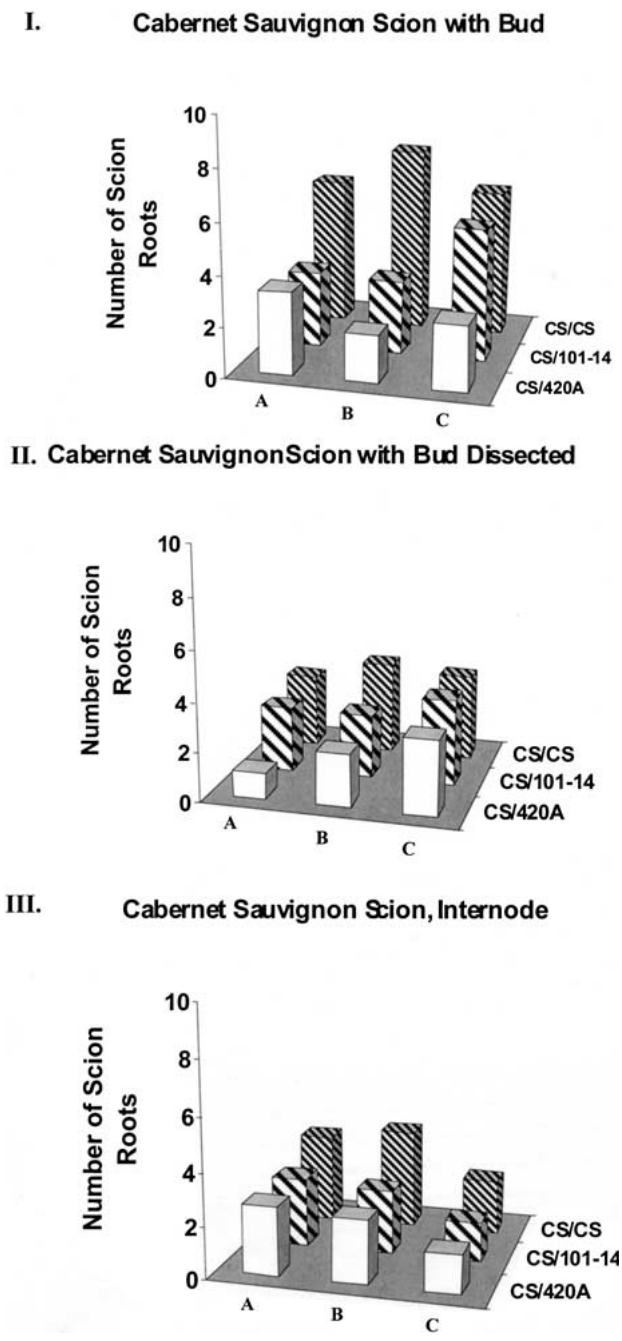

Figure 4. The number of roots that emerged from a 3.0 cm scion cutting of *V. vinifera* cv. Cabernet Sauvignon, when grafted onto a 3.0 cm rootstock cutting using the omega graph. Shown are the means (n ≅ 20 for each bar) when the rootstock piece consisted of (A) a node on which the dormant bud was intact, (B) a node from which the dormant bud was dissected, or (C) an internode. For the first row in the back (CS/CS), the rootstock was *V. vinifera* cv. Cabernet Sauvignon. In the middle row (CS/101-14), *V. riparia* × *V. rupestris* cv. 101-14 was the rootstock. In the front row (CS/420A) *V. berlandieri* × *V. riparia* cv. 420A was the rootstock. Standard deviations were generally less than 20% of the mean.

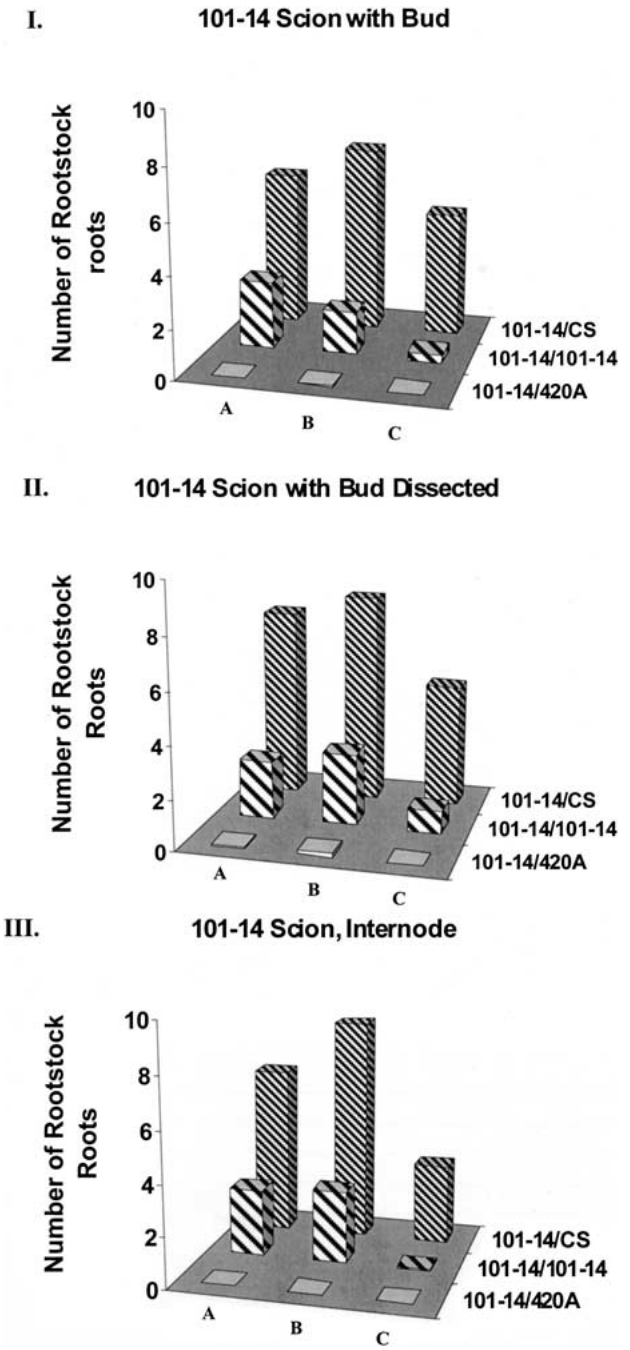

Figure 5. The number of roots that emerged from a 3.0 cm cutting in the rootstock position, when a 3.0 cm *V. riparia* × *V. rupestris* cv. 101-14 scion was grafted on top of it using the omega graph. Shown are the means (n ≅ 20 for each bar) when the rootstock piece consisted of (A) a node on which the dormant bud was intact, (B) a node from which the dormant bud was dissected, or (C) an internode. For the first row in the back (101-14/CS) the rootstock was *V. vinifera* cv. Cabernet Sauvignon. In the middle row (101-14/101-14), *V. riparia* × *V. rupestris* cv. 101-14 was the rootstock. In the front row (101-14/420A) *V. berlandieri* × *V. riparia* cv. 420A was the rootstock. Standard deviations were generally less than 20% of the mean.

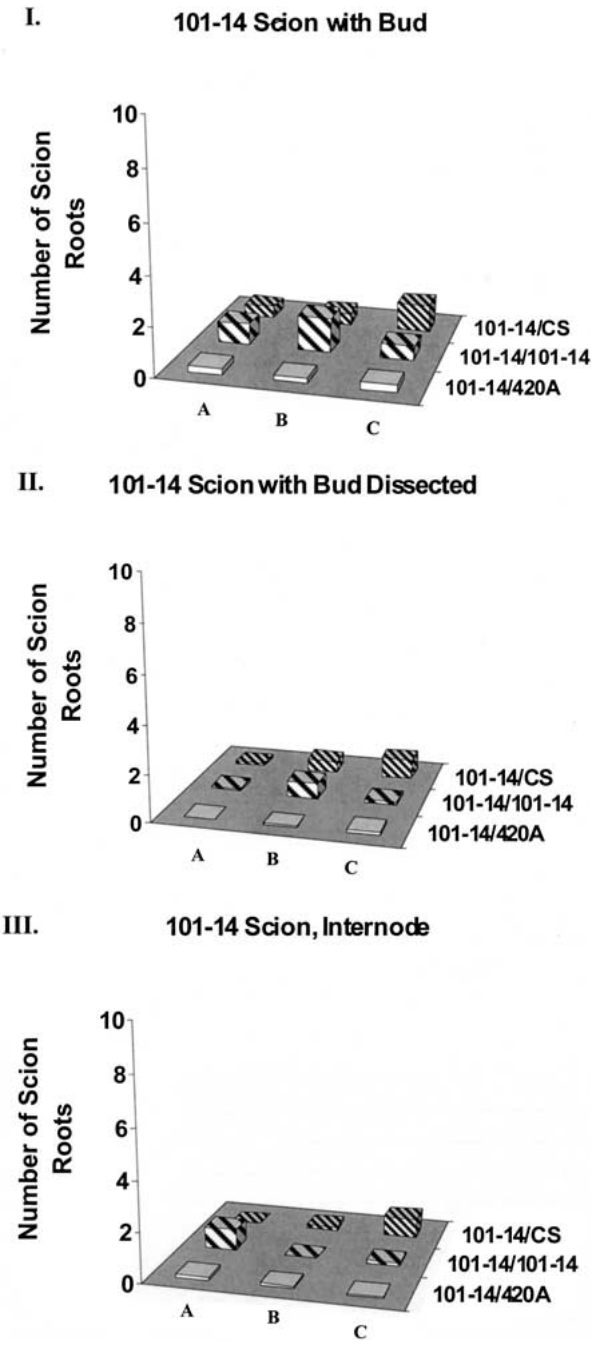

Figure 6. Figure shows the number of roots that emerged from a 3.0 cm scion cutting of *V. riparia* × *V. rupestris* cv. 101-14, when grafted onto a 3.0 cm rootstock cutting using the omega graph. Shown are the means (n ≅ 20 for each bar) when the rootstock piece consisted of (A) a node on which the dormant bud was intact, (B) a node from which the dormant bud was dissected, or (C) an internode. For the first row in the back (101-14/CS), the rootstock was *V. vinifera* cv. Cabernet Sauvignon. In the middle row (101-14/101-14), *V. riparia* × *V. rupestris* cv. 101-14 was the rootstock. In the front row (101-14/420A) *V. berlandieri* × *V. riparia* cv. 420A was the rootstock. Standard deviations were generally less than 20% of the mean.

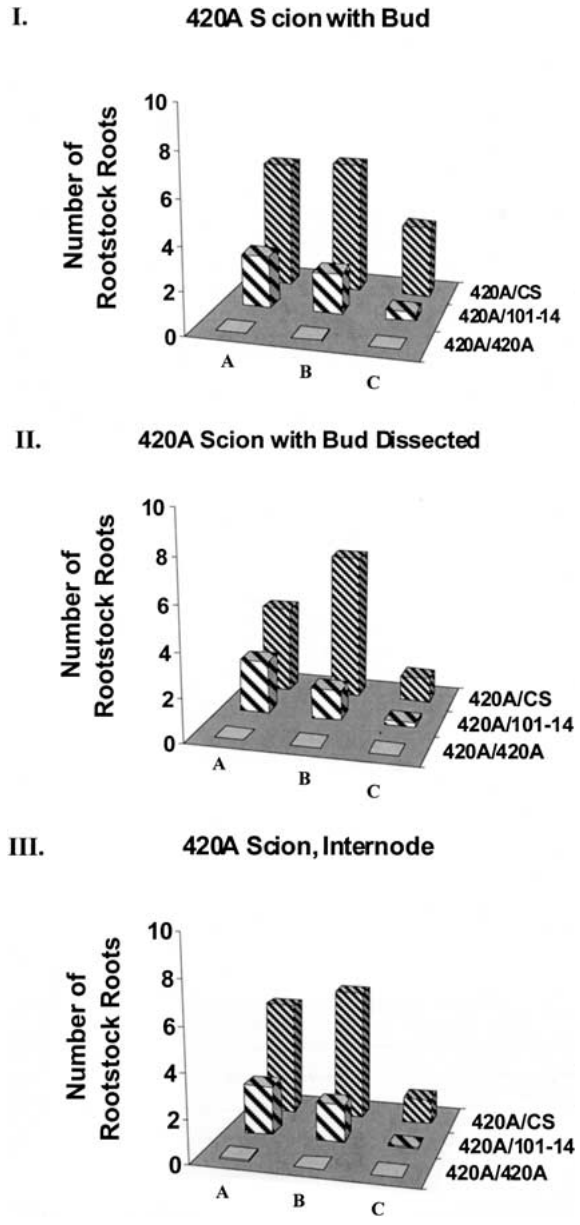

Figure 7. The number of roots that emerged from a 3.0 cm cutting in the rootstock position, when a 3.0 cm *V. berlandieri* × *V. riparia* cv. 420A scion was grafted onto it using the omega graph. Shown are the means (n ≅ 20 for each bar) when the rootstock piece consisted of (A) a node on which the dormant bud was intact, (B) a node from which the dormant bud was dissected, or (C) an internode. For the first row in the back (420A/CS), the rootstock was *V. vinifera* cv. Cabernet Sauvignon. In the middle row (420A/101-14), *V. riparia* × *V. rupestris* cv. 101-14 was the rootstock. In the front row (420A/420A) *V. berlandieri* × *V. riparia* cv. 420A was the rootstock. Standard deviations were generally less than 20% of the mean.

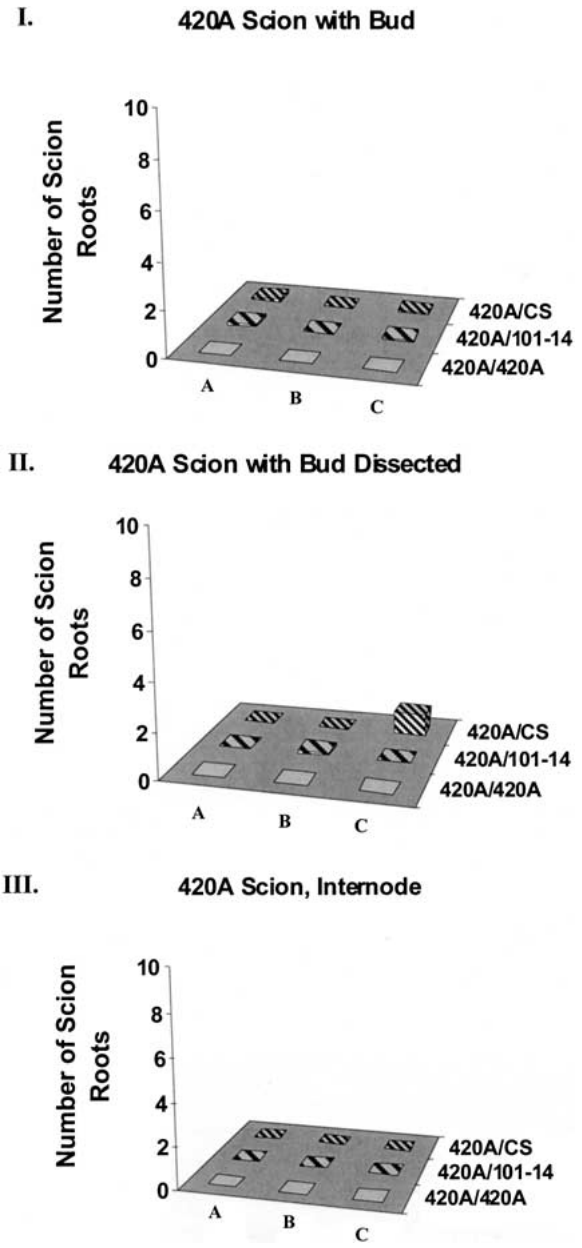

Figure 8. The number of roots that emerged from a 3.0 cm scion cutting of *V. berlandieri* × *V. riparia* cv. 420A, when grafted onto 3.0 cm rootstock cutting using the omega graph. Shown are the means (n ≅ 20 for each bar) when the rootstock piece consisted of (A) a node on which the dormant bud was intact, (B) a node from which the dormant bud was dissected, or (C) an internode. For the first row in the back (420A/CS), the rootstock was *V. vinifera* cv. Cabernet Sauvignon. In the middle row (420A/101-14), *V. riparia* × *V. rupestris* cv. 101-14 was the rootstock. In the front row (420A/420A) *V. berlandieri* × *V. riparia* cv. 420A was the rootstock. Standard deviations were generally less than 10% of the mean.

where all the scions were disbudded, with Figure 4, II). Thus, for CS, dormant bud removal increased adventitious root emergence, but only if the roots that emerged were in a position basipetal with respect to the dormant bud removed.

These observations suggest that a compound inhibitory to adventitious root formation may be transported basipetally from the apical scion bud and several candidate PGRs could be involved (Davis and Haissig 1990). Basipetal transport of PGRs like auxin, or auxin like compounds, can occur quickly (within 20 h) in cuttings of the length used in this investigation (Julliard 1966, 1967). In addition, Epstein and Lavee (1984) found that IAA was not readily transported out of basal internodes once it accumulates in them. But other candidate compounds cannot be ruled out, including cytokinins (van Staden and Harty 1988). Alteration in cytokinin:auxin ratios (Mullins 1967; Brouwer 1983) have been proposed as controlling antagonists in adventitious root formation. Our results did not support this hypothesis in its most simple scenario. Buds on non-dormant cuttings are auxin sources (Jacobs 1979), although it is uncertain when emerging non-photosynthetic buds, like those used in this investigation, become active and strong sources of IAA. Disbudding of pea cuttings results in lowered basal concentrations of IAA and diminished adventitious root formation (Nordström and Eliasson 1991). Indeed, it is often observed that adventitious roots emerge in the vicinity of the dormant bud in grapevine rootstock cuttings that are difficult to root. Thus, one of our hypotheses—that removal of the dormant bud in the case of the nonrecalcitrant to root rootstock (CS) would diminish adventitious root emergence—was not supported by our results. When scions of our most prolific root-forming species (CS) with the bud intact were grafted onto recalcitrant to root 420A, root emergence did not increase (Figure 3). In a like manner, scion pieces of recalcitrant to root rootstocks had no influence on adventitious root emergence in the other rootstock genotypes used in this investigation (Fig. 7). These results, taken together, indicate that the influence of ecodormant buds on adventitious root formation in general is small, with that of CS being mildly inhibitory.

This brings up the issue of the influence of a wound response in the treatments we subjected our cuttings to. Wounding induces callus and root formation, and the two processes are believed to be linked to some extent (Hartmann and others 1997). Nonetheless, all of the cuttings were cut in no less than four positions. All cut pieces with the same combinations of nodes and internodes (internodes always generated less callus independent of genotype, Figure 9), and from the same genotype, produced quantities of callus that were not statistically significantly different (Figure 9). It is interesting to note that 420A is extremely difficult to root, yet it produced statistically significantly more callus than the other genotypes (Figure 9). Any damage made to the cutting when dormant buds were removed also should not interrupt basipetal transport of PGRs because vasculature of the bud is distinct from that of traces that circumvent the bud (Fournioux and Bessis 1979). Thomas and Schiefelbein (2002) found that an actin depolymerizing factor protein was expressed during adventitious root formation in stem cuttings of *V. vinifera* (cv Arka Neelamani), but that wounding only weakly induced its expression. Thus, although it is possible that adventitious root formation is sensitive to wounding of dormant canes, it seems unlikely that wounding, in the specific case where dormant buds were removed from the nodal region, influenced our results. Rather, our results suggest that callus formation and adventitious root formation are subject to very different control mechanisms in dormant woody cuttings of *Vitis*.

Other arguments that can be invoked to explain such results, including the one that carbon competition limits adventitious root formation when the source of such an inhibitory compound (the dormant bud) is removed, were not strongly supported by our results. The total number of roots that emerged from the graftings (scion plus rootstock position) and the mass of roots produced (data not shown) did not differ over all grafting combinations. The callus score and the weight of removable callus produced by disbudding treatments were not statistically significantly affected by bud removal (Figure 9). Again, it is interesting that the recalcitrant to root hybrid 420A produced nearly twice as much callus as either CS or 101-14 (Figure 9). This observation might support the absence of signal for adventitious root formation in this genotype, but grafting buds from a prolific root former (CS) in either the scion or rootstock position did not effect adventitious root formation (Figures 3, 8), indicating the signal is probably not from buds.

It is immediately apparent from all of the figures that CS as rootstock produced adventitious roots prolifically regardless of whether the scion was clonal (Figure 3), consisted of an intermediate to root rootstock such as 101-14 (Figure 5, 101-14/CS) or a recalcitrant to root rootstock like 420A (Figure 7, 420A/CS). In a like manner, the rootstock 101-14 was intermediate to root regardless of whether the scion was clonal (Figure 5, 101-14/101-14), con-

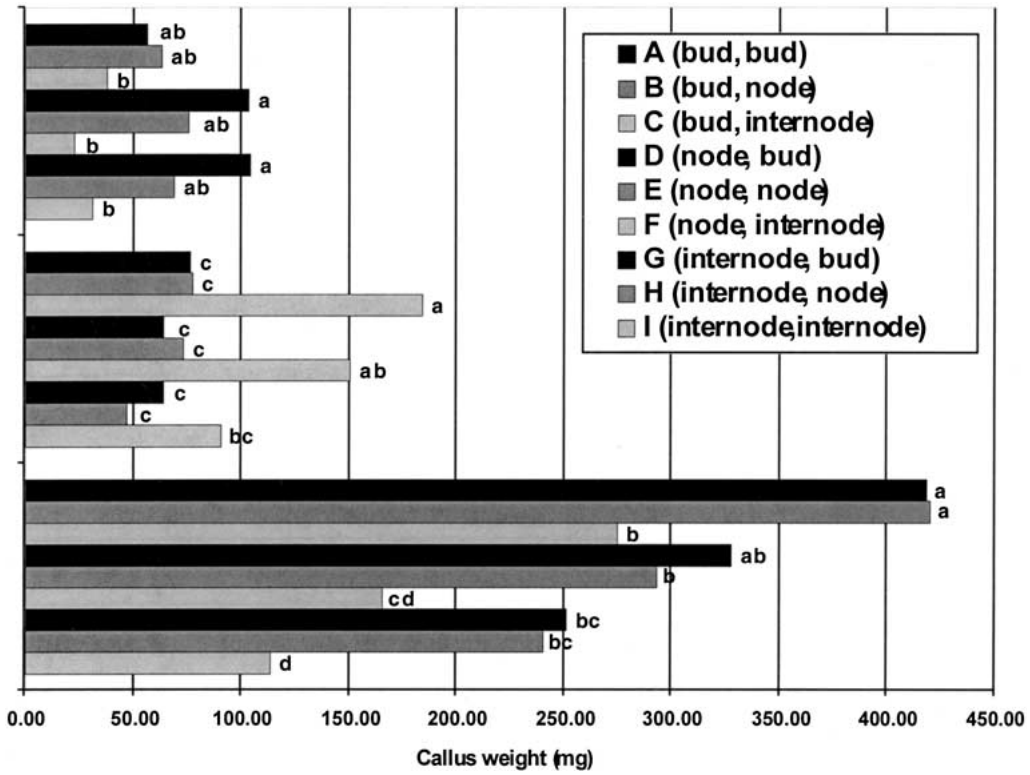

Figure 9. The dry weight of callus tissue that emerged from the basal end of graftings where *Vitis vinifera* cv. Cabernet Sauvignon (CS) comprised the scion and either CS, *V. riparia* × *V. rupestris* cv. 101-14 (101-14) or *V. berlandieri* × *V. rupestris* cv. 420A (420A) was the rootstock. For each of the three scion/rootstock sets, the nine possible combinations of A-I are as shown in Figure 2 and in the inset. Shown are the means of 20 individual observations. A scion/rootstock combination within each set differs significantly ($P < 0.05$) from a scion/rootstock combination within the same set if they do not share the same letter above the bars.

sisted of a prolific root former (Figure 3I, CS/101-14), or a recalcitrant to root species (Figure 7I, 420A/101-14). Finally, 420A was recalcitrant to root regardless of whether or not the scion was clonal (Figure 7, 420A/420A), consisted of a non-recalcitrant to root species (Figure 3, CS/420A) or an intermediate to root rootstock like 101-14 (Figure 5, 101-14/420A). Furthermore, disbudding of a scion or rootstock position did not significantly influence adventitious root formation by either of the more recalcitrant to root rootstocks (Figure 6 for 101-14 and Figure 8 for 420A ($P \geq 0.05$). Finally, for all three cultivars emergence of adventitious roots from the scion position was not statistically significantly influenced by any of the reciprocal transplant experiments ($P \geq 0.05$). CS nodes with dormant buds, disbudded nodes, and internodes in the scion position formed numerous roots (Figure 4), 101-14 nodes with dormant buds, disbudded nodes or internodes in the scion position produced an intermediate number of roots (Figure 6), and 420A nodes with dormant buds, disbudded nodes or internodes formed very few roots (Figure 8).

Concluding Remarks

Numerous rootstocks of woody cultivars that were originally selected for resistance to a number of root borne pests and diseases, are now used throughout the World for a host of other problems. These challenges include resistance to pests and diseases other than those initially targeted, adaptation to non-fertile and sodic- or lime-containing soils, and a range of other environmental problems. A substantial number of *Vitis* rootstocks are recalcitrant to form adventitious roots (Pongrácz 1983), as are rootstocks of other taxa. The economic losses associated with unsuccessful propagation of recalcitrant to root rootstock cultivars has increased in concert with the heightened popularity of such *Vitis* rootstocks. PGRs like auxin and its derivatives have proven effective at increasing the rooting ability of such rootstocks, and cultural practices such as the use of mist chambers and water soaking have emerged as another primary means of improving rooting success.

We have demonstrated that although the dormant bud exerts some control over adventitious root

formation in *Vitis vinifera*, such control was not apparent in two North-American hybrid rootstocks. Thus, the notion that disbudding rootstock cuttings diminishes adventitious root formation was not supported by the results of our investigation. It is not clear whether or not the physiological state of buds used in our study correlated with the conditions under which other researchers have observed changes in grapevine adventitious root formation (age of bud and dormancy). This is a common problem with respect to other woody species as well. Nonetheless, our data clearly support the statement that the bud can influence adventitious root formation and can be inhibitory (Favre 1973). Great strides are being made in our understanding of the ways in which PGRs operate, and information concerning signal transduction pathways is important in this respect (Hwang and Sheen 2001; Leyser 2001). Although there is a clear need to understand the molecular genetic controls on adventitious root formation in grapevines (Thomas and Shiefelbein 2002), their woody habit and long generation times does not make them easily amenable to molecular genetic investigations. Thus, non-dormant tissues and tissue culture methods have become the most effective medium for such investigations. As a consequence, there is still an unmistakable need to understand how environment (trellising and training systems, cultural conditions and harvest practices) interacts with internal factors that apparently improve adventitious root formation (carbon availability or endogenous levels of growth regulators), in order to improve our ability to propagate grapevines.

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