

Biological and environmental factors controlling root dynamics and function: effects of root ageing and soil moisture

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Abstract

Understanding factors controlling root dynamics and functioning can lead to more efficient and profitable vineyard management. However, our current understanding of root dynamics and their regulation by plant and environmental factors is limited, particularly under field conditions. This paper presents current understanding of grape root dynamics, highlighting studies using minirhizotron cameras, which directly assess root dynamics, and experiments on roots of known age, which link root phenology and function.

Data summarised here show timing of grape root production varies widely among different regions, as well as among rootstocks and canopy management systems in the same region. Timing of production can be responsive to differences in soil moisture. Lifespan of grape roots, however, appears less affected by soil moisture because of nocturnal hydraulic redistribution. Root function, such as capacity for P and N uptake, declines rapidly with root age. Differences in timing and spatial distribution of root production can effect above-ground growth and vineyard water-use efficiency.

Improving our understanding of when roots grow and are functionally active in agricultural systems can lead to improved water and fertiliser applications, and more precise vineyard management. Because both environmental and biological factors affect root dynamics, simple predictions of timing of root production or standing populations with shoot development are unlikely to be achieved. However, with multi-year data on root dynamics, and environmental and biological factors, regionally specific models of root populations and their functioning may be possible to develop.

Keywords: *grape root, root function, root production, water-use efficiency, WUE*

Introduction

Optimisation of grapevine management under current and future climates requires better knowledge of both shoot and root system function. Above-ground growth and development in grape have been studied largely independent of the below-ground system due, in part, to technical difficulties involved with investigating roots. Techniques allowing for detailed root observation have permitted some progress in enhancing knowledge of below-ground systems (e.g. Comas et al. 2000), but important aspects of root dynamics and function are still missing. Patterns of grape root growth commonly found in textbooks are based on limited data sets (e.g. Mullins et al. 1992) and have recently shown not to be universal (Eissenstat et al. 2006). Research is still ongoing to uncover the fundamental 'rules' governing root growth. Root growth varies depending on both plant and environmental factors (e.g. Comas et al. 2005, Bauerle et al. 2008b). It may be possible to model root system growth and function over the season with better understanding of plant and environmental controls over root growth, as well as additional root physiological information, such as

nutrient and water uptake, and changes in these functions with root ageing (Comas et al. 2000, 2005).

Understanding the effects of limited water availability on root system growth and function is essential for adapting vineyard management under anticipated changes in agricultural resources (Clingeffer 2009, Schultz 2009). As water availability becomes progressively more limited because of increased agricultural, residential and urban demands, and anticipated climatic changes, there is an increasing need to make vineyard systems more efficient through better management of crop water use (Clingeffer 2009). Vineyard managers will need to adapt current viticultural practices to respond to changes in rainfall patterns, water supplies for irrigation and warmer temperatures. One approach is to select varieties and rootstocks for higher water-use efficiency (e.g. Collins and Loveys 2009, Flexas et al. 2009, de Herralde et al. 2009, Vandeleur et al. 2009). In addition, a more mechanistic understanding of root allocation, distribution and functioning of drought-tolerant versus drought-avoiding varieties and rootstocks under limited soil moisture will enhance efforts at fine-tuning vineyard management. Drought-tolerant strategies may include producing roots

that can survive in periodically dry soil, while drought-avoiding strategies may include shedding roots in dry areas and rapidly growing roots in moist areas to maintain plant water status (Huang et al. 1997). These strategies may affect seasonal as well as spatial (e.g. vertical) root distribution and may have implications for other aspects of management such as timing and method of fertilisation.

Recent contributions made from minirhizotron and rootbox studies in grape will be reviewed to explore implications of this research for management. We will specifically explore current information on the timing of root production and seasonal root standing populations, ageing effects on grape root function and implications for seasonal nutrient absorption by vines, soil moisture effects on grape root production and lifespan, and hydraulic redistribution, and suggest areas where more research is needed.

Timing of root production

There have been long-standing assumptions that grapevines have bimodal root production, with roots growing in spring and fall, and little growth in summer (Lyr and Hoffman 1967, van Zyl 1988, Mullins et al. 1992). This pattern was thought to be driven by root carbon competition with the needs of shoot and fruit development, and lack of soil moisture in many climates in summer months. These assumptions, however, were based on limited data and do not appear to be universal (Eissenstat et al. 2006). Detailed field observations of root populations indicate that root growth primarily occurs between flowering and veraison in both temperate and Mediterranean climates, despite the co-occurrence with summer growth, although years of extremely low soil moisture could limit root growth without supplemental irrigation (Comas et al. 2005, Eissenstat et al. 2006, Bauerle et al. 2008b, Field et al. 2009) (Figure 1). In temperate climates with favourable postharvest growing conditions, some rootstocks produced a smaller postharvest flush of roots in addition to the main peak of fine root growth that occurred around anthesis (Field et al. 2009). In subtropical climates with a short growth period between budburst and harvest but long postharvest period with favourable growing conditions, the primary period of root growth occurred post-harvest with no spring flush (Oag et al. 2009).

In addition to environmental effects on root production, canopy management can also affect the timing of root production (Comas et al. 2005). Minimal pruning in which almost no pruning is done has recently increased in popularity for many grape varieties as a way to increase fruit production while minimising labour costs of pruning (Clingleffer 1984, Poni et al. 2000, Weyand and Schultz 2006, Carbonneau 2009). Minimal pruning leaves more nodes on shoots, leading to more rapid canopy development in the spring and heavier fruit production, but similar final canopy size as heavily pruned vines later in the season (Lakso 1999a,b). Minimal pruning of own-rooted Concord vines led to earlier initiation of root growth, which was produced in more shallow depths, likely because of root production occurring earlier in the

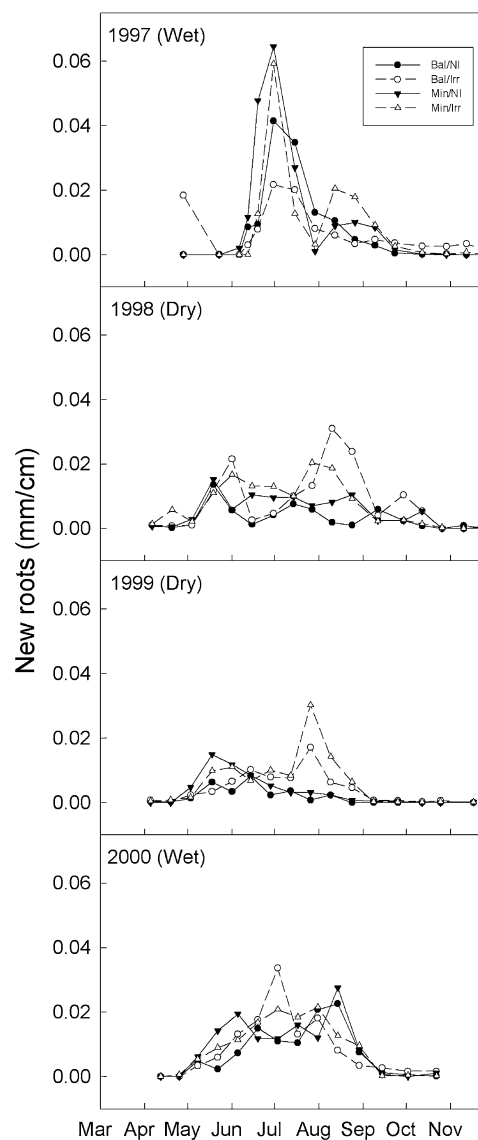


Figure 1. New root production visible in minirhizotrons (root length per observational area) in 4 years of study in heavily pruned/rainfall (Bal/NI), heavily pruned/irrigated (Bal/Irr), minimally pruned/rainfall (Min/NI), minimally pruned/irrigated (Min/Irr) Concord grapevines. Each point of each treatment is the average of root populations from four experimental blocks. The 4 years of study included two wet years (1997 and 2000) and two dry years (1998 and 1999). Adapted from Comas et al. (2005).

season when temperature in shallow soil would be most favourable for root growth (Comas et al. 2005).

Ageing effects on grape root function

Root systems are architecturally complex and have multiple functions. In woody plants such as grape, woody portions of the root system provide the structural framework and are mainly used for transport, anchorage and storage of carbohydrates and nutrients. These roots produce non-woody, fine lateral roots each year that provide the principal means of water and nutrient absorption. The different functions of these portions of the root system can be recognised by considering branching order and secondary development (Pregitzer et al. 2002, Guo

et al. 2008). Using a morphometric classification scheme (*sensu* Fitter 1982), the first-order roots are the ultimate fine laterals with no branches, the second-order roots only have first-order laterals and so on. Anatomical studies have shown that the more permanent woody roots usually begin at the third or fourth order, which is indicated by secondary growth, loss of cortex and mycorrhizae, increased vessel size and development of a cork periderm (Guo et al. 2008, Valenzuela-Estrada et al. 2008). First- and second-order roots, which usually have an intact cortex, make up the majority of the length of the root system and are primarily responsible for water and nutrient acquisition of the vines.

First- and second-order roots are usually determinant in growth; typically, an individual root may not extend more than 2–3 cm in length (Volder et al. 2005, Resendes et al. 2008). Growth and development of these roots are accomplished in often just 1–3 days. Many things change in the first days and weeks of the roots' life that strongly influence their ability to absorb water and nutrients. One important change is mycorrhizal colonisation. Little is known on rates of mycorrhizal colonisation in the first days and weeks of a grape root's life. In apple, mycorrhizal colonisation begins when roots are about 3 days old and peaks after about 2 weeks, based on work in a ripe apple orchard in Pennsylvania (Resendes et al. 2008). Many roots do not become mycorrhizal, and these can be colonised by non-mycorrhizal fungi, some of which are likely pathogenic. Interestingly, faster growing roots at birth are more likely to be colonised by mycorrhizal fungi, and their growth can be promoted following colonisation (Resendes et al. 2008). Rarely are young apple roots colonised by both mycorrhizal and non-mycorrhizal fungi. This study suggested that while many first-order roots may be born at a particular time, they are not all born equal. Some are faster growing, likely to become mycorrhizal and become an important component of the absorptive root system. Others are thinner and slower growing, likely to remain uncolonised by mycorrhizal fungi and have a high probability of being colonised by other kinds of fungi that are not beneficial to the plant and quite possibly pathogenic. Typically in apple (e.g. Wells and Eissenstat 2001) as well as in grape (Anderson et al. 2003, Bauerle et al. 2008b), a portion of any root cohort dies fairly quickly, often within 3–4 weeks. Based on the work of Resendes et al. (2008), we suspect that the portion of the fine root system that rapidly dies may disproportionately include roots that are less vigorous at birth and lack mycorrhizal colonisation compared with those more vigorous at birth and quickly colonised by mycorrhizal fungi.

Roots also change with age in a number of physiological parameters, including respiration, nutrient uptake kinetics and phenolic compounds. Nitrate uptake, for example, is very high when the root is first born, but declines markedly after just a few days (Volder et al. 2005, 2009). Nitrate uptake follows root N concentration presumably because of the linkage of protein N to the carrier enzymes needed for uptake (Volder et al. 2005). In very young roots, nitrate may also serve as an osmoticant

to increase turgor of the elongation region of the root tip (Bloom et al. 2002). Uptake potential of phosphate also has been shown to decline with root age in other fruit crops (Bouma et al. 2001). Root respiration declines with root age (Comas et al. 2000, Bouma et al. 2001, Volder et al. 2005), which tends to reduce the costs of root maintenance in parallel with the benefits associated with root uptake. This tracking of losses in root uptake capacity with root maintenance costs results in fairly stable root efficiency (benefit/cost) with root age (Bouma et al. 2001, Volder et al. 2005).

In grape, declines in root respiration also parallel increases in root pigmentation or root browning (Figure 2) (Comas et al. 2000). Pigmentation may be the result of condensed tannins as found in *Eucalyptus pilularis* and *Pinus banksiana* (McKenzie and Peterson 1995). Often, the internal structures of mycorrhizal fungi and cortical cells die as browning advances (Richards and Considine 1981, Comas et al. 2000). In minirhizotron studies of Concord grape, root browning usually took 3–4 weeks (Anderson et al. 2003). Concord grape roots browned more quickly when born after flowering, rather than before flowering, possibly related to soil temperatures delaying rates of browning in cooler soils typical before flowering in upstate New York (Anderson et al. 2003). Both warmer soil temperatures and low soil moisture have been associated with more rapid browning

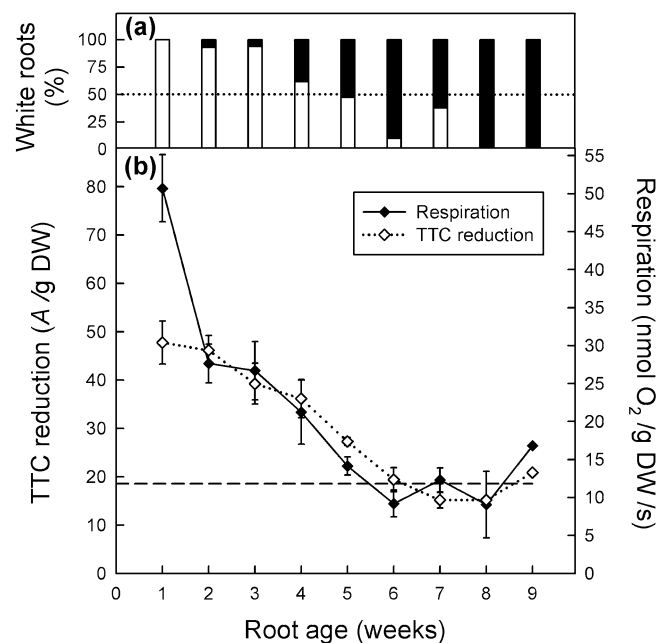


Figure 2. (a) The per cent of root pigmentation with age (in weeks) shown as the proportion of root samples in each age class that were white (white bars) versus the proportion that were brown or black (black bars). Dotted line (.....) indicates the level where 50% of the roots sampled were brown or black. (b) Metabolic activity with root age estimated by tetrazolium chloride (TTC) reduction (measured as absorbance units per gram dry weight) and respiration for Concord grape roots undergoing both balanced- and minimal pruning (\pm standard error). Dashed line (----) indicates absorption determined from control roots. The figure is reproduced with permission from Comas et al. (2000). ©New Phytologist.

(Rogers 1939, Bartsch 1987). Browning has been associated with death of the cortex and, ultimately, root death (Comas et al. 2000). Thus, the accumulation of phenolic compounds associated with browning may either be directly or indirectly linked to loss of root absorptive potential with age.

Soil moisture effects

Grapevines, compared with many other fruit crops, grow well in regions of little to no summer precipitation (Champagnol 1984, Mullins et al. 1992). Although it has been long recognised that grapevines are able to survive in zones of severe water limitation, little attention has been given to the mechanisms underlying their survival. Plants typically preferentially grow roots in regions of soil with moderately high moisture (Coutts 1982, Fort et al. 1998, Green and Clothier 1999). An important aspect in understanding plant response to soil moisture deficits is the potential of plant roots to continue functioning as soil moisture decreases. Moisture within the soil profile is also heterogeneous. Root systems must forage for this resource by adjusting tissue deployment (Stasovski and Peterson 1991, Taleisnik et al. 1999) and physiology (Sharp and Davies 1979, Westgate and Boyer 1985) in order to obtain this limited resource.

Efficient foraging for soil resources through shifting root tissue deployment involves intrinsic plant control over new root production and root survivorship. Plants generally respond to localised patches of water and nutrients by increasing new root production and longevity (e.g. Pregitzer et al. 1993). Species and varieties, however, vary in their capacity for root initiation and growth responses to heterogeneous environments (Campbell et al. 1991, Bauerle et al. 2008b). In field situations, changing root distribution among different patches and layers of soil moisture over the growing season may involve shifting zones of new root produc-

tion and shortening lifespan of existing roots. The portion of the grape root system near the soil surface often encounters extremely different soil moisture conditions than that in deeper soil layers. Grape roots growing in deeper soil layers were found to have prolonged lifespans compared with those in shallow soil (Anderson et al. 2003). However, root lifespan was either not different in irrigated versus rainfall patches or it was shorter in irrigated patches (Anderson et al. 2003, Bauerle et al. 2008a).

Grapevine root growth plasticity in response to soil moisture plays an important role in regulating when and where roots capture resources. Root proliferation of new root laterals in patches of available soil resources increases a plant's chance of local resource capture (Hodge 2004). When plant roots encounter a patch of water during times of limited water supply, they typically proliferate roots within it (Hodge 2004). However, years of breeding have produced rootstocks that vary in their propensity for growth in resource-limited environments (Smart et al. 2006, Bauerle et al. 2008b) (Figure 3). As discussed above, it was previously considered a general rule that root and shoot growths were disparate, with root growth slowing during summer months when shoot growth was most active and soil moisture was most limiting (Lyr and Hoffman 1967, van Zyl 1988). Studies have shown that root growth of some grape species and rootstocks can be greatly reduced under extreme conditions of dry soil without supplemental irrigation (Comas et al. 2005), while in some species and rootstocks, vines can continue to produce new roots during moderate to severe water stress and may be stimulated to produce larger root populations (Freeman and Smart 1976, van Zyl 1988, Gomez-Del-Campo et al. 2005, Bauerle et al. 2008b) (Figure 3).

Inconsistent responses to soil moisture may be due in part to differences between grape species and rootstocks

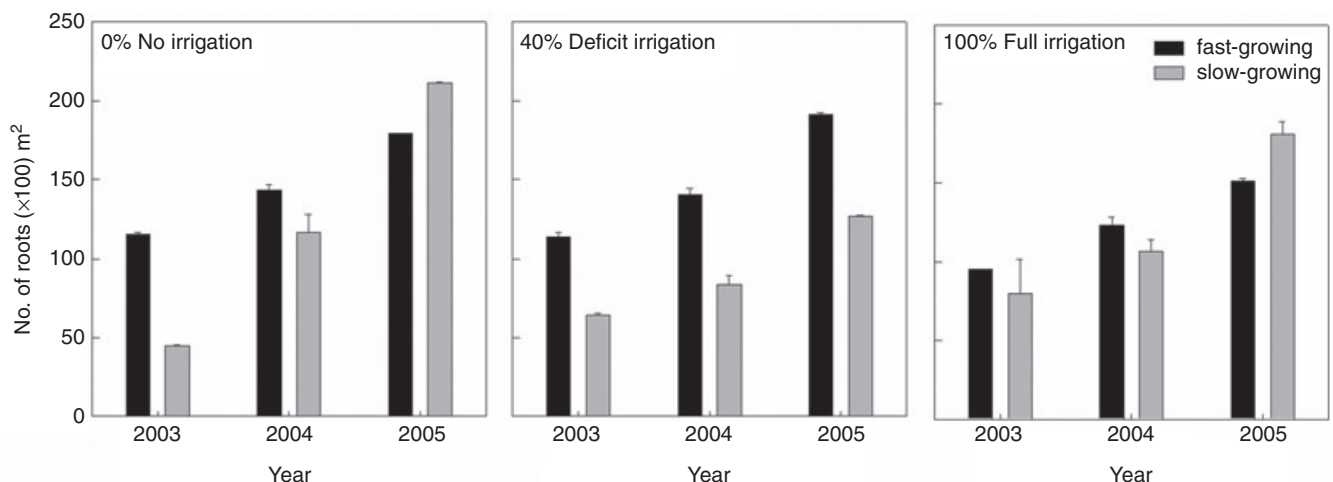


Figure 3. The number of roots produced in minirhizotron windows in a Merlot vineyard in Oakville, California, USA, during the main growing season for a fast-growing rootstock (1103 Paulsen (*Vitis berlandieri* \times *Vitis rupestris*)) and a slow-growing rootstock (101–14 Millardet de Gramanet (*Vitis riparia* \times *V. rupestris*)) over 3 years under three levels of irrigation (no irrigation, 40% (deficit irrigation), and 100% crop evapotranspiration (E_t)). E_t was calculated from the evaporation of a class A pan and the Penman–Monteith equation (E_t), and corrected with crop coefficients (K_c) put forward by Pritchard (1992). Adapted from Bauerle et al. (2008b).

displaying different strategies of coping with drought. In Mediterranean climates, studies of two contrasting rootstocks found a faster-growing rootstock produced the majority of its roots during the warm summer months, while a slower-growing rootstock avoided the hot summer months and tended to grow a greater portion of its roots during the predictable wet winter months (Bauerle et al. 2008b). The faster-growing rootstock also rapidly produced roots in irrigated soil zones, while the slower-growing rootstock limited root production in dry soil and shifted production to deeper soil horizons, where moisture is relatively more constant, or to periods of the year with more favourable water availability (Bauerle et al. 2008b). Greater root production under limited moisture availability is consistent with the optimisation theory of plant growth allocation, which suggests that plant carbon will be deployed to those absorptive tissues whose resource acquisition most limits plant growth (e.g. Bloom et al. 1985). However, when soil moisture is extremely limited, there may be physical barriers to root production because of high soil impedance (e.g. Cornish et al. 1984) for which species and rootstocks may vary in sensitivity. Thus, research indicates that even within the same climate and vineyard, not all grape root systems should be managed the same. In order to optimise and properly manage irrigation and fertiliser application, vine root growth and the growth strategy of the rootstock should be considered.

In addition to shifts in root tissue deployment in response to low soil moisture, internal water transport and, specifically, hydraulic redistribution may mitigate root water stress when water is limiting (Bauerle et al. 2008a). Hydraulic redistribution, the nocturnal movement of water from roots in wet zones to roots in dry zones (Richards and Caldwell 1987), may alleviate vine water stress by rehydrating roots that are subjected to severe moisture stress. Grapevines have relatively large xylem vessels compared with other plants, allowing for low hydraulic resistance. This hydraulic architecture permits relatively rapid redistribution of water to those roots under the greatest moisture stress (Smart et al. 2005).

There are several theories to explain how hydraulic redistribution benefits the plant, including retained cell turgor for plant growth (Hsiao and Xu 2000), refilling of xylem embolisms (McCully 1999) and providing water for nocturnal increases in leaf water content (Nardini and Pitt 1999). Moreover, prolonged root function as a direct result of hydraulic redistribution can extend root lifespan, which may increase nutrient uptake (Matzner and Richards 1996, Eissenstat et al. 1999). Research on grapes grown under a controlled setting where transpiration was controlled by supplemental lighting during nocturnal hours suggests internal hydraulic redistribution extends root lifespan in dry soil (Bauerle et al. 2008a). Thus, hydraulic redistribution can benefit grapevines by allowing them to mitigate adverse effects of soil moisture deficits on roots, including root shrinkage, xylem embolisms and, ultimately, root death (North and Nobel 1997, Caldwell et al. 1998).

Conclusions

Understanding the plasticity of vine growth above- and below-ground, and root functionality under drought conditions is important for effective management of vineyards. Patterns of root growth vary with both environmental and inherent plant-based factors (e.g. exogenous vs endogenous controls) (e.g. Huang and Eissenstat 2000, Comas et al. 2005) (Figures 1,3). While we are beginning to appreciate some of the variables affecting root growth and functioning, more information is needed in order to develop rules that govern general patterns. Economic pressures on vineyard management to reduce labour costs have changed management of the above-ground portions of vines, but there is limited understanding of the consequences of above-ground management on below-ground growth. For example, minimal pruning may save labour costs but may cause earlier canopy development, with shifts in the size and timing of root system development that may require alterations to the application of fertilisation and irrigation (Comas et al. 2005). Optimising vineyard management to effectively shape grape root system growth for avoiding or tolerating drought (e.g. Soar and Loveys 2007) requires more information of growth and functional responses of grape root systems to biotic and abiotic factors.

It may also be possible to directly apply a better understanding of grape root functioning under drought to optimise vineyard management for minimal water use. California wineries and vineyard managers currently use leaf water potential as a means of monitoring vine water status (Williams and Araujo 2002), which may not necessarily give the appropriate information needed to calculate the application of water resources. For several species, researchers have considered root water status as an indication of plant performance under drought conditions (Nobel and Lee 1991, Simonneau and Inra 1991), although never for *Vitis*.

In order to understand the functioning of the root system and best manage the efficient application of nutrients and water, we need to know when fine root populations are produced; when these root populations are functionally active, both for nutrient and water uptake; and how these resources are redistributed within the plant. We need to develop a more predictive understanding of how different environmental and endogenous factors control root growth and function. Undoubtedly, this understanding will help inform more mechanistic models of root growth and function to assist in vineyard management.

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