

# Root foraging in response to heterogeneous soil moisture in two grapevines that differ in potential growth rate

Taryn L. Bauerle<sup>1</sup>, David R. Smart<sup>2</sup>, William L. Bauerle<sup>3</sup>, Christine Stockert<sup>2</sup> and David M. Eissenstat<sup>1</sup>

<sup>1</sup>Department of Horticulture, Penn State University, University Park, PA, USA; <sup>2</sup>Department of Viticulture and Enology, University of California, Davis, Davis, CA, USA; <sup>3</sup>Department of Horticulture & Landscape Architecture, Colorado State University, Fort Collins, CO, USA

## Summary

Author for correspondence:

David M. Eissenstat

Tel: +1 814 863 3371

Fax: +1 814 863 6139

Email: [dme9@psu.edu](mailto:dme9@psu.edu)

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- Linkages between plant growth rate and root responses to soil moisture heterogeneity were investigated.
- Root dynamics were studied using genetically identical shoots (*Vitis vinifera* cv. Merlot) with genetically distinct root systems that promote higher (HSV) and lower (LSV) shoot growth rates (1103P and 101–14 Mgt, respectively). Three quantities of irrigation replenished different amounts of evapotranspiration (0, 40 and 100%  $ET_c$ ) in a California vineyard.
- Roots of HSV vines exhibited more plasticity, as indicated by greater preferential growth in irrigated soil during the summer, and a larger shift in root diameter with a change in soil moisture than LSV vines. Higher tolerance of low soil moisture was not observed in LSV roots – root survivorship was similar for the two rootstocks. LSV vines produced a large fraction of its roots during the winter months and increased root density over the study, while HSV vines produced roots mainly in summer and only exhibited a high initial peak in root biomass in the first year.
- These results demonstrated that a plant of higher vigor has greater morphological plasticity in response to lateral heterogeneity in soil moisture but similar tolerance to moisture stress as indicated by root survivorship in dry soil.

**Key words:** avoidance, localized water stress, minirhizotron, plasticity, root production and survivorship, shoot vigor, tolerance, *Vitis* rootstock.

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## Introduction

Owing to both spatial and temporal heterogeneity of resources in soil, the efficient deployment of roots in resource-rich patches and reduced expenditures to roots in resource-poor patches are often important considerations for success in a resource-limiting environment (Fitter, 1994). Trade-offs between tissue construction and maintenance (Eissenstat & Yanai, 1997), and between root and shoot biomass allocation (Sharp & Davies, 1979), can substantially influence plant foraging for below-ground resources (Caldwell, 1976).

Fast- and slow-growing species may respond differently to low resource availability (Lambers & Poorter, 1992). In this study we examine morphological plasticity or the proportional growth of roots in resource-rich patches relative to total root

growth so as to increase acquisition of limiting soil resources. Studies that have examined the role of plant growth rate on root morphological plasticity have typically focused on nutrient supply (Crick & Grime, 1987; Eissenstat & Caldwell, 1988a; Doussan *et al.*, 2003; Hodge, 2004 and references therein). Fast-growing species generally exhibit more morphological plasticity than slow-growing species, thus allowing them to grow roots more quickly in areas rich in nutrients (Crick & Grime, 1987). It is not clear if these trends hold true for root systems exposed to localized patches of soil moisture. During periods of decreased water availability, increased root production or fine lateral initiation has been observed in field-grown tomatoes (Reid & Renquist, 1997) and perennial ryegrass (*Lolium perenne*; Jupp & Newman, 1987). As soil dries, plants typically reduce root growth (Richards & Cockroft, 1975;

Stuedle, 2000; Comas *et al.*, 2005) and carbon allocation (Kosola & Eissenstat, 1994) to those roots in dry portions of soil and preferentially grow roots in regions of high soil moisture (Courtts, 1982; Fort *et al.*, 1998; Green & Clothier, 1999).

Root foraging during periods of low soil moisture has important consequences for the plant. Resource capture by resource pre-emption, for example, can determine plant success in below-ground competitive interactions (Eissenstat & Caldwell, 1988b; Hodge, 2004). Root systems of high plasticity can incur substantial risk if periods of favorable soil moisture are followed by long periods without rain. Some plants, such as cacti, can produce very inexpensive 'rain roots' that respond very quickly to ephemeral supplies of water (Snyman, 2006), whereas other plants, such as citrus, may utilize a more conservative strategy of modest root growth in wet soil and maintenance of roots in dry soil (Kosola & Eissenstat, 1994; Eissenstat *et al.*, 1999). Allocation of carbon toward the root system to build 'expensive' roots with a well developed exodermis and endodermis has also been shown to limit root desiccation in dry soil (North & Nobel, 1991).

### Soil moisture heterogeneity in the landscape

Spatial and temporal variation in soil moisture can result in distinctively different soil moisture distribution in the surface soil layers. Lateral soil moisture heterogeneity can result from variation in topography, such as depressions or stream channels, water infiltration, differential root competition as well as agricultural irrigation. On an evolutionary timescale, there is little predictability as to whether certain lateral roots might encounter high soil moisture during periods of high moisture stress. Thus root systems with high growth plasticity may allow a plant to exploit lateral soil moisture heterogeneity better.

Unlike lateral heterogeneity in soil moisture, vertical heterogeneity is often predictable in both space and time, especially in climates with distinct wet and dry seasons and where soil water recharge occurs during the wet season. Soils typically dry out in the top soil layers first while deeper soil layers maintain higher amounts of soil moisture. Root system plasticity may contribute to water acquisition at deeper depths in the soil; however, vertical root growth also typically has a strong genotypic component (Doussan *et al.*, 2003).

Exploring how plants with different growth rates respond to heterogeneous water supply contributes to our understanding of how root foraging behavior may be linked to plant potential growth rate in perennial plants. Our study is unique in that we examined genetically identical shoot grafts (scions) on two genetically distinct root systems that differ in their effects on shoot growth rate (vigor). We quantified how root production, seasonal partitioning, and lifespan in grapevines of different potential growth rate respond to soil moisture heterogeneity along a gradient in whole-plant water stress severity. Compared with lower vigor vines, we hypothesized

that vines with higher vigor would display greater plasticity in root growth and morphology, especially to lateral soil moisture heterogeneity, but less tolerance of stress, as indicated by higher root mortality in dry soil. In addition, we predicted that these traits would be most accentuated in vines of moderate to high water stress.

## Materials and Methods

### Experimental site

We compared two rootstock cultivars that differed in potential growth rate. The rootstock 1103 Paulsen (1103P; *V. berlandieri* × *V. rupestris*) is a root system tending to provide high shoot growth (HSV), and commonly referred to as conferring high vigor in horticultural and viticultural disciplines (Wolpert *et al.*, 2002). The other rootstock was 101-14 Millardet de Gramanet (101-14 Mgt; *Vitis riparia* × *V. rupestris*), a root system associated with lower shoot vigor (LSV, see Bauerle *et al.*, 2007). Vines were grown under different quantities of drip irrigation in an established Merlot (*Vitis vinifera* cv. Merlot) experimental block in Oakville, CA, USA (in cooperation with UC Davis). The vines were 11 yr old and planted in Bale (variant) gravelly loam (fine-loamy, mixed, superactive, thermic Cumulic Ultic Haploxeroll). Mineral soils in the 0–20 cm range had total soil N of  $0.21 \pm 0.01\%$ , KCl-extractable  $\text{NH}_4^+ \text{-N}$  of  $3.02 \pm 0.25 \text{ mg kg}^{-1}$  and  $\text{NO}_3^- \text{-N}$  of  $2.75 \pm 0.26 \text{ mg kg}^{-1}$  (Carlisle *et al.*, 2006).

The Oakville region averages 83 cm of precipitation annually and has a mean annual temperature of  $14.3^\circ\text{C}$  (CIMIS, 2003–2005). Precipitation normally occurs from the months of November to April, with the majority of precipitation falling in December and January. The typical growing season of the vineyard begins with budbreak in March until fruit harvest in September and leaf senescence in November.

The vines were trained on a bilateral cordon with vertical shoot positioning (VSP) and oriented SE to NW with rows of vines spaced  $2.4 \times 2.2 \text{ m}$  apart. We utilized a completely randomized block design with irrigation amount (three values) and two rootstock cultivars randomized in each block in a total of six blocks. The entire experimental vineyard comprised 1.05 hectares. In 2002, each experimental vine was reduced from two to one irrigation drip emitter, located 50 cm from the trunk. Irrigation treatments were started when midday stem water potentials (see later description) reached a critical value of  $-1.0$  to  $-1.2 \text{ MPa}$ . Irrigation was applied twice weekly and determined using crop evapotranspiration ( $ET_c$ ), the loss of water to the atmosphere by the combined processes of evaporation (from soil and plant surfaces) and transpiration (from plant tissues), calculated from the Penman–Montieth relationship that was subsequently corrected using a grape crop coefficient ( $K_c$ ) computed as a function of total accumulated growing degree days, and

evaporation from a class A pan (Pritchard, 1992). Irrigation treatments consisted of 0% (no irrigation), 40% (deficit irrigation with 40% replacement of  $ET_c$ ), and 100%  $ET_c$  (full replacement) and were randomly assigned to subplots of each rootstock within the vineyard.

## Environment

Environmental data were obtained from an on-site weather station (CIMIS, 2003–2005). Volumetric soil water content was estimated at 20–50, 50–80 and 80–120 cm depths using time domain reflectometry using the minirhizotrons as access tubes for the soil moisture probe (Model TRIME-FM T3; Mesa Systems Co., Medfield, MA, USA). These soil depth intervals corresponded with the highest root densities. Volumetric soil moisture ( $\theta_v$ ; %) was converted to soil matric potential (MPa) by a soil water retention curve determined using a pressure plate extractor (Soil Moisture Equipment Co., Santa Barbara, CA, USA) under five pressures (–0.01, –0.03, –0.1, –3, and –1.5 MPa). Bulk density measurements, acquired over several time points spanning 2002–03 in a previous study at the same vineyard (Carlisle *et al.*, 2006), were  $1.33 \pm 0.10 \text{ g cm}^{-3}$  at 6–12 cm depth with a slightly compacted layer of  $1.45 \pm 0.05 \text{ g cm}^{-3}$  at 40–46 cm depth.

Predawn and solar noon stem water potentials were monitored throughout the growing season with a pressure chamber (Soil Moisture Inc., Santa Barbara, CA, USA). Approximately every 10–14 d, stem water potentials were determined in all 36 minirhizotron treatment vines by first placing a leaf in a plastic bag and then aluminum foil to prevent light penetration for 15 min before severing the leaf and placing it in the pressure chamber (Shackel *et al.*, 2001).

## Root observations and measurements

Minirhizotron root observation tubes (1.3 m long and 6 cm outside diameter) of clear plastic (cellulose acetyl butyrate) were installed in April 2002 at an angle of 30° from the vertical to a depth of 1.2 m, of which 1.1 m were accessible using the minirhizotron camera. One minirhizotron tube was placed through the dripper zone *c.* 60 cm from the trunk directly below the zone of soil receiving irrigation from the drip emitter. The other minirhizotron for that vine was placed in the unirrigated zone on the opposite side of the vine, at a similar distance from the trunk. A total of 72 minirhizotrons were used with two tubes per vine  $\times$  three irrigations  $\times$  two rootstocks  $\times$  six blocks. Surrounding vines served as buffers to provide environmental continuity for treatment vines and also to separate treatments. Plastic (PVC) plugs prevented water infiltration in the bottoms of the tubes and black electrical tape and rubber stoppers prevented light penetration into the portion of the tube above the soil surface. Radiant heating was minimized by covering the tops of the tubes with white metal radiation shields.

Continuous root images were taken down the length of each tube from January 2003 to December 2005, once every 2 wk during the growing season and once a month during vine dormancy. Each image was approx. 14 mm in height and 18 mm wide. All images were analyzed using specialized software (WinRhizo Tron MF, Regents Inc. Quebec, Canada) for root population counts, survivorship and production. Root births were estimated by calculating the date midway between the observation date when a root was first observed and the previous observation date. Similarly, root death was estimated as being midway between the first date the root was observed dead and the previous observation date. Root death was identified by a black and shriveled appearance (Comas *et al.*, 2000) or if the root had disappeared from the window and did not reappear. Roots that transected more than one minirhizotron observation window vertically within the same minirhizotron observation tube were only counted once. Root growth plasticity was calculated as the growth of the root system during the summer in areas of high soil moisture as a proportion of total root growth observed with the two minirhizotrons per vine, one in moist soil and one in dry soil. Seasonal root production was examined for roots produced during the four seasons by examining the total root length produced over all windows of the minirhizotron tubes per square centimeter of observational window over 3 months for HSV vines (rootstock 1103P) and LSV vines (rootstock 101–14 Mgt) during the years 2003–05. Root standing crop was determined by the difference in cumulative production and cumulative mortality of the fine roots.

## Data analysis

Stem water potentials and soil matric potential were analyzed using GLM repeated measures in SPSS (SPSS Inc. v. 11.0, Chicago, IL, USA). Root lifespan data were analyzed with Cox proportional hazards regression (PROC PHREG, SAS Institute Inc., Cary, NC, USA). This type of analysis allows the influence of all other covariates to be held constant while the ‘hazard’ of an individual covariate is determined (Cox, 1972). The ‘hazard’ of a covariate refers to the risk of mortality of a root at time  $t$ , where  $t$  is the product of a baseline hazard function of  $k$  covariates (Allison, 1995). Statistical Analysis System’s PROC PHREG uses the partial likelihood method of Cox (1972) to estimate a parameter coefficient of  $\beta$  for each tested covariate, and calculates a chi-square statistic to test the null hypothesis that each  $\beta$  equals zero. A parameter estimate can have either a negative or positive sign depending on the effect it has on the covariate. In this case, a negative sign indicates a decreased hazard of mortality with an increase in the covariate (Wells & Eissenstat, 2001). Covariates tested included root diameter, root order and the number of neighboring roots present in the window. Wilcoxon rank sum tests were performed to analyze for differences in survivorship of root systems and roots growing

in wet vs dry soil. Further analyses on the effects of year of observation and depth of roots on root population size were completed using the GLM procedure in SPSS (SPSS Inc. v. 11.0). Soil moisture data were averaged over 2003–2005 and analyzed using analysis of covariance with initial soil moisture values at all three depths before treatment implementation as covariates (PROC ANCOVA, SAS Institute Inc.). Root plasticity in response to lateral heterogeneity was calculated as the average number of roots produced in the top 60 cm of soil observed with the minirhizotron in the irrigated region as a percentage of the total number of roots produced in the top 60 cm observed with two minirhizotrons (wet and dry regions) and analyzed using ANOVA in SPSS. Root plasticity in response to vertical heterogeneity was calculated as the number of roots produced in soil deeper than 60 cm as a percentage of the total number of roots produced over the entire soil profile and likewise analyzed by ANOVA in SPSS.

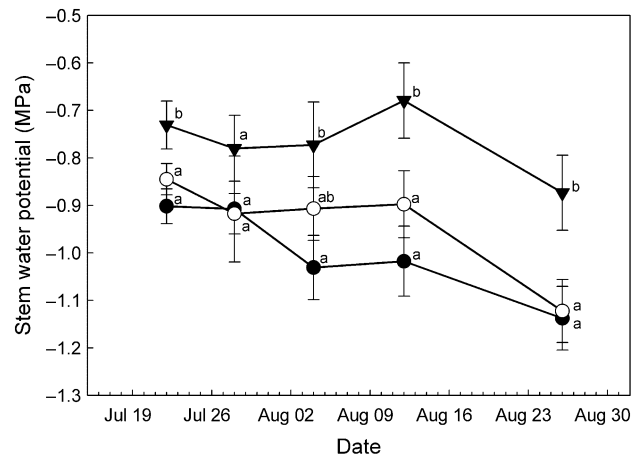
## Results

### Environmental parameters

Weather was characterized as regionally normal for 2003–05 (see description in the Materials and Methods section) with wet, cool winters and warm, dry summers. Although a slightly longer, wet spring occurred in 2005, annual precipitation was similar to the long-term mean (Bauerle, 2007).

No significant differences in soil moisture were found between LSV and HSV vines for irrigated treatments in the irrigated soil (40%  $ET_c$ ,  $P = 0.582$ ; 100%  $ET_c$ ,  $P = 0.727$ ; also no significant interactions with irrigation treatment;  $P > 0.40$ ), and so data for the two rootstocks were combined (Supplementary material, Fig. S1). Significantly drier soil was maintained on the unirrigated side of the vine under the deficit (40%  $ET_c$ ) treatment and full irrigation (100%  $ET_c$ ) treatments ( $P < 0.0001$ ) (Fig. S1). Unirrigated soil had less soil moisture than irrigated soil in the driest part of the year (June–Sept) (28% irrigated, 23% unirrigated;  $P < 0.0001$ ). Soil moisture exhibited slight increases with depth in unirrigated soil (3–4% absolute increase) for the full irrigation treatment (100%  $ET_c$ ;  $P = 0.057$ ) and no increase in unirrigated soil under deficit irrigation (40%  $ET_c$ ;  $P = 0.793$ ). Soil in the unirrigated treatment (0%  $ET_c$ ) had the largest increase in soil moisture with depth compared with other treatments (5–8% absolute increase;  $P < 0.0001$ ). Soil water content on the irrigated side of the vine in the top 20–80 cm zone, the area where the majority of roots were located, averaged 30% (*c.*  $-0.01$  MPa) under irrigation designed to replace 100%  $ET_c$  and 27% (*c.*  $-0.05$  MPa) under 40%  $ET_c$ .

Soil water content on the unirrigated side of the vine was 26% ( $-0.15$  MPa) for 100%  $ET_c$  irrigation, 24% ( $-0.4$  MPa) for 40%  $ET_c$ , and 23% ( $-0.8$  MPa) for no irrigation (0%  $ET_c$ ) during August (a dry month) over the 3 yr of the study ( $P < 0.001$ ). Deeper soil ( $> 80$  cm) retained more water with



**Fig. 1** Midday stem water potential ( $\pm 1$  SE) of 'Merlot' grapevines under different irrigation conditions in Oakville (CA, USA) over the stressed portion of the growing season (July–August) in 2004. Irrigation treatments, applied twice weekly, were 0% (closed circles), 40% (open circles) and 100% (triangles) replacement of estimated evapotranspired water ( $ET_c$ ) (overall irrigation effect:  $P < 0.0001$ ). Data for vines on root systems associated with higher shoot vigor and lower shoot vigor were combined (time  $\times$  rootstock effect,  $P = 0.189$ ).

an average of 29% soil water content ( $-0.02$  MPa) in the irrigated zone and 28% water content ( $-0.03$  MPa) in the unirrigated zone ( $P = 0.150$ ).

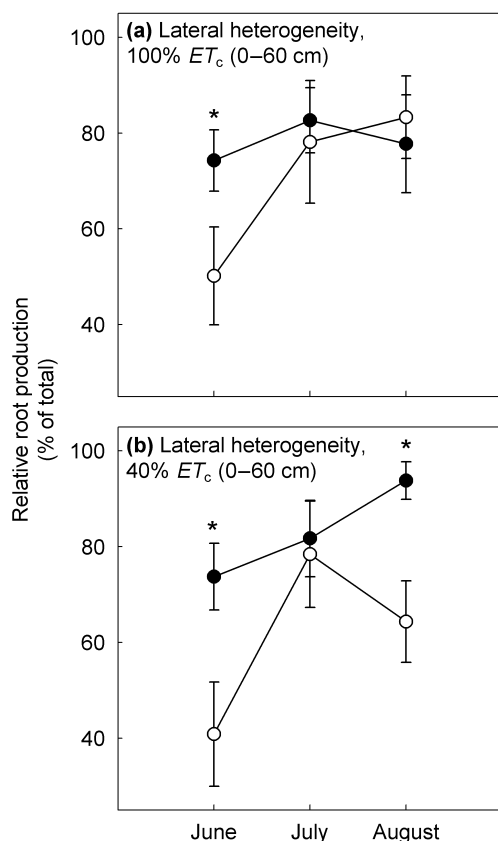
### Shoot responses

Over the course of the study period, vines produced almost two times the amount of dormant-season lignified cane tissue (pruning weights) on the HSV root system compared with that produced by vines on the LSV root system under all water stresses (irrigated vines: HSV,  $2.08 \pm 0.15$  vs LSV,  $1.06 \pm 0.09$  kg; unirrigated vines: HSV,  $1.93 \pm 0.18$  vs LSV,  $1.02 \pm 0.12$  kg;  $P < 0.001$ ) (irrigation effect  $P = 0.160$ ) (irrigation  $\times$  rootstock effect  $P = 0.308$ ).

Irrigation had strong effects on stem water potential through much of July and August, the period of lowest rainfall and highest temperatures of the growing season (Fig. 1). Midday stem water potentials of vines in the 100%  $ET_c$  treatment were *c.* 30% higher than those in the 40%  $ET_c$  treatment ( $P = 0.005$ ) and almost 50% higher than those in the 0%  $ET_c$  treatment ( $P < 0.001$ ). The vines in the 0%  $ET_c$  and 40%  $ET_c$  treatments, however, exhibited similar midday stem water potentials, especially in late July and late August (Fig. 1;  $P = 0.443$ ) (overall rootstock effect:  $P = 0.087$ ; time  $\times$  rootstock effect  $P = 0.189$ ; time  $\times$  irrigation effect  $P = 0.096$ ).

### Root growth in relation to soil moisture heterogeneity

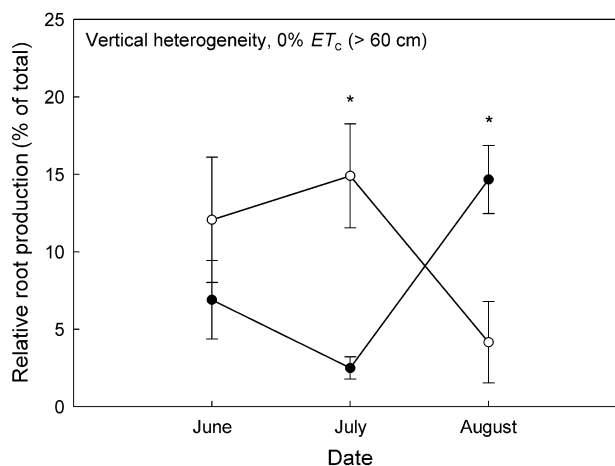
**Lateral heterogeneity** The HSV rootstock generally grew proportionally more of its total roots in irrigated soil compared with the LSV rootstock (Fig. 2; main rootstock



**Fig. 2** Summer fine root production in irrigated soil zones for vines under different drip irrigation conditions. Vines were on a root system associated with high shoot vigor (HSV; 1103P; closed circles) and on a root system associated with lower shoot vigor (LSV; 101–14 Mgt; open circles) for two irrigation treatments: 100% replacement of estimated evapotranspiration ( $ET_c$ ) (a); and 40% replacement of  $ET_c$  (b). Data were calculated as the number of new roots produced over each monthly time period visible with a minirhizotron in the top 0–60 cm of the irrigated region of the soil as a percentage of the total roots produced over the same period in the top 60 cm in both irrigated and dry unirrigated soils (see text). Estimates of monthly new root production were averaged over 3 yr (2003–05). Points of significance are denoted by an asterisk ( $P < 0.05$ ).

effect,  $P < 0.050$ ). At both 40%  $ET_c$  and 100%  $ET_c$ , HSV vines preferentially grew *c.* 20–30% more of their total roots than the LSV vines in the irrigated soil region in June. No significant differences between LSV and HSV vines were evident in July at either irrigation amount. In August, HSV vines grew preferentially *c.* 30% more of their total roots in the irrigated zone than the LSV vines (rootstock effect,  $P = 0.042$ ), but only at 40%  $ET_c$ . Consistent with these patterns, there was a significant irrigation effect ( $P = 0.008$ ) and a significant interaction between irrigation and rootstock ( $P = 0.028$ ) on preferential root growth in response to lateral heterogeneity in soil moisture.

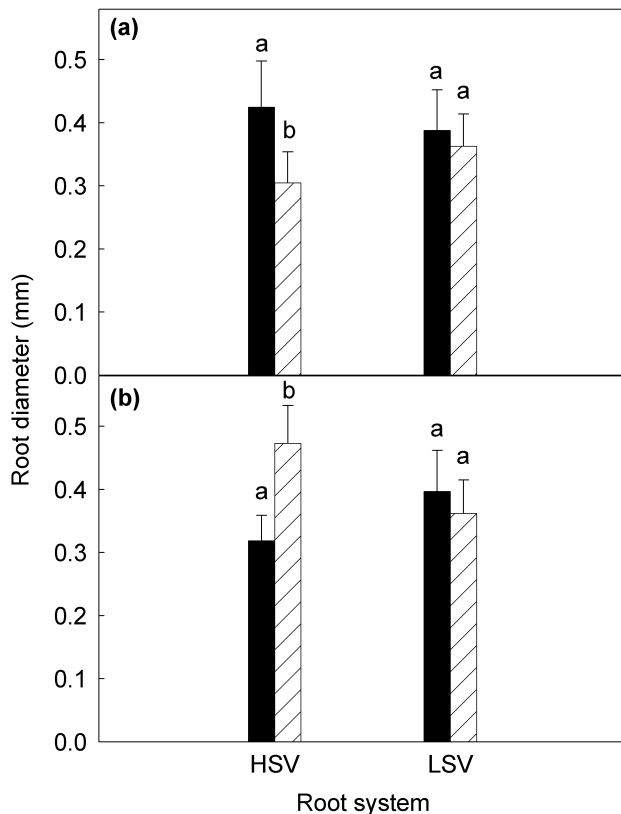
**Vertical heterogeneity** In the unirrigated treatment, there was only limited evidence that the HSV root system



**Fig. 3** Summer fine root production in unirrigated vines in deep soil with little soil moisture depletion (soil depths  $> 60$  cm), as a percentage of the total roots produced over the entire soil profile over the same time period. Data shown are a root system associated with high shoot vigor (HSV; 1103P; closed circles) and a root system associated with lower shoot vigor (LSV; 101–14 Mgt; open circles). Data represent observations made between June and August, averaged over 3 yr (2003–05). Points of significance are denoted by an asterisk ( $P < 0.05$ ).

exhibited greater preferential root production than the LSV root system in the deeper, more moist soil ( $> 60$  cm) as the growing season progressed (Fig. 3). Interestingly, during mid-summer the LSV root system grew a greater percentage of its total roots deeper in the soil compared with the HSV root system ( $P = 0.043$  for July). Only in August was there evidence that HSV vines exhibited proportionally more root growth than the LSV vines in the deeper soil layers ( $P = 0.010$ ).

**Root morphology** The morphology of HSV roots was more affected by dry soil than that of LSV roots. First-order roots (the finest laterals on the root system without daughter roots) of the HSV root system were approx. 30% thinner in diameter in dry soil during the dry season (June–Aug) in the top 20 cm of soil compared with those in irrigated soil (Fig. 4; rootstock effect:  $P = 0.039$ ). In addition, in unirrigated soil regions, HSV roots near the surface were thinner than those in the moister, deeper soil layers ( $> 60$  cm,  $P < 0.001$ ). Root diameters were generally similar for HSV and LSV root systems in both irrigated and unirrigated soil in the middle soil depths (20–60 cm zone, data not shown;  $P = 0.335$ ). Root diameter varied with depth for the HSV root system, with roots in irrigated soil decreasing in root diameter with soil depth, and roots in unirrigated soil increasing in diameter with soil depth ( $P = 0.029$ ). In contrast to the HSV root system, the LSV root system exhibited little variance in root diameter in wet and dry soil ( $P = 0.411$ ) and with depth ( $P = 0.462$ ).



**Fig. 4** Root diameter ( $\pm 1$  SE) in moist and dry soil. Roots of grapevines at two soil depths (a, < 20 cm; b, > 60 cm) growing in irrigated soil (closed bars) and unirrigated soil (hatched bars) during the dry summer months (June–August). Rootstock diameter varied for the high shoot vigor (HSV) root system ( $P = 0.039$ ), but not by amount of irrigation ( $P = 0.844$ ), and so data were pooled. Roots of HSV vines increased in root diameter with soil depth in unirrigated soil ( $P = 0.029$ ). The root system associated with lower shoot vigor (LSV) displayed little variance in root diameter in wet and dry soil ( $P = 0.411$ ) and with depth ( $P = 0.462$ ) (rootstock  $\times$  depth effect  $P = 0.212$ ). Differences in lower-case letters indicate mean separation for root diameter between roots in irrigated soil and roots in unirrigated soil ( $P < 0.05$ ).

### Root tolerance

Patterns of root survivorship indicated similar median lifespans of LSV and HSV roots produced in unirrigated soil zones during periods of low soil moisture when supplemental water was applied to the opposite side of the vine (rootstock effects:  $P = 0.081$  for 40%  $ET_c$ , Fig. 5b;  $P = 0.439$  for 100%  $ET_c$ , Fig. S2b). We recognize that the lifespan of the roots shown extend beyond the period of high moisture deficits. However, during the most water-stressed time period (June–Sept, see shaded area of Fig. 5), root lifespan was very similar between the two rootstocks.

Likewise, roots produced in wet soil during the summer months also had similar lifespans in the two rootstock cultivars (rootstock effects:  $P = 0.573$  for 40%  $ET_c$ , Fig. 5a;

$P = 0.875$  for 100%  $ET_c$ , Fig. S2a). Roots born during dry mid-summer months (July–Sept) in vines receiving no supplemental water (0%  $ET_c$ ) exhibited slightly longer median lifespans for the LSV root system (95 d) than for the HSV system (67 d), but these differences in lifespan were not statistically significant (Fig. 5c;  $P = 0.374$ ). Patterns of root survivorship for roots born in winter were also very similar for the HSV and LSV vines ( $P = 0.627$ ; data averaged over all depths and irrigation sides; data not shown).

### Seasonal patterns of root growth

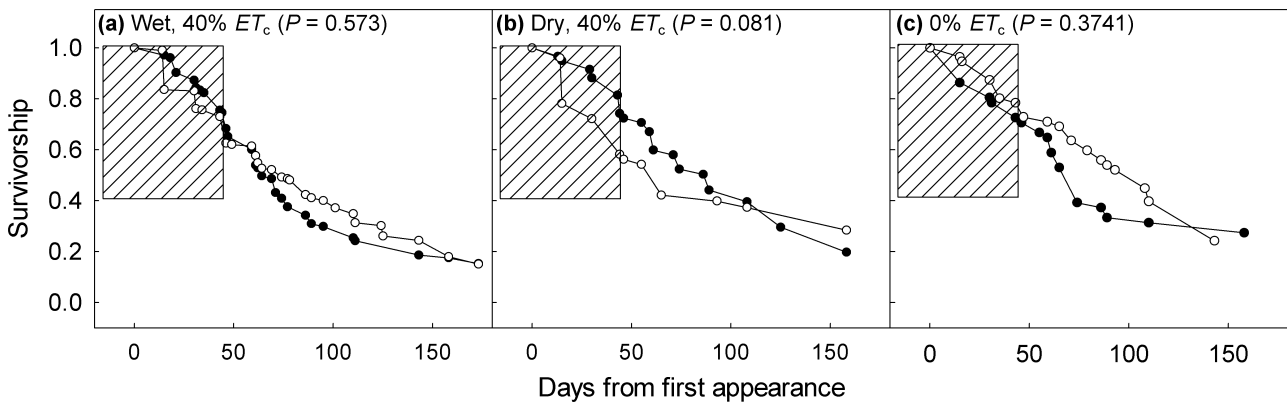
Compared with the HSV root system, the LSV root system exhibited a greater tendency for root growth during periods of little water stress, producing a larger portion of its roots during the cool, wet, winter and, to a lesser extent, during the spring months (Fig. 6; season  $\times$  rootstock interaction:  $P = 0.002$ ). Averaged over all 3 yr, the LSV root system produced approximately threefold more roots in the winter months (December to February) than the HSV root system. Both root systems had similar overall root production after 3 yr of study ( $P = 0.99$ ).

### Root population size (standing crop)

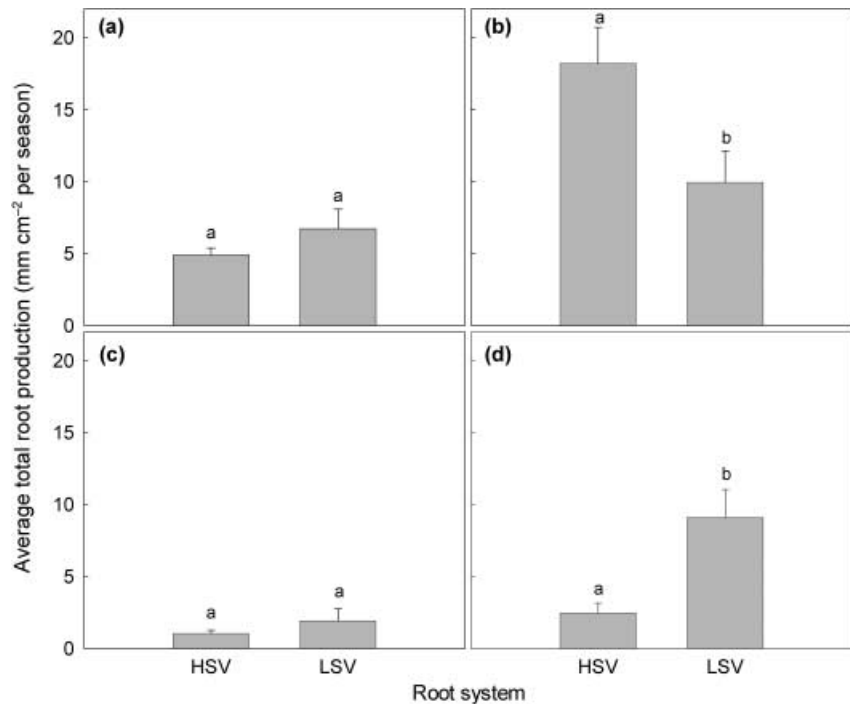
Further indications of differential HSV and LSV root responses to soil moisture deficits were indicated by the root system population size (= standing crop; Fig. 7). The HSV root system exhibited a high initial peak in population size in 2003 in each irrigation treatment, but in subsequent years, populations appeared to reach a more steady-state, stable condition (Fig. 7a–c). By contrast, the LSV root population did not show as substantial a response in 2003 and instead exhibited increases in its root population in the 0–90 cm zone over the following 2 yr in the 0% and 100%  $ET_c$  treatments (Fig. 7a,c). Irrigation affected the root systems differently, with the HSV root system having little overall response to supplemental water (contrast Fig. 7a with Fig. 7b,c), and the LSV root system producing the most growth in root population in the absence of irrigation (Fig. 7a). Indeed, in the no-irrigation treatment, the LSV root system was characterized by a more numerous and extensive root system by the third year of the study, compared with the HSV root system ( $P = 0.001$ ; Fig. 7a).

### Discussion

Various attempts have been made to describe root foraging responses to soil moisture heterogeneity (Richards & Cockcroft, 1975; Coutts, 1982; Fort *et al.*, 1998; Green & Clothier, 1999; Steudle, 2000); however, we are unaware of any studies that have evaluated the role of a plant's potential growth rate. Using a system where genetically identical shoots were grafted on to two genetically diverse root systems, one of known high growth potential (HSV) and one of lower



**Fig. 5** Survivorship of roots in irrigated (a) and unirrigated (b) soils for grapevines of different potential growth rate that were irrigated twice weekly to replace 40% of estimated evapotranspiration ( $ET_c$ ). Data represent roots born during the months of July–August in soil depths of 0–60 cm for vines of high shoot vigor (HSV, rootstock 1103P, closed circles) and lower shoot vigor (LSV, rootstock 101–14 Mgt, open circles) over the years 2003–05. No significant differences between wet and dry sides ( $P > 0.43$ ) or between rootstocks ( $P > 0.08$ ) were observed. (c) Survivorship of roots in the top 0–60 cm in unirrigated soil in the 0%  $ET_c$  vines (rootstock effect:  $P > 0.3741$ ). The shaded area indicates the period of lowest soil moisture (July–September).



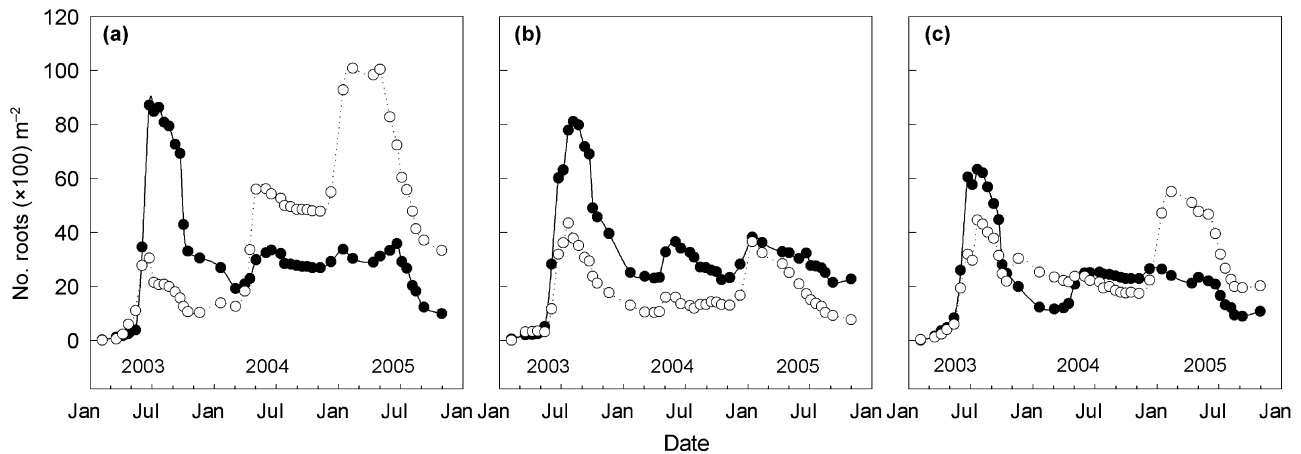
**Fig. 6** Seasonal root production of two root systems that differ in potential growth rate (+ 1 SE). Data represent total root length produced per  $cm^2$  of observational window over 3 months for vines of higher shoot vigor (HSV, rootstock 1103P) and lower shoot vigor (LSV, rootstock 101–14 Mgt) over the years 2003–05 (season  $\times$  root system interaction:  $P = 0.002$ ). Data were pooled over the 3 yr, as there was no interaction of season  $\times$  root system  $\times$  year ( $P = 0.430$ ). Each season corresponded to the following months: (a) spring, March–May (significance of rootstock effect:  $P = 0.230$ ); (b) summer, June–August ( $P = 0.032$ ); (c) fall, September–November ( $P = 0.328$ ); (d) winter, December–February ( $P = 0.009$ ). Significant differences are signified by different letters ( $P < 0.05$ ).

growth potential (LSV), we provide evidence that growth predisposition influenced root responses in both space and time across a gradient in plant water stress.

We found that moderately stressed vines (40%  $ET_c$ ) on the HSV root system exhibited proportionally more root growth in the irrigated soil zone than the LSV root system during the period of most active growth (June and August; Fig. 2a,b). Although the LSV root system also demonstrated preferential root growth in the irrigated zone, the response was less pronounced, supporting the general theory that fast-growing species have greater ability to proliferate roots and therefore a

better chance of competing for ephemeral resources in a patchy environment than slow-growing species (Grime, 1977). Our results indicate this kind of response may be accentuated under moderate stress.

While we manipulated water in this study in creating soil heterogeneity, we cannot exclude the possibility that the increased soil moisture also increased nutrient availability and the roots responded to this as well. Differences in root responses to soil moisture independent of nutrient supply cannot be separated under field conditions, but only under very controlled and necessarily artificial conditions.



**Fig. 7** Population of roots (standing crop) for vines of different potential growth rates under different amounts of drip irrigation. Data represent root system populations from 2003 to 2005 expressed per  $\text{m}^2$  of viewing area. Vines were on a root system associated with higher shoot vigor (HSV; 1103P, closed circles) or on a root system associated with lower shoot vigor (LSV; 101–14 Mgt, open circles) for three irrigation treatments: (a) no irrigation (0%  $ET_e$ ); (b) irrigation added twice weekly to replenish 40% of evapotranspiration (40%  $ET_e$ ); and (c) irrigation added to replenish 100% of evapotranspiration (100%  $ET_e$ ). Root observations from six vines were averaged for each treatment. Two tubes per vine were pooled.

Typically in Mediterranean climates, especially in heavy-textured soils of high water-holding capacity, the surface soil layers are relatively dry later in the growing season, and only the deeper layers have adequate soil moisture to sustain root growth. Under conditions of no irrigation, more plastic plants may more readily grow roots in the deeper, moister soil regions later in the growing season compared with less plastic plants. Alternatively, plants adapted to environments where soil moisture is only available at depth during the growing season may evolve root systems that preferentially grow more roots deeper in the soil earlier in the growing season, regardless of soil moisture conditions at the surface (Harris, 1967; Harris & Wilson, 1970). The HSV root system may be more consistent with the first explanation and the LSV root system seems more consistent with the second. Despite the HSV root system going into the summer stress period with 30% of its total root population in deep unirrigated soil layers ( $> 60 \text{ cm}$ ), relatively few roots were produced in the deeper layers during June and July (Fig. 3). In August, however, after the surface layers had dried, numerous roots were produced in soil layers deeper than 60 cm (Fig. 3). The LSV root system produced *c.* 25% of its root system in the deeper, moister soil layers for two out of the three months of high water stress. The LSV root system may not be growing more roots at depth as a result of environmental cues, but may be simply genetically entrained to establish a deep, extensive root system when photosynthate is available (also see Fig. 7).

In addition to more rapid preferential root production in response to lateral soil moisture heterogeneity, we also observed that the HSV root system exhibited more shrinkage in root diameter than the LSV root system (Fig. 4). We suspect that the thicker-diameter roots in wet soil in the HSV root system were a direct result of the high water availability

leading to larger, and possibly more numerous, cortical cells (Mapfumo *et al.*, 1994; North & Nobel, 1997). The smaller diameter roots in the dry soil in the HSV root system may simply reflect greater susceptibility to root shrinkage compared with that of the LSV root system, an indication of lower tolerance to dry soil (North & Nobel, 1997). It is unclear if this has any functional significance to nutrient or water acquisition for the plant, but it clearly had little impact on root lifespan (Fig. 5, Fig. S2).

Despite previous arguments for extended root lifespan in slow-growing species (Grime, 1977), both root systems demonstrated similar patterns of root survivorship in both wet and dry soil (Fig. 5, Fig. S2). This experiment did not support a hypothesized tolerance strategy of longer root survivorship in dry soil by the LSV root system. Indeed, soil moisture deficits did not influence root longevity in either rootstock cultivar. One way in which grape roots may tolerate exposure to soil moisture deficit is through water movement from roots in wet soil to those in dry soil during periods of minimal transpiration such as the night-time (Bauerle *et al.*, 2008). Plants under higher water stress may be less likely to re-hydrate desiccated tissues nocturnally. Many species, including many desert species, have demonstrated the capability to redistribute water. Hydraulic redistribution has been shown to occur in a cold desert shrub in soils as dry as  $-5.0 \text{ MPa}$  (Williams *et al.*, 1993). In desert succulents, by contrast, roots exposed to severe dry soil ( $< -5.0 \text{ MPa}$ ) have demonstrated large losses in root water permeability and root death, suggesting either a lack of sufficient water reaching the roots through hydraulic redistribution or the absence of the physiological processes itself (Nobel & Huang, 1992).

Root growth during predictable periods of high soil moisture is beneficial to plants in drought-prone environments



(Lyr & Hoffman, 1967; Hayes & Seastedt, 1987). The LSV root system exhibited an entirely different root growth strategy than the HSV root system to seasonal patterns of water and overall root development in response to supplemental water. The LSV root system produced a large number of its roots during the winter months, suggesting ability for root growth in cooler soils using carbohydrate reserves (Fig. 6). During the summer months, LSV vines also grew proportionally more roots during June and July than the HSV vines (Fig. 3). Moreover, in contrast to the HSV root system, the LSV root system slowly accumulated root density, especially under no irrigation (Fig. 7). Rather than rapid root responses to localized environmental cues during the growing season, the LSV root system seemed more adjusted to growing roots during periods when, and in locations where, soil moisture was more predictable. Similar observations of fine root growth during periods of ample soil water are associated with Great Basin cold-desert species under drought-stress conditions (Harris, 1967; Harris & Wilson, 1970; Peek *et al.*, 2005). This strategy, coupled with continued root system development and lower shoot vigor, presumably allows a plant in climatic regions with predictably high soil moisture in winter or spring to cope with severe drought stress during summer.

Water stress severity proved influential in root system response to lateral water heterogeneity and seasonal growth patterns but not necessarily for root lifespan. In the HSV vines, deficit irrigation (40% *ET*) resulted in a greater preferential root production in irrigated soil than that of fully irrigated vines (100% *ET*) in August, consistent with the hypothesized higher degree of morphological plasticity for the faster grower under greater water stress (Fig. 2). Patterns in seasonal and annual shifts in root populations indicated similar responses of the fast grower to water stress severity, while the slow grower produced the largest population of roots under the greatest water stress (Fig. 4). Therefore while the faster grower may out compete for water during localized wetting events, the slower-growing vines displayed a long-term strategy of building a large root system for a predictably dry growing season. Soil moisture severity had little effect on root lifespan, with similar patterns in root survivorship between rootstocks and between wet and dry soils.

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## Supplementary Material

The following supplementary material is available for this article online:

**Fig. S1** Volumetric soil moisture (ls means  $\pm$  1 SE). Data were collected at three soil depths (20–50, 50–80 and 80–110 cm) in irrigated soil zones, with irrigation designed for 40 and 100% replacement of vine evapotranspiration ( $ET_c$ ) (left panels), and in unirrigated soil zones of the same plant (right panels), averaged over 3 yr (2003–05) (year  $\times$  rootstock effect;  $P > 0.40$ ). Significantly drier soil was maintained on the unirrigated side of the vine in the deficit irrigation (40%  $ET_c$ ;  $P < 0.0001$ ) and full irrigation (100%  $ET_c$ ;  $P < 0.0001$ ) treatments (means followed by different letters are significantly different,  $P < 0.05$ ).

**Fig. S2** Survivorship of roots in irrigated (a) and unirrigated (b) soils in the top 0–60 cm for grapevines of different potential growth rate at irrigation added twice weekly to replenish 100% of estimated evapotranspiration (100%  $ET_c$ ). Data represent roots born during the months of July–August for vines of high shoot vigor (HSV, rootstock 1103P, closed circles) and lower shoot vigor (LSV, rootstock 101–14 Mgt, open circles) over the years 2003–05. No significant differences between wet and dry sides ( $P > 0.43$ ) or between rootstocks ( $P > 0.08$ ) were observed. The shaded area indicates the period of lowest soil moisture (July–September).

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