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Article

Rootstocks alter the Seasonal Dynamics and Vertical Distribution of New Root Growth of *Vitis vinifera* cv. *Shiraz grapevines*

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Abstract: Minirhizotron tubes were installed to monitor root growth dynamics of mature Shiraz grapevines in a rootstock trial established in the hot climate Riverina region of New South Wales, Australia. The vertical root distribution and seasonal root growth dynamics of Shiraz on own-roots and Shiraz grafted on the rootstocks Ramsey, 140 Ruggeri and Schwarzmann was studied for five seasons across a seven-year period to a depth of 60 cm. New root production was significantly influenced by genotype, soil depth, season, growth stage and year. Soil moisture and soil temperature were monitored at 10, 30 and 60 cm in the last two seasons. Soil moisture at 30 cm and soil temperature at all three depths were significant predictors of root growth. New root numbers were significantly higher in 140 Ruggeri than the other rootstocks. To the depth studied, 140 Ruggeri roots were evenly distributed from the topsoil down, whereas the majority of roots of Schwarzmann and Shiraz were located at intermediate depths in the 10-40 cm ad 20-40 cm zones respectively, while Ramsey roots were found at 20 cm or below. Depending on genotype, root growth occurred across several phenological stages but tended to peak at flowering. In some years we observed root growth in early and late winter at rates exceeding that of autumn, and this was associated with warmer temperatures during this period. Overall, seasonal rooting dynamics were responsive to abiotic factors but dominated by genotype.

Keywords: genotype; seasonal root growth; vertical root distribution; soil depth; soil temperature; soil moisture

1. Introduction

Optimization and predictions of plant growth responses to present and future environments require an enhanced understanding of below-ground processes. Aboveground growth and development of woody perennials can be influenced by timing of root growth, root distribution and root interactions with their surrounding environment [1-3]. For example, shallow rooting has negative consequences on fruit tree performance in dry years but a positive influence in a wet spring

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[2]. In addition, the manipulation of root growth through rootstocks [4] can reduce excessive shoot growth [5], carbohydrate metabolism and whole plant growth [6]. Tree performance and productivity may be related to constraints in fine root growth and root functioning. In addition, perennial fruit tree root growth may be genetically controlled by rootstocks or the interactions between rootstocks and scions [7-9]. For example, commonly used rootstocks in grapevines are derived from diverse climatic backgrounds and have genotypic differences [8,10]. Generally, these variations may impact both root and shoot growth, and eventually the sustainable productivity of fruit trees [11]. Because of their genetic diversity, rootstocks can effect scion vigor [12], flower induction [9], and may even alter mineral and water uptake [13] due to their different root anatomy. Therefore, a better understanding of root dynamics within fruit crops, such as root growth dynamics and root lifespan, has implications for fertilizer and irrigation management.

Unlike the aboveground tissues, root growth can continue in mature trees all through the year [14-17]. There is little information about root growth dynamics in woody plants, including grapevines. Root growth studies are scarce as methods are complex, time consuming and tedious either through non-destructive direct monitoring or by destructively observation. Long-term studies on larger woody plants are particularly uncommon. However, it has been observed that root growth dynamics of grapevines vary between cultivars, vine age, management practices and environmental stress. Freeman and Smart [18] found that Shiraz vines had rapid root growth 10 weeks after bud break with maximum root development when shoot growth had ceased and also after harvest. In a study with five woody cultivars, grape root activity occurred in early spring prior to bud break and during bud break, and in mid to late summer when shoot growth had ceased [19]. More recently, Callejas et al. [15] reported that grapevine roots displayed several growth peaks; they were most pronounced at flowering, veraison and harvest and these dynamics were different at three soil depths.

The varying root growth dynamics at different soil depths results in different root distribution dynamics. Bassoi et al. [13] found that grapevine rootstocks had a similar rooting dynamics under micro-sprinkler irrigation conditions. Roots were present to a 100 cm depth and approximately 90 % of the roots were distributed down to a 60 cm depth, with a larger root occurrence in the first 40 cm. Some studies have reported that the distribution of roots in the soil profile can be related to genetic factors which also regulate the density of roots [20,21]. In addition, the distinct distribution of grapevine roots is a result of different soil environments [22,23], particularly soil temperature and soil moisture [15,16,24,25]. When soil temperature is not a limiting factor, soil water content may regulate root development [26]. However, when all the factors that impact on root growth are optimal, soil temperature is the main impacting factor of root development. The ideal range of soil temperature for maximum root growth of walnut was between 21 and 24 °C [27]. In citrus, maximum root growth was observed around 29 °C and declined below 22 °C [28]. Woodham and Alexander [29] and Kliewer [30] indicated that the optimal soil temperature for grapevine root growth is close to 30 °C. The warm soils can stimulate root growth and nutrient uptake of grapevines [31,32].

In Australia, South Burnett, Riverina and Hunter Valley are the warmest grape growing regions with median growing season temperatures of 22.9, 21.5 and 20.7 °C, respectively [33]. Wagga Wagga, in the Riverina region of southern NSW, is the second warmest grape growing region in Australia. However, our study would be the longest hot climate study that has been attempted since studies on root lifespan in Merlot vineyard at Oakville, California, USA [26]. Therefore, in hot climates, it would be informative to understand seasonal root growth and distribution in hot soils [34]. In addition, in terms of vineyard management, potential genotypic differences between rootstocks in seasonal fine root growth dynamics and root distribution are another important aspect. Therefore, we selected two of the most widely planted rootstocks (Ramsey and Schwarzmann) and another important grapevine rootstock (140 Ruggeri) as they are believed to be the most favourable rootstocks for Shiraz vineyards in warm and hot climates [35] and relevant to the Australian industry. Finally, a two-stage seasonal root growth study was conducted in a four-year comparison of rootstocks, and temperature and soil moisture were monitored in the last three years.

2. Materials and Methods

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2.1. Location and vines

The field experiment was carried out in a Shiraz rootstock field trial within a commercial vineyard located at Charles Sturt University, Wagga Wagga, NSW Australia (35º05'S 147º 35'E) over five growing seasons within a seven-year period from 2007 to 2014. The trial was established in 1998 with *Vitis vinifera* (cv. Shiraz, clone PT23) and nine different rootstocks planted as own-rooted vines in a Latin square design across 10 vine rows and then field-grafted to the same Shiraz clone in the following year. The vines were planted at 2 m spacing along the row with 3 m between rows, trained to a bi-lateral permanent cordon, spur pruned and drip irrigated. There were six adjacent vines of each graft combination in each of the 10 replicate rows. For this study, we selected four replicates of the self-grafted Shiraz, and four replicates of the rootstocks 140 Ruggeri (V. berlandieri × V. rupestris), Ramsey (V. champinii), Schwarzmann (V. riparia × V. rupestris). Herbicides were used to maintain bare ground in the undervine area as part of the standard management for the vineyard, but during the root observation period any weeds that appeared between herbicide applications were removed manually. Nutrition, pest management, and other vineyard operations were consistent with common commercial vineyard practices. The major phenology stages were recorded using the modified E-L system [36].

2.2. Installation of minirhizotron tubes

Two clear polycarbonate (minirhizotron) tubes of 100 cm length with an external diameter of 55 mm were installed in each replicate in autumn 2007, three months prior to the start of the study. The tubes were installed 20 cm from the trunk of the two centre vines in each replicate, aligned with the vine row to avoid damage from vineyard machinery, and angled under the vines at 30 degrees from vertical (Figure 1). This resulted in 8 observation tubes per genotype and 32 tubes in total in the trial. The bottom of each tube was permanently sealed with a clear acrylic plastic end cap glued in position to prevent water ingress. The top of the minirhizotron tube that extended above the soil surface were painted black and enclosed within removable opaque covers made from heavy duty white PVC pipe with the top end sealed with a matching PVC end-cap to exclude light, water and insects. These covers were held in place with a tight rubber seal and the base of the tube cut at an angle to sit flush with the soil surface.

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Figure 1. Installation of minirhizotron tubes. The tubes were installed 20 cm from the trunk of the two centre vines in each replicate, aligned with the vine row to avoid damage from vineyard machinery, and angled under the vines at 30 degrees from vertical.

2.3. Soil water and temperature monitoring

Soil moisture was recorded during the 2012/2013 and 2013/2014 seasons using 16 MEA Gbugs (Measurement Engineering Australia Pty. Ltd, SA) installed in two of the four replicates of each rootstock. Each logger was connected to three gypsum blocks (measurement range of -50 to -500 kPa) at depths of 10 cm, 30 cm and 60 cm under an emitter and logged every 2 hours. In one replicate, soil temperature was recorded at the same depths along the irrigation line either directly under an emitter or in the non-wetter area between two emitters using T-type thermocouples connected to a 12-channel digital thermometer (BTM-4208SD, Lutron Instruments, Taiwan). Subsequent statistical analysis used the average temperature of the two readings at each depth.

2.4. Weather data

We used analysis of variance (ANOVA) to analyse the mean light interception in both experiments. All significance testing was performed at the 0.05 level and where a significant effect was found, the pairwise 95% least significant difference (lsd) was used to make comparisons. Linear and non-linear models were used to investigate relationships between variables measured within the light interception experiments. We used a log10 transformation to improve the assumptions underlying the ANOVA performed on data from the planting systems experiment.

2.5. Weather data

Weather data from 2007 to 2014 were collected at a weather station located at the New South Wales Department of Primary Industries in Wagga Wagga. This weather station was located approximately 1.5 km from the experiment. Rainfall, maximum, average and minimum air temperature were recorded daily.

2.6. Root observation and digital image collection

A minirhizotron camera system was used for non-destructive root observation (BTC-100X, Bartz Technology LLC, CA, USA) of the four genotypes, from the soil surface to an equivalent vertical depth of 60 cm. Digital images were captured fortnightly from 50 consecutive 1.2 cm fixed windows in each tube over the period of August 2007 to October 2010 and June 2012 to June 2014. Throughout these five seasons, 169600 digital images were collected.

For root image analysis, we used a simplified visual assessment procedure where the number of new white roots appearing at each date were counted rather than traced. Due to the very large number of images tracing all individual roots manually was not possible, and the definition of roots in the images was not always clear enough to rely on automated detection. Partly due to a slow accumulation of a fine layer of clay particles covering some windows which progressively obscured the view of roots with time, and partly due to the use of extruded polycarbonate tubes which had a slightly textured surface that reduced the optical clarity. Information from the images was therefore

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extracted manually, with the images for each tube viewed by depth and date using Rootfly software (Wells and Birchfield, Clemson University, SC, USA), and then the number of new roots that had appeared in the image since the last date entered into a spreadsheet manually.

2.7. Statistical analysis

2.7.1. Analysis across all observation dates

Based on the objectives of this research, we classified a root as growing or not growing to enable the investigation of growth dynamics across the soil profile and seasons. Roots that were 'not growing' were those that were not visibly growing as assessed by the minirhizotron images. We used a generalised linear mixed model, in the form of a binomial logistic regression to analyse this binomial data. This model was fitted in the statistical software R (version 3.2.0) using the ASReml-R (asreml-3.0) package. The model used for this analysis (Model 1) can be symbolically written as:

Binomial growth ~ average air temperature + genotype + season + phenological stages + year + observation date + replicate + tube + soil depth (and all the interactions of these variables)

To match the root observation data to the daily air temperature data, averages for the period until the observation date were calculated.

An alternative assessment of the data was achieved by concentrating on only the growing roots and newly appearing roots. The number of new roots at each observation date was recorded and used as the response variable in a linear mixed model fitted in the statistical software R (version 3.2.0) using the ASReml-R (asreml-3.0) package. It was necessary to log transform this data, so the model assumption of homogeneity was met. The model used for this analysis (Model 2) can be symbolically written as:

ln (Number of new roots) ~ average air temperature + genotype + season + phenological stages + year + observation date + replicate + tube+ soil depth (and all the interactions of these variables)

A log-likelihood ratio test was used to determine whether the random terms were significant in both Models 1 and 2. Year refers to the calendar year while season refers to spring, summer, winter or autumn. Phenological stage refers to the developmental stage of the vine, and observation date refers to the day the image was taken. Soil temperature was recorded at the depth of 10, 30 and 60 cm. It was categorical. However, root images are collected from the top of the soil to 60 cm and it was a continuous variable. Soil depth is included as a random factor in our Model because the root image locations were a continuous variable in this experiment.

2.7.2. Analysis across last three years of observation dates

Soil temperature and moisture in the last three years of data collection were recorded at hourly intervals and air temperature was recorded on a daily basis. To match the root observation data to the environmental factors, averages for the period until the observation date were calculated. Before deciding which environmental factors to use in the analysis, we calculated the correlation between the factors as one of the assumptions of the analysis methods used is that the independent variables need to be uncorrelated with each other.

Soil moisture at 30 and 60 cm were correlated with each other (Figure 2), and therefore 10 and 30 cm were used in our model. Air temperature and soil temperature were strongly correlated, therefore, only one of these measurements was used in the model. Air temperature was retained for this analysis to maintain consistency with the analysis across all observation dates. The model we used for this analysis (Model 3) can be symbolically written as:

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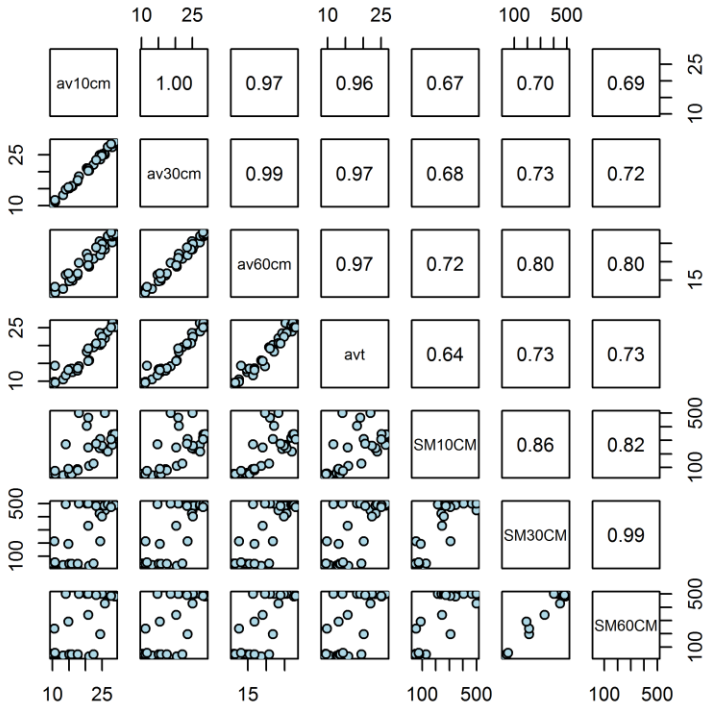

Figure 2. Correlation map of air temperature, soil temperature and moisture at different depths. "av10 cm" = average soil temperature at 10 cm; "av30 cm" = average soil temperature at 30 cm; "av60 cm" = average soil temperature at 60 cm; "avt" = average air temperature; "SM10CM" = average soil moisture at 10 cm; "SM30CM" = average soil moisture at 30 cm; "SM60CM" = average soil moisture at 60 cm.

ln (Number of new roots) ~ average air temperature + genotype + season + phenological stages + year + observation date + soil moisture at depth 10 cm + soil moisture at depth 30 cm + replicate + tube + depth (and all the interactions of these variables)

We used the 5% significance level as statistically significant in this analysis. The model assumptions were that the residuals were normally distributed; they had a constant variance and were independent.

3. Results

3.1. The model outcomes

The root parameters related to genotypes and other abiotic factors computed for the ASReml described in the Methods section are shown in Tables 1 and 2. The outcomes of each model are explained in detail in the subsequent sections.

Table 1. Outcome from the analysis based on Model 1 and Model 2 described in the methodology. "***; ** and *" indicate significance at the 0.1, 1 and 5 % respectively. The non-significant interaction terms are not included in the table. In Model 1, significance is shown for the factors which resulted in no root growth. In Model 2, significance is shown for the factors that affected the number of new roots produced.

Predictor variables	**Response**	
	No root growth (Model 1)	**New roots (Model 2)**

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Air temperature	***	***
Genotype	***	**
Season	***	***
Depth	*	*
Phenological stages	***	***
Year	***	***
Observation date	***	***
Air temperature: Genotype	***	***
Genotype: Season	***	**
Genotype: Phenological stages	***	***
Genotype : Year	***	***
Genotype : Observation date	***	***

Table 2. Outcome from the analysis based on Model 3 described in the methodology. "***; ** and *" indicate significance at the 0.1, 1 and 5 % respectively. "ns" indicates no significant interaction when a term was used. The non-significant interaction terms are not included in the table.

Predictor variables	**Response**
	New roots
Air temperature	**
Genotype	**
Season	***
Depth	*
Phenological stages	**
Year	ns
Observation date	ns
Soil moisture at 10 cm	ns
Soil moisture at 30 cm	**
Air temperature: Genotype	***
Genotype: Soil moisture at 10 cm	*
Genotype: Soil moisture at 30 cm	**

3.2. Soil moisture, soil and air temperature, phenological stages

Soil water tension was higher at the depth of 10 cm compared to the other two depths, 30 cm and 60 cm. The soil became very dry once summer started with the driest period occurring during summer and autumn with some fluctuations at the depths of 30 cm and 60 cm (Figure 6-2 b). Notably, the soil water content at 30 cm was highly correlated with soil moisture at 60 cm (Figure 2). Soil water at 10 cm was higher due to its proximity to the point of irrigation and rainfall.

Maximum summer soil temperatures in the 2013/2014 season were between 35-37 °C and greater by approximately 5 °C relative to the 2012/2013 season at the 10 cm and 30 cm depths. Soil temperatures in winter, spring and autumn were similar, in the range of 5-15 °C, 10- 30 °C and 30-10 °C respectively (Figure 3 a). In addition, the soil temperature at the depth of 30 cm was highly correlated to the temperature at the 60 cm depth (Figure 2). The maximum air temperature in 2009 reached 44 °C and are compared to other six years in Figure 4. The maximum air temperature was lower than 40 °C in year one and year five. However, we found no year-to-year difference in average air temperatures which was calculated based on the values between each two observation dates (data not shown in the table as those not significant terms were removed).

The timing of the major phenological stages varied between years, fluctuating between 4 to 10 days. However, the harvest date of 2009 was around 20 days earlier than the other years (Table 3) in this study and this could be related to the higher air temperature in that season and/or management factors.

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Table 3. Date of onset of the major phenological stages in grapevine development over five seasons. These dates are based upon the Eichhorn and Lorenz system modified by Coombe [36].

Phenological stages	Season				
	Season 1 (2007/2008)	Season 2 (2008/2009)	Season 3 (2009/2010)	Season 4 (2012/2013)	Season 5 (2013/2014)
Bud-break (E-L 02)	12/09/2007	17/09/2008	8/09/2009	18/09/2012	18/09/2013
Flowering (E-L 08)	08/11/2007	29/10/2008	02/11/2009	30/10/2012	02/11/2013
Veraison (E-L 31)	02/01/2008	07/01/2009	30/12/2009	08/01/2013	30/12/2013
Harvest (E-L 35)	29/02/2008	10/02/2009	23/02/2010	06/03/2013	09/03/2014

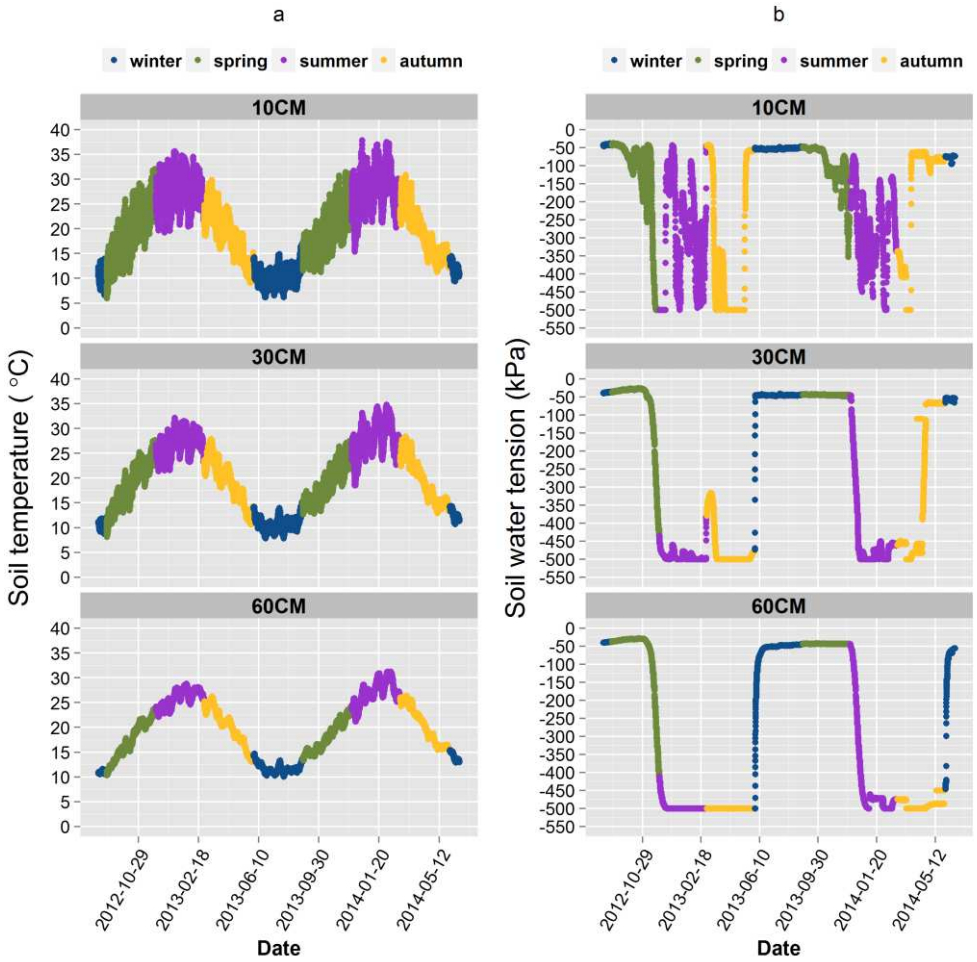

Figure 3. Seasonal dynamics of soil temperature (a) and soil moisture (b) at 10 cm, 30 cm and 60 cm depths adjacent to minirhizotron tubes over two seasons (2012/2013 and 2013/2014). Values are means of four locations for each of the four genotypes. The colour of the symbol refers to winter, spring, summer and autumn.

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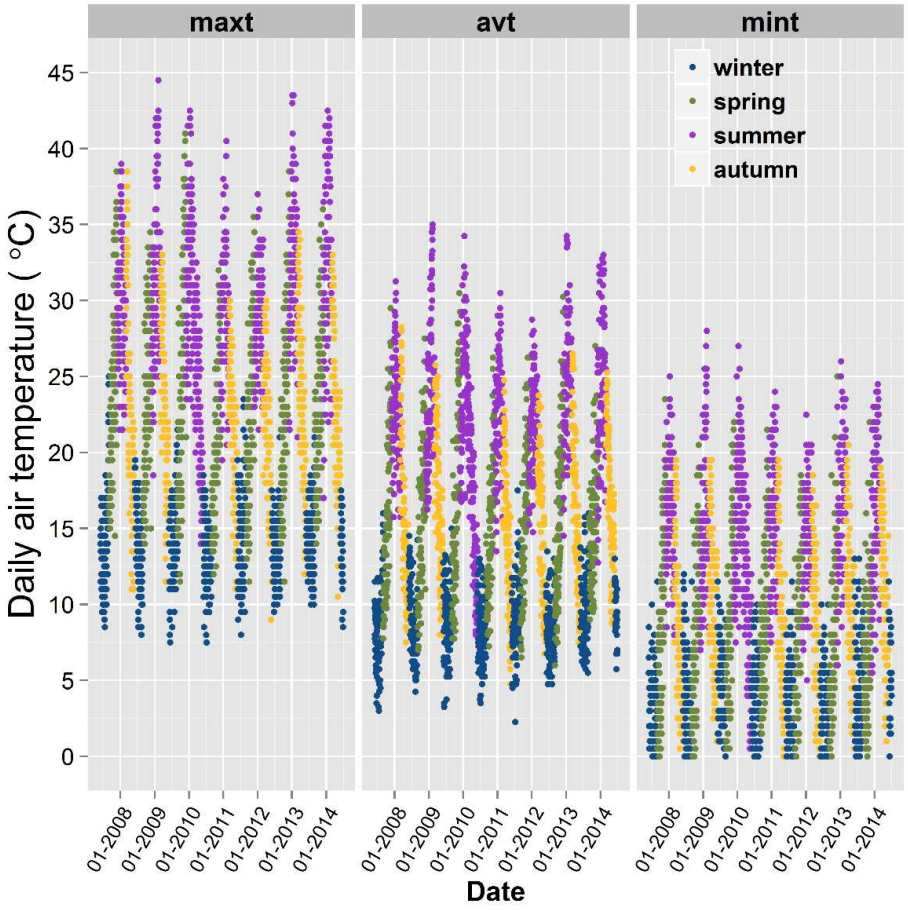

Figure 4. Seasonal dynamics of maximum, mean and minimum air temperature over seven years. On the figure, the "avt" is average air temperature; "maxt" is maximum air temperature and "mint" is minimum temperature. Values are daily air temperature from June 2007 to June 2014. The colour of the symbol refers to winter, spring, summer and autumn.

3.3. Total new root production in different seasons and phenological stages

Total new root numbers varied between genotype, with 140 Ruggeri having the greatest total root numbers compared to Ramsey, followed by Schwarzmann and Shiraz. Maximum new root production was observed in spring at bloom in each species while it reached a minimum in autumn at harvest. Interestingly, Ramsey had more new root production in winter and at bud-break compared to the other genotypes (Table 4). Notably, the new root population in winter was higher than autumn growth.

Table 4. A genotype comparison of the total number of new roots produced over a seven-year period in each of the four seasons and around the major phenological stages.

		Genotypes			
		Shiraz	**140 Ruggeri**	**Schwarzmann**	**Ramsey**
Seasons	Spring	1157	2621	1440	1603
	Summer	254	470	414	333
	Autumn	50	156	156	109
	Winter	245	331	205	514
	Bud-break	93	136	41	191

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Phenological stages	Flowering	594	1563	1075	972
	Veraison	132	136	164	124
	Harvest	99	203	81	69
Year total		1706	3578	2215	2559

3.4. New root production, vertical root distribution dynamics and seasonal root growth dynamics of grapevines

We non-destructively observed substantial new root production through the visible sides of the minirhizotrons. Year to year variability was found in new root growth among the genotypes and new root populations also varied through the soil profile (Figure 5). New root numbers were significantly different between rootstocks ($p < 0.001$) (Table 2). In this vineyard, vertical root distribution to the depth studied was unique for each genotype over the period of seven years. The depth of roots was one of the influencing factors in this new production ($p < 0.05$) (Table 1). Roots of 140 Ruggeri were distributed most evenly with depth, while most new Shiraz roots were found below 20 cm. Higher root numbers were present in Schwarzmann between the 10 cm and 40 cm soil layers, while there was a tendency for greater root numbers in Ramsey rootstocks below the 20 cm soil depth with only a few new roots in the upper part of the soil (Figure 6).

Distinctive seasonal root growth activity occurred over the seven years. Root growth was most pronounced around flowering, followed by veraison, bud-burst and harvest (Figure 5). New roots formed in spring were greater than those produced later in the season. The seasonal dynamics in root growth were similar in the different rootstocks, but the amount of root growth varied between the rootstocks. Overall, when considering the significant interactions between new root production with direct or indirect related factors, we found that new root growth was significantly affected by genotype ($p < 0.01$), air temperature ($p < 0.001$), season ($p < 0.001$), development stage ($p < 0.001$), year ($p < 0.001$) and observation date ($p < 0.001$) (Table 2). In the last three years, we found that new root production also was significantly related to soil temperature ($p < 0.01$) and soil moisture at the depths of 30 cm or 60 cm ($p < 0.01$). Additionally, the combination of genotype with soil temperature ($p < 0.001$) or with soil moisture at the depth of 10 cm ($p < 0.05$) influenced new root growth (Table 1).

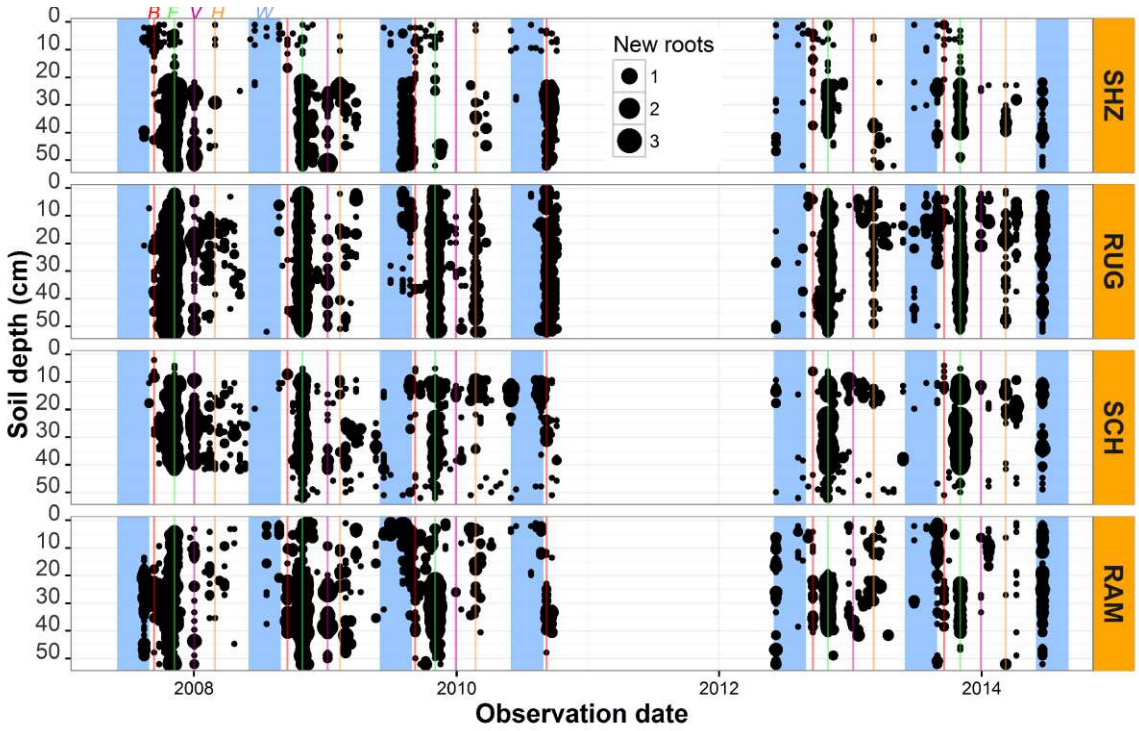

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Figure 5. Number of new roots and their seasonal distribution dynamics by soil depth as monitored in minirhizotron window positions over 2007/2008, 2008/2009, 2009/2010, 2012/2013 and 2013/2014. Values are means of new roots counted at each image location (depth), by observation date. SHZ = Shiraz, RUG = 140 Ruggeri, SCH = Schwarzmann, RAM = Ramsey. The italicized symbols on the left corner of the figure indicates phenological stages of grapevines and winter period (dormancy); B = Bud break, F= Flowering, V = Veraison, H = Harvest, W = Winter. No growth (zeros) not shown in this figure. Average new root numbers at each particular depth is shown on the figure legend as 1, 2 and 3 with the size of the symbol proportional to the number of new roots.

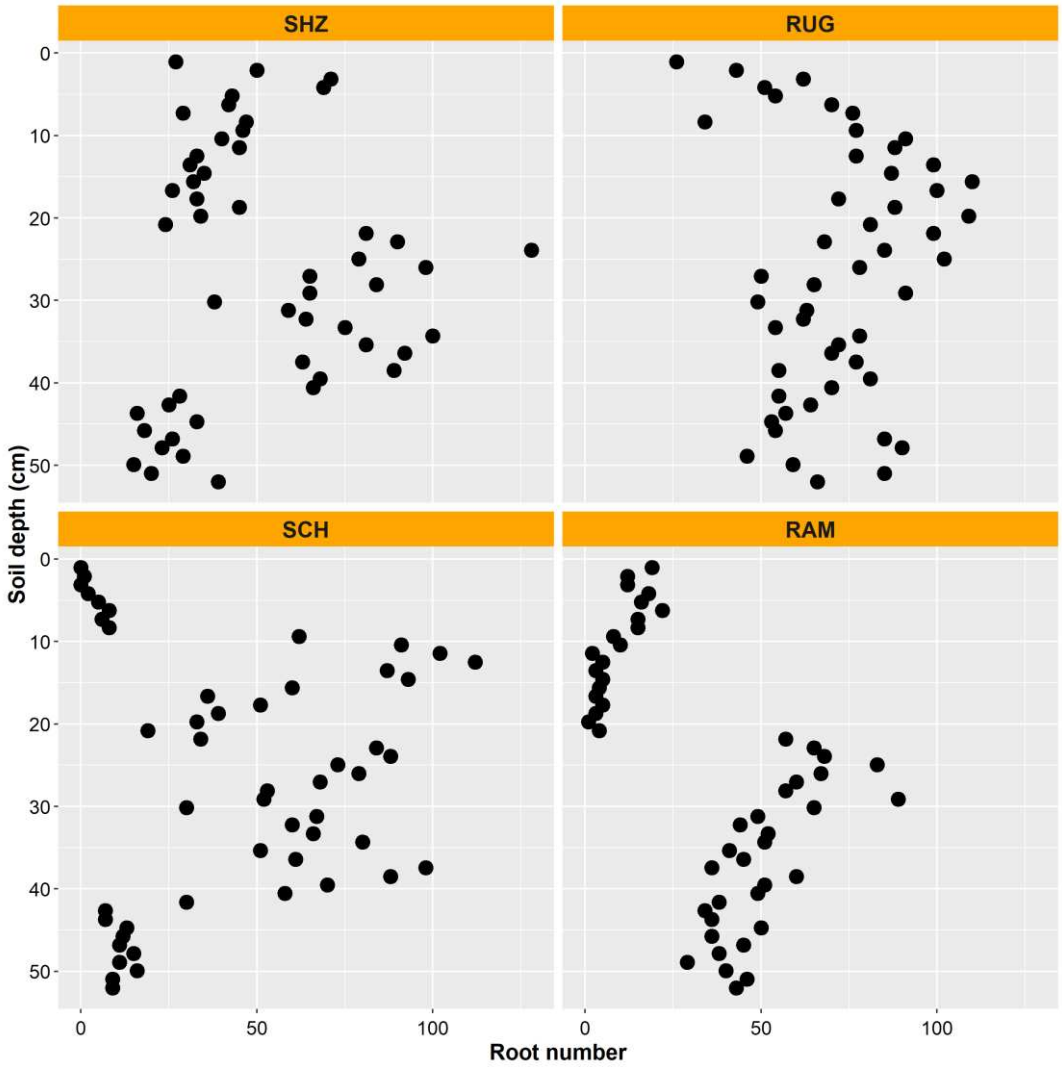

Figure 6. Total number of new roots of the four genotypes and their distribution dynamics by soil depth as monitored in minirhizotron window positions. Values are the means of 2007/2008, 2008/2009, 2009/2010, 2012/2013 and 2013/2014. SHZ = Shiraz, RUG = 140 Ruggeri, SCH = Schwarzmann, RAM = Ramsey.

4. Discussion

4.1. New root production, vertical root distribution dynamics and seasonal root growth dynamics of grapevines

New root production in grapevines was a function of biotic and abiotic factors such as genotype, phenological stage, temperature, moisture, season and year. We found that the seasonal dynamics in root production were consistent over the five seasons. New root production began in late winter and peaked at flowering in spring when soil temperature reached between 15 and 30 °C throughout the

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soil profile. The active root population declined in mid or late summer and after harvest. Based on these periodic changes in new root growth over the seven years, we suggest that the initiation of new root production in grapevines could be partially influenced by soil temperature and/or plant demand for nutrient/water resources. Year to year difference were found in timing of root growth (Table 1) over the seven years. However, we analysed new root growth presence of soil temperature and moisture in the model from the last three years of this study, and we found that new root production had no significant difference in observation date (Table 1).

Unimodal dynamics of root production, with one clear flush of new roots through the season, have been found in several fruit crops including grapevines. This unimodal curve may relate to a temperate environment where dormancy starts soon after crop harvest [2,10,24]. In contrast, a multimodal distribution in new root production was evident here with a major flush occurring at flowering and minor modes at other phenological stages. The amplitude between the major and minor modes varied between rootstocks. Unlike in other cooler grape growing regions, where dormancy begins shortly after harvest, the vine leaves in our warm climate vineyard remained functional for two to three months prior to leaf senescence. This may provide vines with enough carbohydrates that go beyond root reserve replenishment requirements and allow more root flushes during the post-harvest period and even after leaf fall.

According to the previous study, maximum root growth in grapevines occurs before flowering and after harvest [18]. Van Zyl [37] found that root production of grapevines began after bud-break and maximum growth rates occurred at the bloom stage, after which the growth rate decreased. However, in that study, a new root flush period started after harvest. Alternatively,, the main root flushes of Merlot and Concord were observed in summer between bloom and veraison and little root production occurred before harvest and during dormancy when conditions were favourable [3]. We found that the main period of new root production occurred in spring, followed by summer, winter and autumn. This variability in when root production occurs may be related to varying soil temperatures and root carbon availability during the major phenological stages. The presence of new root production during dormancy can be explained by Bhar [14]. He showed that some grapevine roots can grow continuously during dormancy where the ambient soil temperature was 3 °C or higher. Furthermore, Eissenstat et al. [3] found year to year differences were evident in the specific timing of root production and dynamics appeared to be influenced by cultural practices such as irrigation [38] and pruning [39,40].

4.2. Influence of soil temperature on grapevine root growth

When other abiotic factors are not limiting, soil temperature initiates root growth and influences distribution [15,24,31,41]. We found that the soil temperature at 10, 30 and 60 cm was highly correlated to the air temperature (Figure 2). Soil temperature and air temperature were also highly correlated therefore only one of these could be used in our model. We recorded soil temperature data in the last three years. Thus, air temperature was used as this data was collected over the full 7 years. Generally, the soil temperature was lower than the air temperature and the seasonal fluctuation occurred with depth depending on the changes of soil moisture and aboveground plant growth [25]. In grapevines, the optimal soil temperature for root growth is close to 30 °C [29,30]. The average annual root growth of table grapes (Vitis Vinifera L.) cv. Thompson Seedless was not correlated with the annual soil temperature and higher thermal diffusivity in soil profile favoured root production [15]. Based on our last three years of results, the maximum root growth occured in spring at the flowering stage when the soil temperature was in the range of 15 to 30 °C and then new root production decreased over summer until autumn. However, the roots started to grow during early dormancy while the soil temperature was 10 to 15 °C. Interestingly, in autumn, there was little new root growth after harvest when soil temperature was around 10-30 °C, a similar temperature range during spring when root production was prolific.

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4.3. Influence of soil moisture on grapevine root growth

Efficiency of water-use affects grapevine performance and lack of water will cause limitations to plant growth and yield [42]. We found that there was no apparent influence of soil moisture at 10 cm on the production of new roots, however there was an effect at 30 cm. Irrigation was successful at consistently wetting only the top 10 cm while most of the roots were further down the profile where the presence of irrigation water was more sporadic. The soils at 30 cm may have been sufficiently dry to limit root production at this depth. Irrigation methods in vineyard management have a significant effect on moisture diffusion within the soil profile, resulting in different root growth dynamics and water use efficiency of the grapevine [37,43,44]. The data of the more recent years indicate that there are fewer new roots forming relative to the previous years and this might be the consequence of the irrigations not reaching the 30 cm depth due to less applied water. Unfortunately, no irrigation records are available to verify this. Further studies wetting the entire soil profile would give a better indication of new root production in response to soil moisture.

4.4. Influence of genotype on grapevine root distribution

We found that the four different rootstocks had different root production behaviours. Maximum root production peaks appeared at flowering in each rootstock. The rootstocks behaved differently at the other stages. For example, Schwarzmann and Shiraz had greater root populations at veraison than harvest and this was followed by bud-break. Conversely, 140 Ruggeri had a contrary result. Ramsey had greater new root production at bud-break, followed by veraison and harvest (Figure 5). Other fruit crops such as peach grafted on five different rootstocks had similar seasonal dynamics of new root production. Fine root populations reached a minimum in winter and declined during the final stages of fruit development [7]. In the same study, spring some rootstocks produced greater root length compared to those produced later in the season.

We found that the genotypes had different amounts of new roots through the soil profile (Figure 6) and total new root production was significantly different at the different soil depths (Table 1). Information on these differing root growth behaviours can potentially be used to plan time of fertiliser application and irrigation amounts. A peach rootstock with a different genetic background (K119-50) formed a large amount of new roots below 69 cm, unlike four other rootstocks [7]. Consistent with our study, different grapevine species had different root numbers. For example, the greatest root numbers were observed in Dogridge followed by Barbera and Concord (intermediate), then Noble with the smallest amount of roots [45]. In addition, the root distribution dynamics varied between cultivars. Noble had shallow roots, with approximately 35 % of the total roots in the 0-15 cm depth whereas most of the roots of Dogridge occurred in the 90- 105 cm soil profile. We found that new root production by 140 Ruggeri occurred in the 0 - 52 cm layer with the greatest root numbers between 10 - 30 cm. Shiraz had a maximum number of new roots in the 20- 40 cm depth, whereas Schwarzmann had the greatest root populations between 10-40 cm. Ramsey had a very unique root distribution dynamic and most of the new roots occurred in the soil zone at 20 – 52 cm (Figure 6). The installation angle and the observation direction did not influence root counts [46]. Based on the wide range in root distribution and seasonal dynamics in root growth of grapevine species and rootstocks, we suggest that they have adapted to the soil environmental conditions from which they originate.

5. Conclusions

We conclude that grapevine rootstocks displayed genetic variability in root development in response to changes in soil depth, developmental stage, season, year, temperature and soil moisture. We suggest that the genetic diversity of rootstocks could be drawn upon as a management tool for specific soil environments, based on these particular root distribution characteristics in different soil depths and seasonal root growth dynamics of grapevine rootstocks. In addition, climatic background of these rootstocks and their ability to adapt to different environmental conditions was one of the important aspects contributing to these variations between rootstocks. These rootstocks with differing root growth dynamics may influence whole vine performance, carbohydrate reserves and

nutrient and water uptake dynamics through the season. Most importantly, our findings can be added to models that estimate whole grapevine performance and yield in changing soil environments in those grape growing regions which are the hottest.

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