1-1-2009

Effects of novel hybrid and traditional rootstocks on vigour and yield components of Shiraz grapevines

T H. Jones
CSIRO

B R. Cullis
NSW Department of Primary Industries, bcullis@uow.edu.au

P R. Clingeleffer
CSIRO

E H. Ruhl
CSIRO

Recommended Citation

Jones, T H.; Cullis, B R.; Clingeleffer, P R.; and Ruhl, E H.: Effects of novel hybrid and traditional rootstocks on vigour and yield components of Shiraz grapevines 2009, 284-292.
https://ro.uow.edu.au/infopapers/2105

Effects of novel hybrid and traditional rootstocks on vigour and yield components of Shiraz grapevines

Abstract

Background and Aims: The influence of grapevine rootstocks on vine vigour and crop yield is recognized as an integral part of viticultural management. However, the genetic potential of Vitis species rootstock hybrids for vigour and yield control is not fully exploited in Australian viticulture. The effect of 55 novel inter- and intra-species hybrids and five traditional hybrid rootstock cultivars on winter pruning weight, berry size and fruit yield of grafted Shiraz vines is presented. The genetic predictions that resulted from this analysis were used to illustrate how rootstocks that best perform for a combination of traits may be selected.

Methods and Results: The use of linear mixed models and residual maximum likelihood procedures took into account repeated measures and spatial variation within a large field trial (720 vines). Over 6 years of assessment, variation of up to 93.9% in winter pruning weight, 81.9% in fruit yield and 21.0% in berry weight between rootstocks was estimated.

Conclusions: The effect of rootstock genotype accounted for marked differences in conferred pruning weight, berry weight and fruit yield from trial averages. Comparison of statistical analysis techniques illustrated that the choice of such techniques may influence the outcome of genetic selection from field trial data.

Significance of the Study: Such quantification of the variation between vines in vigour, fruit yield and berry size due to rootstock genotype provides a framework for selection of well-performing genotypes for inclusion in advanced generations of the CSIRO vine rootstock breeding program.

Keywords

traditional, novel, effects, vigour, yield, components, shiraz, rootstocks, hybrid, grapevines

Disciplines

Physical Sciences and Mathematics

Publication Details

Jones, T. H., Cullis, B. R., Clingeleffer, P. R. & Ruhl, E. H. (2009). Effects of novel hybrid and traditional rootstocks on vigour and yield components of Shiraz grapevines. Australian Journal of Grape and Wine Research, 15 (3), 284-292.

Effects of novel hybrid and traditional rootstocks on vigour and yield components of Shiraz grapevines.

T.H. Jones[1,4], B.R. Cullis[2], P.R. Clingeleffer[1], and E.H. Rühl[1,3]

[1]CSIRO Division of Plant Industry, PMB, Merbein, Vic., 3505
[2]NSW Department of Primary Industries Wagga Wagga Agricultural Institute
[3]Current address: Geisenheim Research Centre, Section for Grapevine Breeding and Grafting, 65366 Geisenheim, Germany
[4]Corresponding Author: Tim H. Jones. Current address: Yalumba Nursery, PO Box 10, Angaston, SA, 5355. Facsimile: + 61 8 85687710. Email: tjones@yalumba.com.

Running title: Rootstock effects on Shiraz

Abstract

Background and Aims

The influence of grapevine rootstocks on vine vigour and crop yield is recognised as an integral part of viticultural management. However, the genetic potential of *Vitis* species rootstock hybrids for vigour and yield control is not fully exploited in Australian viticulture. The effect of 55 novel inter- and intra-species hybrids and five traditional hybrid rootstock cultivars on winter pruning weight, berry size and fruit yield of grafted Shiraz vines is presented. The genetic predictions that resulted from this analysis were used to illustrate how rootstocks that best perform for a combination of traits may be selected.

Methods and Results

The use of linear mixed models and residual maximum likelihood procedures took into account repeated measures and spatial variation within a large field trial (720 vines). Over six years of assessment, variation of up to 93.9% in winter pruning weight, 81.9% in fruit yield and 21.0% in berry weight between rootstocks was estimated.

Conclusions

The effect of rootstock genotype accounted for marked differences in conferred pruning weight, berry weight and fruit yield from trial averages. Comparison of statistical analysis techniques illustrated that the choice of such techniques may influence the outcome of genetic selection from field trial data.

Significance of Study

Such quantification of the variation between vines in vigour, fruit yield and berry size due to rootstock genotype provides a framework for selection of well performing genotypes for inclusion in advanced generations of the CSIRO vine rootstock breeding program.

Keywords: *Grapevine breeding, BLUP, rootstock, yield components, vigour.*

Introduction

The use of non *Vitis vinifera* rootstocks in wine grape production provides a platform for manipulation of a broad range of vine characteristics which can consequently improve vineyard efficiency (Whiting 2004). Since the initial adoption of non *V. vinifera* rootstocks, primarily to provide grafted vines with resistance to the grape phylloxera (*Daktulosphaira vitifoliae*) (de Castella 1921), rootstocks have been selected to confer a wide range of other traits for grapevine improvement. These include resistance to nematodes (Stirling and Cirami 1984; McKenry and Anwar 2006) as well as other soil-borne pathogens (Ferreira and Marais 1987; Walker *et al.* 1994; Sule and Burr 1998), adaptability to soil pH (Conradie 1983; Bavaresco *et al.* 2003), salinity tolerance (Sauer 1968; Downton 1977; Walker *et al.* 2002; Walker *et al.* 2004), drought tolerance (Carbonneau 1985; McCarthy *et al.* 1997), adaptability to water logging (Whiting and Orr 1990; Striegler *et al.* 1993), ability to mediate nutrient uptake and juice and wine composition (Bénard *et al.* 1963; Hale and Brien 1978; Ruhl *et al.* 1988; Walker *et al.* 1998; Walker *et al.* 2000; Mpelasoka *et al.* 2003), and the ability to control vine vigour and yield components (Rives 1971; Ruhl *et al.* 1988; May 1994; Reynolds and Wardle 2001).

With grapevine vigour and yield closely related to fruit composition and wine quality (Kliewer and Weaver 1971; Bravdo 1985; Clingeleffer *et al.* 2000; Kliewer and Dokoozlian 2005), considerable resources may be required to manage these traits in commercial vineyards that aim to maximize profitability by optimizing yield and quality (Clingeleffer and Sommer 1995; Dry *et al.* 1999). Rootstocks may be utilized to influence vigour and fruit yield, with the potential to reduce reliance on standard traditional viticultural techniques such as vine training, pruning and fruit thinning (Pouget 1987; Delas 1992; Clingeleffer *et al.* 1999; Clingeleffer *et al.* 2000).

Significant variation in conferred vigour and yield have been identified between traditional rootstock varieties (Harmon 1949; Lipe and Perry 1988; Pouget and Delas 1989; Prior *et al.* 1993; Main *et al.* 2002; Zerihun and Treeby 2002), most of which are non *V. vinifera* species hybrids or pure non *V. vinifera* species (Pongrácz 1983; May 1994). Specifically, such rootstocks have been shown to directly influence vigour and yield controlling physiological processes such as nitrogen uptake (Williams and Smith 1991; Keller *et al.* 2001b; Keller *et al.* 2001a; Zerihun and Treeby 2002) and photosynthesis (Düring 1994; Koblet *et al.* 1997; Soar *et al.* 2006).

With the influence of rootstock variety on vigour and yield potentially under strong genetic control, the potential for breeding to improve rootstock effects on wine grapes is clearly evident (Alleweldt and Possingham 1988; Read and Gu 2003; Cousins 2005). However, despite other reports in the literature, a level of ambiguity still remains around the genetic potential that resides within the broad range of rootstock germplasm available, perhaps due in part to the interaction of management techniques and other environmental variables on the performance of the traditional rootstock varieties (May 1994; Read and Gu 2003). Indeed, relatively few grapevine rootstock varieties are used extensively by the grape industry, with preference given to varieties that have historically proven to perform well (May 1994; de Andres *et al.* 2007). In comparison to the European industry, grafted vines are still a minority in Australian vineyards with 18.9% of the total area of Australian vineyards planted with grafted vines in 2006 (Dry 2007). Hence, in recent years, rootstock breeding in Australia has moved towards the screening of non-traditional multi-species hybrids for suitability to local conditions (Clingeleffer 1996; Wheal *et al.* 2002).

The efficacy of such breeding programs depends foremost on the accurate genetic assessment (e.g. Cotterill and Dean 1990; Cullis *et al.* 2000) of the effect of rootstock varieties on scions (Rives 1971) which will lead to a more accurate prediction of the outcome of selective breeding. In this paper, we used linear mixed models and residual maximum likelihood procedures (Gilmour *et al.* 1995) to take into account various aspects of the environmental, temporal, and genetic variation residing within the trial to more accurately partition the variance due to each variable (Gilmour *et al.* 1997). This allowed the calculation of the best linear unbiased predictions (BLUPs, Robinson 1991) of the effects of 55 non-traditional multi-species hybrid rootstocks and 5 traditional rootstock varieties on mature grafted Shiraz grapevines. We investigated rootstocks effects on vine vigour (measured as winter pruning weight following Ravaz (1911) and Rives (1971)), berry weight and fruit yield over six years of observations. In addition, the genotypes identified by this contemporary statistical analysis that best satisfied a predefined multi-trait selection regime were compared to those identified with the use of arithmetic trial means alone. This comparison clearly illustrated how the choice of statistical analysis technique may influence the outcome of genetic selection from field trial data.

Materials and Methods

Trial site and design

The trial was established in 1989 at Koorlong (34° 15' 32" S, 142° 7' 59" E) in the warm climate inland irrigation region of Sunraysia (Victoria, Australia). The trial is situated on sandy calcareous earths (Northcote 1988), on a slight north-south slope with east-west running rows 3 m apart, with 1.8 m between vines along rows.
The trial, consisting of 6 replicates (2 vine plots) of each rootstock genotype, was planted in 1989, with vine propagation and grafting carried out in 1988. Vines were bench grafted and planted in the same season. It was assessed over 6 years from 1993 to 1998. The trial was designed with 5 of the 6 replicates planted as adjacent complete blocks, with the sixth replicate split into two incomplete blocks situated at either end of the five adjacent complete blocks. Once established, the vines were spur pruned (bud load approximately 80 buds per vine) with cordons developed on a two wire vertical trellis. Standard commercial management practices for the region were applied to the field trial, with approximately 0.7 m of water applied per year by overhead sprinklers.

Data collection

Winter pruning weights were recorded, measuring total fresh pruning wood weight for each vine. Total fruit yield (whole bunches) was recorded for each vine, with 5 berries (two from the top, two from the middle and one from the base) from ~20 bunches weighed to calculate average berry weight for each vine. When sampling berries, bunches were sampled in equal numbers from both sides of the vine, sampling bunches evenly along cordons where possible, immediately prior to harvesting all bunches.

Genetic background of material

All rootstocks were grafted to Shiraz clone PT23. The five traditional rootstocks consisted of two *V. candicans* x *V. rupestris* natural hybrids Dog Ridge and Ramsey, both previously regarded as *V. champinii* (see Pongrácz 1983), two *V. berlandieri* x *V. rupestris* hybrids 1103 Paulsen and 140 Ruggeri, and the multispecies complex hybrid Freedom with a pedigree involving *V. vinifera*, *V. labrusca*, *V. riparia*, and *V. rupestris*. The 55 non-traditional rootstocks consisted of intra- and inter-species hybrids (Table 1), including some selections that did not have a fully resolvable pedigree (denoted *u.p.*). Three of these hybrids (2 - Merbein 5489, 3 – Merbein 5512 and 12 – Merbein 6262) are CSIRO selections that have recently been released to the Australian viticultural industry.

Statistical Analysis

Trial data was analysed using linear mixed models and the residual maximum likelihood procedure with ASREML-R (Butler *et al.* 2007). Rootstock genotype (i.e., a factor with 60 levels) defined the "treatment" structure while block, field row, field column and field plot (with 6, 12, 60, 360 levels respectively) were included in all models as random terms to account for either the design randomisation processes or extraneous variation arising from spatial heterogeneity in the field.

As a small number of vines were replaced after early stage mortality (propagated in the same way as the original vines), a covariate based on the year of re-planting was created and included in all models as a fixed term. Where necessary additional covariance models were included at the residual level, typically based on the separable first order autoregressive model described in Cullis and Gleeson (1991). To account for spatial variation not adequately dealt with by the randomized trial design, spatial covariance models were applied in the field row and field column direction where appropriate (Cullis and Gleeson, 1991). Similarly, to account for temporal correlation across years (e.g. Verbyla and Cullis 1992; Jaffrezic and Pletcher 2000), covariance models were included for each random term which contributed in a major way to the total variation. Covariance models used included the uniform and ante-dependence models as appropriate (Wolfinger 1996; Jaffrezic *et al.* 2003). An antedependence covariance model was also used for the residuals.

To best describe the effect of rootstock genotype on grafted vine performance, Best Linear Unbiased Predictors (BLUPs) (Robinson 1991) of rootstock genotype values and standard errors were calculated. The accuracy of these was computed using a generalised measure of broad-sense heritability (Cullis *et al.* 2006) which is defined as the square of the correlation between predicted and true genetic effects (Falconer and Mackay 1996; Oakey *et al.* 2006). Total genetic correlations (combining additive and non-additive effects) over years were also obtained from the fitted REML models.

Arithmetic means across all years were also calculated for each trait to allow comparison with rootstock genotype predictions based on BLUP estimates. An arbitrary selection regime that identified potential commercially favourable rootstocks, in terms of the traits examined in this study, was then applied to illustrate how the identification of optimal genotypes may differ depending on the statistical technique used for genotype evaluation. This selection regime identified rootstocks that conferred low to medium vine vigour, medium to high yield, small berry size whilst maintaining vine balance (Smart 1991).

Results

The three traits examined in this study where strongly influenced by rootstock genotype, illustrated by comparisons of the genotype BLUP values that predict the effect of each rootstock genotype on grafted vine performance. A 93.9% decrease in pruning weight between vines with the most and least vigourous rootstock genotypes (Figure 1a), an 81.9% decrease in fruit yield between vines with the most and least productive rootstock genotypes (Figure 1b) and a 21.0% decrease in berry weight between vines with the largest and smallest berry producing rootstock genotypes (Figure 1c) was observed. REML estimates of total genetic correlations between years ranged between $r_g = 0.85$ and $r_g = 0.99$ for pruning weight and $r_g = 0.69$ and $r_g = 0.93$ for fruit yield. Such high genetic correlations indicate relatively high consistency from year to year. However in both traits (in particular fruit yield, Table 2), a decrease in genetic correlation with increasing time between observations was evident, hence, the ante-dependence covariance structure over years described earlier was fitted in the model. Genetic correlations between years in berry weight ranged between $r_g = 0.53$ and $r_g = 0.82$, however there was no such pattern of decline in correlation over time. Single year generalised broad-sense heritabilities for pruning weight and fruit yield ranged from $h^2_g = 0.87\text{-}0.90$ (mean = 0.89) and $h^2_g = 0.81–0.91$ (mean = 0.89) over the six years of assessment (Table 3), indicating a high level of accuracy in the prediction of rootstock genotype values. The generalized heritability of berry weight was more variable over years ($h^2_g = 0.50 – 0.76$, mean = 0.69), however still suggesting a considerable correlation between predicted and real genetic values.

All traditional rootstock varieties produced more vigourous, productive vines with larger berry size than the trial means. The two CSIRO selections Merbein 5512 (3) and Merbein 6262 (12) displayed considerably lower pruning weight, yield and berry size than the trial mean (Figure 1). Merbein 5489 (2) displayed a pruning weight and yield not significantly different from the trial mean, while displaying smaller berry size (Figure 1).

The ranking of rootstock genotype performance based on BLUPs showed marked differences to that based on trial means (Figure 2). Of the 21 low vigour genotypes that would be selected under an arbitrary low vigour pruning weight range of 1.0 to 2.0 kg based on BLUP values, sixteen genotypes were selected in common with those identified for the same selection range using trial means, with two additional genotypes identified using trial means, that fell outside the specified range of BLUP genotype values. Similarly, differences were identified when applying a medium to high yield selection range of between 10.0 and 11.0 kg, and a low berry weight selection range of 1.2 to 1.3 g (Figure 2). When genotypes were ranked by the commonly used Ravaz Index (ratio of vine yield (kg) to pruning weight (kg), Ravaz (1911)), differences between estimates based on the two approaches were magnified, especially in genotypes that produced vines which showed a larger yield to vigour ratio (Figure 2d).

When an arbitrary selection range for the Ravaz Index of between 8.0 and 10.0 was applied, that would identify vines that exhibit relative high yield per mass of prunings, but remain "in balance" (Bravdo *et al.* 1984; Bravdo 1985; Smart 1991), none of the four genotypes selected using BLUP values of yield and pruning weight were identified using the trial means approach (Figure 2d). Instead, three different genotypes were identified when trial means for yield and pruning weight of genotypes were used.

When the rootstock yield BLUPs were plotted against those for pruning weight, the positive relationship between yield and vine vigour identified by past studies (e.g. Walker *et al.* 2002) was evident (Figure 3). This plot also provides the opportunity to graphically illustrate how genotypes that satisfy both the yield and pruning weight selection ranges discussed above can be rapidly identified (Figure 3). On this basis, three optimal genotypes (19, 43, 45) are identified. However, with none of these genotypes satisfying the initial berry weight selection range and Ravaz Index selection range (displaying vigour (kg)/pruning weight (kg) = 6.3, 7.2 and 5.3 respectively) applied, it was necessary to loosen constraints to allow selection of an appropriate number (10%) of best performing genotypes.

When applying a pruning weight selection range of between 1.0 and 2.0 kg, a yield selection range of between 8.0 and ll.0 kg, a berry weight criterion of less than 1.4 g and a Ravaz Index range of between 5.0 and 10.0 (indicative of “vine balance”, Smart 1991), 10% of the genotypes examined are identified as optimal genotypes under the management conditions of this trial with Shiraz as the scion variety (Table 4). It was interesting to note that all traditional rootstock varieties showed low Ravaz Indices (< 5.0) under the trial management conditions (Figure 3).

Discussion

The performance of Shiraz grapevines in the replicated field trial environment was heavily influenced by rootstock genotype, reflecting the genetic diversity conferred by the broad range of *Vitis* species (de Andres *et al.* 2007) that comprise the genetic backgrounds of the rootstocks examined in this experiment. Marked differences between rootstock genotypes in conferred vigour, yield and berry weight, over six years of observations, were estimated with the use of Best Linear Unbiased Predictions (BLUPs, e.g. Robinson 1991, Welham *et al.* 2004). These predictions clearly illustrate the considerable potential of rootstocks to mediate vine performance. In addition, such variability between genotypes clearly suggests that significant gains may be realised by selective breeding to combine and amplify beneficial traits (Cotterill and Dean 1990; Falconer and Mackay 1996).

In woody perennial species that generally require a number of years between germination and reproductive (and fully productive) maturity, it is imperative that such predictions of breeding values are as accurate as possible to optimise efficiency of selection and advanced generation breeding (Cotterill and Dean 1990; Falconer and Mackay 1996). When spatial and temporal variables were appropriately modelled in this analysis, substantial differences in the predicted performance of genotypes to that estimated by arithmetic trial means were identified.

In the case of vine vigour in the current study, measured as total winter pruning weight, genetic correlations between the six years of observations were high ($r_g \geq 0.85$) indicating that observations carried out over a shorter number of years may provide adequate information in this trial, depending on the desired level of accuracy.

Consistently high values of generalised broad-sense heritability ($h^2_g = 0.87 - 0.90$) for rootstock genotype effect on vine pruning weight over the six years of observations suggest a high level of accuracy in the BLUP predictions. Dog Ridge (*V. candicans* x *V. rupestris*) produced the most vigourous vines within the trial over the six years of observations. Conversely, the inter-species hybrid genotype 32 (a complex hybrid with a pedigree dominated by *V. Vinifera* and *V. rotundifolia* that was not-completely resolved due to an open-pollination event in the selection's background) conferred the lowest winter pruning weights of the 60 genotypes analysed, producing 93.9% less pruning weight than Dog Ridge. The five traditional rootstock varieties in this trial conferred moderately high to very high vigour, with each variety closely matching that described in the literature (summarised by Whiting 2004). It is interesting to note that studies of ungrafted table grape hybrids have identified a much lower heritability of vine vigour (broad-sense heritability not significantly different from zero, Firoozabady and Olmo 1987, narrow-sense $h^2 = 0.22$, Wei *et al.* 2003a). Genetic correlations for total fruit yield among years declined with increasing time between observations. However, beyond the first year of observations (vine age of 5 years), predicted rootstock genotype values from each year correlated well with each other ($r_g \geq 0.80$). Following an expected close association between fruit yield and vine vigour (Walker *et al.* 2002), genotype 32 also conferred the lowest fruit yield, producing 81.9% less fruit than the highest yielding genotype 23 (*V. candicans* x *V. rupestris* x *V. vinifera* hybrid, Table 1). As was the case for conferred vine vigour, a high level of accuracy in the predicted effects of rootstock genotypes on conferred fruit yield was indicated by consistently high generalised broad-sense heritabilities ($h^2_g = 0.81 - 0.91$) over the six years of observations. Assuming our generalized broad-sense heritability estimates are describing a significant proportion of additive genetic variation, this again contrasted with that observed in ungrafted table grape hybrids, with Wei *et al.* (2003a) reporting a narrow sense heritability (Falconer and Mackay 1996) estimate of ($h^2 = 0.18$) for fruit yield among the diverse range of table grape bi-parental progeny studied. This raises the possibility that genetic variation in conferred winter pruning weight and fruit yield conferred by rootstocks of such a diverse species background may be somewhat greater than that residing among pure *V. vinifera* varieties. However, the population specific estimates of generalized broad-sense heritability in this study of a relatively small population do not take into account genetic by environment interactions, and do not partition additive and non-additive components of genetic variation (e.g. Oakey *et al.* 2006). Rootstock field trial designs that include appropriate family pedigree size and structure to allow accurate narrow-sense heritability estimates of rootstock genotype effects are necessary to quantify this with more accuracy (Falconer and Mackay 1996).

Genetic correlations in berry weight across years were as low as $r_g = 0.53$ (between 1993 and 1994) and did not display any clear trend with time between observations, indicating that selection for rootstock influence on berry weight may not be able to be made reliably from any one single year of results. This also indicated that the inclusion of the standard exponential decay covariance structure for repeated measures in the model was not appropriate for this trait. The lower heritability values for conferred berry weight in comparison to fruit yield and pruning weight could be caused by weaker genetic control in this situation, reduced genetic variability in this trait within the genetic material studied (as seen in the relatively narrow range of berry weight BLUP values), a sampling methodology that is prone to more error than the total yield and pruning weight measures, or a combination of these factors. Nonetheless, with an average generalised heritability of $h^2_g = 0.69$ and significant variation between genotypes in BLUP values under trial conditions, berry size is clearly influenced by rootstock genotype. It is interesting to note that the largest berries occurred on vines grafted to the *V. vinifera* x *V. longii* hybrid genotype 37, with 72% of these particular hybrids conferring larger berry sizes than the trial mean. In addition, the five traditional rootstock varieties produced larger berries than the trial mean. Narrow-sense heritability estimates for berry size among *V. vinifera* table grape hybrids was estimated at $h^2 = 0.63$ by Wei *et al.* (2002), indicating that berry weight in the ungrafted grapevines is under strong additive genetic control and that significant genetic improvement in berry size may be achieved with selective breeding (Wei *et al.* 2003b).

Under the management conditions applied to the field trial, all traditional rootstock varieties produced vines that had a yield to pruning weight ratio of less than 5.0, below the optimal threshold suggested by authors such as Bravdo *et al.* (1984) Bravdo (1985) and Smart (1991) for optimal vine balance in terms of fruit quality (e.g. Kliewer and Dokoozlian 2005). With a reduction in yield response to pruning weight evident in high vigour rootstocks in this study, it is apparent that the non-traditional hybrid genotypes that conferred less vigour than the traditional varieties in the field trial maintained preferable yield to pruning weight ratios under the trial environment and management regime. By considering the BLUP genotype values for all three traits, it was possible to illustrate how ten percent of the genotypes studied that best satisfied predefined yield, vigour and berry weight prerequisites could be selected, in the absence of genotype by environment information. While this provides an example of multi-trait selection (Falconer and Mackay 1996) in its most simplistic form, it illustrates the significant potential that exists for development of improved grapevine rootstocks that are specific to industry requirements. Recently, highly replicated grafted rootstock genetic trials that comprise a broad range of germplasm and include the pedigree structure required to allow estimation of additive genetic effects (Falconer and Mackay 1996), have been implemented. These trials will provide information on the genetic control of a range of crucial traits with high resolution and facilitate the development of a functional multi-trait selection index that will significantly improve the efficiency of grapevine rootstock breeding in Australia.

Acknowledgements

David Emanuelli for data collection. Steve Sykes, Craig Hardner, Jo Stringer, Brady Smith, Alison Smith and Paul Petrie for advice on the manuscript and analysis.

References

Alleweldt G., Possingham J. V. (1988) Progress in Grapevine Breeding. Theoretical and Applied Genetics **75**, 669-673.

Bavaresco L., Giachino E., Pezzutto S. (2003) Grapevine rootstock effects on lime-induced chlorosis, nutrient uptake, and source-sink relationships. Journal of Plant Nutrition **26**, 1451-1465.

Bénard P., Jouret C., Flanzy M. (1963) Influence des porte-greffes sur la composition minérale des vins. Annales de technologie agricole **12**, 277-285.

Bravdo B. (1985) Effect of crop level and crop load on growth, yield, must and wine composition, and quality of Cabernet Sauvignon. American Journal of Enology and Viticulture **36**, 125.

Bravdo B., Hepner Y., Loinger C., Cohen S., Tabacman H. (1984) Effect of crop level on growth, yield and wine quality of a high yielding Carignane vineyard. American Journal of Enology and Viticulture **35**, 247-252.

Butler D., Cullis B. R., Gilmour A. R., Gogel B. J. (2007) 'ASReml-R reference Manual Release 2.0.' (Queensland Department of Primary Industries and Fisheries. Available online at http://www.vsni.co.uk/resources/doc/asreml-R.pdf.: Brisbane)

Carbonneau A. (1985) The early selection of grapevine rootstocks for resistance to drought conditions. American Journal of Enology and Viticulture **36**, 195-198.

Clingeleffer P. R. (1996) Rootstocks: A means to control scion pH, ion composition and spectral parameters and meet juice and wine quality specifications. In 'Quality Management in Viticulture: ASVO Viticulture Seminar'. Mildura Arts Centre, 2 August. (ASVO)

Clingeleffer P. R., Krstic M. P., Sommer K. J. (2000) Production efficiency and relationships among crop load, fruti composition, and wine quality. In 'Proceedings of the American Society for Enology and Viticulture 50th Anniversary Meeting, Seattle, June 19-23' pp. 318-322

Clingeleffer P. R., Sommer K. J. (1995) Vine development and vigour control. In 'Canopy management: proceedings of a seminar organized by the Australian Society of Viticulture and Oenology, Mlidura, 1994'. (Ed. P Hayes). (Winetitles, Adelaide)

Clingeleffer P. R., Sommer K. J., Walker R. R. (1999) Hollistic system approach for sustainable vineyard management for grape and wine quality. In 'Proceedings of the Tenth Australian Wine Industry Technical Conference'. Sydney. (Eds RJ Blair, AN Sas, PF Hayes and PB Høj) pp. 188-196. (The Australian Wine Research Institute Urrbrae)

Conradie W. J. (1983) Liming and choice of rootstocks as cultural techniques for vines in acid soils. South African Journal of Enology and Viticulture **4**, 39-44.

Cotterill P. P., Dean C. A. (1990) Successful Tree Breeding with Index Selection (CSIRO: Melbourne)

Cousins P. (2005) Evolution, genetics and breeding: Viticultural applications of the origins of our rootstocks. In 'Grapevine Rootstocks: Current Use, Research and Application Proceedings of the 2005 rootstock symposium'. Osage Beach, Missouri. (Eds P Cousins and K Striegler). (Mid-America Viticulture and Enology Center Southwest Missouri State University Mountatin Grove Campus)

Cullis B. R., Smith A. B., Hunt C., Gilmour A. (2000) An examination of the efficiency of Australian crop variety evaluation programmes. Journal of Agricultural Science **135**, 213-222.

Cullis B. R., Gleeson A.C. (1991) Spatial-analysis of field experiments - an extension in 2 dimensions. Biometrics **47**, 1449-1460.

Cullis B. R., Smith A. B., Coombes N. E. (2006) On the design of early generation variety trials with correlated data. Journal of Agricultural, Biological and Environmental Statistics **11**, 381-393.

de Andres M. T., Cabezas J. A., Cervera M. T., Borrego J., Martinez-Zapater J. M., Jouve N. (2007) Molecular characterization of grapevine rootstocks maintained in germplasm collections. American Journal of Enology and Viticulture **58**, 75-86.

de Castella F. R. (1921) Resistant Stocks. The Journal of the Department of Agriculture of Victoria **19**, 490-499.

Delas J. J. (1992) Criteria used for rootstock selection in France. In 'Rootstock Seminar: A Worldwide Perspective'. Reno, Nevada. (Eds JA Wolpert, MA Walker and E Weber) pp. 1-14. (American Society for Enology and Viticulture)

Downton W. J. S. (1977) Chloride accumulation in different species of grapevine. Scientia Horticulturae **7**, 249-253.

Dry P. R., Loveys B. R., Illand P. G., Botting D. G., McCarthy M. G. (1999) Vine manipulation to meet fruit specifications. In 'Proceedings of the Tenth Australian Wine Industry Technical Conference'. Sydney. (Eds RJ Blair, AN Sas, PF Hayes and H P.B.) pp. 208-214. (The Australian Wine Research Institute)

Dry N. (2007) Grapevine Rootstocks Selection and Management for South Australian Vineyards. (Lythrum: Press Adelaide)

Düring H. (1994) Photosynthesis of ungrafted and grafted vines: effects of rootstock genotype and plant age. American Journal of Enology and Viticulture **45**, 297-299.

Falconer D. S., Mackay T. F. C. (1996) Introduction to Quantitative Genetics. (Addison Wesley Longman Ltd.: Dinburgh Gate, Harlow, Essex)

Ferreira J. H. S., Marais P. G. (1987) Effect of rootstock cultivar, pruning method and crop load on *Botrytis cinerea* rot of *Vitis vinifera* cv. Chenin Blanc grapes. South African Journal of Enology and Viticulture **8**, 41-44.

Firoozabady E., Olmo H. P. (1987) Heritability and correlation studies of certain quantitative traits in table grapes, *Vitis* spp. Vitis **26**, 132-146.

Gilmour A., Cullis B. R., Verbyla A. P. (1997) Accounting for natural and extraneous variation in the analysis of field experiments. Journal of Agricultural, Biological, and Environmental Statistics **2**, 269-293.

Gilmour A. R., Thompson R., Cullis B. R. (1995) Average information REML: An efficient algorithm for variance parameter estimation in linear mixed models. Biometrics **51**, 1440-1450.

Hale C. R., Brien C. J. (1978) Influence of Salt Creek rootstocks on composition and quality of Shiraz grapes and wine. Vitis **17**, 139-146.

Harmon F. N. (1949) Comparitive value of thirteen rootstocks for ten *vinifera* grape varieties in the Napa Valley in California. Proceedings of the American Society of Horticultural Science **54**, 157-162.

Jaffrezic F., Pletcher S. D. (2000) Statistical models for estimating the genetic basis of repeated measures and other function-valued traits. Genetics **156**, 913-922.

Jaffrezic F., Thompson R., Hill W. G. (2003) Structured antedependence models for genetic analysis of repeated measures on multiple quantitative traits. Genetical Research **82**, 55-65.

Keller M., Kummer M., Vasconcelos M. C. (2001a) Reproductive growth of grapevines in response to nitrogen supply and rootstock. Australian Journal of Grape and Wine Research **7**, 12-18.

Keller M., Kummer M., Vasconcelos M. C. (2001b) Soil nitrogen utilisation for growth and gas exchange by grapevines in response to nitrogen supply and rootstock. Australian Journal of Grape and Wine Research **7**, 2-11.

Kliewer W. M., Dokoozlian N. K. (2005) Leaf area/crop weight ratios of grapevines: Influence on fruit composition and wine quality. American Journal of Enology and Viticulture **56**, 170-181.

Kliewer W. M., Weaver R. J. (1971) Effect of crop level and leaf area on growth, composition, and coloration of 'Tokay' grapes. American Journal of Enology and Viticulture **22**, 172-177.

Koblet J. R., Keller M., Candolfi-Vasconcelos M. C. (1997) Effects of training system, canopy management practices, crop load and rootstock on grapevine photosynthesis. Acta Horticulturae **427**, 133-140.

Lipe W. N., Perry R. L. (1988) Effects of Rootstocks on Wine Grape Scion Vigor, Yield, and Juice Quality. Hortscience **23**, 317-321.

Main G., Morris J., Striegler K. (2002) Rootstock effects on Chardonel productivity, fruit, and wine composition. American Journal of Enology and Viticulture **53**, 37-40.

May P. (1994) Using Grapevine Rootstocks: The Australian Perspective. (Winetitles: Adelaide)

McCarthy M. G., Cirami R. M., Furkaliev D. G. (1997) Rootstock response of Shiraz (*Vitis vinifera*) grapevines to dry and drip-irrigated conditions. Australian Journal of Grape and Wine Research **3**, 95-98.

McKenry M. V., Anwar S. A. (2006) Nematode and grape rootstock interactions including an improved understanding of tolerance. Journal of Nematology **38**, 312-318.

Mpelasoka B. S., Schachtman D. R., Treeby M. T., Thomas M. R. (2003) A review of potassium nutrition in grapevines with special emphasis on berry accumulation. Australian Journal of Grape and Wine Research **9**, 154-168.

Northcote K. H. (1988) Soils and Australian Viticulture. In 'Viticulture Volume 1 Resources'. (Eds BG Coombe and PR Dry) pp. 81. (Australian Industrial Publishers: Adelaide)

Oakey H., Verbyla A., Pitchford W., Cullis B., Kuchel H. (2006) Joint modeling of additive and non-additive genetic line effects in single field trials. Theoretical and Applied Genetics **113**, 809-819.

Pongrácz D. P. (1983) Rootstocks for Grape-vines. (David Philip: Cape Town)

Pouget R. (1987) Usefulness of rootstocks for controlling vine vigour and improving wine quality. Acta Horticulturae **206**, 109-113.

Pouget R., Delas J. J. (1989) Le choix des porte-greffe de la vigne pour une production de qualité. Connaissance de la Vigne et du Vin **Hors série**, p 27-31.

Prior L. D., Cullis B. R., Sarooshi R. A. (1993) Influence of rootstock and trellis systems on the productivity of sultana grapevines. Australian Journal of Experimental Agriculture **33**, 935-943.

Ravaz L. (1911) L'effeuillage de la vigne. Annales de l' Ecole Nationale d' Agriculture de Montpellier **11**, 219-245.

Read P. E., Gu S. (2003) A century of American viticulture. Hortscience **38**, 943-951.

Reynolds A. G., Wardle D. A. (2001) Rootstocks impact vine performance and fruit composition of grapes in British Columbia. HortTechnology **11**, 419-427.

Rives M. (1971) Statistical analysis of rootstock experiments as providing a definition of the terms vigour and affinity in grapes. Vitis **9**, 280-290.

Robinson G. K. (1991) That BLUP is a good thing: The estimation of random effects. Statistical Science **6**, 15-51.

Ruhl E. H., Clingeleffer P. R., Nicholas P. R., Cirami R. M., McCarthy M. G., Whiting J. R. (1988) Effect of rootstocks on berry weight and pH, mineral-content and organic-acid concentration of grape juice of some wine varieties. Australian Journal of Experimental Agriculture **28**, 119-125.

Sauer M. R. (1968) Effects of vine rootstocks on chloride concentration in Sultana scions. Vitis **7**, 223-226.

Smart R. E. (1991) Sunlight into Wine. (Winetitles: Adelaide)

Soar C. J., Dry P. R., Loveys B. R. (2006) Scion photosynthesis and leaf gas exchange in *Vitis vinifera* L. cv. Shiraz: Mediation of rootstock effects via xylem sap ABA. Australian Journal of Grape and Wine Research **12**, 82-96.

Stirling G. R., Cirami R. M. (1984) Resistance and tolerance of grape rootstocks to South Australian populations of root-knot nematode. Australian Journal of Agriculture and Animal Husbandry **24**, 277-282.

Striegler R. K., Howell G. S., Flore J. A. (1993) Influence of rootstock on the response of seyval grapevines to flooding stress. American Journal of Enology and Viticulture **44**, 313-319.

Sule S., Burr T. J. (1998) The effect of resistance of rootstocks to crown gall (*Agrobacterium* spp.) on the susceptibility of scions in grape vine cultivars. Plant Pathology **47**, 84-88.

Verbyla A. P., Cullis B. R. (1992) The analysis of multistratum and spatially correlated repeated measures data. Biometrics **48**, 1015-1032.

Walker M. A., Clingeleffer P. R., Kerridge G. H., Ruhl E. H., Nicholas P. R., Blackmore D. H. (1998) Effects of the rootstock Ramsey (*Vitis champini*) on ion and organic acid composition of grapes and wine, and on wine spectral characteristics. Australian Journal of Grape and Wine Research **4**, 100-110.

Walker M. A., Wolpert J. A., Weber E. (1994) Viticultural characteristics of Vr hybrid rootstocks in a vineyard site infected with grapevine fanleaf virus. Vitis **33**, 19-23.

Walker R. R., Blackmore D. H., Clingeleffer P. R., Correll R. L. (2002) Rootstock effects on salt tolerance of irrigated field-grown grapevines (*Vitis vinifera* L. cv. Sultana). 1. Yield and vigour inter-relationships. Australian Journal of Grape and Wine Research **8**, 3-14.

Walker R. R., Blackmore D. H., Clingeleffer P. R., Correll R. L. (2004) Rootstock effects on salt tolerance of irrigated field-grown grapevines (*Vitis vinifera* L. cv. Sultana) 2. Ion concentrations in leaves and juice. Australian Journal of Grape and Wine Research **10**, 90-99.

Walker R. R., Read P. E., Blackmore D. H. (2000) Rootstock and salinity effects on rates of berry maturation, ion accumulation and colour development in Shiraz grapes. Australian Journal of Grape and Wine Research **6**, 227-239.

Wei X., Clingeleffer P. R., Sykes S. (2003a) Narrow-sense heritability estimates for yield and quality characteristics in CSIRO's table grape breeding program. Acta Horticultura **603**, 173-179.

Wei X., Sykes S. R., Clingeleffer P. R. (2003b) Effects of selection on early stage genetic evaluation for berry weight in breeding table grapes. Plant Breeding **122**, 77-82.

Wei X. M., Sykes S. R., Clingeleffer P. R. (2002) An investigation to estimate genetic parameters in CSIRO's table grape breeding program. 2. Quality characteristics. Euphytica **128**, 343-351.

Welham S., Cullis B., Gogel B., Gilmour A., Thompson R. (2004) Prediction in linear mixed models. Australian & New Zealand Journal of Statistics **46**, 325-347.

Wheal M., Clingeleffer P. R., Sykes S. (2002) Grapevine rootstocks for Australian conditions. In ''Plant Breeding for the 11th Millenium' Proceedings of the 12th Australasian Plant Breeding Conference 15-20th September'. Perth, Western Australia. (Ed. JA Coomb) pp. 161-166. (Australasian Plant Breeding Association Inc.)

Whiting J. R. (2004) Grapevine Rootstocks. In 'Viticulture'. (Eds PR Dry and BG Coombe) pp. 167-188. (Winetitles: Adelaide)

Whiting J. R., Orr K. (1990) 99 Richter and 101-14 rootstocks susceptible to waterlogging. The Australian Grapegrower and Winemaker **321**, 60.

Williams L. E., Smith R. J. (1991) The effect of rootstock on the partitioning of dry weight, nitrogen and potassium, and root distribution of Cabernet Sauvignon grapevines. American Journal of Enology and Viticulture **42**, 188-122.

Wolfinger R. D. (1996) Heterogeneous variance: covariance structures for repeated measures. Journal of Agricultural, Biological, and Environmental Statistics **1**, 205-230.

Zerihun A., Treeby M. T. (2002) Biomass distribution and nitrate assimilation in response to N supply for *Vitis vinifera* L. cv. Cabernet Sauvignon on five Vitis rootstock genotypes. Australian Journal of Grape and Wine Research **8**, 157-162.

Table 1: Species pedigrees of hybrid rootstock genotypes examined within the field trial. Where possible, the species of the grandparents of the hybrid genotypes within the field trial are shown. In some cases, it was not possible to resolve the pedigree of a particular rootstock genotype: *u.p.v.r* = unresolved pedigrees including *V. Vinifera* and *V. rotundifolia*; *u.p.* = completely unresolved pedigrees. *V. can* x *V. rup* = natural *V. candicans* x *V. rupestris* hybrid.

Hybrid Code	Pedigree	
	Parent 1	Parent 2
1-5	*V. berlandieri* x *V. berlandieri*	*V. berlandieri* x *V. berlandieri*
6	*V. berlandieri* x *V. berlandieri*	*u.p.*
7-13	*V. cinerea* x *V. cinerea*	*V. cinerea* x *V. cinerea*
14-15	(*V. can* x *V. rup*) x *V. riparia*	*V. berlandieri* x *V. rupestris*
16-18	(*V. can* x *V. rup*) x *V. riparia*	*V. berlandieri* x *V. riparia*
19-21	(*V. can* x *V. rup*) x *V. riparia*	*V. berlandieri* x *V. berlandieri*
22-23	(*V. can* x *V. rup*) x (*V. can* x *V. rup*)	*V. vinifera* x *V. vinifera*
24-28	*u.p.v.r*	*u.p.*
29-31	*V. vinifera* x *V. rotundifolia*	*u.p.*
32	*u.p.v.r*	*V. rotundifolia*
33-55	*V. longii* x *V. longii*	*V. vinifera* x *V. vinifera*

Table 2: Genetic correlation coefficients (r_g) for fruit yield between years obtained from the REML model indicate a gradual decline in the correlation between genotype performance over the six years of observations.

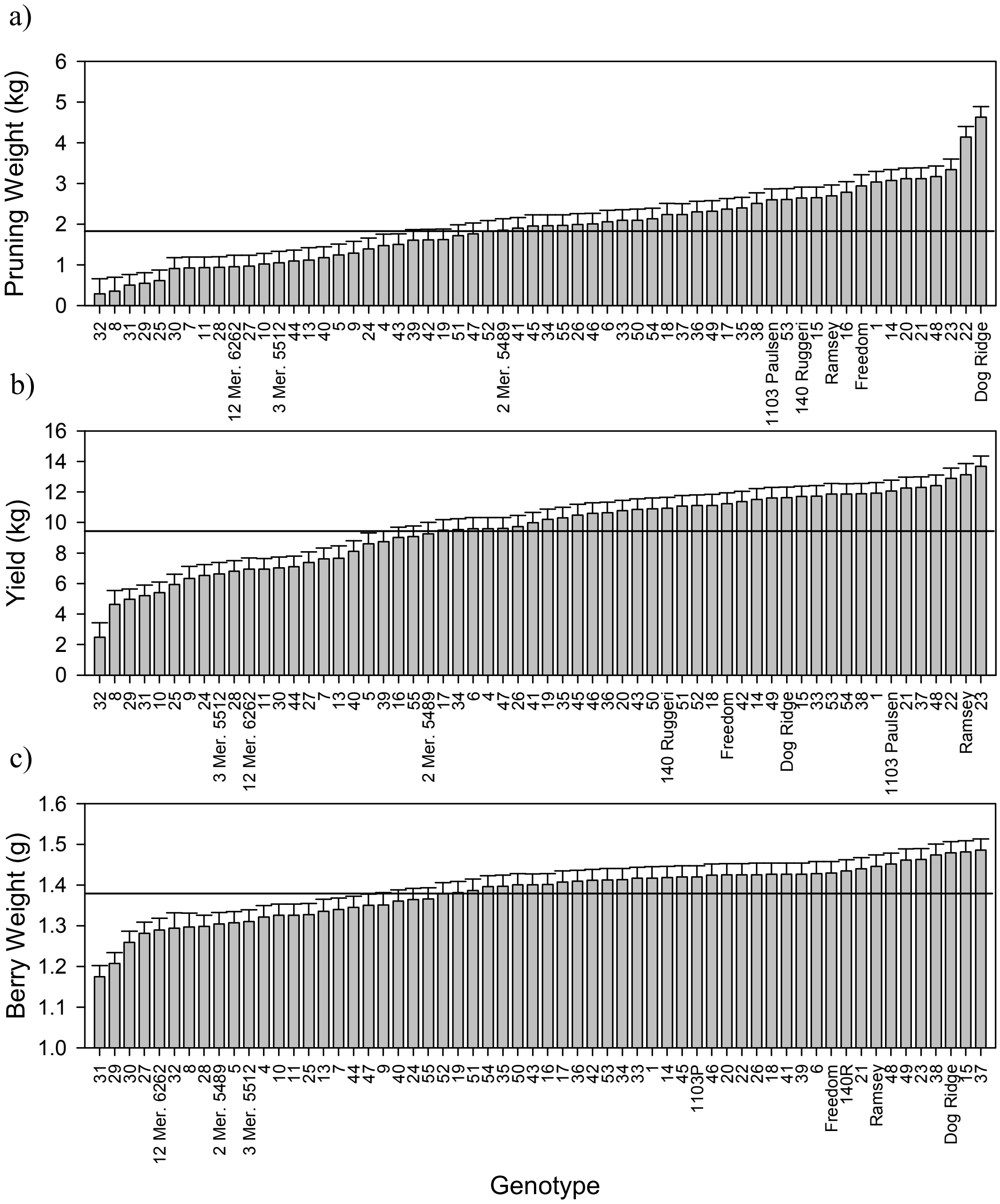
Year	1994	1995	1996	1997	1998
1993	0.83	0.80	0.76	0.74	0.69
1994	.	0.87	0.90	0.83	0.80
1995	.	.	0.86	0.87	0.86
1996	.	.	.	0.91	0.92
1997	.	.	.	.	0.93

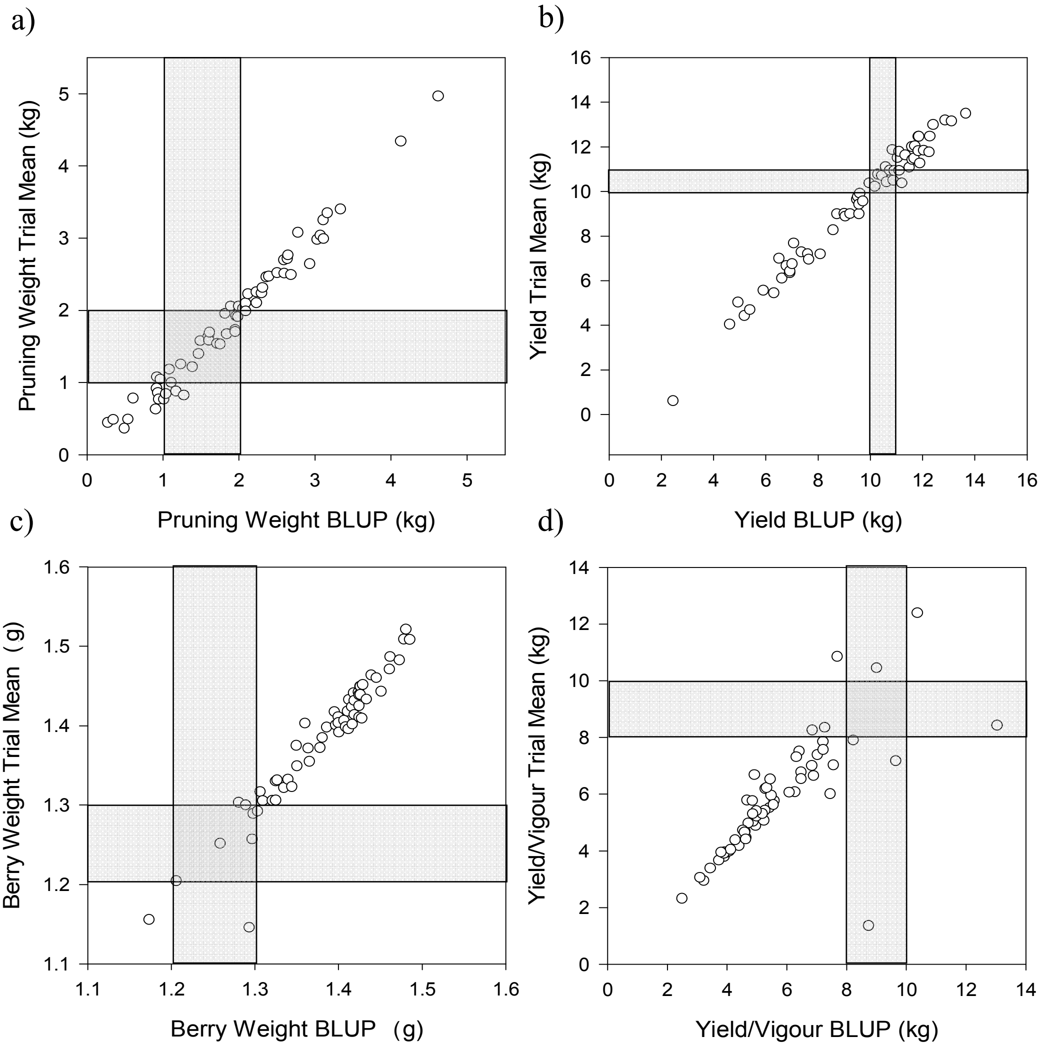
Table 3: Generalised broad-sense heritability estimates for pruning weight, yield and berry weight, calculated for each year of the study. Mean values for all years are presented.

Year	Pruning Weight	Yield	Berry Weight
1993	0.90	0.81	0.63
1994	0.90	0.88	0.75
1995	0.90	0.86	0.78
1996	0.89	0.91	0.73
1997	0.90	0.88	0.50
1998	0.87	0.89	0.76
Mean	0.89	0.87	0.69

Table 4: The six genotypes (10% of those examined) that best fit a selection range designed to identify rootstock genotypes that confer intermediate vigour while maintaining suitable yield levels, berry size, and Ravaz Index (yield/pruning weight) are shown. Mean BLUP values over the six years of observations are provided for each trait.

Genotype	PrunWt (kg)	Yield (kg)	BeWt (kg)	Ravaz Index
4	1.48	9.59	1.32	6.50
5	1.24	8.60	1.31	6.92
19	1.62	10.20	1.38	6.29
40	1.18	8.11	1.36	6.87
47	1.76	9.62	1.35	5.46
2 Mer. 5489	1.85	9.25	1.30	5.01


a)
Pruning Weight (kg)
6
5
4
3
2
1
0
32
8
31
29
25
30
7
11
28
12 Mer. 6262
27
10
3 Mer. 5512
44
13
40
5
9
24
4
43
39
42
19
51
47
52
2 Mer. 5489
41
45
34
55
26
46
6
33
50
54
18
37
36
49
17
35
38
1103 Paulsen
53
140 Ruggeri
15
Ramsey
16
Freedom
1
14
20
21
48
23
22
Dog Ridge
b)
Yield (kg)
16
14
12
10
8
6
4
2
0
32
8
29
31
10
25
9
24
3 Mer. 5512
28
12 Mer. 6262
11
30
44
27
7
13
40
5
39
16
55
2 Mer. 5489
17
34
6
4
47
26
41
19
35
45
46
36
20
43
50
140 Ruggeri
51
52
18
Freedom
42
14
49
Dog Ridge
15
33
53
54
38
1
1103 Paulsen
21
37
48
22
Ramsey
23
c)
Berry Weight (g)
1.6
1.5
1.4
1.3
1.2
1.1
1.0
31
29
30
27
12 Mer. 6262
32
8
28
2 Mer. 5489
5
3 Mer. 5512
4
10
11
25
13
7
44
47
9
40
24
55
52
19
51
54
35
50
43
16
17
36
42
53
34
33
1
14
45
1103P
46
20
22
26
18
41
39
6
Freedom
140R
21
Ramsey
48
49
23
38
Dog Ridge
15
37
Genotype


a)
Pruning Weight Trial Mean (kg)
Pruning Weight BLUP (kg)
0
1
2
3
4
5
b)
Yield Trial Mean (kg)
Yield BLUP (kg)
0
2
4
6
8
10
12
14
16
c)
Berry Weight Trial Mean (g)
Berry Weight BLUP (g)
1.1
1.2
1.3
1.4
1.5
1.6
d)
Yield/Vigour Trial Mean (kg)
Yield/Vigour BLUP (kg)
0
2
4
6
8
10
12
14

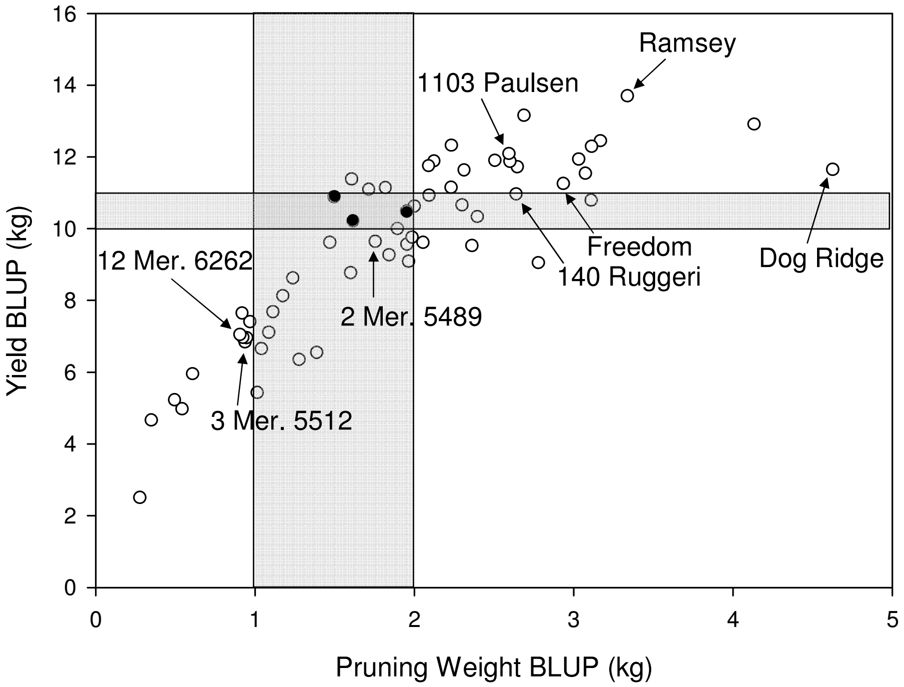

Yield BLUP (kg)
0
2
4
6
8
10
12
14
16
Pruning Weight BLUP (kg)
0
1
2
3
4
5
Ramsey
1103 Paulsen
12 Mer. 6262
3 Mer. 5512
2 Mer. 5489
Freedom
140 Ruggeri
Dog Ridge

Figure legends:

Figure 1: The Best Linear Unbiased Predictors (provided with prediction standard errors) for the pruning weight (a), fruit yield (b) and berry weight (c) of Shiraz grapevines grafted to the 60 rootstock genotypes. The trial mean of the BLUP values for all rootstock genotypes is displayed with a horizontal bar for each trait. Genotypes 2, 3 and 12 are CSIRO selections and have been additionally labelled to allow ease of comparison with traditional varieties.

Figure 2: Comparisons of genotype performance calculated with Best Linear Unbiased Predictions (BLUPs) and trial arithmetic means for pruning weight (a), yield (b) and berry weight (c) indicate clear differences in the predicted performance of genotypes based on the two approaches. The ratio of yield to vigour calculated from genotype trial means is compared to that calculated from genotype BLUPs (d) showing a magnification in the discrepancies between predictions based on the two approaches. The shaded areas allow comparison of the genotypes that would be selected under an arbitrary selection range based on BLUP values versus arithmetic means.

Figure 3: Best Linear Unbiased Predictions (BLUPs) for yield are plotted against pruning weight. The performance of the traditional rootstock varieties and the three CSIRO rootstock selections included in the study are shown. When a selection range of between 10.0 and 11.0 kg for fruit yield and 1.0 and 2.0 kg for pruning weight is applied, three genotypes (filled black) that satisfy these criteria are identified.