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Coast Redwood in New Zealand – Analysis of the Kuser Clones and the Interaction between Clones and Environment

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EXECUTIVE SUMMARY

Very little data exists on the genetic performance of redwood clones across different environments. Not knowing possible genotype by environment interactions makes it difficult to recommend clones to growers if they are not located in a similar site to where the clone(s) have been tested.

This report is the first well-replicated experiment with clonal material from a range of provenances from the United States (known as the Kuser trial) to answer some of the questions on how redwood growth and wood quality vary with site.

In this project, two nine-year-old Kuser clonal trials were analysed and ranked for growth, wood density and epicormic shoots. Each trial had 170 clones with eight single-tree replicates. Trees were measured at two North Island sites, Awaho 14 km south of Wairoa, and Thompson 17km north of Stratford.

Results indicate that:

The rankings of the different clones were consistent across these two sites. This suggests that when grown on sites that are suitable for redwood, the best clones at one site would likely remain the best clones at another. This is encouraging news.

- Medium-to-high genetic control was found for all growth and wood property traits measured, except epicormic shoots. The clonal broad sense heritabilities for each trait at the Awaho and Thompson sites were the following; 0.35 and 0.52 for DBH, 0.52 and 0.30 for wood density, and 0.4 and 0.50 for percentage heartwood. This means that breeding is likely to produce significant gains for these traits.

- Epicormic shoots were under low genetic control (0.11 and 0.27) for Awaho and Thompson, respectively. This means clone-to-clone you could make small gains for selection for this trait, but expression of epicormic shoots is mostly under the control of the environment and management (including thinning and pruning and stand conditions).

- On average, faster growing trees were genetically correlated with trees with lower density (-0.52 to -0.58) and higher incidence of epicormic shoots (0.36 to 0.44). This means that growing redwoods too fast will likely be detrimental to the wood density of the final crop.

- Selection scenarios will need to be developed to look for “correlation breakers” where both density and DBH can be improved simultaneously (where the population trend is that these traits are negatively correlated, individuals are likely to exist where this is not the case). If these “correlation breakers” do not exist, robust selection criteria with economic weights for both traits should be developed.

Important caveats:

- Only two sites were measured. More sites are needed to get a better understanding of the consistency of the results in environments where this species is grown.
- Heritability was not estimated as it was not possible to separate the additive genetic variance and the non-additive genetic variance. This was because no parents were known for the clones in the trials. Clonal repeatability represents the same concept, but for clones, and includes additional non-additive variance from within-family effects of recombination.
- Non-additive genetic variance cannot be passed from parent to offspring. Clonal repeatability is therefore an over-estimate of the genetic variance that will be passed down to offspring through breeding, but indicative of what genetic variation exists for exploitation in a clonal system.

INTRODUCTION

The Kuser collection, named after Professor John Kuser of Rutgers University, is a clonal provenance trial of Coast Redwood (*Sequoia sempervirens*, (D.Don) Endl.) that was established in the 1980s. Based on consultations with local foresters, his research team systematically sampled trees throughout its natural range in Western United States, from Curry County in southern Oregon (44.22 North) to Monterey County (35.83 North) in California (Libby, 2002 unpublished). Two random cuttings were taken from selected stands, with cuttings taken from young seedlings if possible. A total of 198 clones were collected from 99 sites [1]. Some US Counties were more heavily sampled than others. For example, there were a large number of samples taken from Del Norte, Humbolt, and Mendicino Counties. The cuttings were established as a hedge-orchard in Korbel, California, and replications were provided to the California Division of Forestry, University of California at Berkeley, France, Spain, and possibly Chile (Libby, 2002 unpublished). The Kuser trial is the largest provenance trial known for Coast Redwood.

In 2001, Jim Rydelius of the Soper Wheeler Company, imported 182 clones from the Kuser collection into New Zealand[1]. Stool beds were established from these imports at Southernwoods Nursery in Christchurch[1]. With assistance from Scion and industry, cuttings were taken from the stool beds to establish 11 replicated provenance trials throughout New Zealand between 2003 and 2006.Locations range from Mangamuka in Northland to Nightcaps in Southland. These trials have the potential to provide valuable information on which provenances perform the best in New Zealand conditions, and how much the environmental conditions influence growth and wood properties. This report analyses the results from the oldest trials that were established in 2003.

METHODS

Trials and Traits Assessed

170 of the 182 Kuser clones were planted out in 2003 at two trial sites in the North Island, one at Awaho (39° 2' 32.2"S, 177° 18' 12.3"E), 14 km south of Wairoa, and the other at Thompson (39° 15' 4.9"S, 174° 19' 5.4"E), 17 km north of Stratford. A third trial established in 2003, Conway Hills in Canterbury, was suppressed by broom and is not included in this study. Each trial used a single-tree randomised incomplete block design. Each replicate had space for 180 trees with an additional 10 trees (seedling control or filler) planted to complete the design. At each site, eight replicates of the Kuser clones were established to account for within-site environmental variation.

Both trials were assessed at age 10 for the following traits:

DBH	diameter at breast height (cm)
DEN	basic wood density (kg/m^3) at breast height
HWAP	heartwood area percentage (%) at breast height
EPI	epicormic shoots, 0 to 3 score; 0 = none, 1 = few, 2 = moderate, 3 = lots

Tree DEN and HWAP were measured on 5-mm diametric cores extracted at breast height from a subset of four of the eight replicates at each site. DEN was measured using the maximum moisture content method [2]. The length of the core containing heartwood (HWL) and the core length (CL) were measured to determine the HWAP of each tree:

$$HWAP = \left(\frac{\pi(HWL/2)^2}{\pi(CL/2)^2}\right) \times 100 \qquad [1]$$

Statistical Analysis

Controls within each trial series were dropped from datasets before analysis. Clonal material was open pollinated and had no complex pedigree structure, being first generation selections, meaning clonal effects were the only effect that could be accounted. Individual clones were treated as repeated measures. All traits were analysed using an individual-tree linear mixed effects model in ASReml-R, which is an implementation of ASReml [3]. The following model was used to estimate variance components for individual traits within each trial:

$$\boldsymbol{y} = \boldsymbol{Xd} + \boldsymbol{Z}_1\boldsymbol{r} + \boldsymbol{Z}_2\boldsymbol{r.b} + \boldsymbol{Z}_3\boldsymbol{a} + \boldsymbol{e} \qquad [2]$$

where ***y*** is the vector of observations on a trait, ***d*** is a vector of fixed effects (i.e., replicate, and mean), ***r*** is a vector of random replicate effects, ***r.b*** is a vector of random block-within-replicate effects, ***a*** is a vector of random genetic effects estimated from individual genotypes, and ***e*** is a vector of random residual effects. Where sets effects were insignificant for a particular trait they were excluded from Model 1. ***X, Z***$_1$,***Z***$_2$ and ***Z***$_3$ are known incidence matrices relating the observations in ***y*** to effects in ***d***, ***r***,***r.b,***and ***a*** respectively.

Estimated variance components from each model were used to estimate the clonal repeatability (H_c^2) for each trait:

$$\widehat{H}_c^2 = \frac{\hat{\sigma}_g^2}{\hat{\sigma}_{ag}^2 + \hat{\sigma}_e^2} \qquad [3]$$

where σ_g^2 is the genetic variance of individual clones, and σ_e^2 the residual effects. Standard errors of statistics were based on approximations using Taylor series expansion [4] within ASReml.

Genetic correlations between traits were estimated as:

$$r_{g_{xy}} = \frac{\hat{\sigma}_{g_{xy}}}{\sqrt{\hat{\sigma}^2_{g_x}\hat{\sigma}^2_{g_y}}} \quad [4]$$

where $\sigma_{a_{xy}}$ is the covariance between the traits, σ^2_g is the genetic (additive and non-additive) variation for trait *x* and $\hat{\sigma}^2_{g_y}$ is the genetic (additive and non-additive) variation for trait *y*. The estimated additive genetic correlation $r_{g_{xy}}$ between traits *x* and *y* was obtained directly using the CORR directive to structure the **G** matrix for each model. Ramets of each clone were represented as replicates of the same genotype.

Equation [1] was adjusted to include site effects, site was fitted as a fixed effect and all model terms fitted within site. Type-B genetic correlation estimates (r_B) between genotypes at different environments for each trait[5] were obtained directly using the CORR command within ASReml to structure the **G** matrix for the additive genetic component estimated by each model; all other model terms were considered independent at each site.

RESULTS

Survival at each site was generally good; 76% at Awaho and 93% at Thompson.

Clonal repeatabilities estimated were moderate to high (Table 1).

Heritability was not estimated, as it was not possible to separate the additive genetic variance and the non-additive genetic variance. This was because no parents were known for the clones in the trials. Clonal repeatability represents the same concept, but for clones, and includes additional non-additive variance from within-family effects of recombination.

Non-additive genetic variance cannot be passed from parent to offspring. Clonal repeatability is therefore an over-estimate of the genetic variance that will be passed down to offspring through breeding, but indicative of what genetic variation exists for exploitation in a clonal system.

Four things were interesting:

- EPI was heritable (Table 1), but these values are low for clonal repeatabilities. This suggests that it would be difficult to select clones that will consistently produce few epicormic shoots.
- HWAP repeatability was moderate-to-high. This suggests that this trait is under strong genetic control and large gains could be made from selection for this trait.
- DBH and DEN had moderate-to-high repeatabilities. This suggests that good gains may be made from selecting both these traits.
- Repeatabilities for DBH and DEN did change somewhat with site. The expression of genetic gain for these traits may vary across different sites. This would suggest that site has a degree of influence on these traits. However, the degree influence is unknown.

Table 1: Clonal repeatability estimates for all traits measured at individual sites

Trait and site	Repeatability	Trait and site	Repeatability
DBH Awaho	0.35±0.04	DBH Thompson	0.52±0.03
DEN Awaho	0.52±0.04	DEN Thompson	0.30±0.05
HWAP Awaho	0.40±0.06	HWAP Thompson	0.50±0.05
EPI Awaho	0.11±0.03	EPI Thompson	0.27±0.03

Across-site (Type B) genetic correlations are measures of genotype x environment interaction. The genetic correlations estimated for the two sites that were assessed were high to very high (0.70-0.98; Table 2). This indicates very low genotype x environment interaction. This is very encouraging, as it means that rankings are not changing between the sites. Thus, the best clones found at one site will likely remain the best clones at the other sites. Although only two sites were available to test the across-site genetic correlations, they represent sites that are highly suitable for redwood.

EPI had the lowest genetic correlation across sites (0.7, Table 2), but even this trait, which had lower repeatability (Table 1), had very consistent rankings across sites, so the ranking of the genotypes were the same/very similar on both sites.

Table 2: Genetic correlations (rB) between the same trait across sites.

Across-site genetic correlations (age 10)		
Trait	r_B	**s.e.**
DBH	0.89	0.04
DENS	0.98	0.07
HWAP	0.92	0.07
EPI	0.70	0.11

Genetic correlations between traits were as follows:

- DBH and density were negatively genetically correlated (Table 3). The larger the DBH, the less dense the wood. Thus, the selection for faster growing trees will have a detrimental effect on the density and vice versa.
- HWAP and DBH were highly genetically correlated (Table 3).This would suggest that trees with a larger DBH would also likely have a higher percentage of heartwood.
- DBH and EPI and HWAP and EPI were both moderately genetically correlated (Table 3). This project did not attempt to understand what this relationship means, but it suggests that trees with high growth rates also had a propensity to produce a high number of epicormic shoots.

In summary, fast growth is associated with lower wood density and a higher number of epicormic shoots. The genetic parameters estimated in this study were for only two sites that were highly suitable for redwood. More Kuser trials will need to be assessed from more sites when they reach age 9, to determine if the same genetic correlations are consistent across different site types. Three sites will reach age 9 in 2014, and the remaining three in 2015. These sites will have a wide range of productivity and different environmental limitations to growth. This will help determine if the indicative good genetic control, and low genotype x environment interaction is consistent throughout New Zealand.

Table 3:Genetic correlations between traits at the same site.

	DEN Awaho	**HWAP Awaho**	**EPI Awaho**
DBH Awaho	-0.52±0.07	0.60±0.08	0.44±0.12
DEN Awaho		-0.37±0.10	-0.18±0.14
HWAP Awaho			0.38±0.15
	DEN Thompson	**HWAP Thompson**	**EPI Thompson**
DBH Thompson	-0.58±0.08	0.73±0.05	0.36±0.08
DEN Thompson		-0.30±0.11	-0.22±0.11
HWAP Thompson			0.38±0.09

Variance components are given in Appendix One.

CONCLUSIONS

- The rankings of the different clones were consistent across sites. This suggests that when grown on sites that are suitable for redwood, the best clones at one site would likely remain the best clones at another – at least on sites favourable for redwood. This is encouraging news.

- Medium-to-high genetic control was found for all growth and wood property traits measured, except epicormic shoots. This means that breeding is likely to produce significant gains for these traits.

- Epicormic shoots were under low genetic control. This means clone-to-clone you could make small gains for selection for this trait, but expression of epicormic shoots is largely under the control of the environment (including thinning and pruning and stand conditions).

- On average, faster growing trees were correlated with trees with lower density and higher incidence of epicormic shoots. This means that growing redwoods too fast will likely be detrimental to the wood density of the final crop.

- Selection scenarios will need to be developed to look for “correlation breakers” where both density and DBH can be improved simultaneously (where the population trend is that these traits are negatively correlated, individuals are likely to exist where this is not the case). If these “correlation breakers” do not exist, robust selection criteria with economic weights for both traits should be developed.

Important caveats

- Only two sites were measured. More sites are needed to get a better understanding of the consistency of the results.

- The genetic correlations are estimated for clones. There is no family (male and female parent) structure in this analysis. This means that the additive (heritable) and non-additive (not heritable but captured in clones) genetic variation could not be separated. The inheritance of traits from parents to offspring is likely to be smaller than is indicated here, but is not fully predictable until these components are separated.

- The non-additive variation will include c-effects (factors that artificially inflate differences among clones) which are likely to include differences in physiological maturation among clones. This may have inflated heritability estimates.

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APPENDIX

Appendix1: Variance Components

Site	Trait	Variance due to additive genetic effects	Variance due to replicate effects	Variance due to blocks nested within replicates effects	Residual (error) variance
Awaho	**DBH**	13.06	0.39	1.17	24.09
Awaho	**DEN**	432.4	0.00	2.11	398.1
Awaho	**HWAP**	38.80	1.61	2.40	57.62
Awaho	**EPI**	0.07	0.00	0.01	0.59
Thompson	**DBH**	12.50	0.42	0.61	11.66
Thompson	**DEN**	250.6	29.09	7.85	587.5
Thompson	**HWAP**	52.79	1.18	2.23	52.72
Thompson	**EPI**	0.24	0.01	0.02	0.64