



# Quambalaria shoot blight resistance in marri (*Corymbia calophylla*): genetic parameters and correlations between growth rate and blight resistance

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## Abstract

Quambalaria shoot blight (QSB) has emerged recently as a severe disease of *Corymbia calophylla* (marri). In this study, QSB damage and growth were assessed in *Corymbia calophylla* trees at 4 and 6 years of age in two common gardens consisting of 165 and 170 open-pollinated families representing 18 provenances across the species' natural distribution. There were significant differences between provenances for all traits. The narrow-sense heritability for growth traits and QSB damage at both sites were low to moderate. The genetic correlation between QSB damage and growth traits was negative; fast-growing families were less damaged by QSB disease. Age-age genetic correlations for individual traits at four and six years were very strong, and the type-B (site–site) correlations were strongly positive for all traits. Provenances from cooler wetter regions showed higher resistance to QSB. The QSB incidence at 6 years was significantly correlated with environmental factors of the provenance's origin. The QSB incidence at years four and six was not correlated with the QSB expression in 3-month-old seedlings. Based on these results, selection for resistance could be undertaken using 4-year-old trees. There is potential for a resistance breeding program to develop populations of marri genetically diverse and resistant to QSB.

**Keywords** Breeding for disease resistance · Genetic variation · Heritability · Genetic correlation · *Quambalaria pitereka*

## Introduction

Globally, while natural ecosystems are in balance with their native pathogens, non-native invasive pathogens have major impacts on forest tree species, often causing widespread mortality in native forests, plantations, and urban plantings (Sniezko 2006; Kenis et al. 2017; Nahrung and Carnegie 2020). Management protocols to slow the spread

of the pathogens in native forests may be partially effective, but the development of resistant plants will be the key to restoring and reforesting areas impacted by diseases. Using quantitative genetic methods, breeding for disease resistance has been successful in some forest tree species (Carson and Carson 1989). Good examples of resistance breeding programs include resistance to *Dothistroma* needle blight on *Pinus radiata* in New Zealand (Carson 1989) and white pine blister rust resistant western white pine (*Pinus monticola*) in North America. For both species, resistant lines have been used in reforestation for decades (Sniezko et al. 2016). The *Phytophthora lateralis* resistance program also shows promise to help stabilize Port Orford cedar (*Chamaecyparis lawsoniana*) in its native range of north-western California and southwestern Oregon, USA (Sniezko et al. 2020).

*Corymbia calophylla* (*Eucalyptus* sensu lato, family Myrtaceae) is a keystone species of the biologically rich Mediterranean-type forests and woodlands of the southwest of Western Australia. Endemic to the area, it is distributed from Geraldton in the north, to Cape Riche in the south and east to Narrogin and the wheat-belt (Churchill 1968). *Corymbia calophylla* occurs together with *Eucalyptus*

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*diversicolor*, *E. gomphocephala*, *E. marginata*, and *E. patens*, and is often present in urban parks and woodlands. *Corymbia calophylla* produces large quantities of kino veins and is therefore not suitable as structural timber, but it can be used for wood chips for pulp and paper production (Farrell et al. 2010). Its heavy annual flowering makes it an important species for honey production. It is also an important food source and nesting provider for many bird species, including the region's three cockatoo species, two of which are vulnerable or endangered (Cooper et al. 2003). An analysis of *C. calophylla* chloroplast DNA revealed three lineages: a geographically central one, from which a northern, then later, a southern lineage diverged (Sampson et al. 2018). The *C. calophylla* populations from contrasting climates vary in their physiological acclimation to temperature, likely influencing how this ecologically important tree species will respond to climate change (Aspinwall et al. 2017).

Marri is currently displaying a severe decline in health with trees damaged by cankers and shoot dieback. Previous studies have implicated a complex interaction between biotic and abiotic factors (Paap et al. 2017; Sapsford et al. 2021). A study of the canker pathogen (*Quambalaria coyrecup*) showed that there is a higher prevalence of canker in the field in regions with higher rainfall (Paap et al. 2017) and in a glasshouse study on drought stress in a *C. calophylla* provenance from a high rainfall area (Hossain et al. 2018); canker development was greater in well-watered saplings than in droughted saplings (Hossain et al. 2018). Factors such as leaf litter depth and fragmentation that impact abiotic soil properties and ectomycorrhizal fungi were also shown to be drivers of canker incidence in *C. calophylla* (Sapsford et al. 2021). In addition, the presence of *Phytophthora* makes *C. calophylla* more vulnerable to canker attack (Paap et al. 2017).

Quambalaria shoot blight (QSB), caused by *Quambalaria pitereka*, is a disease that results in the repeated destruction of the growing tips and the subsequent formation of a bushy crown or death of trees in severe cases. In the eastern states of Australia, QSB was considered as the main pathogen in *Corymbia* spp. plantation, caused shoot death, affecting growth and form (Carnegie 2007), and increasing threat to eucalypt plantation (Pegg et al. 2009). However, some provenances were identified as being more tolerant and within these provenances, family level resistance was identified (Johnson et al. 2009; Brawner et al. 2011). As such, spotted gum has been identified as a viable option for plantation development. The pathogen has been introduced to Western Australia (WA), where it is found on *C. calophylla* and amenity planted *C. ficifolia* (Paap et al. 2008), and to China, where it occurs on *C. citriodora* and its hybrids (Zhou et al. 2007; Chen et al. 2017). The extent of this pathogen's current and potential effect on *C. calophylla* necessitates the identification of resistant lines for disease breeding programs

to enable reforestation and restoration on severely impacted sites.

A better understanding of the genetic control of growth and disease resistance in *C. calophylla* is required to support genetic improvement efforts. A glasshouse screening for resistance to QSB of 59 families from 11 provenances of 3-month-old *C. calophylla* seedlings showed a significant difference in QSB resistance between provenances (unpublished data). Two common garden trials of *C. calophylla*, which included 165–170 open-pollinated families from 18 provenances (which included those screened as seedlings) were established in 2014 and have been naturally infected by blight disease caused by *Q. pitereka*. These common garden trials provide an excellent opportunity to investigate the genetic control of growth and blight resistance in marri in older trees. After 2 years of growth in the field (trees were 6 months of age at planting), an assessment showed that tree growth and blight resistance traits were heritable and differed significantly among populations (Ahrens et al. 2019), but also indicated a lack of correlation between the resistance observed in the seedlings and that shown by the 2-year-old trees. This paper reassesses these trials at 4 and 6 years of age to obtain information from more mature trees. The most efficient age for selecting for growth traits is between 5 and 10 years for rotations of 25–50 years for eucalypts (Leksono et al. 2006) and pines (Gwaze 2009; Johnson et al. 1997; McKeand 1988). Understanding the genetic variation and the expression of genetic parameters and their stability over time is important for the efficient selection and development of a *C. calophylla* breeding program in Western Australia.

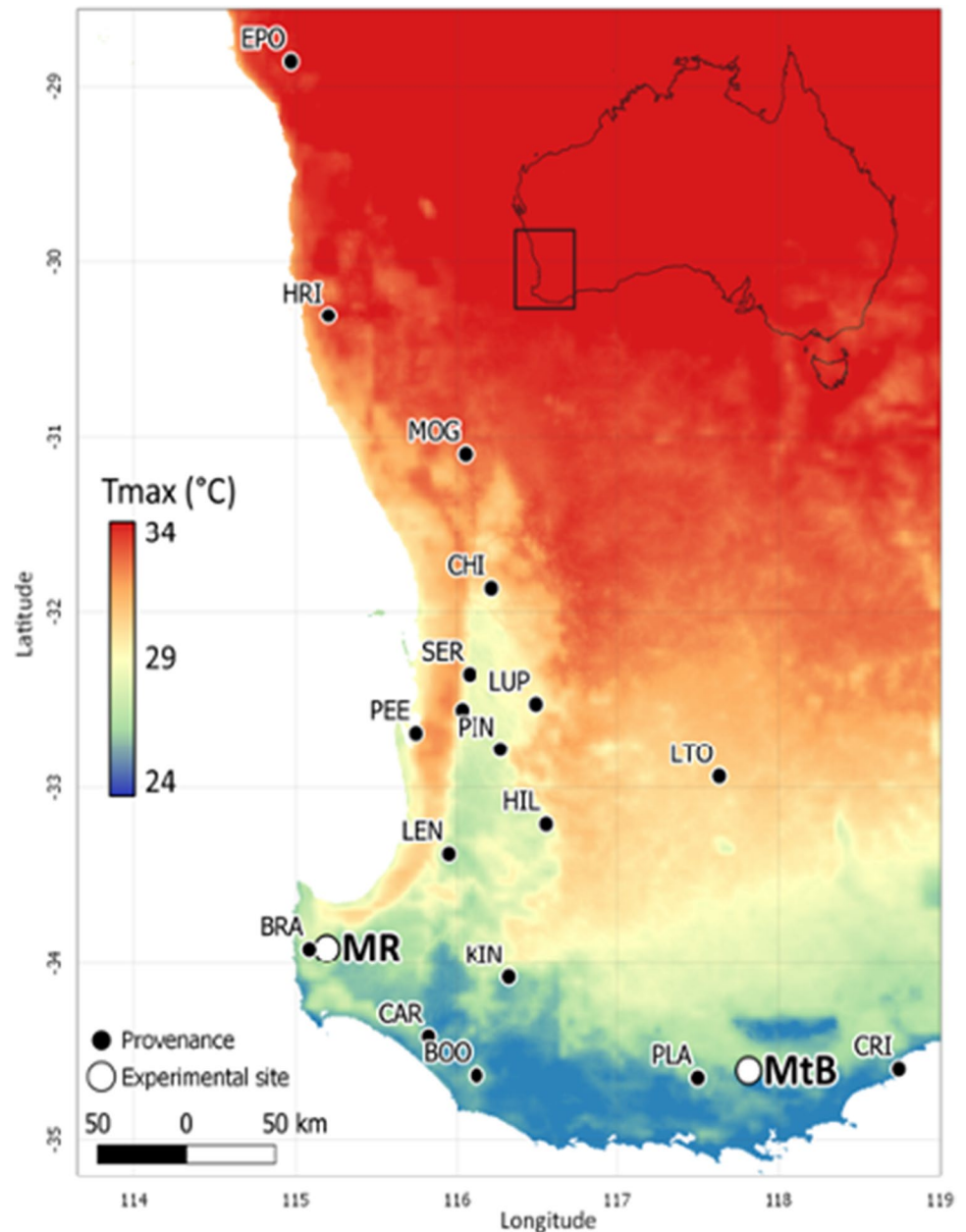
Our hypotheses were (1) growth and QSB resistance of *C. calophylla* varies on different sites and in different provenances (2) growth traits and QSB damage scores are heritable and genetic correlation exists between paired traits, and (3) resistance to QSB expressed in seedlings and trees at 2 years of age will be correlated with the levels of resistance observed in trees of four and six years of age.

## Materials and methods

### Marri provenances and trial designs

Two common garden trials were established at Mount Barker and Margaret River in Western Australia in 2014 (Fig. 1). These two sites, 300 km apart, have similar temperature regimes but Margaret River has substantially higher rainfall (Table 1). The Margaret River site was established within a cleared area previously used for pasture grazing and the Mount Barker site on land managed as a *Eucalyptus* plantation. For both trials, seeds were sourced from 18 provenances from across the

**Fig. 1** Map of southwestern Western Australia showing the location of the *Corymbia calophylla* provenances and the two experimental sites Margaret River (MR) and Mount Barker (MtB) Provenance abbreviations (see Table 2)



natural distribution of *C. calophylla* (Table 2, Fig. 1). Trial designs were generated using Cycdesign 4.1. Both trials were latinized row-column designs with latinization applied to rows and columns across replicates. There were six replicates with families randomly allocated to four-tree row plots. The spacing was 2 m within rows and 4 m between rows. The Margaret River trial was established with 3960 trees from 165 mother trees with 15 rows and 11 columns. The Mount Barker trial contained 170 families, with 4080 trees and was designed with 17 rows and 10 columns. Two buffer rows of trees surrounded trials to minimize edge effects. They were infected naturally with QSB.

### Growth and disease assessment

Trees at both sites were measured in 2018 and 2020 (4 years and 6 years after planting respectively). At 4-year-old, all trees were measured for height, stem diameter 10 cm above ground level, and blight incidence score. At 6 years old, all trees were measured for height, diameter at breast height, blight incidence, and blight severity. A Nikon Laser Rangefinder Forestry Pro was used to measure tree height. The blight score included blight incidence and blight severity and was based on a modified method of Brawner et al. (2011). Briefly, blight incidence was assessed by visually determining the percentage of

**Table 1** Description of trial sites and the numbers of *Corymbia calophylla* provenances used in the present study

Descriptions	Margaret River trial	Mount Barker trial
Planting date	Oct 2014	August 2014
Latitude	33.96°S	31.77°S
Longitude	115.08°E	116.45°E
Mean annual rainfall (mm)	1130	764
Trial area (ha)	3.6	3.8
Design	6 reps, 15 rows, 11 columns, 4 trees/plot	6 reps, 17 rows, 10 columns, 4 trees/plot
Spacing	2 m × 4 m	2 m × 4 m
Marri	3960 trees, 165 families from 18 provenances	4080 trees, 170 families from 18 provenances

shoot tips on a tree with evidence of blight on a five-point scale (0 = no evidence of blight disease on the whole canopy; 1 = 1–25%; 2 = 26–50%; 3 = 51–75%, and 4 = 76–100%) of tips of the canopy blighted. In year 6, but not in year 4, blight severity was also scored on a five-point scale (0 = no damage; 1 = low damage; 2 = moderate damage; 3 = high damage; and 4 = severe damage). These rankings were opposite to those used by Ahrens et al. (2019), who used 1 for high and 5 for low QSB damage, respectively.

**Table 2** Number of families of *Corymbia calophylla* included in this study and the climatic conditions at the provenance origin

Provenance	Code	MR F	MtB F	Latitude	Longitude	T <sub>MAX</sub>	MAP	1/AI
Ellendale Pool	EPO	2	4	−28.859°	114.969°	34.1	467	3.33
Hill River	HRI	9	10	−30.311°	115.202°	31.7	563	2.56
Mogumber	MOG	10	10	−31.099°	116.051°	33.3	579	2.56
Chidlow	CHI	10	10	−31.868°	116.223°	32.2	900	1.54
Serpentine	SER	10	10	−32.353°	116.076°	30.5	1173	1.12
Lupton	LUP	10	10	−32.521°	116.499°	31.6	635	2.22
Whittaker	WHI	10	10	−32.556°	116.031°	30.0	1187	1.10
Peel Inlet	PEE	8	8	−32.685°	115.743°	30.4	885	1.49
Pindalup	PIN	10	10	−32.781°	116.278°	30.3	935	1.43
Toolibin Lake	LTO	10	10	−32.937°	117.632°	31.2	358	3.85
Hillman	HIL	9	9	−33.208°	116.562°	30.2	678	2.00
Lennard	LEN	10	10	−33.377°	115.947°	30.7	912	1.47
Bramley	BRA	9	9	−33.916°	115.083°	26.1	1072	1.04
Kingston	KIN	10	10	−34.081°	116.330°	27.7	820	1.49
Carey	CAR	10	10	−34.420°	115.821°	25.9	1,106	1.02
Cape Riche	CRI	8	10	−34.602°	118.743°	26.2	579	2.08
Boorara	BOO	10	10	−34.639°	116.124°	25.6	1159	0.95
Plantagenet	PLA	10	10	−34.653°	117.499°	26.7	733	1.59

MR F, number of families at Margaret River; MtB F, number of families at Mount Barker; T<sub>MAX</sub>, maximum temperature of the warmest month (°C); MAP, mean annual precipitation (mm); 1/AI, 1/aridity index

## Statistical analysis

Before analysis, all trees identified by Ahrens et al. (2019) as runts plus a small number of trees for which there were no diameter data were removed from the analysis. Additional trees possibly fitted into the “runt” description based on size, but they were left in the data set. All descriptive statistics (mean, standard errors, coefficient of variation) and correlation were performed in R (R Core Team 2021), and all figures were created in GGPlot2 (Wickham 2016). The data were checked for normality and homogeneity of variance, and due to violation of assumptions, the Wilcoxon rank-sum test was used instead of Welch’s *t*-test to determine whether site means for each trait differed significantly. The Kruskal–Wallis rank-sum test was used to compare trait means between provenances and between families within each provenance, followed by the post hoc Dunn test to calculate pairwise multiple comparisons between groups.

Pearson’s correlation was used to examine the relationship between traits (QSB incidence and tree height) and environmental factors (annual precipitation, maximum temperature, and the aridity index). Similarly, Pearson’s correlation was used to investigate the resistance of QSB expressed in plants of different ages, including 3-month-old seedlings screened in the glasshouse trial (unpublished data), trees in the same field trials at 2 years of age (Ahrens et al. 2019), and the trees of 4 and 6 years of age.



Genetic data analysis was performed using ASReml version 4.1 (Gilmour et al. 2015). Individual site variance parameters and across site correlations were estimated using the linear mixed model:

$$\mathbf{Y} = \mathbf{X}\mathbf{b} + \mathbf{Z}\mathbf{u} + \mathbf{e}$$

where  $\mathbf{Y}$  is the column vector of individual phenotypic values of the response variable,  $\mathbf{X}$  is the design matrix associating observations with fixed effects,  $\mathbf{b}$  is the vector of fixed effects,  $\mathbf{Z}$  is the design matrix associating observations with random effects,  $\mathbf{u}$  is a vector of random effects, and  $\mathbf{e}$  is the vector of residual errors assumed to be identically and independently normally distributed with  $E(\mathbf{e})=0$ . Within the framework of the linear mixed model, three sets of analyses were conducted as described below.

### Univariate family analyses

Elements in  $\mathbf{b}$  comprised the intercept, site, and provenance effects, while elements in  $\mathbf{u}$  comprised row replicate, column replicate, long row, long column, rows within replicates, columns within replicate, plot and family effects, and the residual error. Trial design effects were treated as a random effect to maximize the potential for information recovery. Residual plots were examined for homoscedasticity, and potential transformations were identified using the methodology outlined by Gilmour et al. (2015). Tree height at age 4 years was transformed using the formula  $x^{0.7}$ , and tree height at age 6 years was transformed using the formula  $x^{0.3}$ . Diameter at age 4 years was transformed using the formula  $x^{0.7}$ , and diameter at age 6 years was transformed using the formula  $x^{0.6}$ . Transformation for the QBS blight incidence and severity made little difference, so it was left untransformed. In this and all subsequent models, fixed effects were tested for significance using Wald  $F$  statistics (Gilmour et al. 2015). Variance components in univariate models were tested for significance using the one-tailed log-likelihood ratio test with 0.5 degrees of freedom (Gilmour et al. 2015; Self and Liang 1987). Those terms which were not significant were removed from the subsequent analyses to enable some bivariate models to converge.

### Univariate cross-site analyses

Terms in  $\mathbf{b}$  comprised the intercept, site effects, population effects, and site  $\times$  population effects, while terms in  $\mathbf{u}$  were the same as for the univariate individual tree model, nested within sites. All design effects were assumed independent between sites. Fixed effects were tested for significance using Wald  $F$  statistics (Gilmour et al. 2015).

The cross-site model was used to generate the best linear unbiased estimated means for sites, populations, narrow-sense heritability, and cross-site genetic correlation. To determine if a genetic correlation was significantly different from unity, the correlation was constrained to one and tested using a one-tailed log-likelihood ratio test with 0.5 degrees of freedom (Self and Liang 1987; Gilmour et al. 2015). To test if a genetic correlation was significantly different from zero, the correlation was constrained to zero, and a two-tailed log-likelihood ratio test with 1 degree of freedom was used.

### Within-site multivariate analyses

Model terms in  $\mathbf{u}$  and  $\mathbf{b}$  were described for univariate analysis, nested within the trait. Variances and covariances for terms in  $\mathbf{b}$  were used to calculate genetic parameters for height, diameter, QSB blight incidence, and QSB blight severity. Bivariate analyses between traits were used to estimate phenotypic and genetic correlations between traits.

Mixed mating systems in open-pollinated eucalypts may produce inflated heritability estimates for growth traits (Costa et al. 2010; Griffin and Cotterill 1988); therefore, a coefficient of the relationship of  $p = 1/2.5$  was applied when estimating the additive variance component to compensate for selfing rates of about 30%. This coefficient was appropriate for first-generation eucalypt progeny, suitable correcting variance components, and heritability estimates (Bush et al. 2011). Narrow-sense heritability was estimated according to the formula:

$$\hat{h}^2 = \sigma_a^2 / (\sigma_a^2 + \sigma_p^2 + \sigma_e^2)$$

where  $\hat{h}^2$  is the narrow-sense heritability,  $\sigma_a^2$  is the additive component of variance,  $\sigma_p^2$  is the plot component of variance, and  $\sigma_e^2$  is the error component of variance. The standard errors for heritability estimates were calculated using Dickerson's approximation.

Genetic and phenotypic correlations were calculated according to the formula:

$$r = \sigma_{12}^2 / \sqrt{\sigma^2_1 * \sigma^2_2}$$

where  $r$  represents either the genetic correlation ( $r_g$ ) or the phenotypic correlation coefficient ( $r_p$ ) between traits or between ages of the same trait. For the genetic correlation,  $\sigma^2_{12}$ ,  $\sigma^2_1$ , and  $\sigma^2_2$  represent the additive genetic covariance and additive genetic variances, respectively. For phenotypic correlation estimation,  $\sigma^2_{12}$ ,  $\sigma^2_1$ , and  $\sigma^2_2$  are the phenotypic covariance and phenotypic variances for the relevant traits.

The type-B genetic correlations were calculated at the family level, which measures the genetic correlation between the same trait expressed on two sites (Burdon 1977).

## Results

### Growth traits and QSB resistance of *Corymbia calophylla* provenances

The mean heights and diameters of trees in Mount Barker were higher than those in Margaret River, and trees were less damaged by QSB in Mount Barker than in Margaret River (Table 3). The Wilcoxon rank-sum test showed significant differences in all growth traits and QSB damage at the two sites, except for QSB incidence at age six and tree height at age of four. However, the increments in height and diameter between 4 and 6 years of age at Margaret River were greater than at Mount Barker. Between 4 and 6 years of age, tree height at Margaret River increased by 128.5 cm and only 35.6 cm at Mount Barker. The increase in mean diameter at the two sites (from age four to six) could not be compared as two different methods were used to measure the diameter (see Methods section). At Margaret River, there were significant differences ( $P < 0.001$ ) in growth traits and QSB disease resistance among provenances (Table 4). The four provenances Boorara, Bramley, Carey, and Plantagenet were in the fastest growing group and showed a high level of QSB resistance. In contrast, the outlier provenance at Toolibin Lake was the most susceptible provenance and among the slowest growing provenances (along with Chidlow and Hill River). At Mount Barker, there were also significant differences ( $P < 0.001$ ) in height, diameter, QSB incidence, and QSB severity between provenances (Table 5). Of all the provenances tested, Boorara was the fastest growing and the most resistant, followed by the provenances Bramley, Carey,

and Plantagenet. Chidlow and Toolibin Lake were the most susceptible provenances and were also in the group of slow-growing provenances.

Provenances at the extreme ends of the range of resistance and susceptibility frequently showed more uniformity among families for disease expression at year six than did the intermediate provenances (Supplementary Table 1).

### Genetic parameters

#### Heritability estimates

The narrow-sense heritability ( $h^2$ ) for all growth traits and QSB damage at individual sites were low to moderate (Table 3), ranging from  $0.14 \pm 0.03$  to  $0.26 \pm 0.04$  at Margaret River and from  $0.11 \pm 0.03$  to  $0.19 \pm 0.04$  at Mount Barker. The heritability for each trait varied considerably across sites, with values were higher at Margaret River than at Mount Barker.

#### Phenotypic and genetic correlation

The negative phenotypic correlation between all QSB scores (BI4, BI6, and BS6) and growth traits (height and diameter) indicated that the fast-growing provenances were less damaged by QSB disease (Table 6). The ranking for height and QSB severity at 6 years old Margaret River and Mount Barker clearly showed this trend (Supplementary Table 2). At both sites, these correlations were low at the age of 4 years (from 0.00 to 0.14), and increased at the age of 6 years; however, the correlations remained weak ( $-0.25$  to 0.42).

**Table 3** Mean values with standard errors, coefficient of variation, and narrow-sense heritability ( $h^2$ ) of growth traits and Quambalaria shoot blight incidence and severity of *Corymbia calophylla* for the two provenance trials. Data for  $h^2$  for year two are from Ahrens et al. (2019)

Traits	Margaret River			Mount Barker			Wilcoxon rank-sum test
	Mean ( $\pm$ SE)	CV (%)	$h^2$	Mean ( $\pm$ SE)	CV (%)	$h^2$	
HT2	155.1		$0.14 \pm 0.03$	280.3		$0.18 \pm 0.04$	
HT4 (cm)	$265.0 \pm 1.36$	30.9	$0.16 \pm 0.03$	$370.0 \pm 2.07$	33.4	$0.16 \pm 0.03$	<0.001
HT6 (cm)	$393.5 \pm 2.56$	38.7	$0.24 \pm 0.04$	$405.6 \pm 2.54$	37.3	$0.19 \pm 0.04$	0.16
DB2			$0.12 \pm 0.03$			$0.11 \pm 0.03$	
DB4 (cm)	$7.8 \pm 0.04$	30.6	$0.14 \pm 0.03$	$12.3 \pm 0.06$	28.7	$0.11 \pm 0.03$	<0.001
DBH6 (cm)	$8.7 \pm 0.07$	46.0	$0.18 \pm 0.03$	$11.5 \pm 0.07$	37.9	$0.13 \pm 0.03$	<0.001
BI2			$0.08 \pm 0.03$			$0.19 \pm 0.04$	
BI4	$1.90 \pm 0.02$	56.8	$0.19 \pm 0.04$	$1.59 \pm 0.01$	54.1	$0.13 \pm 0.03$	<0.001
BI6	$2.11 \pm 0.03$	73.9	$0.26 \pm 0.04$	$2.09 \pm 0.03$	71.3	$0.19 \pm 0.04$	0.81
BS6	$2.09 \pm 0.03$	71.8	$0.26 \pm 0.04$	$1.95 \pm 0.02$	74.9	$0.11 \pm 0.03$	<0.05

HT2, HT4, HT6, height at the age of 2, 4, and 6; DB2, DB4, diameter at the height of 10 cm above the ground level at the age of 2 and 4; DBH6, diameter at breast height at the age of 6; BI2, BI4, BI6, blight incidence at the age of 2, 4, and 6 years; BS6, blight severity at the age of 6 years; SE, standard error; CV, coefficient of variation. Wilcoxon rank-sum test for the mean value of growth and QSB traits

**Table 4** Mean growth and Quambalaria shoot blight incidence and severity scores (untransformed data) with standard errors for *Corymbia calophylla* provenances at the ages 4 and 6 at Margaret River trial

Provenances	HT4	DB4	HT6	DBH6	BI4	BI6	BS6
Boorara	330±5.71	8.7±0.18	519±11.10 <sup>a</sup>	11.4±0.31	1.1±0.05	0.8±0.07	1.1±0.09 <sup>a</sup>
Bramley	322±5.67	8.7±1.75	500±9.64 <sup>a</sup>	11.4±0.25	1.2±0.04	0.7±0.07	1.3±0.12 <sup>a</sup>
Cape Riche	255±5.10	7.7±0.17	387±10.00 <sup>bc</sup>	9.2±0.27	1.6±0.07	1.7±0.12	1.7±0.11 <sup>b</sup>
Carey	322±5.51	8.7±0.15	504±9.56 <sup>a</sup>	11.2±0.24	1.4±0.05	0.9±0.07	1.4±0.11 <sup>a</sup>
Chidlow	232±3.95	7.3±0.14	298±6.99 <sup>d</sup>	6.4±0.22	2.6±0.07	3.2±0.08	2.8±0.08 <sup>de</sup>
Ellendale pool	249±9.39	7.1±0.25	340±14.30 <sup>c</sup>	7.1±0.37	2.0±0.15	2.5±0.21	2.1±0.20 <sup>bc</sup>
Hillman	250±5.57	7.5±0.17	356±9.28 <sup>c</sup>	7.7±0.27	2.2±0.07	2.6±0.10	2.4±0.10 <sup>cd</sup>
Hill River	199±5.74	6.3±0.21	293±10.20 <sup>d</sup>	6.4±0.31	1.6±0.07	2.2±0.11	2±0.11 <sup>bc</sup>
Kingston	296±5.43	8.1±0.16	477±9.87 <sup>ab</sup>	1.1±0.26	1.7±0.06	1.7±0.10	1.8±0.10 <sup>b</sup>
Lennard	278±4.58	7.7±0.14	440±8.76 <sup>b</sup>	9.5±0.23	1.7±0.07	1.7±0.10	1.9±0.10 <sup>bc</sup>
Lupton	241±4.92	7.4±0.15	339±8.28 <sup>c</sup>	7.4±0.24	2.2±0.07	2.9±0.09	2.5±0.09 <sup>d</sup>
Mogumber	252±4.08	7.4±0.13	345±7.72 <sup>c</sup>	7.4±0.21	2.4±0.07	2.9±0.09	2.5±0.09 <sup>d</sup>
Peel Inlet	236±5.32	7.7±0.19	333±9.19 <sup>c</sup>	8.2±0.30	2.7±0.08	2.6±0.11	2.5±0.10 <sup>d</sup>
Pindalup	249±4.36	7.8±0.15	347±7.55 <sup>c</sup>	8.1±0.24	2.4±0.07	2.7±0.10	2.6±0.09 <sup>de</sup>
Plantagenet	311±6.01	8.5±0.18	519±11.10 <sup>a</sup>	11.1±0.28	1.3±0.05	1±0.07	1.7±0.11 <sup>b</sup>
Serpentine	248±5.36	7.9±0.16	366±9.82 <sup>bc</sup>	8.7±0.26	2.0±0.08	2.3±0.11	2.1±0.11 <sup>bc</sup>
Toolibin lake	227±4.15	7.3±0.15	292±6.17 <sup>d</sup>	6.2±0.19	2.6±0.07	3.3±0.07	2.9±0.08 <sup>e</sup>
Whittaker	256±4.63	7.7±0.14	391±9.50 <sup>bc</sup>	8.6±0.25	2.0±0.07	2.3±0.11	2.2±0.10 <sup>c</sup>

HT4, HT6: height at the age of 4 and 6; DB4, diameter at the height of 10 cm above the ground level at the age of 4; DBH6: diameter at breast height at the age of 6; BI4, BI6, blight incidence at the age of 4 and 6 years; BS6, blight severity at the age of 6 years. Means with the same letter are not significantly ( $p > 0.05$ ) different in Duncan’s multiple range test

**Table 5** Mean growth and Quambalaria shoot blight incidence and severity scores (untransformed data) with standard errors for *Corymbia calophylla* provenances at the ages 4 and 6 at Mount Barker

Provenances	HT4	DB4	HT6	DBH6	BI4	BI6	BS6
Boorara	449±11.20	13.2±0.31	521±14.30 <sup>a</sup>	13.4±0.34	1.1±0.04	1.5±0.10	1.3±0.10 <sup>a</sup>
Bramley	416±10.30	13.3±0.26	460±12.40 <sup>b</sup>	12.9±0.35	1.1±0.05	1.4±0.10	1.4±0.10 <sup>ab</sup>
Cape Riche	349±9.18	12.6±0.28	393±10.80 <sup>cd</sup>	11.6±0.36	1.6±0.06	2.1±0.10	1.9±0.10 <sup>bc</sup>
Carey	426±8.55	12.8±0.25	464±11.40 <sup>b</sup>	12.6±0.31	1.2±0.04	1.8±0.10	1.6±0.10 <sup>ab</sup>
Chidlow	327±6.50	11.4±0.21	352±8.05 <sup>d</sup>	10.0±0.27	2.0±0.06	2.8±0.09	2.7±0.09 <sup>d</sup>
Ellendale pool	325±13.80	9.6±0.42	346±17.80 <sup>d</sup>	8.9±0.52	1.9±0.12	2.3±0.17	1.8±0.15 <sup>bc</sup>
Hillman	354±8.68	12.1±0.26	385±10.4 <sup>cd</sup>	12.2±0.31	1.7±0.06	2.2±0.11	1.9±0.10 <sup>bc</sup>
Hill River	321±6.70	11.4±0.24	354±8.61 <sup>d</sup>	9.9±0.30	1.7±0.06	2.2±0.10	2.0±0.10 <sup>bc</sup>
Kingston	390±7.95	12.7±0.26	433±10.40 <sup>bc</sup>	12±0.30	1.5±0.06	1.9±0.10	1.7±0.10 <sup>b</sup>
Lennard	398±8.43	12.7±0.25	435±10.50 <sup>bc</sup>	12.3±0.31	1.4±0.05	1.6±0.10	1.6±0.10 <sup>ab</sup>
Lupton	371±8.14	12.3±0.24	396±1.00 <sup>cd</sup>	11.4±0.29	1.6±0.06	2.3±0.10	2.3±0.10 <sup>cd</sup>
Mogumber	376±7.34	12.1±0.20	405±8.38 <sup>c</sup>	11.1±0.23	1.9±0.06	2.6±0.10	2.1±0.10 <sup>c</sup>
Peel Inlet	334±8.07	12.2±0.25	352±9.39 <sup>d</sup>	10.6±0.33	1.8±0.07	2.4±0.10	2.3±0.11 <sup>cd</sup>
Pindalup	349±7.11	12.3±0.23	372±8.27 <sup>d</sup>	11.3±0.29	1.7±0.06	2.5±0.10	2.2±0.10 <sup>cd</sup>
Plantagenet	423±9.40	12.9±0.25	476±11.89 <sup>ab</sup>	12.6±0.31	1.3±0.05	1.3±0.10	1.5±0.10 <sup>ab</sup>
Serpentine	349±7.05	12.1±0.21	396±9.29 <sup>cd</sup>	11.7±0.28	1.5±0.06	1.8±0.10	1.9±0.10 <sup>bc</sup>
Toolibin lake	336±5.59	12.1±0.20	357±7.28 <sup>d</sup>	10.6±0.24	1.9±0.06	2.8±0.10	2.4±0.10 <sup>d</sup>
Whittaker	347±7.32	11.8±0.22	377±8.54 <sup>d</sup>	10.8±0.26	1.7±0.06	2.3±0.10	2.2±0.10 <sup>cd</sup>

HT4, HT6: height at the age of 4 and 6; DB4, diameter at the height of 10 cm above the ground level at the age of 4; DBH6, diameter at breast height at the age of 6; BI4, BI6, blight incidence at the age of 4 and 6 years; BS6, blight severity at the age of 6 years. Means with the same letter are not significantly ( $p > 0.05$ ) different in Duncan’s multiple range test

**Table 6** Phenotypic ( $r_p$ ) and genetic ( $r_g$ ) correlation with the standard error between various growth traits, and Quambalaria shoot blight incidence and severity in *Corymbia calophylla* field trials at Mount Barker and Margaret River

Trait–trait	Margaret River		Mount Barker	
	$r_p$	$r_g$	$r_p$	$r_g$
BI4-HT4	$-0.1 \pm 0.02$	$-0.54 \pm 0.13$	$-0.14 \pm 0.02$	$-0.45 \pm 0.16$
BI4-DB4	$0.00 \pm 0.02$	$-0.26 \pm 0.16$	$-0.09 \pm 0.02$	$-0.24 \pm 0.19$
BI6-HT6	$-0.42 \pm 0.02$	$-0.82 \pm 0.06$	$-0.29 \pm 0.02$	$-0.61 \pm 0.11$
BI6-DBH6	$-0.39 \pm 0.02$	$-0.71 \pm 0.08$	$-0.25 \pm 0.02$	$-0.44 \pm 0.13$
BS6-HT6	$-0.25 \pm 0.02$	$-0.68 \pm 0.13$	$-0.26 \pm 0.02$	$-0.6 \pm 0.14$
BS6-DBH6	$-0.25 \pm 0.02$	$-0.57 \pm 0.14$	$-0.25 \pm 0.02$	$-0.48 \pm 0.15$
BI6-BS6	$0.57 \pm 0.01$	$0.99 \pm 0.07$	$0.55 \pm 0.01$	$0.92 \pm 0.07$
HT4-DB4	$0.67 \pm 0.01$	$0.64 \pm 0.09$	$0.62 \pm 0.01$	$0.69 \pm 0.09$
HT4-HT6	$0.77 \pm 0.01$	$0.93 \pm 0.03$	$0.78 \pm 0.01$	$0.97 \pm 0.03$
DB4-DBH6	$0.68 \pm 0.01$	$0.82 \pm 0.06$	$0.75 \pm 0.01$	$0.92 \pm 0.04$
BI4-BI6	$0.41 \pm 0.02$	$0.97 \pm 0.07$	$0.13 \pm 0.03$	$0.74 \pm 0.13$

HT4, HT6: height at the age of 4 and 6; DB4, diameter at the height of 10 cm above the ground level at the age of 4; DBH6, diameter at breast height at the age of 6; BI4, BI6, blight incidence at the age of 4 and 6; BS6, blight severity at the age of 6

The genetic correlation between tree height and QSB incidence or QSB severity was higher than the diameter. At Margaret River, the genetic correlations between growth traits and QSB damage were moderate to high ( $-0.54$  to  $-0.82$ ), except for the correlation between QSB blight incidence and diameter at 4 years ( $-0.26$ ). At Mount Barker, these correlations were from low to moderate ( $-0.24$  to  $-0.61$ ). The genetic correlations between tree height and diameter were strong and positive at both sites and, except for the correlation between tree height and diameter at year 4 at Mount Barker, were significantly different from unity ( $P < 0.001$ ).

### Age-age genetic correlation

Age-age genetic correlations (or genetic correlation between the same traits at different ages) were generally strong and positive, varying from 0.82 to 0.97 at Margaret River and 0.74 to 0.99 at Mount Barker (Table 6). At Mount Barker, the genetic correlation of height, diameter, and QSB incidence at different ages was significantly different from unity ( $P < 0.05$ ). However, at Margaret River, only the genetic correlation of tree diameter between the two ages was significant ( $P < 0.001$ ).

### Genotype by environment interactions

The type-B genetic correlation measures the importance of environment interactions on genotype, and it provides the estimates of G x E interactions. Estimated type-B correlations were generally strongly positive for all traits and ranged from 0.71 to 0.87 (Table 7). All correlations were significantly different from unity ( $P < 0.05$ ) except for tree height at year four, diameter at year six, and QSB blight severity at year six.

**Table 7** Estimates of type-B genetic correlations with the standard error between sites for the height, diameter, stem volume, and Quambalaria shoot blight disease incidence and severity of *Corymbia calophylla*

Traits	Type-B genetic correlation
HT4 (cm)	$0.87 \pm 0.12$
HT6 (cm)	$0.86 \pm 0.08$
DB4 (cm)	$0.75 \pm 0.15$
DBH6 (cm)	$0.87 \pm 0.1$
BI4	$0.71 \pm 0.15$
BI6	$0.72 \pm 0.11$
BS6	$0.80 \pm 0.2$

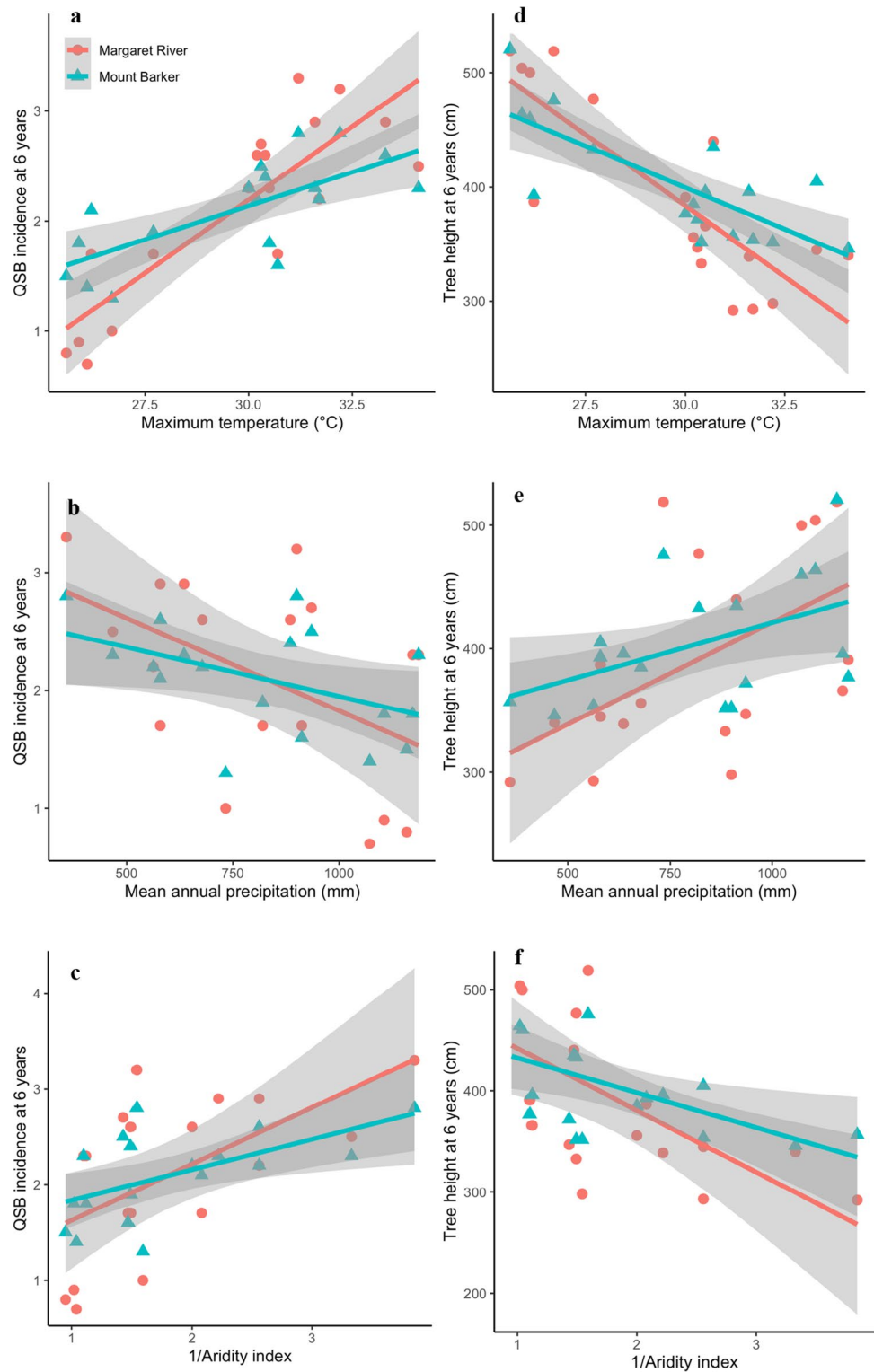
HT4, HT6: height at the age of 4 and 6; DB4, diameter at the height of 10 cm above the ground level at the age of 4; DBH6, diameter at breast height at the age of 6; BI4, BI6: QSB incidence at the age of 4 and 6

### Correlation between traits and environmental factors

Pearson's correlation between provenance QSB incidence at 6 years and the environmental factors at the provenance origin (maximum temperature, annual precipitation, and aridity index) were all significant ( $P < 0.05$ ) (Supplementary Table 3). The strongest positive correlations were between QSB incidence and maximum temperature or aridity index, while there was a weaker, negative correlation with annual precipitation. Similarly, there were significant correlations between tree height at 6 years old and these environmental factors, with the strongest correlation between maximum temperature and tree height. The correlation was similar at both the Margaret River and Mount Barker trials (Fig. 2).



**Fig. 2** Correlation between QSB resistance or height of *Corymbia calophylla* provenances at six years of age and climatic factors of the origin of each provenance: mean annual precipitation, maximum temperature of the warmest month, and 1/aridity index (see also Supplementary Table 3)



**Comparison of the relative level of QSB resistance in plants of different ages**

Eleven of the 18 provenances in the field trials were screened for QSB resistance as seedlings in a glasshouse

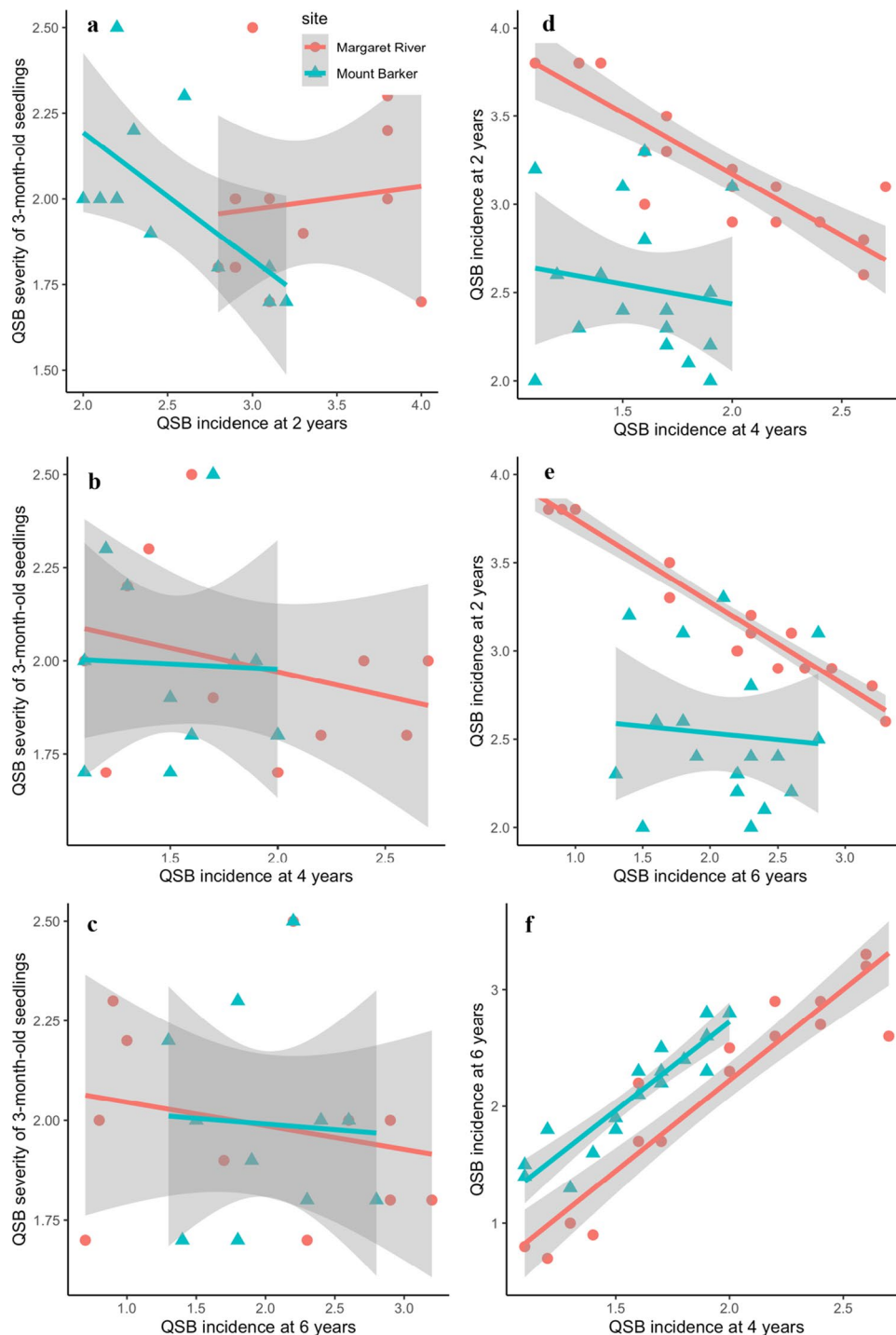
trial (unpublished data). Overall, there was no correlation between the provenance resistance of seedlings and resistance of 4 or 6-year-old trees at both sites or 2-year-old trees at Margaret River. However, there was a significant correlation between the resistance of seedlings and

2-year-old trees at Mount Barker ( $r = -0.64$ ,  $p < 0.05$ ) (Fig. 3) (Note: this correlation is negative due to the scoring methods used: at year two, the range was from 1 to 5 with 5 being disease free (Ahrens et al. 2019), while in the scoring for the older trees rank 5 was the most affected). Of the provenances showing the highest resistance as seedlings, only Bramley also showed high resistance at both field sites. In contrast, Chidlow and Serpentine, which

were highly resistant as seedlings, were the least resistant of the field-grown trees.

When the data for resistance of provenances at 2, 4, and 6 years were compared, there was no correlation between the 2-year-old trees and the older ones at Mt Barker, but a significant correlation at Margaret River between 2-year-old tree and 4-year-old tree ( $r = 0.87$ ;  $P < 0.001$ ) and 6-year-old tree ( $r = 0.97$ ,  $P < 0.001$ ) (Fig. 3d, e). A further difference

**Fig. 3** Relative level of QSB resistance of 3-month-old seedlings of *Corymbia calophylla* provenances in a glasshouse and the same provenances in field trials at Margaret River and Mount Barker after 2, 4, and 6 years of growth (data for 2-year-old trees from Ahrens et al. (2019)) (see also Supplementary Table 4)



between the seedlings and the 4- or 6-year-old trees in the field was that some families in the Chidlow, Kingston, and Serpentine provenances at the seedling stage exhibited 100% of plants resistant to QSB. No family of any provenance in the field showed all plants to be resistant and the results for the seedlings are no doubt due to the low number of seedlings tested per family compared to the number of trees in the field. At both sites, a strong positive correlation between QSB incidence at 4 years and QSB incidence at 6 years was evident (Fig. 3f). The QSB incidence at the age of six was also very highly correlated with QSB severity at the same age (Supplementary Table 4).

## Discussion

Our results confirmed the first hypothesis that there would be significant variation in tree height, diameter, and QSB resistance among provenances and families at both sites. The second hypothesis was also confirmed; all traits in the present study showed low to moderate heritability. Genetic correlations were found between paired traits, and especially significant was the moderate to a strong genetic correlation between tree height and QSB resistance, suggesting that there is potential to indirectly select resistant families based on the selection of tree height. The third hypothesis was only partially confirmed; disease resistance in seedlings was correlated with that recorded for 2-year-old trees at Mount Barker, but there was no correlation at Margaret River, and no correlation between the seedlings and 4- or 6-year-old trees on both field sites. Data from 2-year-old trees correlated with that from years 4 and 6 at Margaret River, but not at Mount Barker. There was, however, a correlation between the disease resistance of provenances at ages 4 and 6 years on both field sites.

The large variation in QSB resistance among provenances indicates that selecting elite provenances would result in significant genetic improvement in resistance to QSB. Four provenances, Boorara, Plantagenet, Carey, and Bramley were fast growing, exhibited a high overall level of QSB disease resistance and, particularly at the Margaret River site, frequently showed no significant variation between families within a provenance in disease incidence or severity; these provenances have high value as a source of resistant seed. The most resistant provenances originated from the most southern area of southwest Western Australia, where the climate is cooler and wetter than the northern parts, except for the Plantagenet provenance, where the annual rainfall was only 733 mm. This finding matches analysis of results from the same field trials at the age of two (Ahrens et al. 2019), which also showed that provenances from cool wet environments had the highest levels of growth and resistance. The high resistance level displayed by the Plantagenet

provenance is unlikely to be because it originates from a location close to the field trial where it has had the opportunity to develop resistance to local *Q. pitereka* isolates, as it performed equally well at the Margaret River site. Research on *C. citriodora* in Eastern Australia by Dickinson et al. (2004) also reported a good correlation between disease resistance and rainfall at provenance origin, but Pegg et al. (2011) found very high variability in disease resistance within provenances and no correlation with rainfall at provenance origin.

Precipitation at the planting site also affects disease expression. On the Margaret River site, which has significantly more rainfall than Mount Barker, the trees showed less growth but more QSB damage than Mount Barker. Similar provenance trials examining QSB on *C. citriodora* in the eastern states of Australia and China have yielded some results aligned with ours and others in conflict. Dickinson et al. (2004) also reported that when *C. citriodora* plantations were established on trial sites with a range of annual rainfall, the disease was more severe on the wetter sites. However, Lan et al. (2011) and Chen et al. (2021) found more disease linked with lower rainfall.

In the present study, the narrow-sense heritability ( $h^2$ ) for all growth traits and QSB damage at the individual sites was low to moderate, generally indicating low to moderate levels of additive genetic control of growth and QSB resistance. Estimates of heritability for disease incidence remained relatively constant over 2, 4, and 6 years at Mount Barker (0.13–0.19) but at Margaret River  $h^2$  was 0.08 at year two and increased to 0.26 at year six (Table 3). It is possible that the inoculum load on the trees at 2 years of age particularly at Margaret River may not have been high enough to give an accurate assessment of resistance.

The heritability estimated in the present study was higher than the heritability estimated for QSB resistance in *C. citriodora* in China ( $h^2=0.06$ –0.27), but lower than heritability estimated in *C. citriodora* trials in NSW ( $h^2=0.31$  for 25-month-old trees (Johnson et al. 2009)) and in Queensland ( $h^2=0.18$ –0.49 (Brawner et al. 2011)). The explanation for the relatively lower  $h^2$  values than those for *C. citriodora* may be associated with the fact that *Q. pitereka* was only recently introduced to Western Australia but is endemic to eastern Australia (Paap et al. 2008; Zhou et al. 2007). The level of heritability from the present study was also lower than some of those in successful examples of resistance breeding in tree species as in fusiform rust resistance in loblolly pine ( $h^2=0.68$ –0.85 (Kinloch and Stonecypher 1969)) or white pine blister rust resistance ( $h^2=0.38$  (Becker and Marsden 1972)).

The strong genetic correlation between growth traits and QSB resistance found in the present study suggests that selection for either growth traits or disease expression could be used to identify more productive and QSB

resistant provenances and families. This finding supports previous studies where the relationship between growth and QSB tolerance is strong (Carnegie 2007; Brawner et al. 2011; Pegg et al. 2011). It is also similar to the relationship between growth and fusiform rust resistance in *Pinus taeda* (Sierra-Lucero et al. 2002). Also, the positive strong genetic correlation between QSB incidence and QSB severity on the 6-year-old trees indicated that either QSB incidence or severity could be used to assess the QSB disease damage; QSB incidence is the easiest to assess. The strong positive genetic correlation between the same traits at ages four and six supports the idea that the selection for growth and QSB resistance could be conducted at age four.

The estimated type-B correlations were generally strongly positive for all traits and ranged from 0.71 to 0.87, indicating no provenance  $\times$  location interaction. Therefore, we can select the best performing provenances (such as Boorara, Bramley, Carey, and Plantagenet) to plant in all locations with similar ecology and climate conditions to present field trials. Introduction of resistance genes to populations in hotter, drier areas may require controlled pollination or possibly resistant scions grafted onto rootstocks from the drier locality.

The third hypothesis that resistance to QSB would be similar in 3-month-old seedlings, trees at 2 years of age, and those at 4 and 6 years of age was only partially supported. The QSB resistance of provenances recorded for seedlings was similar to that of 2-year-old trees at the Mount Barker site where trees grew more quickly, but the slower-growing trees at Margaret River, and trees at both sites at 4 and 6 years of age showed no correlation with seedlings. The lack of correlation between present data with the seedlings could be due to the protocols (particularly inoculum levels) and environmental conditions used for seedling infection and differences in leaf anatomy and tree physiology between seedlings and adult trees.

Selection for resistance to QSB in marri poses different problems than selection for disease-resistant lines of a species for use in a plantation harvested after 10–15 years. Selection for resistance at year four is likely resulted in trees that are resistant until a plantation is harvested, but less certain for trees in natural forests where they may persist for 100 years or more. Observation on the infection status of trees in the Margaret River and Mount Barker in future years is needed to give more certainty of the validity of selection at year four or six.

The southwest of Western Australia has experienced declining rainfall for several decades (Spickett et al. 2011), and this, together with increasing temperatures, is predicted to result in more frequent water stress, particularly in northern areas (Williams et al. 2013, 2013). More frequent and hotter fires might make for ideal conditions for QSB with masses of young susceptible regrowth. The speed of climate

change, together with the difficulty of assessing the relative disease resistance of saplings and mature trees, means that demonstration of the heritability of QSB resistance at age four, and its correlation with fast growth is a valuable tool for the development of adaptive management strategies for marri.

## Conclusions

There was significant genetic variation in growth rate and QSB resistance between provenances in *C. calophylla*. The narrow-sense heritability for growth traits and QSB damage were low to moderate. The genetic correlation between QSB damage and growth traits was significant; age-age genetic correlations were strongly suggesting the selection for resistance could be undertaken using 4-year-old trees. Type-B (site–site) correlations were strongly positive for all traits indicating no provenance  $\times$  location interaction. Environmental factors at the provenance's origin could be the indicator for QSB resistance. The information developed in this study will assist with developing populations of *C. calophylla* that are more resistant to QSB.

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**Data availability** All data generated or analyzed during this study are included in this published article and its electronic supplementary material.

## Declarations

**Conflict of interest** The authors declare no competing interests.

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