



Genetic variation in fire recovery and other fire-related traits in a global eucalypt species

Mariano A. Hernández^{1,2} · Jakob B. Butler¹ · Hans Ammitzbohl¹ · Jules S. Freeman^{1,3} · Julianne O'Reilly-Wapstra¹ · René E. Vaillancourt¹ · Brad M. Potts¹

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Abstract

To understand the potential of forests to adapt to wildfire, we studied the genetic architecture of fire-related structural, damage and recovery traits in a globally important Australian forest tree species, *Eucalyptus globulus*. Fourteen traits were evaluated in an outcrossed F₂ population in a field trial in Tasmania, Australia, which was burnt by a wildfire 14 years after planting. The trial also included open-pollinated families of the grandparental dwarf and tall ecotypes used to produce the F₂ population. We studied the phenotypic correlations within the F₂ population and performed quantitative trait loci (QTL) analyses using a linkage map comprised of 472 markers. Ecotype comparisons revealed that almost all traits were under genetic control, with trees of the dwarf ecotype significantly more damaged and mainly recovering from lignotubers, whereas tall ecotype trees mainly recovered from epicormic resprouts extending for a variable height up the stem. Within the F₂, tree size was negatively correlated with fire damage and positively correlated with recovery. Genetic control of fire-related traits was confirmed by the detection of 38 QTL in the F₂ population. These QTL accounted for 4 to 43% of the phenotypic variation in these traits. Several QTL co-located and likely reflect pleiotropic effects. However, many independent QTL were detected, including QTL for crown consumption and trunk scorch, epicormic resprouting, resprout herbivory, and seedling establishment. The QTL detected argue that many genetically controlled mechanisms are responsible for variation in fire damage and recovery.

Keywords Epicormic resprouting · *Eucalyptus globulus* · Herbivory · QTL analysis · Seedling recruitment · Wildfire

Introduction

Fire is an important ecological process in many forest communities, affecting species composition and coexistence (McLauchlan et al. 2020). Many tree species have strategies to resist or recover from the effect of fire (Keeley et al. 2011; Clarke et al. 2013; Pausas and Keeley 2014). However, such strategies are increasingly being challenged by changes in fire regimes, with the frequency and intensity of forest fires

projected to increase globally due to increased droughts and extreme temperatures caused by climate change (Miller et al. 2019; Bowman et al. 2020; Kelly et al. 2020; Nolan et al. 2021).

Australia is one of the most fire-prone countries in the world (Burrows 2008), and future climate change scenarios show an increase in fire risk over a large portion of the continent because of warming, reduction in relative humidity (Pitman et al. 2007), and increase in dry lightning (Dowdy 2020). A large component of the Australian vegetation is dominated by the genus *Eucalyptus* and other sclerophyllous species of the *Myrtaceae* family, which have evolved in the presence of fire (Crisp et al. 2011; Paramjyothi et al. 2020). Eucalypts have numerous traits which are direct- or pre-adaptations to survive or recover from fire (Gill 1997). Among the most notable of these are the storage of seed in closed fruits in the canopy (serotiny, Lamont et al. 2020) and recovery traits such as the capacity to resprout vegetatively (Burrows 2013). Resprouting from basal lignotubers allows eucalypts to survive after high-intensity fires when their crown is completely killed, while epicormic resprouting

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✉ Jakob B. Butler
jakob.butler@utas.edu.au

¹ School of Natural Sciences and ARC Training Centre for Forest Value, University of Tasmania, Hobart, TAS 7001, Australia

² Instituto Nacional de Tecnología Agropecuaria (INTA), Route 27 - Km 38.3, Bella Vista, 3432 Corrientes, Argentina

³ Forest Genetics, Scion, Rotorua 3046, New Zealand

from stems or branches allows individuals to rapidly restore photosynthetic capacity (Burrows 2002; Pausas and Keeley 2017). The latter is facilitated by bud-bearing meristematic strands which reside in the bark, outer-wood, and vascular cambium (Burrows 2002; Clarke et al. 2013). Recovery after fire can also occur by seedling recruitment from canopy-stored seed which is usually shed en masse following canopy damage (Ashton 1979). Fire increases the availability of nutrients in the soil, removes other vegetation, and alters soil microbial dynamics, which promotes seed germination and establishment (Aguas et al. 2018; Ammitzball et al. 2022).

Many plant traits have been postulated to affect the response of trees to fire (Midgley et al. 2010; Bowman et al. 2014; Pausas et al. 2017; Karavani et al. 2018). For example, tree size is positively correlated with the likelihood of survival after fire because trees with larger diameter are less likely to have the whole circumference of the cambium killed by exposure to high temperatures (Gutsell and Johnson 1996; Lawes et al. 2011). Bark thickness is another trait positively associated with fire resistance, with thicker bark thought to shield the cambium and the dormant epicormic buds or meristematic tissue beneath the bark from heat damage (Rosell 2016; Pausas 2017; Pausas and Keeley 2017; Karavani et al. 2018). While bark thickness is generally a function of tree size (Lawes et al. 2013), relative to tree diameter, it can also differ between species (Hengst and Dawson 1994; VanderWeide and Hartnett 2011; Graves et al. 2014) and populations of the same species (López et al. 2002; Bdeir et al. 2019). The association of other traits with fire resistance is less studied, but a multi-species study has shown that wood density has a strong positive correlation with post-fire survival (Brando et al. 2012), suggesting an increased capacity of trees with denser wood to compartmentalize fire damage, which may lead to reduced xylem damage and susceptibility to cavitation (Nolan et al. 2021). Although the contribution of all these traits to resistance and recovery from fire has been previously studied at the phenotypic level, this has rarely been addressed at the genetic level, which is required to understand the potential for forest tree populations to genetically adapt to various fire regimes.

Depending on whether it is the direct or indirect result of natural selection by fire or other selective pressures, particular traits may be said to provide an adaptation or a pre-adaptation (i.e., fire-exaptation) to fire, respectively (Keeley et al. 2011; Lamont and He 2017; Lamont et al. 2019). Regardless, the potential for adaptation and pre-adaptation depends on the existence of genetic variation (Bradshaw et al. 2011), which is required for an evolutionary response to selection (Le Rouzic and Carlborg 2008). Common garden field trials testing provenance or family differences are a long-standing approach to reveal the genetic basis to phenotypic variation in forest trees (Alberto et al. 2013; Ramírez-Valiente et al. 2021). Such trials have shown a quantitative genetic basis to

variation in fire-related traits associated with reproduction (e.g., precocity, serotiny) and tree structure (e.g., trunk size and relative bark thickness) (Chambers et al. 1997; Dutkowski and Potts 1999; Hernández-Serrano et al. 2014). In forest trees, both family-level quantitative trait locus (QTL) mapping and population-level association genetic studies are also frequently used to provide insights into the genetic architecture underlying phenotypic variation and for identifying the putative loci influencing this variation (Neale and Kremer 2011). However, there is a paucity of studies linking genotype with phenotype for fire-related traits, especially recovery traits. Furthermore, post-fire factors that affect resprouting, such as insect attack and mammalian herbivory, are scarcely addressed, even at the phenotypic level (Woolley et al. 2012; Hutchen et al. 2017).

Eucalyptus globulus Labill. (Tasmanian blue gum) occurs naturally in Tasmania, the Bass Strait Islands, and adjacent coastal regions of Victoria (Dutkowski and Potts 1999) and is widely planted in other regions of Australia where it is the most important plantation eucalypt species (Downham and Gavran 2019). As one of the nine *Eucalyptus* species that dominate the world's eucalypt plantations (Harwood 2011), *E. globulus* is also grown in temperate regions of the world such as Chile, Portugal, and Spain where it is a valuable resource for pulp, paper, and timber production (Potts et al. 2004). The effect of fire on this species is therefore important because of the potential impact on both natural populations and the plantation industry in Australia (Battaglia and Bruce 2017) and overseas (Tomé et al. 2021). The species is well-adapted to regenerate from wildfire through vegetative recovery and canopy-stored seed. It is a "combination sprouter" having the potential to vegetatively recover from crown destruction through both epicormic shoot production from the stem and branches, and resprouting from basal lignotubers (Nicolle 2006; Burrows 2013). Wildfire is also important for seedling establishment, creating a suitable seed bed and causing the release of canopy-stored seed from its woody capsules (Larcombe et al. 2013; dos Santos et al. 2015). There is considerable genetic variation, both within and between provenances of *E. globulus*, for traits which could potentially affect damage and recovery of trees from wildfire, and thus the adaptive potential of the species. Such fire-related traits include lignotuber size and vegetative recovery (e.g., resprouting following harvesting (Whitlock et al. 2003)), composition and abundance of foliar terpenes (O'Reilly-Wapstra et al. 2011), and stem traits associated with growth rate, bark and wood density (Freeman et al. 2013).

There has been extensive research on the response of *E. globulus* to wildfire, particularly in Portugal where a large expanse of the plantation estate has been impacted by wildfire in the last decade (Tomé et al. 2021). This research shows that tree damage and recovery are not only related to fire intensity and landscape features (Larcombe et al.

2013; Catry et al. 2015; Aguas et al. 2017), but also physical attributes such as tree size (Marques et al. 2011; Catry et al. 2013a). Despite these previous studies, there is no empirical evidence as to whether other structural traits affect damage or recovery of *E. globulus* trees from wildfire at the phenotypic level nor if there is a genetic basis to the variation in fire response. This lack of information includes the post-fire vegetative and reproductive regeneration, both of which can be affected by herbivory (Midgley et al. 2010), to which *E. globulus* exhibits considerable genetic variation in susceptibility (McGowen et al. 2004b; O'Reilly-Wapstra et al. 2014). Such information is required to understand the potential long-term consequence of fire on natural and planted forests, and assess the potential of the species to adapt to altered wildfire regimes.

The present study uses a QTL mapping population of *E. globulus* that was burnt during a wildfire and aims to determine: (i) whether there is genetic variation in fire damage and recovery, including herbivory of resprouting foliage and seedling recruitment; and (ii) the phenotypic and genetic associations among the fire-related structural, damage, and recovery traits.

Materials and methods

Genetic material

Genetic and phenotypic analyses were performed on a trial of *Eucalyptus globulus* that included a large outcrossed F_2 mapping population, comprising a full-sib family generated by crossing two F_1 individuals (parents), one originating from crossing a tree with a dwarf ecotype from Wilsons Promontory in Victoria (see Jordan et al. 2000) with a tree of the tall ecotype (normal ecotype of the species) from King Island in Bass Strait, the other from crossing another unrelated Wilsons Promontory tree with one of the tall ecotype from Taranna in southeast Tasmania (Hudson et al. 2014). Open-pollinated families representing the dwarf and tall ecotype grandparents (from open-pollinated seed collected from surviving grandparental trees) were also randomly interspersed within the planting blocks of the F_2 family. The number of F_2 and open-pollinated individuals used in the analyses of the various traits is shown in Table 1.

Trial description and fire event

The trial studied was planted in 2006 on an ex-native forest site near Geeveston, in southern Tasmania, Australia (43° 13' 8.60" S, 146° 53' 54.81" E, 382 m a.s.l.). The site was clear-felled, remaining vegetation cleared, and debris windrowed to produce four planting bays. Following typical silviculture practices used to establish eucalypt plantations

in Tasmania, the windrows were burnt, bays then rip-lined to produce planting rows 4 m apart into which trees were planted at a spacing of 4 m apart. The trial was thus effectively established into bare soil. It was embedded in the routine plantations established at the same time by Sustainable Timber Tasmania, but was surrounded by a fence for protection against marsupial browsing. The four planting bays of the trial were divided into a total of 14 blocks, which were of variable size dependent on bay and row configurations. The F_2 and open-pollinated families were spread across these blocks and planted into random positions within each block.

The trial was burnt by a wildfire between January and February 2019. The fire was initiated by a dry lightning storm that registered more than 2000 lightning strikes and burned nearly 64,000 hectares of tall eucalypt forests (Wardlaw 2021). The fire burnt through all of the trial and the trial fence was damaged allowing post-fire access by marsupial browsers. Three months after the fire, a first inspection showed all surface litter and understorey plants were burnt (Fig. 1a, b); the bark of 98% of trial trees showed signs of fire damage, and the canopies of all trial trees were damaged to some extent. Of the 350 trial trees, 280 (80%) had their pre-fire foliar canopies completely killed (100% consumed or scorched) by the fire (see Supplementary Figure S1) and 44 of these 280 had their canopies completely consumed. The 70 (20%) trees that had some part of their pre-fire canopy alive tended to be spatially clustered (see Supplementary Figure S1), resulting in statistically significant differences among blocks in fire damage scores (one-way ANOVA, $P < 0.001$). Despite canopy leaf death, no tree mortality occurred in the F_2 following the fire, and recovery occurred by both epicormic and basal resprouting.

Assessment of fire-related traits

Fourteen fire-related traits were measured on the trial trees at different stages of the stand development, both pre- and post-fire. These traits were separated into four categories: structural traits, fire damage traits, post-fire recovery traits, and post-fire herbivory traits (Table 1). Structural traits were assessed prior to the fire and were putatively linked to the capacity of trees to respond to fire (e.g., bark thickness). Traits associated with fire damage were those that reflected burn severity on individual trees (e.g., crown consumption). Recovery traits were those that represented a direct response of trees to fire by restoring the photosynthetic capacity of pre-established trees (e.g., through stem epicormic shoots or basal resprouts) or measured the ability of a tree to produce a new generation through seedling establishment. Post-fire herbivory traits were those associated with herbivory on vegetative shoots generated following post-fire resprouting (e.g., mammalian browsing).

Three structural traits were assessed up to 3 years prior to the fire. Diameter at breast height (1.3 m) was measured

Table 1 Statistics for traits assessed in the genetic trial of *Eucalyptus globulus*, pre- and post-fire

Trait	Year of evaluation	Code	Variable type	Units	Genetic material									
					Dwarf ecotype grandparents			Tall ecotype grandparents			<i>p</i> -level	F ₂ population		
					<i>n</i>	Mean	SE	<i>n</i>	Mean	SE		<i>n</i>	Mean	SE
<i>Structural traits</i>														
Diameter at breast height ^{a, †}	2016	DBH ₁₆	Continuous	mm	18	71.9	8.5	18	169.5	15	<0.001	303	145.5	3.0
	2020	DBH ₂₀	Continuous	mm	14	74.9	8.8	16	217.4	16.6	<0.001	312	172.5	3.8
Bark thickness ^{a, b}	2016	BT ₁₆	Continuous	mm	6	10.8	0.3	16	8.8	0.6	0.004	247	9.9	0.1
Pilodyn penetration ^a	2016	PP ₁₆	Continuous	mm	6	11.2	0.8	16	14.4	0.3	0.007	247	13.0	0.1
<i>Fire damage traits</i>														
Trunk scorch	2019	TS ₁₉	Continuous	%	18	55.3	8.4	17	32.9	8.3	0.040	245	30.2	1.5
Crown consumption	2019	CC ₁₉	Continuous	%	18	83.9	5.0	17	48.5	9.1	0.002	245	41.3	2.1
Crown scorch ^{††}	2019	CSC ₁₉	Continuous	%	7	100	-	14	100	-	-	215	100	-
<i>Post-fire recovery traits</i>														
Seedlings established	2020	SE ₂₀	Count		13	1.1	0.4	14	0.93	0.4	0.486	245	0.7	0.1
Number of basal resprouts	2019	NBR ₁₉	Count		14	1.7	0.5	14	0.9	0.7	0.037	245	1.2	0.1
Number epicormic clusters	2019	NEC ₁₉	Count		14	10.6	2.1	14	9.6	4.0	0.288	245	18.7	1.0
Epicormic shoots in crown	2020	ECR ₂₀	Bivariate (0,1)		14	0	0	14	0.2	0.1	0.079	245	0.2	0
Height of the last epicormic	2019	HLE ₁₉	Continuous	%	14	16.8	4.1	14	51	12.1	0.188	245	42.8	2.5
	2020	HLE ₂₀	Continuous	%	14	14.9	5.3	14	42.9	9.0	0.021	245	42.8	2.5
Epicormic shoot coverage	2020	EC ₂₀	Continuous	%	14	12.1	4.1	14	28.4	6.6	0.058	245	42.7	2.1
<i>Post-fire herbivory traits</i>														
Insect attack	2019	IA ₁₉	Ordinal (0–3)		12	0.9	0.2	13	0.6	0.2	0.339	218	0.7	0.1
	2020	IA ₂₀	Ordinal (0–3)		13	1.1	0.1	14	1.0	0	0.335	242	1.2	0
Mammalian browsing	2019	MB ₁₉	Ordinal (0–3)		13	1.2	0.3	14	0.4	0.3	0.028	233	0.5	0.1
	2020	MB ₂₀	Ordinal (0–3)		13	1.2	0.2	14	0.5	0.2	0.029	242	0.6	0.1

Statistics for the post-fire damage, recovery and herbivory traits are based on the filtered data set which only included trees with complete death of their foliar canopy (i.e., canopy-killed subset).

Note. *SE*, standard error; *p*-level, statistically significant difference between populations of dwarf and tall ecotype grandparents.

^aTraits where the means were compared with Welch's *t*-test. Other traits were compared with Wilcoxon-Mann-Whitney test.

^bStatistics refer to adjusted bark thickness (ADBT₁₆).

[†]Ten F₂ trees were alive in 2020 but were not measured for DBH in 2016 and one re-spouting tree could not be reliably assessed for DBH in 2020. Not all ecotype controls were assessed in 2020.

^{††}When individuals had their crown completely consumed, no measurements of crown scorch (CSC₁₉) were possible, which explains the difference in sample sizes for the damage traits. As CSC₁₉ was invariant in the canopy-killed subset of trees, no SE is shown.

on trees before (DBH₁₆) and after the fire (DBH₂₀). Ten F₂ trees were alive in 2016 but were missed in the DBH assessment, leading to more trees being assessed for DBH₂₀. Bark thickness and wood density were measured 2.5 years before the fire. To measure bark thickness and wood density, a bark hole-punch was used to remove a bark window (10 × 70 mm) at breast height from the outer rough bark to the cambium on the north facing side of the main stem of each tree. Due to the requirement for removal of the bark window, we did not assess trees with DBH less than 10 cm. Wood density was measured from the cambium layer into the stem xylem using a 6 J-Forest pilodyn penetrometer. The depth of the pilodyn penetration into the stem xylem of the standing tree is strongly negatively correlated with wood density in *E.*

globulus (Callister and England 2010). Pilodyn penetration was averaged after taking a pilodyn measurement from the top and bottom of the bark window on the surface of the exposed wood (PP₁₆). Following this, bark thickness from the outer rough bark to the cambium was measured using the depth gauge of the pilodyn (BT₁₆). Given the proximity between the age of assessment of structural traits and the time of the fire, coupled with the strong age-age correlations observed in *E. globulus* for diameter, wood density (Stackpole et al. 2010), and bark thickness (Nickolas et al. 2020), it is assumed that the phenotypic differences among individuals in 2016 reflect that at the time of the fire.

Three traits associated with fire damage were visually assessed 3 months post-fire by a single observer. Following



Fig. 1 Fire damage, post-fire recovery, and herbivory traits measured on the common garden field trial. **a** Trees with 100% of their crown scorched. **b** Trees with 100% of their crown consumed. **c** Maximum stem height scorched by the fire (indicated by red arrow). **d** Basal resprout. **e** Epicormic clusters. **f** Seedling established on the forest

floor (indicated by red arrow). **g** Damage from mammalian browsing (indicated by red arrow). **h** Insect herbivory by larvae of the leaf beetle, *Paropsisterna cloelia*. Photographs **a**, **b**, and **e** were taken 3 months after the fire, while the rest were taken 1 year after the fire

Thies et al. (2006), the trunk (bole) scorch (TS_{19}) was considered as the percentage of tree height that was scorched by the fire (Fig. 1c). Crown consumption (CC_{19}) was defined as the percentage of pre-fire live foliar crown volume consumed, therefore gone, by active combustion (McHugh et al. 2003) and visually estimated, based on the observers' prediction of the pre-fire crown volume from remaining crown branches. Similarly, crown scorch (CSC_{19}) was visually estimated as the percentage of the leaves remaining in the crown (i.e., that had not been consumed by the fire) assessed as scorched (brown and desiccated) and assumed dead (McHugh and Kolb 2003).

Recovery traits were assessed twice, at 3 months and 12 months post-fire. Some traits were evaluated on both occasions, while others only once when taking a second measurement was impractical. Seedling establishment (SE_{20}) was assessed by counting the number of seedlings alive on

the burnt area of ground in a 1-m radius around the trunk of each tree 1 year after the fire. Because eucalypts have (i) very limited seed dispersal (Booth 2017), particularly heavy-seeded species such as *E. globulus* (Cremer 1977; Larcombe et al. 2013), (ii) little soil stored seed (Florence 1996), and (iii) seedlings established after wildfire are usually directly derived from seeds stored in woody capsules in the tree canopy (dos Santos et al. 2015), the seedlings counted in the circular plot were assumed to be from seed shed from the central tree following the fire. As the maker genotypes are expected to be randomly distributed in the trial, any seed flow-over from adjacent trees in the trial would only diminish the probability of QTL detection. Recovery traits also included assessments of resprouting from the lignotuber, stem, crown, and the whole tree. Following Catry et al. (2013a), the number of resprouts (NBR_{19}) originating from basal lignotubers was counted 3 months post-fire. In

addition, we also counted the number of epicormic clusters (i.e., number of clusters of vegetative shoots (NEC_{19})) between the ground and 2 m height on the four cardinal faces of each tree stem (Fig. 1e). Epicormic shoots in the crown (ECR_{20}) were also evaluated as a bivariate trait, defining the tree crown as the top section of the stem which starts with the main branches. Another resprouting trait considered was the height to the highest cluster of epicormic shoots on the stem, expressed as a percentage of the total tree height. This trait was assessed twice using two different methods. The first measurement was performed 3 months post-fire (HLE_{19}), using a visual estimation in the field, while a second measurement was performed using photos taken of every tree 1 year after fire (HLE_{20}). The photos covered the entire tree from the base to the top, making it possible to identify and measure tree height as well as any resprouting

along the stem (Fig. 2). To assess the photos, digital measurements were taken with the software ImageJ v. 1.52a (Schneider et al. 2012). We also assessed the epicormic shoot coverage (EC_{20}) on the stem using the photos and ImageJ, defined as the length of the stem covered by epicormics, expressed as a percentage of total tree height.

Post-fire herbivory traits were visually evaluated across epicormic and basal shoots located between the ground and 2 m up the stem, 3 months and then 1 year after the fire (Fig. 1g, h). Separate estimates in the field by the same experienced observer in both years were made of the percentage leaf area lost through insect and mammal browsing based on relatively distinctive symptoms. The loss through insect attack (IA_{19} and IA_{20}) integrated damage which was mainly ascribed to sawfly larvae (*Perga affinis*), eucalypt leaf beetle larvae (*Paropsisterna cloelia*), and nymphs of *Amorbus* sp.,

Fig. 2 Photos taken in 2020 for assessing the traits epicormic shoot coverage and height to the last epicormic (1 year after trees were burnt by wildfire). **a** Tree with epicormic shoots covering the first third of stem from the ground. **b** Tree with epicormics on most of the stem



which have relatively distinctive symptoms and are species previously reported as pests of *E. globulus* plantations (de Little et al. 2008). The mammalian browsing damage (MB₁₉ and MB₂₀) was caused by the common brushtail possum (*Trichosurus vulpecula*), a marsupial commonly reported as responsible for damaging trees in Tasmanian eucalypt plantations (Miller et al. 2009). Their damage is often associated with the presence of typical scratch marks on the tree trunk. Both insect attack and mammal browsing were assessed using an ordinal scale (0 = no damage, 1 = minor damage, 2 = medium damage, 3 = heavy damage).

Analysis

Diameter at breast height, bark thickness, and pilodyn penetration were analyzed using all the phenotypic measurements available for the trait (Table 1). Since these traits did not represent a response to the effect of fire, no exclusion of trees was needed to standardize the analysis. However, we performed the analyses of damage, recovery, and post-fire herbivory only on trees with no pre-fire leaves left alive in the crown, that is, trees with foliar crowns either 100% consumed by the fire or trees with crowns 100% scorched. This selection was aimed at reducing the variation in fire exposure among trees and restricts our analysis to the subset of trees with pre-fire foliar canopies that were completely killed by the fire. It also was aimed at avoiding interference from living pre-fire canopy foliage in the recovery response due to hormonal/nutrient mechanisms (Meier et al. 2012). This filtered subset is hereafter referred to as the “canopy-killed” trees. This exclusion meant that there was no variation in crown scorch in the subset of trees analyzed, so this trait was dropped from further analyses, but there was variation in crown consumption (CC₁₉) and trunk scorch (TS₁₉). While this variation likely includes a residual effect of spatial variation in fire intensity, this will not bias our QTL results as segregating markers are expected to have a random distribution throughout the trial.

To determine whether there was genetic variation for fire-related traits, trait means of dwarf and tall ecotype grandparent families were compared. Since trees of these two groups were randomly distributed in the trial blocks, statistical differences in fire-related traits were not due to the spatial distribution of trees, but genetic-based group differences. The group means of traits which had Gaussian distributions (i.e., diameter at breast height, bark thickness, and pilodyn penetration) were compared with Welch's *t*-tests, while comparison of group differences for other traits was performed with Wilcoxon-Mann-Whitney test. Because bark thickness is associated with stem size (Lawes et al. 2013), the effect of diameter was removed by linear regression with DBH measured at the same time and adjusted values analyzed as well as non-adjusted values. This regression was based on

all data (F₂ plus open-pollinated families), and the adjusted bark thickness was the sum of the overall mean bark thickness and the residuals derived from the linear regression of bark thickness on DBH (Table 1).

To examine the genetic architecture underlying variation in the above traits, quantitative trait loci (QTL) analysis was performed on the F₂ family with the software MapQTL 6 (Van Ooijen 2009). A high density linkage map has been previously constructed using this F₂ population (Hudson et al. 2012) and several QTL analyses have already been performed (Hudson et al. 2014; Butler et al. 2016; Ammitz-boll et al. 2018). To decrease the computational demand in QTL analyses, the linkage map was reduced to 472 markers (422 DArT and 50 SSR) located at intervals of 2 to 5 cM by removing most 3:1 segregating DArT markers and retaining all SSR markers and an even distribution of DArT markers segregating in a 1:1 ratio while preserving their cM position following the methodology used by Hudson et al. (2014). Permutation tests (1000 permutations) were run to determine the significance thresholds of the logarithm of odds (LOD) at the genome-wide and chromosome-wide levels (Churchill and Doerge 1994). Putative QTL were declared as significant (i.e., genome-wide type I error rate < 0.05) or suggestive (i.e., chromosome-wide type I error rate < 0.05) depending on LOD score (Freeman et al. 2008). Initially, interval mapping was used, choosing various traits as covariates when removing the effect of these was meaningful to the analysis. For example, DBH was included as the covariate for bark thickness given their high phenotypic correlation (see the “Results” section); thus, the QTL reported refer to relative bark thickness. When QTL peaks exceeded the suggestive LOD threshold in interval mapping, the closest markers were added as cofactors in a subsequent analysis by restricted multiple-QTL model (rMQM) mapping. rMQM analyses were conducted using an iterative approach until no more QTL were detected, cofactor markers were the closest marker to each QTL, and QTL positions were stable (Van Ooijen 2009). To determine if parental segregation of QTL effects was solely on the maternal or paternal sides, or both, Kruskal-Wallis single marker analyses were conducted in MapQTL 6, and the significance of markers with different segregation adjacent to each significant QTL was examined. This analysis permitted the classification of QTL effects into three main classes: male segregation, where the markers inherited solely from the female parent showed no significant effect; female segregation, where the markers inherited solely from the male parent showed no significant effect; and both parents, where markers inherited from the male and female parents were significant ($P < 0.05$). When segregation came from both parents and the effect of one of the parents was more pronounced than the other, we indicated which of the parents had the major contribution to segregation in the region. In addition, associations between

traits were explored by estimating Spearman correlations (ρ) within the F_2 population.

Results

Ecotype comparison

Comparison of means between dwarf and tall ecotypes showed statistically significant differences for all structural traits (DBH_{16} , DBH_{20} , BT_{16} , PP_{16} ; Table 1). The samples of the dwarf ecotype had higher wood density (density is the inverse of pilodyn penetration) and higher values of adjusted bark thickness than samples of the tall ecotype, but lower average values of stem diameter. As BT_{16} and PP_{16} were not measured from small stems, a disproportionately high number of the dwarf trees were not assessed, which could potentially underestimate the difference between the ecotypes. Nevertheless, additive genetic inheritance in the F_2 population are likely for stem diameter, adjusted bark thickness, and pilodyn penetration, since its sample means were close to midway between that of the grand-parental means of the dwarf and tall ecotypes (Table 1, Supplementary Figure S2). The F_2 population encompassed the full range of phenotypic variation in DBH_{20} exhibited between the dwarf and tall ecotypes, but there was also much variation in the tall ecotype (Supplementary Figure S3).

Traits associated with fire damage (TS_{19} and CC_{19}) also showed statistically significant differences between the means of dwarf and tall ecotypes using the filtered data set of canopy-killed trees (Table 1). The dwarf ecotypes were more damaged and the F_2 mean was closer to that of the tall ecotype. For example, 61% for the dwarf ecotype trees studied experienced complete crown consumption during the fire, which compares with 18% for the tall ecotype and 12% for the F_2 trees. Based on the observed absence of epicormic shoots below 2 m in the first year following the fire (NEC_{19}) and the absence of epicormic shoots on the trunk in the second year (HLE_{20}), 20 of the 245 canopy-killed F_2 trees (8%) would classify having been top-killed by the fire (i.e., total death of the above ground aerial biomass), but 60% of these were observed with basal shoots in the first post-fire assessment and all were alive at the second post-fire assessment. By comparison, there were two top-killed trees of the dwarf ecotype (14%, both of which survived to the second assessment) and no top-killed trees of the tall ecotype.

Within the F_2 , phenotypic correlations (Table 2) revealed an inverse and statistically significant relationship of tree size (i.e., DBH_{20}) with trunk scorch (TS_{19} , $\rho = -0.49$) and crown consumption (CC_{19} , $\rho = -0.50$), showing that the smallest trees suffered the greatest fire damage. These correlations were calculated using the canopy-killed F_2 trees.

Very similar correlations were obtained using all F_2 trees without filtering based on fire damage (TS_{19} , $\rho = -0.47$; CC_{19} , $\rho = -0.44$). This finding was consistent with the ecotype comparisons. Most recovery traits (SE_{20} , NEC_{19} , ECR_{20} , HLE_{19} , and EC_{20}) did not show statistical differences between the dwarf and tall ecotype (Table 1). Thus, despite being more damaged, the dwarf ecotype recovered as well as the tall ecotype. The number of seedlings established (SE_{20}) beneath tall versus dwarf ecotypes was not significantly different, and there was no significant association between tree size (DBH_{20}) and SE_{20} within the F_2 (Table 2). Only the number of basal resprouts (NBR_{19}) and height of last epicormic (HLE_{20}) showed statistical differences between the grand-parental groups, with the dwarf ecotype having more basal resprouts and a lower proportion of the stem with epicormic shoots than the tall ecotype. The same trait-size association was evident within the F_2 (Table 2). No differences between ecotypes were found for insect attack (IA_{19} and IA_{20}), but there were statistically significant differences in mammal browsing for the two assessments (MB_{19} and MB_{20}). In each year, mammal browsing was more intense on the dwarf than the tall ecotypes (Table 1) but was unrelated to tree size within the F_2 (Table 2).

QTL analysis

In the absence of fitting covariates, exploratory QTL analyses indicated that many of the QTL detected for fire damage and recovery traits collocated with QTL for DBH_{20} or bark thickness (results not shown), as expected from the significant phenotypic correlations observed with the F_2 (Table 2). Accordingly, the QTL analyses reported for the damage and recovery traits (Table 3) account for the effects of tree size (and where relevant fire damage) to focus on additional genetic factors which influence fire damage and recovery. For example, the QTL we report for fire damage traits accounted for differences due to tree size by fitting DBH_{20} as a covariate and QTL for recovery traits additionally accounted for variation in fire damage by also fitting TS_{19} or CC_{19} . These QTL analyses allowed the detection of 38 QTL, of which 13 were significant and 25 suggestive (Table 3). QTL were detected for all traits and time periods except insect attack in 2020 (IA_{20}). Since linkage group, position, and statistical significance of the QTL detected were the same for both assessments of diameter at breast height (DBH_{16} and DBH_{20}), only QTL for the last measurement is reported. The number of QTL detected per single trait ranged from 1 to 7 and the percentage of variance explained by each QTL ranged from 1.4 to 12.5%. There were 21 QTL that occupied unique genomic regions, whereas 17 QTL were co-located. Overall, QTL were detected in 28 discrete genomic regions, here defined as regions in which no QTL had LOD peaks within 5 cM of

Table 2 Spearman correlations (ρ) among fire-related traits for the F₂ population of *Eucalyptus globulus*

	DBH ₂₀	BT ₁₆	ADBT ₁₆	PP ₁₆	TS ₁₉	CC ₁₉	SE ₂₀	NBR ₁₉	NEC ₁₉	ECR ₂₀	HLE ₁₉	HLE ₂₀	EC ₂₀	IA ₁₉	IA ₂₀	MB ₁₉
Bark thickness (BT ₁₆)	0.81 ***															
Adjusted bark thickness (ADBT ₁₆)	0.00 ns	0.50 ***														
Pilodyn penetration (PP ₁₆)	0.02 ns	-0.06 ns	-0.07 ns													
Trunk scorch (TS ₁₉)	-0.49 ***	-0.17 *	0.04 ns	-0.22 **												
Crown consumption (CC ₁₉)	-0.50 ***	-0.24 ***	-0.05 ns	-0.12 ns	0.57 ***											
Seedlings established (SE ₂₀)	0.11 ns	0.07 ns	-0.03 ns	0.26 *	-0.20 **	-0.11 ns										
Number of basal resprouts (NBR ₁₉)	-0.34 ***	-0.23 **	0.04 ns	-0.17 *	0.23 ***	0.20 **	-0.16 **									
Number of epicormic clusters (NEC ₁₉)	0.27 ***	-0.21 **	0.05 ns	0.08 ns	-0.30 ***	-0.28 ***	-0.06 ns	0.16 *								
Epicormic shoots in crown (ECR ₂₀)	0.40 ***	0.23 **	-0.02 ns	0.01 ns	-0.32 ***	-0.39 ***	-0.02 ns	-0.12 ns	0.20 **							
Height of the last epicormic (HLE ₁₉)	0.68 ***	0.34 ***	0.01 ns	0.13 ns	-0.49 ***	-0.49 ***	0.09 ns	-0.31 ***	0.39 ***	0.36 ***						
Height of the last epicormic (HLE ₂₀)	0.74 ***	0.44 ***	0.05 ns	0.08 ns	-0.52 ***	-0.48 ***	0.05 ns	-0.27 ***	0.42 ***	0.65 ***	0.74 ***					
Epicormic shoot coverage (EC ₂₀)	0.63 ***	0.29 ***	0.04 ns	-0.02 ns	-0.38 ***	-0.40 ***	-0.10 ns	-0.16 *	0.56 ***	0.57 ***	0.65 ***	0.86 ***				
Insect attack in 2019 (IA ₁₉)	0.02 ns	-0.07 ns	-0.02 ns	-0.07 ns	0.04 ns	-0.01 ns	-0.09 ns	0.16 *	0.21 **	0.04 ns	-0.11 ns	-0.01 ns	0.08 ns			
Insect attack in 2020 (IA ₂₀)	0.26 ***	-0.08 ns	-0.05 ns	-0.01 ns	0.03 ns	0.02 ns	0.09 ns	-0.06 ns	-0.07 ns	0.1 ns	0.11 ns	0.21 **	0.07 ns	-0.14 ns		
Mammalian browsing in 2019 (MB ₁₉)	-0.12 ns	-0.03 ns	0.09 ns	0.02 ns	0.06 ns	-0.04 ns	0.05 ns	0.19 **	0.20 **	0.02 ns	-0.16 *	-0.02 ns	-0.02 ns	0.34 ***	-0.02 ns	
Mammalian browsing in 2020 (MB ₂₀)	0.07 ns	-0.07 ns	-0.06 ns	0.08 ns	-0.04 ns	0.05 ns	0.01 ns	0.01 ns	0.07 ns	-0.12 *	0.07 ns	0.01 ns	-0.02 ns	-0.02 ns	-0.01 ns	0.17 *

Statistical significance was indicated by ***= $p < 0.001$, **= $p < 0.01$, *= $p < 0.05$, ns not significant

Numbers in bold indicate statistical significance after Bonferroni correction for multiple comparisons ($p < 0.05/136$). DBH₁₆ and DBH₂₀ were highly correlated ($\rho = 0.97$); thus, only correlations for DBH₂₀ are presented. Correlations were calculated based on the canopy-killed trees used in the QTL analysis. Virtually identical results were obtained when the correlations are calculated using all F₂ trees (data not shown)

Table 3 Quantitative trait loci (QTL) for fire-related traits in an F₂ population of *Eucalyptus globulus*

Trait	Covariable	LG	cM	Marker	LOD	PVE	Seg
Diameter at breast height (DBH ₂₀)		10	39.5	Embra153	10.82***	12.5	—
		7	9.7	562769	9.55***	10.9	M
		4	60	570780	4.62*	5.1	F
		3	75.7	570139	3.11	3.4	B (>F)
Bark thickness (BT ₁₆) ^a	DBH ₁₆	9	83.3	569303	6.28**	3.2	—
		10	26.9	567691	5.30*	2.7	F
		2	108.2	638845	4.06	2.0	—
		1	53.2	Embra222	2.79	1.4	—
Pilodyn penetration (PP ₁₆)	DBH ₁₆	4	12.4	600106	8.51***	10.7	M
		6	46	568743	6.12***	7.5	B (>M)
		1	86.6	644046	4.61***	5.6	B (>M)
		2	87.9	564988	3.85	4.6	M
		3	83.4	600338	4.42	5.3	F
		4	70.2	574628	4.06	5.3	F
		10	26.9	567691	3.39	4.1	F
Trunk scorch (TS ₁₉)	DBH ₂₀	11	67.6	502828	3.58	4.2	F
Crown consumption (CC ₁₉)	DBH ₂₀	1	75	638702	2.92	3.4	—
		9	60.8	641541	2.89	3.3	—
		3	59.8	573637	2.86	3.3	B (>F)
Seedlings established (SE ₂₀)	DBH ₂₀	6	5	569441	4.74*	8.3	F
Number of basal resprouts (NBR ₁₉)	DBH ₂₀	7	3	564899	5.84*	9.1	M
Number epicormic clusters (NEC ₁₉)	DBH ₂₀	7	5.8	570301	3.95	5.6	M
		8	61.8	640208	3.55	5.1	M
		10	51.6	573717	3.45	4.9	B (>M)
		11	27.9	571793	3.17	4.5	F
Epicormic shoots in crown (ECR ₂₀)	DBH ₂₀ +CC ₁₉	3	75.7	570139	3.85	5.8	B (>F)
Height of the last epicormic (HLE ₁₉)	DBH ₂₀ +TS ₁₉	2	11.4	564330	3.30	3.5	F
Height of the last epicormic (HLE ₂₀)	DBH ₂₀ +TS ₁₉	2	14	642292	3.71	3.1	—
		3	59.8	573,637	3.42	2.8	F
Epicormic shoot coverage (EC ₂₀)	DBH ₂₀	3	75.7	570139	3.34	3.4	B (>F)
		11	31.3	566749	3.11	3.1	F
Insect attack (IA ₁₉)		3	35	640311	3.13	6.4	M
		11	6.6	638367	2.89	5.5	B
Mammalian browsing (MB ₁₉)		3	39.3	570900	4.67**	8.3	M
		2	45.3	599725	3.52*	6.2	M
Mammalian browsing (MB ₂₀)		3	59.8	573637	3.11	5.3	M
		3	6.9	644409	4.30*	7.2	M
		4	77.6	565463	2.52	4.3	F

LG, linkage group; cM, map position in centimorgan; Marker, marker closest to the QTL peak; LOD, significance; PVE, percentage of variance explained; Seg, parent from which the QTL effect segregated (M = male, F = female, B = both, or “—” = undetermined due to dominant markers). Where QTL segregated from both parents, whether a more significant effect was found from the male or female parent is indicated in parentheses. Genome-wide significance was indicated by *** = $p < 0.001$, ** = $p < 0.01$, * = $p < 0.05$. The remaining QTL were significant at the suggestive level (chromosome-wide type I error rate < 0.05). DBH₁₆ and DBH₂₀ were highly correlated ($r = 0.97$); thus, only those for DBH₂₀ are presented and it is this measurement which was fitted as a covariate for the QTL for recovery traits. Adding more co-variates to the analysis of recovery traits did not change the results substantially

^aThe bark thickness QTL detected refer to adjusted bark thickness as DBH₁₆ has been fitted as a covariate. For each trait, the number of F₂ trees used in the QTL analysis corresponds to the sample size given in Table 1

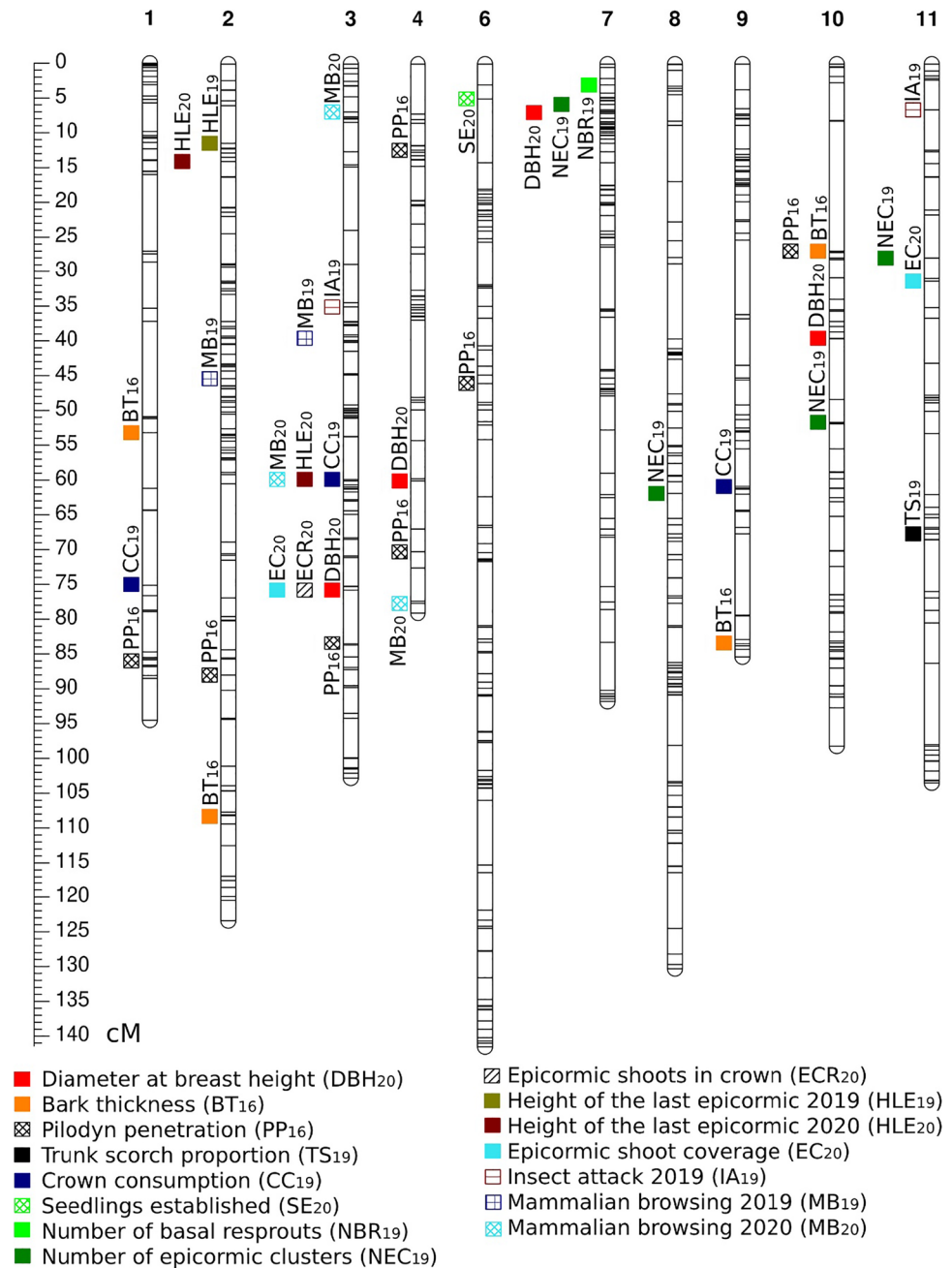
another QTL (Fig. 3). These regions occurred across 10 of the 11 linkage groups of *E. globulus*.

Structural traits (DBH₂₀, BT₁₆, PP₁₆) showed QTL with the highest LOD compared to traits associated with fire damage and recovery. These structural trait QTL mapped to 14 genome regions in 8 different linkage groups (Fig. 3). The number of QTL that influenced each structural trait ranged from 4 to 7, explaining 9.3 to 43.1% of the total variance of the trait. Eight of the structural trait QTL were declared significant at the genome-wide level. Overall, seven QTL were detected for pilodyn penetration (PP₁₆) and four for bark thickness (BT₁₆ adjusted within the QTL analysis for

DBH₁₆). While the phenotypic correlation between these two traits within the F₂ was insignificant (Table 2), their QTL co-located on linkage group 10. QTL for both traits segregated from the female parent (Table 3), suggesting that these QTL are the pleiotropic effect of a single segregating QTL. Examining the phenotypic means for the different genotypes at the markers underlying this QTL showed that the genotypes with relatively thicker bark also had denser wood (Supplementary Figure S4).

Fire damage (TS₁₉, CC₁₉) was negatively phenotypically correlated with tree size (DBH₂₀) (Table 2). After adjusting for co-variation with tree size, 1 QTL was detected for trunk

Fig. 3 The genomic distribution of quantitative trait loci (QTL) associated with fire-related traits in *Eucalyptus globulus* on 10 of its 11 linkage groups (chromosomes). Markers are indicated by dashes across linkage groups



scorch (TS_{19}) and 3 QTL for crown consumption (CC_{19}). Note that because of the exclusion of trees that were burnt less severely from the analysis, these QTL represented the genetic variation in crown consumption among trees with 100% crown scorching. These QTL occupied 4 genomic regions on different linkage groups and overall explained 4.2% of the total variance for trunk scorch and 10% of that for crown consumption.

Vegetative recovery was phenotypically associated with tree size (Table 2). Bigger trees inherently have thicker bark ($\rho = 0.81$; Table 2), and thus, epicormic recovery was positively phenotypically correlated with both tree size and bark thickness (BT_{16}), but not with adjusted bark thickness which accounted for tree size (Table 2). Epicormic regeneration assessed in both years (NEC_{19} , HLE_{19} , ECR_{20} , HLE_{20} , and EC_{20}) was phenotypically negatively correlated with fire damage traits (TS_{19} , CC_{19} , Table 2), indicating that the smaller trees with more severe damage had less epicormic regeneration from the upper trunk and canopy. After adjusting for covariation with tree diameter and relevant fire damage traits (epicormic height traits were adjusted for TS_{19} and epicormics in the canopy adjusted for CC_{19}), twelve QTL were found for recovery traits (SE_{20} , NBR_{19} , NEC_{19} , ECR_{20} , HLE_{19} , HLE_{20} , EC_{20}) occurring on 7 linkage groups (Table 3). Note that adding more co-variables did not change the results substantially (results not shown). The number of QTL that influenced each recovery trait ranged from 1 to 4 and explained 3.5 to 20.1% of the total variance of the trait. Most of the recovery QTL were suggestive, but the QTL for seedlings established (SE_{20}) and number of basal resprouts (NBR_{19}) were significant (Table 3).

Consistent with the significant positive correlations among the epicormic recovery traits within and across years (Table 2), many of the suggestive QTL detected for these traits were co-located and the genotype segregation patterns suggest pleiotropic effects of the same locus. For instance, the region at 30 cM on linkage group 11 was shared by QTL for two recovery traits, number of epicormic clusters (NEC_{19}), and epicormic shoot coverage (EC_{20}) (Fig. 3). Both QTL segregated from the female parent (Table 3) and the effects of the common marker (Supplementary Figure S4) were consistent with the direction expected based on their weak positive phenotypic correlation ($\rho = 0.20$, Table 2). The region at 76 cM on linkage group 3 included co-located QTL for epicormic shoot coverage (EC_{20}) and epicormic shoots in the crown (ECR_{20}). The genotype segregation at the nearest marker to these QTL is from the same parent (Table 3), and the positive correlation between EC_{20} and ECR_{20} ($\rho = 0.57$; Table 2) is in the same direction as the marker effects (Fig. 4a), consistent with this co-location potentially being the pleiotropic effect of a single segregating locus. Similarly, for the co-located QTL for epicormic clusters (NEC_{19}) and number of basal resprouts (NBR_{19}) on

linkage group 7 (4 cM), there was male segregation of both QTL (Table 3), the traits were weakly positively correlated ($\rho = 0.16$; Table 2), and the patterns of marker segregation were in the same direction (Fig. 4b).

QTL for vegetative recovery on linkage group 3 and 7 continued to co-locate with QTL for DBH_{20} , despite their phenotypic covariation with DBH_{20} being accounted for. It is possible that these recovery QTL reflect residual and pleiotropic effects of tree size QTL. For example, the co-located QTL on linkage group 3 at 76 cM show a pattern of genotype segregation consistent with genotypes with larger stems having greater epicormic coverage of the stem and more shoots in the crown (Fig. 4a). In both cases, the markers underlying the QTL indicate segregation consistent with increased fire intensity or decreased tree size causing greater epicormic bud mortality in the upper trunk and crown. However, the co-located QTL for height of the last epicormic in both years (HLE_{19} , HLE_{20}) on linkage group 2 and the epicormic QTL on linkage groups 8 (NEC_{19}), 10 (NEC_{19}), and 11 (NEC_{19} and EC_{20}) are independent of structural QTL. There was no significant phenotypic correlation of recovery traits with adjusted bark thickness ($ADBT_{16}$) or wood density (PP_{16}) (Table 2), and these recovery QTL did not co-locate with any of the QTL associated with bark thickness (BT_{16}) or wood density (Fig. 3). The single QTL for seedling establishment detected after adjusting for tree size (SE_{20}) was independent of all other QTL and was one of the two recovery QTL significant at the genome-wide level (Table 3).

For traits related to herbivory on resprouting vegetative shoots (IA_{19} , MB_{19} , MB_{20}), 7 QTL were detected in 6 genomic regions, explaining 11.9 to 16.8% of the trait variance. There were three QTL for mammalian browsing that had genome-wide significance. One of these QTL (MB_{20}) co-located with QTL for crown consumption (CC_{20}) and height of last epicormic (HLE_{20}) on linkage group 3 (60 cM) (Fig. 3). However, parental segregation was different for each of these traits (Table 3), arguing against these co-locations being due to a pleiotropic effect. The other browsing QTL did not co-locate with any structural, fire damage, or recovery QTL. It is interesting that the QTL for mammalian browsing in different years (MB_{19} , MB_{20}) did not co-locate, and QTL for insect attack were only detected in the first but not the second assessment. However, co-location was detected for mammalian browsing and insect attack scored in the first year after the fire (MB_{19} and ID_{19}) on linkage group 3 (35 cM), suggesting a possible common QTL for herbivory of vegetative shoots. The marker genotype segregation underlying this QTL co-location shows susceptibility to both mammalian and insect herbivores, consistent with the significant positive phenotypic correlation between these two traits (Table 3). However, the other QTL detected insect damage (ID_{19}) on linkage group 11

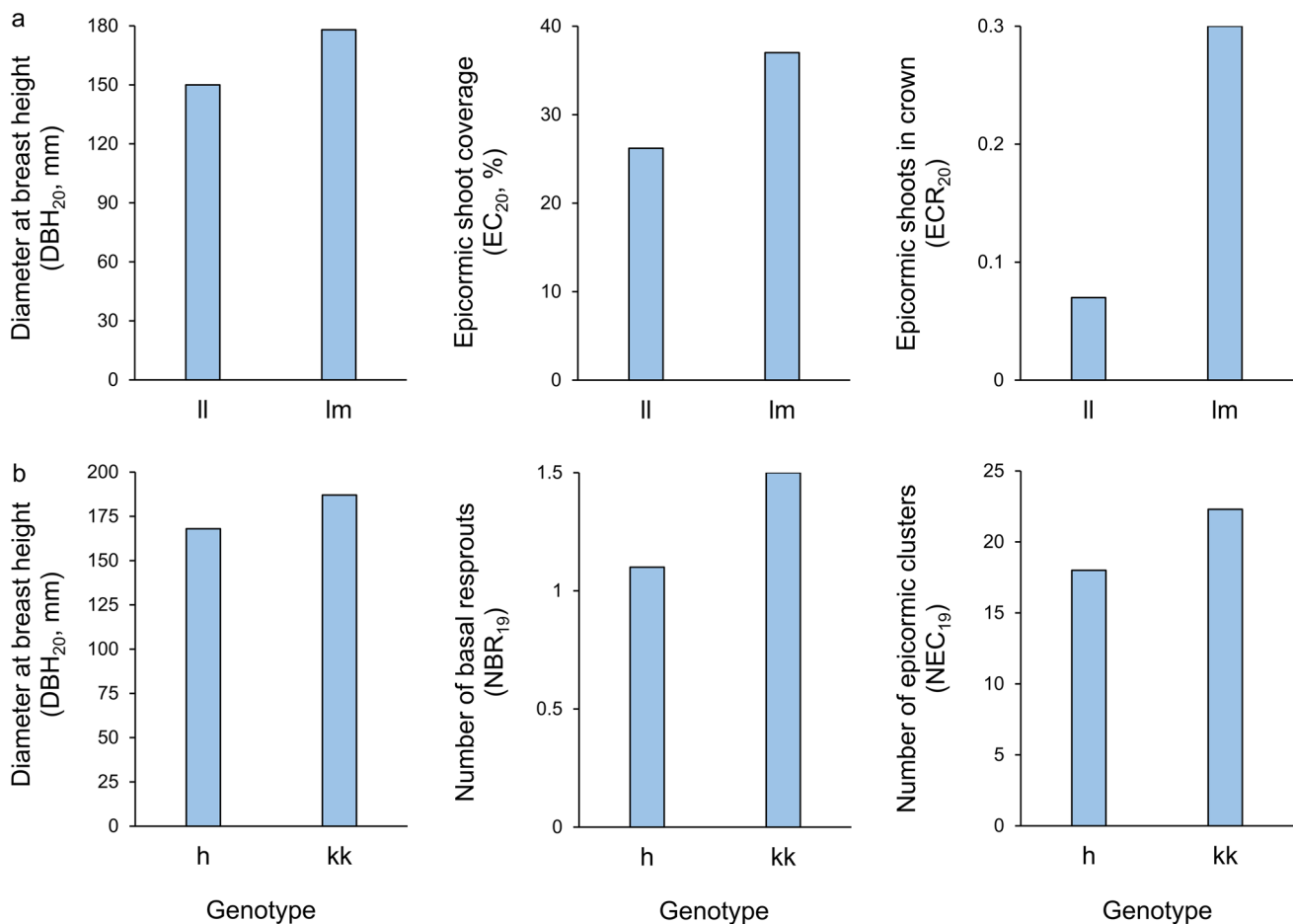


Fig. 4 Genotype average of co-located QTL for fire-related traits based on a common marker. The co-located QTL were on linkage group 3 (75.7 cM, marker 570139) and linkage group 7 (5.8 cM, marker 570301). The common markers were DArTseq markers (where ll/lm indicates a female segregating marker, and h/kk indi-

cates a dominant marker with unknown parental segregation). **a** Co-location for trait diameter at breast height, epicormic shoot coverage and epicormic shoots in crown. **b** Co-location for trait diameter at breast height, number of basal resprouts and number of epicormic clusters

(6 cM) was not co-located with any other QTL detected (Fig. 3).

Discussion

Phenotypic variation in fire damage has been previously reported in several forest trees, including *E. globulus*. These studies identified exogenous (e.g., fire intensity, site) and endogenous (e.g., plant traits) factors that influence the level of fire damage (Kobziar et al. 2006; Hanson and North 2009; Catry et al. 2013b). We here show a genetic basis to variation in fire damage among trees of the same age, which to a large extent is mediated by genetic variation in tree size. A significant difference in fire damage traits was shown between the dwarf and tall grandparents, along with strong phenotypic correlations between stem diameter and the amount of both trunk scorch and

crown consumption in the F₂, which suggests that decreasing tree size increases the risk of stem and crown damage in a wildfire. This finding is consistent with models developed for *Eucalyptus* spp. (including *E. globulus*) to predict topkill (Catry et al. 2013a; Fairman et al. 2019). However, the QTL detected for both crown consumption and trunk scorch accounted for phenotypic variation in tree size by fitting DBH as a covariate, and thus likely reflects the influence of other underlying plant traits. For example, while stem scorch and crown consumption were positively phenotypically correlated reflecting their common phenotypic association with stem size, the QTL detected for these traits after fitting DBH as a covariate were independent.

There are multiple plant traits which could influence the severity of fire damage apart from tree size. Although bark thickness QTL (after accounting for DBH) did not co-locate with QTL associated with fire damage, unmeasured

characteristics of the bark may affect the severity of fire damage on trees (Florence 1996). For example, at the intraspecific level, eucalypt species differ markedly in the amount of decorticated bark which may accumulate on the trunk and branches or at the base of the tree, and funnel fire to the upper canopy (Gill and Ashton 1968). In this respect, Barbour et al. (2009b) reported significant genetic variation among *E. globulus* races in the amount and type of loose decorticated bark on the trunks of trees in a common garden trial. Similarly, it is also possible that the QTL underlying variation in canopy consumption could reflect genetic variation in attributes specifically affecting canopy flammability such as leaf moisture content, retention of dead leaves, leaf functional traits (Murray et al. 2013; Alam et al. 2020), and leaf chemistry (Bowman et al. 2014; Pausas et al. 2017). In the latter cases, essential oils (e.g., terpenes; Pausas et al. 2016; Ganteaume et al. 2021) and waxes (Tumino et al. 2019; Ormeño et al. 2020) have been implicated in foliar flammability. Indeed, one of the three QTL for crown consumption on linkage group 3 was near a QTL reported for a foliar terpene in *E. globulus* (O'Reilly-Wapstra et al. 2011) and another on linkage group 1 near a QTL for cuticular wax also in *E. globulus* (Gosney et al. 2016).

Eucalypts are renowned for the propensity of most species to vegetatively recover from fire damage (Gill 1997), and *E. globulus* is no exception. In the present study, the amount of epicormic resprouting was highly variable and negatively correlated with the amount of basal resprouting and positively correlated with tree size (Table 2). These trends agree with Fairman et al. (2019), who developed models to predict resprouting from stem diameter in *Eucalyptus* spp., showing a propensity for small trees to resprout from the base, large trees from the stem, and medium trees from both base and stem. This phenotypic association between tree size and resprouting characteristics is confounded with the negative association of tree size with trunk scorching and crown consumption, which effectively means that the greater stem and crown damage, the less epicormic resprouting from the upper stem and the more basal resprouting. This is consistent with the rapid development of an epicormic-derived canopy leading to suppression of basal resprouting. However, the only QTL detected for the number of basal resprouts (linkage group 7) was not co-located with fire damage QTL nor QTL for height and amount of epicormic shoot coverage, suggesting that at the genetic level, other factors are at play. This QTL for the number of basal resprouts was co-located with a QTL for the number of epicormic clusters on the bottom 2 m of the stem and DBH, and as all three collocated QTL segregated from the same parent and showed common directionality, these co-located QTL likely reflect a pleiotropic effect of a QTL for greater general resprouting at the base of bigger trees which was not removed by fitting DBH as a covariate.

Relative bark thickness increases rapidly near ground level in many eucalypts (Bowman and Kirkpatrick 1986), including *E. globulus* (Hamilton et al. 2007), and this QTL could reflect a disproportionate increase in relative bark thickness in bigger trees resulting in greater protection of basal epicormic and lignotuber buds.

Within the F₂ family, there were two cases where co-located QTL suggested that the QTL for epicormic resprouting could be a pleiotropic effect of QTL for stem diameter (linkage groups 3 and 7). These co-locations were evident even after accounting for the phenotypic covariation with stem diameter as well as stem and canopy damage. These co-locations could reflect a residual genetic effect of the stem diameter, with the greater absolute bark thickness of larger stems offering better thermal protection of the cambium (Gutsell and Johnson 1996) and embedded bud-forming structures (Burrows 2013; Nolan et al. 2021). Nevertheless, most of the detected QTL associated with recovery traits were independent of QTL associated with stem diameter and even adjusted bark thickness. While thicker bark may offer greater protection of bud-forming structures, Burrows (2013) notes that there is still not strong anatomical and ecological evidence to support this role in the *Myrtaceae*. Indeed, the present study suggests that after accounting for the effects of stem diameter, there are independent QTL affecting epicormic recovery and thus other mechanisms that contribute to genetic variation in epicormic recovery. For example, differences in bark characteristics other than thickness may affect the rate of heat penetration, such as water content, density, proportion of inner and outer bark, structure, and texture (Gill and Ashton 1968; Pausas 2017; Karavani et al. 2018; Resco de Dios 2020). Variation in wood density is another possibility, as previous studies comprising multiple tree species have shown that high wood density delays wood ignition and compartmentalizes damage and mortality due to fire (Brando et al. 2012; Frejaville et al. 2013). However, in the present study, there was no significant phenotypic correlation and no QTL co-location involving wood density and epicormic recovery traits, despite the detection of multiple QTL for wood density and fire recovery, arguing against wood density influencing fire recovery in the present case. Other possible mechanisms underlying fire recovery QTL include the amount of carbohydrate reserves and mobilization (Clarke et al. 2013; Smith et al. 2018), as well as hydraulic limitations arising from xylem embolism and damage (Midgley et al. 2011; Nolan et al. 2021).

The ecotype comparisons and QTL results indicated that browsing by insects and marsupials was genetically variable. The susceptibility of eucalypt foliage to browsing is affected by leaf toughness, nutritional, and defensive chemistry (O'Reilly-Wapstra et al. 2005; Andrew et al. 2007). Newly flushed foliage is particularly attractive to

browsing mammals and insects (Steinbauer et al. 1998; Lawrence et al. 2003). We found co-location of QTL for insect and mammal herbivory in the first year, which could reflect pleiotropy and a shared susceptibility mechanisms associated with traits such as leaf sideroxylonal content (Matsuki et al. 2011) or toughness (Loney et al. 2006). However, as the same trees were assessed and the co-located QTL detected in the same year, the possibility of induced effects arising from the initial browsing (Borzak et al. 2015a) cannot be dismissed. The QTL change across years may reflect differences in the foliage quality following the initial post-fire flush of regrowth from basal or epicormic buds. In eucalypts, foliage quality varies with leaf age (Steinbauer et al. 2015; Marsh et al. 2018) and ontogeny (Lawrence et al. 2003; Borzak et al. 2015b), as does the interaction of herbivores with these traits (Steinbauer and Matsuki 2004). Such variation may have led to different mechanisms causing variation in susceptibility or a change in herbivore species, resulting in different herbivory QTL across years. Alternatively, different herbivory QTL could reflect host independent change in the herbivore communities through post-fire succession, climate variation, or simply season-season stochasticity (Gosper et al. 2015; Gosney et al. 2021). While eucalypts, such as *E. globulus*, are relatively resilient to foliar loss (Pinkard et al. 2004; Borzak et al. 2016), the detected QTL could affect regrowth performance and ultimately tree fitness. However, as we found year-year variation in the browsing QTL, our study suggests that any evolutionary impact of the observed herbivory on regrowth at the genome level would be diffuse and the fitness consequences of specific QTL likely transitory.

Fire is important for *E. globulus* seedling establishment and recruitment (Larcombe et al. 2013; Catry et al. 2015; Aguas et al. 2017). Thus, genetic-based differences in the maternal contributions to the new cohort may reflect differences in a component of their Darwinian fitness (Dall et al. 2015). For example, the discovery of a significant QTL on linkage group 6 for post-fire seedling establishment at the base of the planted F_2 trees reflects a differential contribution of QTL alleles to the new cohort and is independent of tree size. This seedling establishment QTL was not co-located with any other QTL discovered, signaling an underlying mechanism unrelated to the measured structural traits, fire damage, and vegetative recovery. There are several stages at which this QTL could influence the abundance of established seedlings. First, it may be a direct reflection of differences in maternal reproductive output (Deus et al. 2019), which in terms of capsule abundance, seed per capsule or inherent seed germination characteristics have been shown to be under significant genetic control in *E. globulus* (McGowen et al. 2004a; Rix et al. 2015). Such variation could reflect inherent constitutive difference

in reproductive strategies or adaptative differences between maternal trees. Second, it may reflect genetic differences in the loss of canopy-stored capsules and seeds following wildfire, due to variation in traits such as capsule size and wall thickness, moisture content, and capacity to shed seed (dos Santos et al. 2015; Silva et al. 2016). Third, it could reflect a genetic effect on the seedling establishment niche at the base of the focal tree. Litter acts as a physical barrier to *E. globulus* seedling emergence as well as reduces available light (Calviño-Cancela et al. 2018), while burnt soil promotes seedling establishment, since the fire removes litter and other vegetation, as well as increases the availability of nutrients (Tomkins et al. 1991). Genetic-based differences among the races of *E. globulus* have been shown to differentially affect litter communities, as well as condition soil chemistry, with the later revealing quantifiable differences in seed germination in bioassays using soil extracts (Barbour et al. 2009a; Bailey et al. 2012). Basal resprouting can also degrade the seedling recruitment niche close to the maternal tree through resource competition (Potts 1986). While a co-located QTL was not evident, it is noteworthy that there was a low negative phenotypic correlation between the number of established seedlings and the number of basal resprouts.

Regardless of the mechanisms involved, our demonstration of genetic variation in fire-related traits at the intra-specific level is important from a micro-evolutionary perspective as this is a requirement for an evolutionary response to selection (Le Rouzic and Carlborg 2008). While an evolutionary response will be dependent on numerous factors, including genetic constraints and trade-offs (Costa e Silva et al. 2020), we show the potential for wildfire to modify the genetic structure of a forest and accentuate performance-based differences in fitness among genotypes. Trees which do survive and rapidly recover canopies following wildfire are expected to have enhanced competitive ability (Resco de Dios 2020). In even-age plantings of *E. globulus*, mortality has been shown to be size dependent (Chambers et al. 1996; Nickolas et al. 2019). Consistent with this finding, the present study shows that smaller trees are more fire damaged, and more likely to resprout from lower on the stem or tree base. In the extreme case of the dwarf ecotype which mainly resprouted from the base, this would result in a transition from a single-stemmed to a multi-stemmed habit (Nicolle 2006), as commonly observed in wild populations (Jordan et al. 2000). Thus, in a competitive environment such as our uniform-age common garden, wildfire will accentuate the competitive disadvantage of smaller trees as they would be even more prone to be shaded by taller trees whose higher epicormics shoots would allow them to rapidly establish a high canopy and intercept light (Burrows 2013).

In conclusion, our study of the post-fire recovery of uniform age *E. globulus* trees in a common garden revealed genetic variation for fire damage and recovery. We identified QTL for key traits that define the regeneration strategies of eucalypts—stem and basal vegetative resprouting and seedling recruitment (Nicolle 2006). While some of these QTL co-located with structural and fire damage QTL, many represented independent QTL affecting vegetative resprouting and even seedling recruitment. A significant component of the phenotypic and genetic variation in fire damage is linked to pre-fire tree size which has flow-on effects on the extent to which resprouting occurs on the tree stem and base. Our study highlights these effects at the intraspecific level. However, the extent to which the observed differences in fire damage and recovery translate to differences in long-term performance of the different genotypes in this competitive environment will require long-term monitoring. Such information is important for understanding the potential of forest tree populations to adapt to fire, which is predicted to increase in frequency and intensity in many regions of the world under climate change.

Data availability statement

Linkage map and genetic marker data for all members of the mapping population are freely available in the open access repository of the University of Tasmania (<https://eprints.utas.edu.au/22705/>) (Butler et al. 2016). Phenotypic data is available at <http://rdp.utas.edu.au/metadata/8dc20722-4706-4413-99fe-18686b47c6af> (Hernández et al. 2022).

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Author contribution M.A.H., R.E.V., and B.M.P. conceived the ideas and designed methodology. Pre-fire data was collected by H.A. and J.S.F., whereas post-fire data was collected by all authors except H.A. Post-fire herbivory was assessed by J.O.W. The QTL analysis was conducted by M.A.H. under the supervision of J.B.B and J.S.F. M.A.H. performed statistical analyses and led the writing of the manuscript. All authors contributed to the drafts and gave final approval for publication.

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Declarations

Competing interests The authors declare no competing interests.

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