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# Longer duration flooding reduces the growth and sexual reproductive efforts of a keystone wetland tree species

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**Abstract** Wetland forests are dependent on flooding; however, general relationships between flooding and tree responses have been elusive, partly due to often coarse characterisations of flooding. In a novel approach, we used individual tree-scale water level data to assess the effect of flooding duration on a keystone wetland tree species. We surveyed 140 *Eucalyptus camphora* (Mountain Swamp Gum) trees across a swamp forest in both 2012 and 2019. We used TUFLOW to model daily water levels for the period from 2009 to 2019 and determined the flooding history for each surveyed tree. We then assessed the effect of flooding duration and tree size on the survival, growth, condition and extent of sexual reproduction of individual trees. Longer flooding durations limited the basal area growth of larger trees and reduced extent of sexual reproduction. Larger trees had greater basal area growth and signs of sexual reproduction overall. There were no clear effects of flooding duration or tree size on survival or condition. We suggest that for flood-tolerant tree species, prolonged (but not chronic) flooding is likely to result in slower-growing smaller trees potentially without impacts on condition or survival, and that slow tree growth and vegetative regeneration are important strategies for persistence in swamps.

**Keywords** Floodplain tree · Seed production · Sexual reproduction · Swamp forest · Tree growth · Water regime

## Introduction

Wetland forests are dependent on regular flooding, although flooding can both promote and inhibit the growth of wetland trees. Tree responses vary depending on species-specific adaptations to grow in flooded conditions and the hydrological characteristics (duration, depth, timing, etc.) of the flooding (Kozłowski 1986). However, there is contradictory evidence for many flooding-tree response relationships and as such they are difficult to generalise (Mitsch and Rust 1984; Rodríguez-González et al. 2010)—possibly due to the lack of long-term ecohydrological data at the level of individual trees. A better understanding of wetland tree responses to flooding may be possible if long-term tree-level data were assessed.

Flooding regime has long been recognised as important for individual tree growth rates (Conner et al. 1981). For example, regulation-induced altered streamflow patterns and reduced over-bank flooding are associated with declines in riparian tree growth (Reily and Johnson 1982). Conversely, even flood-tolerant trees may exhibit reduced growth or be killed when soils are depleted of oxygen in association with

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chronic flooding, e.g. in impoundments following dam construction (Ernst and Brooks 2003; Kozłowski 1986). Flooding may also affect the growth of individual trees indirectly through controlling stand density and thus competition for resources (Allen et al. 2019).

Complexities in the relationships between wetland trees and flooding are reflected in the numerous studies which have reported both positive and negative effects of flooding on tree growth (e.g. see reviews in Mitsch and Rust 1984, Allen et al. 2019). Studies which have reported hydrological and tree growth variables to be poorly correlated have highlighted that flooding can have both positive (e.g. nutrient and water replenishment) and negative (e.g. anaerobic root zone) influences and thus the relationship between flooding and tree growth is likely to be nonlinear (Mitsch and Rust 1984). Flooding typically promotes tree growth in drier environments where flooding is infrequent (Ellis et al. 2017; Robertson et al. 2001; Stromberg and Patten 1990), while in wetter, flood-prone environments, flooding may be more likely to limit growth (Ernst and Brooks 2003).

Responses to flooding also vary between tree species (Dicke and Toliver 1990; Dudek et al. 1998; Kozłowski 1986; Mitsch and Rust 1984). Flood-tolerance can be expected to increase with the extent to which tree species possess adaptive traits such as the habit of surface rooting, and ability to develop aerenchyma and adventitious roots under flooded conditions (Blom and Voeselek 1996; Colmer and Voeselek 2009). Our study species, *Eucalyptus camphora* (mountain swamp gum), possesses such traits and is considered exceptionally flood-tolerant (Greet 2016; McMahon and Franklin 1993).

While numerous studies have explored the growth responses of trees to flooding, the effect of flooding on the reproductive output of wetland trees is much less researched. Similar to growth effects, flooding in semi-arid regions is likely to promote the reproductive output of floodplain trees (Jensen et al. 2008; Moxham et al. 2018), while in wetter environments, a negative effect of prolonged flooding on reproductive output might be expected. It could be expected that when tree growth is limited by flooding, so is its reproductive output, e.g. reducing flowering and/or seed production, as has been found for herbaceous wetland plants (Warwick and Brock 2003).

Flood-tolerant tree species may grow best in regularly flooded sites (Allen et al. 2019; Callado et al. 2004), but even they may be adversely affected by chronic flooding (Dicke and Toliver 1990; Ernst and Brooks 2003). Within-species growth responses of individual trees to flooding are also dependent on tree size, with larger trees potentially more susceptible to the negative effects of prolonged flooding (Dicke and Toliver 1990; Ernst and Brooks 2003).

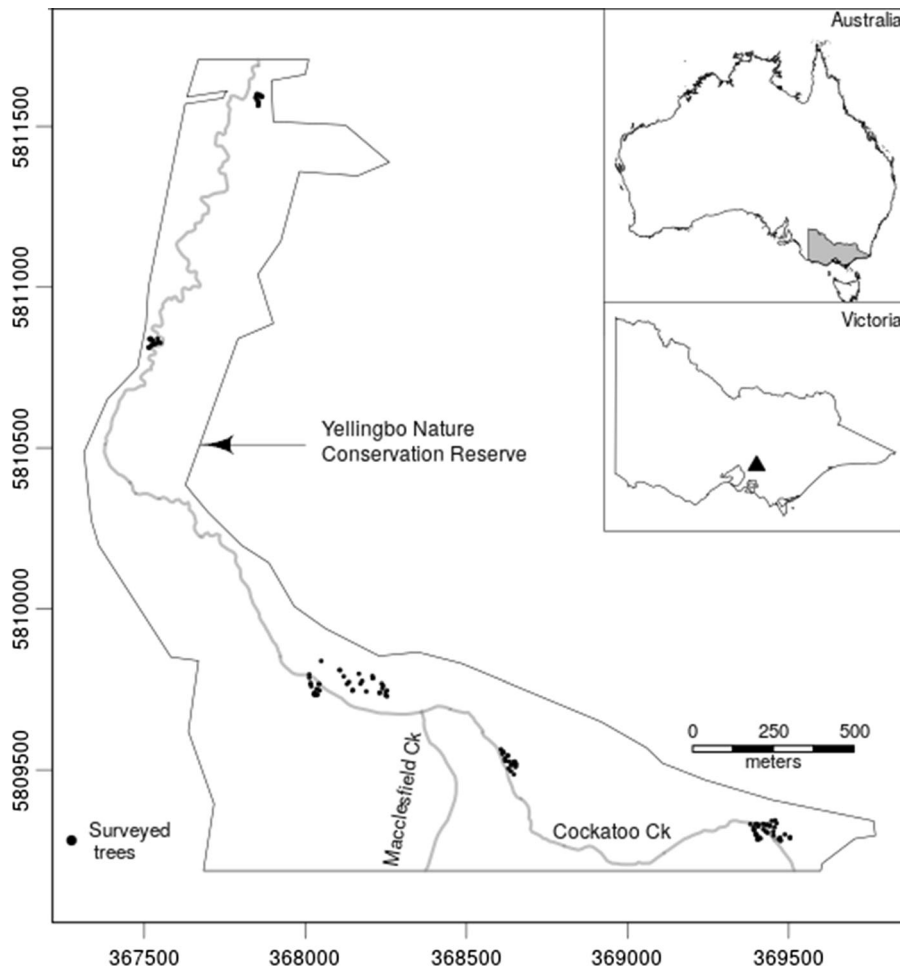
A major impediment to elucidating general relationships between flooding and tree responses may be within-site variability between trees (Day 1985). Studies have typically used site-level characterisation of streamflow or flooding to assess effects of flooding on tree growth (e.g. low/high elevation or more/less flooded sites; e.g. see meta-analysis in Allen et al. 2019). There is a recognised need to develop quantitative models at the scale of individuals (Solari et al. 2016). Hydrodynamic modelling approaches are needed to characterise flooding at individual trees across large areas and long time periods, but have not been widely applied for vegetation response studies (Casas-Mulet et al. 2016).

Using repeated field surveys and modelled daily water levels at the scale of individual trees, our study aimed to assess the relationships between flood duration and the survival, growth, change in condition and signs of sexual reproduction of a flood-tolerant wetland tree, *Eucalyptus camphora*. Despite the marked flood tolerance of *E. camphora*, we expected that longer duration flooding would reduce its survival, growth, vigour and sexual reproductive activity.

## Materials and methods

### Study site

Our study focuses on *Eucalyptus camphora* swamp forests within the Yellingbo Nature Conservation Reserve (Yellingbo NCR, 37° 51' S, 145° 29' E; c. 110 m a.s.l), south-eastern Australia (Fig. 1). The area receives c. 1100 mm of rainfall annually and experiences mean daily maximum temperatures of 13.6 °C in winter and 25.6 °C in summer. The reserve comprises c. 680 ha of remnant, riparian and swamp forest stretching along four watercourses, the Woori Yallock, Sheepstation, Macclesfield and Cockatoo Creeks. Its low-lying floodplains are dominated by



**Fig. 1** Tree locations within the Yellingbo Nature Conservation Reserve, Victoria, south-eastern Australia

swamp forests that are seasonally to near permanently inundated, where *E. camphora* is the sole dominant occurring as a continuous canopy or scattered emergent in association with paperbark (*Melaleuca* spp.) and tea-tree (*Leptospermum* spp.) thickets (McMahon and Franklin 1993). This community varies in structure from open forest to woodland with a variable canopy height (6–25 m) and supports a diversity of sedges, rushes grasses and forbs (Turner 2003).

*E. camphora* swamp forests at Yellingbo represent the largest remnant of this forest type and provide habitat for the last remaining wild populations of the critically endangered helmeted honeyeater and lowland Leadbeater possum (Harley et al. 2005; Pearce and Minchin 2001). The reserve is currently managed for conservation purposes. Its swamp forests are dieback-affected, particularly in an area known as

the Cockatoo Swamp subject to prolonged flooding due to hydrological alterations resulting from stream channelisation upstream (Greet 2016).

#### Tree surveys

In response to accelerating tree dieback at the site, a commissioned survey of tree condition was conducted at the Yellingbo NCR in May 2012 (austral autumn) by Australian Ecosystems (2013). They surveyed 140 *E. camphora* trees across seven sites with one of the authors (JG) assisting. Twenty live trees (> 100 mm diameter at breast height, DBH) were selected at each of seven locations surrounding a core dieback-affected area of the Cockatoo Swamp within Yellingbo NCR (Fig. 1). Trees were haphazardly selected but with an endeavour to survey a representative sample, i.e. a

proportional sample of good and poorer condition trees at each site. Each tree was assigned a unique identifier, permanently marked with a stamped metal tag and its location recorded using a handheld GPS.

Tree condition was assessed using The Living Murray (TLM) method. This method was developed to monitor the condition of floodplain trees and involves visual assessments of tree condition attributes against an absolute reference tree—a tree in best possible condition (Souter et al. 2009). This method has proven to be robust and its measures consistently scored across different groups of observers (Cunningham et al. 2007; Souter et al. 2010). For each tree, several tree condition attributes were initially assessed, including categorical scale assessments of crown extent (proportion of all existing branches which are foliated) (Table 1), crown density (proportion of skylight intercepted by foliated parts of the crown), and extent of sexual reproduction (Table 2). For each tree, the diameters of all stems > 100 mm were measured at 1.3 m using a DBH tape. Exploratory analyses indicated that crown extent and extent of sexual reproduction displayed adequate variability for assessment of change in relation to flooding. In May 2019, all trees were relocated (where possible, e.g. some had fallen over and/or lost their tags and could not be positively identified) using a handheld GPS, and their survival, DBH (mm) of each stem > 100 mm, crown extent and extent of sexual reproduction resurveyed by the same author who assisted with the initial survey (JG).

### Flooding model

Flooding of the swamp was modelled using TUFLOW ([www.tuflow.com](http://www.tuflow.com)) a two-dimensional hydrodynamic model to simulate water levels from hydrologic time-

**Table 2** Category scale for assessments of extent of sexual reproduction—abundance of buds, flowers and capsules (sensu Souter et al. 2009)

Score	Description	Definition
0	Absent	Not visible
1	Scarce	Present but not readily visible
2	Common	Clearly visible
3	Abundant	Dominates the appearance of the tree

series and topographic data. The strengths of this approach are (i) the ability to simulate flooding across a large, complex floodplain, with limited calibration data; (ii) the ability to hindcast inundation history before vegetation monitoring began; (iii) flexibility in allowing data to be extracted for areas that may not have originally been part of the study, or for other studies; (iv) representation of complex two-dimensional flow paths; and (v) representation of storage and evaporation fluxes. This approach addresses the limitations of common vegetation inundation modelling approaches such as water balance and steady state modelling, but has only been applied in a small number of studies (e.g. Benjankar et al. 2011).

The inundation modelling method is described in detail in Russell and Greet (2018). Key aspects of the method are presented in the following sections.

### Hydrology

Flow data were available for two gauges just upstream of the swamp, on Cockatoo Creek (Gauge No. 229248) and Shepherds Creek (Gauge No. 229677), for the period April 1998 to December 2018. Flow estimates for the ungauged Macclesfield Creek that enters

**Table 1** Category scale used for crown extent assessments (sensu Souter et al. 2009)

Score	Description	Percentage of assessable crown baring leaves
0	None	0
1	Minimal	1–10
2	Sparse	11–20
3	Sparse–medium	21–40
4	Medium	41–60
5	Medium–major	61–80
6	Major	81–90
7	Maximum	91–100

Cockatoo Swamp were based on a linear scaling of the Cockatoo and Shepherds Creek combined flow.

### *Hydrodynamic model development*

The hydrodynamic model was built in TUFLOW Classic, a two-dimensional grid-based model. The model was adapted from a previous MIKE FLOOD model developed by Water Technology (2014) and subsequently used by Jacobs (2015), and then improved using recent survey data and further calibration.

The topography was based mainly on a LiDAR 1 m digital elevation models (DEM) collected by the University of Melbourne for this project using an unmanned aerial vehicle (Phoenix Alpha AL3-32 sensor capturing 250 points per m<sup>2</sup> and vertical accuracy of 0.01 m in 2017), resampled at a 5 m grid resolution for input to the model. A 2008 government-provided LiDAR product (Greater Melbourne South-East LiDAR 1 m DEM) collected by manned aircraft with vertical accuracy of  $\pm 0.1$  m was used to infill areas not covered by the 2017 LiDAR. Neither LiDAR product captured elevations below water level, but both were flown during relatively low-water conditions in the swamp, ensuring good definition of inundation-prone areas and representation of hydraulic conveyance.

Comparison with feature surveys were used to apply constant offsets to each DEM to make them consistent with each other and with survey datasets, and to adjust the DEM locally where required. Hydraulic resistance was represented by a Manning's coefficient of 0.067, based on guidance documents (Chow 1959) and calibration.

Inflow boundaries were defined at the upstream ends of Cockatoo, Shepherd and Macclesfield Creeks. A water level boundary was applied to the 2D model at the downstream end of the model, based on nearby gauged water levels. Evapotranspiration (ET) was included in the model based on gridded daily Morton's actual ET data (Morton 1983) for the study area (<https://www.longpaddock.qld.gov.au/silo/>).

### *Hydrodynamic model calibration and validation*

A July 2014 event, and the February to December 2015 period were selected as calibration events to allow for calibration of water levels over a peak flow

event, and over the course of a whole wet season, including filling and draining behaviour. Calibration was undertaken using continuously gauged water levels at three locations and measured point water levels at 11 locations on 25 April 2015 and 34 locations on 29 October 2015. Validation was undertaken using gauged water levels for 2014–2018.

### *Data analyses*

#### *Data curation*

Firstly, we extracted the water-level time series data for the period 2009–2019 from the TUFLOW model for the relevant cell for each surveyed tree. We then calculated flooding duration and depth for each tree. Flooding duration was calculated as the mean number of days per year for which surface water was present within the cell in which the surveyed tree was located. Mean depth was calculated as the average depth of water for that cell, averaged across all days (including dry days). Because flooding duration and mean depth were highly correlated, and the former was more variable and less skewed across trees, we used flooding duration for analyses.

For survival, growth and condition analyses, flooding duration was averaged across the years between the surveys, i.e. Apr 2012–2019. For reproduction, flooding duration of the three-year period preceding each survey was used with tree data combined for both surveys. This period is considered relevant for the production of reproductive structures—crops of buds, flowers and capsules—that were assessed in each of the surveys (Jensen et al. 2007).

Of the 140 trees tagged in 2012, we were able to relocate 117 individuals in 2019 (unlocated trees may have died and/or fallen over, lost their tags, etc.). Unlocated trees were unbiased with regard to flooding history. Of the relocated trees, 4 were incorrectly tagged and 2 had fallen over (but were still alive), these were excluded from further analyses. Of the remaining 111 trees, 13 had died. Dead trees were included in analyses and attributed a '0' for tree growth and a condition score of 0%.

All 111 trees were included in assessments of flooding effects on survival, tree condition and extent of reproduction. Of the 111 trees, 104 were deemed suitable for growth comparison between 2012 and 2019. One tree was excluded due to unrealistic

flooding model outputs (likely due to errors in local topography representation). A further six trees were excluded due to large decreases in measured DBH (typically in cases of main stem breakage).

### Data analyses

We used generalised linear models to assess the effects of flooding duration and tree size and their potential interaction on tree survival, growth (basal area growth), change in condition (based on crown extent) and extent of sexual reproduction. Because the effects of wetland on tree growth have been reported to be dependent on tree size (Dicke and Toliver 1990), all models initially included an interaction term; if the interaction term was non-significant it was removed to ensure it was not masking any main effects of interest. Tree survival was modelled using logistic regression, tree growth using normal linear regression, change in condition using beta regression, and extent of sexual reproduction using ordinal regression.

All models included a random factor of Site to account for the spatially clustered nature of the tree locations. An additional random factor of Tree was included for the reproduction model because data from both surveys were used to account for that fact that each tree was surveyed twice. We fit all GLM models using the *glmmTMB* package (Brooks et al. 2017) except for the ordinal regression model for reproduction which was fit using the *ordinal* package (Christensen 2019). We performed all analysis in R version 3.6.0 (R Core Team 2019).

We defined growth as the increase in basal area between the 2012 and 2019 surveys. In cases of trees with multiple stems (29 out of 104 trees used in the analysis had 2 + stems), we considered only growth of the largest stem. Tree size used in the models for tree growth was the initial basal area of the largest stem. For tree survival, change in condition, and extent of reproduction the initial total DBH (inclusive of all stems) was used to model tree size, because these tree responses considered the whole tree. For analyses of tree condition, midpoints of categories used for crown extent assessments (Table 1) scaled to between 0 and 1 (e.g. score of 1 = 0.05, 2 = 0.15, 3 = 0.3, etc.) were used.

We present all raw data in box plots or scatterplots with regression lines where appropriate. For all models we report results of tests of relevant fixed

effects (flooding duration and tree size, and flooding  $\times$  tree size interaction where relevant) and marginal  $R^2$  values, a measure of the variation explained by the fixed effects in the model. Where the flooding duration  $\times$  tree size interaction term was significant, we defined large trees as those greater than the 75th percentile, and small trees as those smaller than the 25th percentile, for presentation of regression lines. All data and code are freely available via the Open Science Framework (<https://osf.io/s3t8b/>).

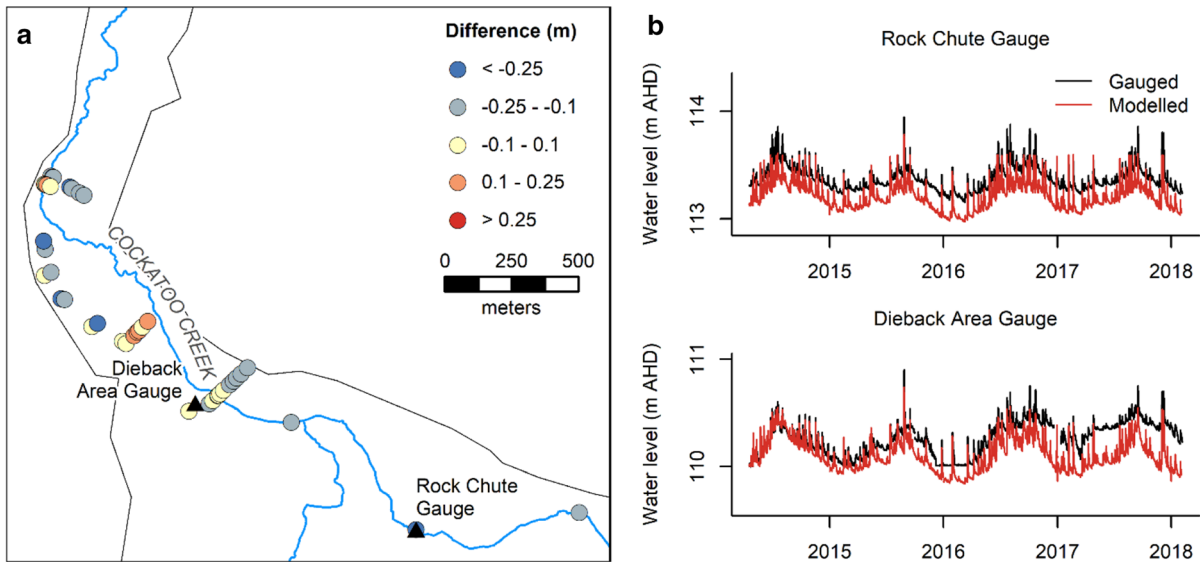
## Results

### Hydrodynamic model calibration and validation

Calibration resulted in a good match with measured water levels (Fig. 2a), albeit with a tendency to underpredict slightly (by around 0.1 m on average). Validation results were very similar to the calibration results, with slight underprediction of water levels (by around 0.1–0.2 m; Fig. 2b). High flow events produced a better match than periods of low inflows or drainage flows, and drainage tended to be slightly too quick. The model is not capable of simulating exchange with groundwater, which is probably why the model does not fully match drainage and low-flow behaviour. As well as influencing surfacewater behaviour, groundwater levels can have a direct influence on vegetation growth and condition. However, groundwater and surfacewater levels are known to be highly correlated at the site (Zacks et al. 2018) and therefore including only surfacewater data in our hydrodynamic and statistical models is considered adequate. After assessing these limitations, the model was judged fit for the purpose of estimating tree-level flooding characteristics.

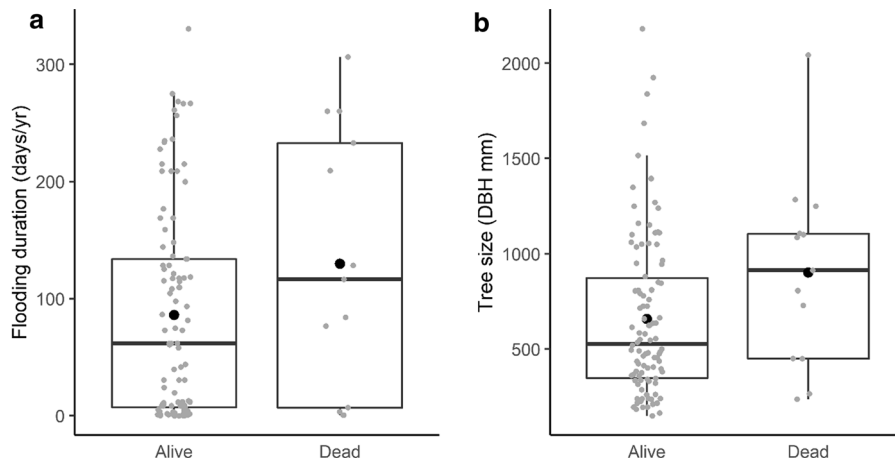
### Tree survival

The 13 trees that died between the 2012 and 2019 surveys tended to be larger (mean total DBH = 901 mm c.f. 658 mm) and flooded for longer (mean flooding duration = 130 days/year c.f. 86 days/year) than those that remained alive ( $n = 98$ ). However, these differences were not statistically significant (Fig. 3; Table 3).



**Fig. 2** Calibration and validation of modelled water levels. **a** Difference between modelled and measured point water levels on 23 Apr 2015 and 29 Oct 2015; **b** gauged and modelled water

levels for 2014–2018 at two gauges (locations shown in **a**). See Fig. 1 for location of study area



**Fig. 3** Boxplots of **a** flooding duration (days/year) and **b** tree size (DBH mm) and survival status (alive or dead) of the resurveyed trees. Bolded lines represent median values; boxes comprise the interquartile range (IQR: 25th to 75th percentile

values); and whiskers comprise all data within 1.5\*IQR from the 25th to 75th percentiles. Grey circles indicate raw data (n = 111) and black circles indicate mean values

Tree growth

The mean basal area (including all stems) of all surveyed live *E. camphora* trees was 0.28 m<sup>2</sup> in 2012 (n = 136) and 0.32 m<sup>2</sup> in 2019 (n = 98). For the 104 trees deemed appropriate for growth assessments between 2012 and 2019, the mean basal area growth rate was 0.01 m<sup>2</sup>/year (range = - 0.004 to 0.036 m<sup>2</sup>/

year). The average flooding duration for these trees was 90 days/year (range = 0–306 days/year).

For all trees flooded for > 200 days/year, their growth was below average regardless of tree size, i.e. < 0.01 m<sup>2</sup>/year. The effect of flooding duration on basal area growth was dependent on tree size (initial basal area), with the growth of larger trees limited most by flooding (i.e. there was an interaction effect of flooding duration and tree size on growth: P < 0.05,

**Table 3** P-values from tests for fixed effects of flooding duration, tree size, and flooding duration  $\times$  tree size (where appropriate) on tree survival, basal area growth, change in condition and extent of sexual reproduction

	Flooding duration	Tree size	Flooding duration $\times$ tree size	Marginal R <sup>2</sup>
Survival	0.638	0.429	NA	0.01
Growth	0.898	<b>0.001</b>	<b>0.025</b>	0.14
Condition	0.505	0.371	NA	NA
Reproduction	<b>0.033</b>	<b>&lt; 0.001</b>	NA	0.20

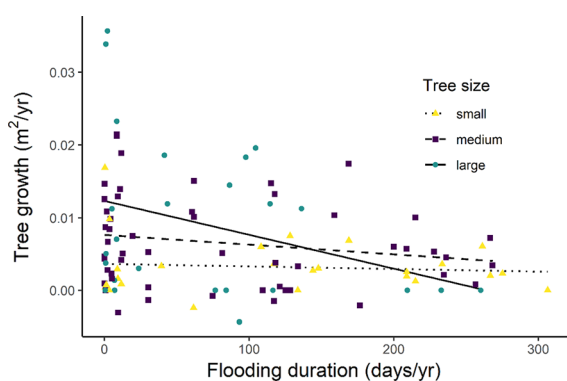
Bolding indicates significant effects,  $p < 0.05$

NA indicates the interaction term was not significant and was not included in the final model. Marginal R<sup>2</sup> values indicate the proportion of variance explained by fixed effects in the model where appropriate

Table 3). Where flooding durations were short, larger trees tended to grow more than smaller trees. Thus, reduced growth with longer duration of flooding was only apparent for larger trees (Fig. 4).

#### Tree condition

Mean crown extent of all live *E. camphora* trees surveyed was 73% for both years (i.e. 73% of the condition of a reference tree, on average). Considering only the 111 resurveyed trees (including the 13 trees that died), tree condition was, on average, 12% less in 2019 compared with 2012. Nonetheless, there were no effects of flooding duration or tree size on change in condition of trees between surveys.



**Fig. 4** Relationship between flooding duration (days/year), tree size and tree growth (basal area growth  $m^2/year$ ). Lines indicate best fits for small ( $0.02$ – $0.06 m^2$ ), medium ( $0.06$ – $0.35 m^2$ ), and large ( $0.41$ – $1.30 m^2$ ) sized trees;  $n = 104$  in total. Note size categories are for illustrative purposes only, size was modelled as a continuous variable, see data analyses section for details

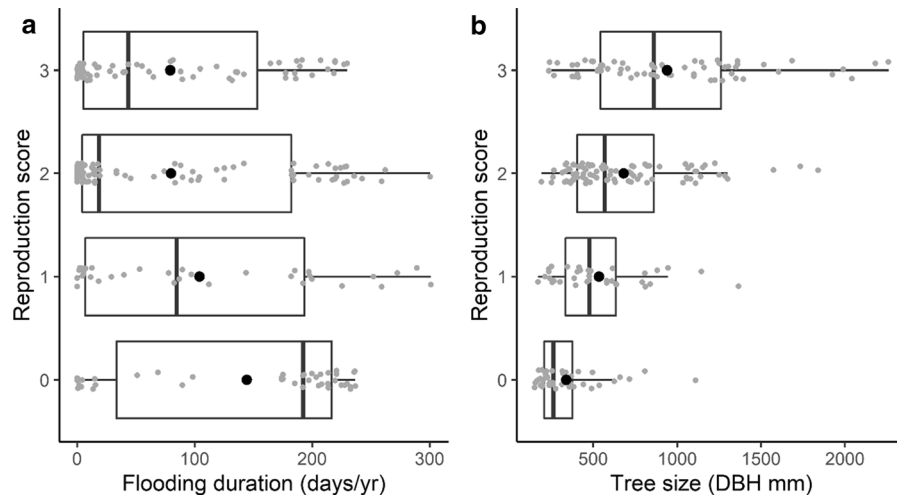
#### Sexual reproduction

Signs of sexual reproduction (buds, flowers and capsules) were more apparent in 2019 than in 2012, with 80% of trees recording a score of 2 or 3 for extent of sexual reproduction in 2019 compared with 57% in 2012. Notably, the three-year period preceding the 2019 survey was drier than that preceding the 2012 surveys (2010–2012 was a particularly wet period), with trees flooded for a mean duration of 67 days/year compared to 115 days/year, respectively.

Prolonged flooding was associated with decreased signs of sexual reproduction. For trees with no signs of sexual reproduction, the mean duration of flooding in the three-year period preceding was longer (144 days/year) than for those with reproduction scores of 1 (104 days/year), 2 (80 days/year) or 3 (79 days/year). There was also a clear effect of tree size on extent of sexual reproduction, with trees with abundantly apparent sexual reproductive activity almost three times larger than trees with no signs of sexual reproduction on average (Table 3; Fig. 5).

#### Discussion

We did not find evidence that prolonged flooding (up to 300 days/year) affected the survival or condition of the flood-tolerant wetland tree, *E. camphora*. Conversely, we found evidence that longer duration flooding was associated with the reduced basal area growth of larger *E. camphora* trees, and fewer signs of sexual reproduction (buds, flowers and capsules). We also found that larger trees had greater basal area growth where flooding durations were short and had more apparent signs of sexual reproduction overall.



**Fig. 5** Boxplots of reproduction scores and **a** flooding duration (days/year) and **b** tree size (DBH mm) combining data from both the 2012 and 2019 surveys. Bolded lines represent median values, boxes comprise the interquartile range (IQR: 25th to

75th percentile values) and whiskers comprise all data within 1.5\*IQR from the 25th to 75th percentiles. Grey circles indicate raw data ( $n = 111$ ) and black circles indicate mean values

Using novel methods combining modelled daily water levels and repeated field surveys, our study provides good evidence that prolonged flooding (e.g. > 200 days/year) promotes slower growth of wetland trees and reduces their efforts to reproduce sexually.

It is perhaps not surprising that our study did not show evidence for an association between flooding duration and survival or condition of *E. camphora* given its exceptional flood-tolerance (Greet 2016; McMahon and Franklin 1993). The seven-year period between the two surveys did not include any large flood events and flooding was not as prolonged as it is during wetter periods. For instance, a notable dieback event in 2011–12 (preceding and motivating the initial tree survey) is thought to have been driven by near continually flooded conditions between 2010 and 2012 (Greet 2016). We suggest the absence of continual flooding spanning multiple years and the small number of trees that died between our surveys precluded greater insights into the relationship between flood duration and survival in this study.

Despite the flood tolerance of *E. camphora*, we did find evidence that longer duration flooding limits its basal area growth. We only found this to be the case for larger trees, likely because of their greater capacity for basal area growth where flooding was not limiting, whereas growth of smaller trees is more likely to be still limited by competition in the absence of flooding (Coomes and Allen 2007). Furthermore, smaller stems

are more flexible, provide a higher surface area for oxygen transport to roots and have lower maintenance costs than bigger stems (Rodríguez-González et al. 2010). Therefore, in contrast to larger trees, smaller trees might experience less physical and physiological stress when subjected to flooding (and consequently their growth rates are less impacted). Our results are concordant with those found for bald cypress (*Taxodium distichum*), a widespread wetland tree of southeastern US, for which continual flooding over five years reduced growth only for larger trees (> 25 cm diameter) (Dicke and Toliver 1990).

It is likely that growth of larger trees is limited by flooding due to hypoxia. Although some floodplain trees remain physiologically active during inundation (Dang et al. 1991; Parolin and Wittmann 2010), energy production via altered metabolic pathways (i.e. anaerobic metabolism) is typically less efficient (Colmer and Voesenek 2009). Therefore, resources (i.e. carbohydrates) from photosynthesis and storage are likely to be predominantly allocated to metabolic maintenance and the construction of morphological adaptations rather than radial growth. Moreover, for trees at regularly flooded sites accumulation of above ground biomass can be slow even during growth in non-flooded periods, because an increased proportion of the acquired carbon is reserved for storage formation in order to maintain the ability to survive and to

recover from such disturbance via resprouting (Vesk and Westoby 2004).

Our findings are also consistent with previous studies that have found wetland tree growth is dependent on tree size (Allen et al. 2019; Dicke and Toliver 1990). However, despite our use of modelled tree-level flooding data, there was considerable variation in our tree response models not explained by either flooding or tree size. As previously suggested, while flooding is an important driver of tree growth, several factors are likely to determine how well a wetland tree survives and grows (Conner and Day Jr 1992; Mitsch and Rust 1984) including climatic (Dudek et al. 1998), soil and water quality (Allen et al. 2019) factors. Several studies have shown that wetland tree growth is also limited by stand density (something not measured in our study), with stand density in turn limited by flooding (Allen et al. 2019; Conner et al. 1981; Horner et al. 2009; Johnson and Bell 1976).

Our study provides evidence that longer flooding durations reduce the sexual reproductive output of *E. camphora*. While prolonged flooding is thus likely to limit stand seed production (just as water-stress does; Jensen et al. 2008), we suggest that this may not necessarily limit the maintenance of populations of wetland trees able to reproduce clonally. *E. camphora*, like many willows (*Salix* spp.), readily resprouts from epicormic buds along the trunk of fallen trees in wet conditions, which may then develop into mature trees (Karrenberg et al. 2002; Pearce 2000). Furthermore, opportunities for seedling establishment are often limited in regularly flooded sites thus seed production, particularly during wet periods, is unlikely to be a fruitful enterprise for wetland trees of regularly flooded environments. We suggest that wetter conditions are likely to promote greater investment in asexual reproduction (e.g. epicormic bud development) over sexual reproduction (flowering and seed production) in flood-tolerant trees capable of reproducing vegetatively.

Slow tree growth should not necessarily be of concern in non-timber production forests. Rather, slower growth may be a successful persistence strategy for trees growing in stressful environments (e.g. swamps) that may allow trees to live longer and attain great ages (> 300 years) (Bigler 2016; Vieira et al. 2005). Indeed, previous dendroecological studies of *E. camphora* at Yellingbo suggest that *E. camphora*

growth is slow and continuous and tree age difficult to determine and poorly correlated with size on water-logged sites (Pearce 2000). In our study, there was no evidence that flooding up to 300 days/year affected tree survival or condition suggesting the slower growth rates of long-flooded trees were sustainable and not an indicator of poor tree health.

Flooding effects on tree growth characteristics can have important implications for their value as habitat (Ellis et al. 2017). *E. camphora* swamp forests at Yellingbo provide critical habitat for both of the State of Victoria's faunal emblems, the helmeted honeyeater and Leadbeater's possum. Both bird and possum prefer structurally complex forests of high stem density (Pearce et al. 1994; Greet et al. unpublished data). We suggest that slower tree growth and reduced sexual reproductive output (and potentially increased propensity for asexual reproduction, i.e. resprouting), may provide for the appropriate habitat characteristics for such swamp-adapted fauna. Similarly, Ernst and Brooks (2003) found prolonged flooded wetland forests were dominated by denser stands of smaller shrubbier trees of flood-tolerant species supported by clonal regeneration. We recommend further research into the potential effects of flooding on trade-offs between sexual and asexual reproduction of wetland trees and implications for wetland tree growth and stand characteristics.

Our study used novel methods to characterize long-term flooding regimes at the individual tree scale. Common methods neglect within-site variability (e.g. use of site-level inundation data), do not allow hindcasting prior to the measurement period (e.g. direct measurement), and are not able to represent key processes in wetland forests (e.g. water balance models, steady-state flow models and one-dimensional models such as HEC-RAS). The dynamic, two-dimensional hydraulic modelling approach used in this study overcomes these limitations, allowing simulation across large areas and long time periods, and representation of complex flow paths, flood storage, antecedent conditions and evaporation. This approach has rarely been adopted but is becoming more accessible with advances in computing (e.g. Benjankar et al. 2011).

## Conclusions

Our study assessed tree responses to flooding modelled at the level of individual trees. We found evidence that the growth of *E. camphora* trees and their sexual reproductive efforts are limited by prolonged flooding. We suggest that slow growth may be a good persistence strategy for trees inhabiting swamps and such growth conditions produce smaller trees (and potentially denser stands) which invest greater energy supporting asexual rather than sexual reproduction.

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