Author/s:
Fischer, S;Greet, J;Walsh, CJ;Catford, JA

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Authors:

Sarah Fischer[a], Joe Greet[a], Christopher J. Walsh[a], Jane A. Catford[b,c]

Institutional affiliations:

[a] School of Ecosystem and Forest Sciences, Burnley Campus, The University of Melbourne, 500 Yarra Bld, Richmond, 3121, Victoria, Australia;

[b] Department of Geography, King's College London, 40 Aldwych, London, WC2B 4BG, UK;

[c] School of BioSciences, The University of Melbourne, Royal Parade, Parkville, 3052, Victoria, Australia.

Corresponding author:

Sarah Fischer, rettichretter@hotmail.de, 0061448049172

Co-author email addresses:

Joe Greet: greetj@unimelb.edu.au;

Christopher J. Walsh: cwalsh@unimelb.edu.au;

Jane A. Catford: jane.catford@kcl.ac.uk

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Suggested reviewers:

Judith Sarneel (judith.sarneel@umu.se);

Claire Moxham (claire.moxham@delwp.vic.gov.au);

Paula Meli (paula.meli@ufrontera.cl);

Alejandra Zuñiga-Feest (alejandrazunigafeest@gmail.com)

RESTORED RIVER-FLOODPLAIN CONNECTIVITY PROMOTES WOODY PLANT ESTABLISHMENT

Sarah Fischer[a*], Joe Greet[a], Christopher J. Walsh[a], Jane A. Catford[b,c]

[a] School of Ecosystem and Forest Sciences, Burnley Campus, The University of Melbourne, 500 Yarra Bld, Richmond, 3121, Victoria, Australia; [b] Department of Geography, King's College London, 40 Aldwych, London, WC2B 4BG, UK; [c] School of BioSciences, The University of Melbourne, Royal Parade, Parkville, 3052, Victoria, Australia.

*Corresponding author: rettichretter@hotmail.de

Abstract

Riparian forest ecosystems are declining globally. Many floodplains no longer flood and thus cease to satisfy the hydrologic requirements for riparian tree maintenance and regeneration. To promote woody riparian plant recruitment where flood regimes have been altered by flow regulation, effective approaches to restoration need to be developed. We implemented a landscape-scale experiment in a remnant, temperate floodplain forest. By constructing two weirs within channelized reaches of a stream, we redirected flows into networks of historic distributary channels, which facilitated widespread floodplain inundation. Using a control-reference-impact study design, we assessed the establishment and growth of planted seedlings of three woody species (*Eucalyptus camphora*, *Leptospermum lanigerum* and *Melaleuca squarrosa*) over 13 months in response to flooding achieved by floodplain reconnection. Planted seedlings had higher height and diameter growth rates at both induced (19–29 cm, 1 mm) and naturally flooded (34–44 cm, 3–5 mm) than at non-flooded (4–10 cm, -5–-3 mm) sites. However, survival rates and temporal growth patterns differed between species according to variation in flood duration and soil moisture, illustrating the different hydrological requirements of the coexisting species. This highlights

that variable flooding and drying patterns are essential to create recruitment niches for different riparian plant species and shows the importance of river-floodplain connectivity for providing adequate flooding regimes. Our study demonstrates the suitability of two complementary restoration approaches – restoring hydrology and active revegetation – for promoting the regeneration of riparian forests.

1. Introduction

Riparian forests host a vast biodiversity, purify air and water, regulate climate and drive biogeochemical cycles at global and local scales. These ecological benefits are largely created by key elements of riparian forests: woody plants. Riparian trees have evolved under natural flooding and drying patterns provided by the stream with which they are connected (Junk *et al.*, 1989). However, throughout much of the world, this connectivity has been disrupted by human activity such as water extraction, damming or channelization (Grill *et al.*, 2019). Consequently, many floodplains no longer flood and thus cease to satisfy the hydrologic requirements for riparian tree maintenance and regeneration (Kingsford, 2000; Tonkin *et al.*, 2018). Most remaining riparian forests display symptoms of degradation and decline, impairing their environmental and societal functions (Tockner and Stanford, 2002; Tonkin *et al.*, 2018). This has prompted efforts to restore native riparian forests and develop effective restoration strategies (Palmer and Ruhi, 2019).

Successful restoration likely requires implementation of complementary approaches to address abiotic and biotic constraints to riparian forest regeneration. Aspects of the historic flooding regime need to be reinstated in order to support native vegetation (Poff *et al.*, 1997; Laub *et al.*, 2020). However, reestablishing physical conditions does not *per se* lead to the reversion of the altered ecosystem to the pre-degraded state (Suding *et al.*, 2004). Regeneration of degraded riparian forests might be further constrained by reduced adult plant health, propagule availability, altered dispersal vectors, lack of suitable nursery sites or competition from invasive understory species (Jensen *et al.*, 2008; Moxham and Dorrough, 2008; Moxham *et al.*, 2018). To address these constraints, replanting of native woody vegetation may compensate for absent or low recruitment and accelerate riparian forest rehabilitation. Planting can facilitate local reestablishment of species, though seedlings' vulnerability to environmental stressors makes establishment a critical hurdle for ecological restoration (Greet *et al.*, 2020a; Laub *et al.*, 2020; Meli *et al.*, 2021). With their high environmental variability, riparian ecosystems exemplify these challenges and thus provide a good model ecosystem for studying establishment processes.

The juvenile phase is a particularly stress-sensitive life-history stage of plants, and the establishment (i.e. survival and growth) of woody plant seedlings has profound implications for the persistence of riparian forests (Walls *et al.*, 2005). Seedlings of many woody riparian species require specific hydrologic conditions during establishment (Mahoney and Rood, 1998; Carter Johnson, 2000; Elias and Vieira, 2020). Therefore, seed release of such species typically coincides with natural flow pulses, which enhance the likelihood that seedlings will be exposed to conditions favorable for recruitment (Pettit and Froend, 2001; Stella *et al.*, 2006). Replicating this synchronization of biological and hydrological processes via management activities is challenging. While the flooding response of early recruitment stages (i.e. dispersal and germination) has been well studied, later recruitment processes (i.e. establishment) in response to flooding often remain unclear (Andersen, 2005).

Woody riparian plant recruitment is likely entwined with flooding, but particular flooding regime characteristics such as depth, duration, frequency and timing may be critical (Vreugdenhil *et al.*, 2006). Seedlings inhabiting dynamic riparian habitats are naturally confronted with contrasting hydrological extremes: flooding and drought. An overexposure to either can compromise plant establishment. While flooding may evoke stress, the metabolic costs of adaptation to flooding may be compensated for by nutrient supply and moisture recharge, which fuel plant growth during the post flooding period (Odum *et al.*, 1979). Shoot elongation and leaf expansion are crucial for harvesting light, thereby producing energy necessary for root expansion and the acquisition of water and nutrients that in turn enables further growth. Aligning hydrological restoration and planting to optimize seedling establishment requires an improved understanding of seedling hydrological requirements.

To date, the response of seedlings to different water regimes has mostly been tested over short periods of time in controlled pot experiments (e.g. Smith and Bourne 1989, Pryor *et al.* 2006, Maxwell *et al.* 2016), and often focused on either the effects of drought, or flooding (Capon *et al.*, 2009). Studies on species from environments where water is abundant or at least sufficient for adult trees with extensive root systems typically concentrate on flooding stress (e.g. Kogawara *et al.* (2006), Greet (2015); Marks and Atia (2020)). While some species perform well, greenhouse trials have reported declines in plant growth and survival for many riparian plant seedlings subjected to flooding (Urquhart, 2004; Pryor *et al.*, 2006; Zacks *et al.*, 2019). This variation in response to flooding may reflect distinct hydrological niches of coexisting species, but to what extent niches are segregated by flooding patterns during seedling establishment in complex environmental contexts remains unresolved. The complexity of hydro-biological linkages is difficult to mimic ex-situ. This calls for more field studies that address natural fluctuations of flooding over time and the ability of plants to both survive and recover from certain stresses (Argus *et al.*, 2015).

In this study we combine restoration works and ecological research to advance our understanding of globally threatened riparian forest ecosystems and guide future restoration practice. We empirically examined the hydrological requirements for the establishment of key riparian species (woody plant seedlings) and evaluated the efficacy of the restoration approach undertaken. We conducted a field-based, landscape-scale experiment in a remnant, temperate riparian forest to investigate the success of restored river-floodplain connectivity in conjunction with revegetation to promote riparian forest regeneration. Specifically, we asked: i) are the survival and growth of planted seedlings of three co-existing woody riparian species affected by flooding? ii) Do species respond in different ways? And iii) does flooding achieved by floodplain reconnection and natural flooding have the same effect?

2. Methods

2.1. Study area

Our study was undertaken within the Yellingbo Nature Conservation Reserve located ~50 km east of Melbourne, Australia (37°50′ S 145°29′ E, ~110 m above sea level) (Figure 1). The area has a cool-temperate climate, experiences maximum temperatures of 25.6°C in summer and 13.6°C in winter and receives ~1100 mm of annual rainfall (Greet *et al.*, 2020b). Seasonally inundated riparian zones within the reserve support threatened 'Sedge-rich *Eucalyptus camphora* swamp forest', which is globally unique (Turner, 2003). This vegetation community typically features a canopy of larger *Eucalyptus camphora* R.T.Baker trees accompanied by thickets of smaller *Leptospermum lanigerum* (Aiton) Sm. and *Melaleuca squarrosa* Donn. ex Sm. trees or shrubs (Turner, 2003). However, tree mortality, deteriorating plant condition and an absence of natural regeneration has resulted in the local decline of these swamp-adapted species. These changes are thought to be partly driven by past human alterations of local watercourses, levee bank construction and drainage (Greet, 2016; Harley, 2016). Conservation and restoration efforts are being made in the reserve because Yellingbo is home to the last wild lowland population of the critically endangered Leadbeater's possum (Harley, 2016). The largest remnant habitat for the possum is swamp forest found along the Macclesfield creek floodplain, our study site. Restoring the floodplain hydrology in combination with revegetation is a potential yet untested means to arrest further riparian swamp forest loss and promote its recovery.

2.2 Study design

In September 2018, we used sandbags to construct two temporary weirs within channelized reaches of Macclesfield Creek to re-engage disconnected floodplain areas. Both diversion weirs were designed to elevate upstream water levels sufficiently to redirect flow into a network of historic distributary channels and thereby achieve widespread and more frequent floodplain inundation. The weirs had built-in pipes that facilitated some in-channel flow.

Over 19 months we continuously monitored water levels at 15-min intervals within re-engaged distributary channels as well as upstream of the weirs and in the non-channelized creek section further downstream (near the reference sites). Monitoring was conducted using Odyssey® Capacitance Water Level Loggers (Dataflow Systems Ltd).

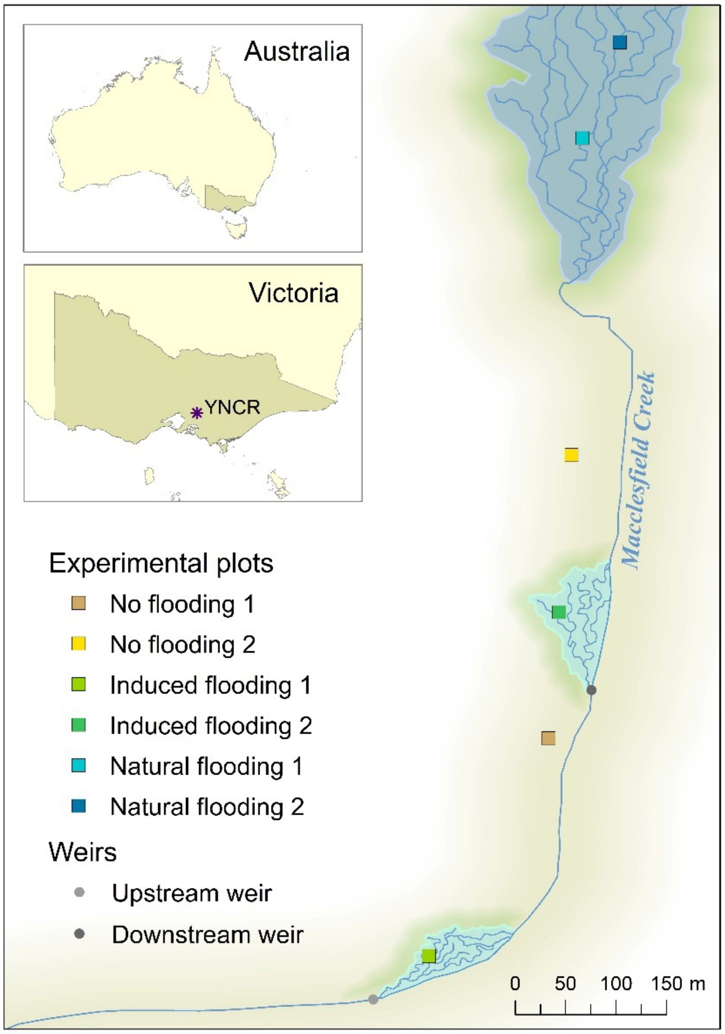

Figure 1 Study site (Yellingbo Nature Conservation Reserve; YNCR) location and sketch of experimental setup showing the two diversion weirs within Macclesfield creek, inundated floodplain areas and the six experimental plots, two for each treatment: no flooding, induced flooding, natural flooding.

To examine effects of restored hydrology on seedling establishment and development we set up an experimental trial using a multiple control-reference-impact study design. Six ~64-m^2 plots were established on the Macclesfield creek floodplain (Figure 1). There were two plots for each of three treatments: impact sites named “induced flooding” (disconnected floodplain areas re-engaged by induced flooding, one per weir); control sites named “no flooding” (disconnected floodplain areas unaffected by the flow diversion and therefore not receiving flooding) and reference sites named “natural flooding” (unmodified, connected floodplain areas with natural flooding featuring *Eucalyptus camphora* swamp forest in good condition). We took manual water level measurements (n = 45) in each of the four naturally or induced flooded plots during the inundation period. We compared the averaged plot water levels to those monitored instream with water level loggers and calculated flooding periods for the natural and induced flooding treatments for the duration of the experiment (Figure 2).

Shallow flooding remained in patches with depths ranging from 0-10cm within all four flooding treatment plots at the start of the experiment when seedlings were planted in early November 2018 (Figure 2). Naturally flooded plots remained flooded for one month after planting whereas floods receded after ~1 and ~3 weeks, respectively, in the two plots with induced flooding (which had both been flooded intermittently over the previous two months since weir construction) (Figure 2). All plots were dry during summer and autumn until the onset of the next flooding period six months after planting (in May 2019) which reflooded the four treatment plots with induced and natural flooding (Figure 2). According to personal observation natural flooded plots flooded at the same time as plots with induced flooding. However, due to water-level logger malfunction, plot water level data are missing for the reference plots at that time. The second flooding period ended in the middle of month twelve after planting (November 2019) in both naturally flooded plots and a few weeks earlier in the plots with induced flooding (Figure 2).

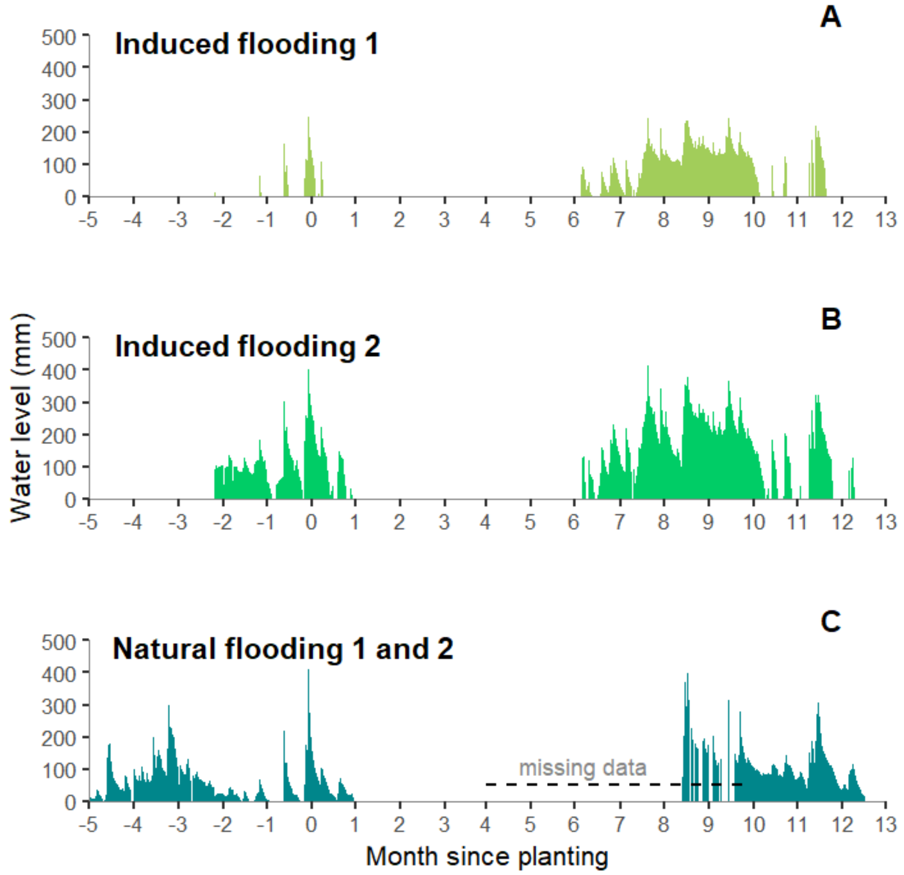

Figure 2 Hydrographs for plot water levels for the two induced flooded plots (top and middle) and plots with natural flooding (bottom, both flooded similarly). Diversion weirs were installed more than 2 months before planting. Note that data is missing for natural flooded plots for the period between month 4 to mid-month 8 and for occasional shorter periods after that as indicated by the dashed line.

Within each plot, we randomly planted 15 tube-stock seedlings of each of three woody species, *E. camphora*, *L. lanigerum* and *M. squarrosa*. Planting was undertaken at the onset of the growing season in early November. We obtained plants from the Friends of the Helmeted Honeyeater Indigenous Plant Nursery at Yellingbo where they were grown from locally sourced seeds. All plots were fenced to exclude browsing mammals.

2.3. Survey protocol

We monitored seedling survival (apparent as the presence of green foliage) and height every month until plots were reflooded seven months after planting (June 2019) and then once again at 13 months following flood recession. We measured basal stem diameter at 2 cm above ground level using calipers in months 0, 7 and 13 on all live individuals.

During each survey we also recorded the volumetric soil moisture content of the top 12 cm of soil at the base of each plant using a HydroSense II soil moisture measurement system (Campbell Scientific) with a 12 cm water content sensor. Soil moisture could only be measured in half of the plots in month 4 as the probe broke during fieldwork. For inundated seedlings, soil moisture content was assumed to be 81%, which corresponds to full saturation of silty clays, the dominant substrate at Macclesfield Creek floodplain (Kasel, 1999).

Soils were nearly saturated (~80%) at the beginning of the experiment in both flooding treatments and soil moisture content was ~25–35 % without flooding (Figure 3). Soil moisture differences between flooded and unflooded plots decreased over the first three months. Notably, soil moisture in the induced flooding treatment dropped quicker than in the naturally flooded treatment. Measured soil moisture minimums were on average 8, 11 and 16 % in no flooding, induced flooding and natural flooding treatments, respectively. Soil moisture increased independent from flooding in all plots from month 4. During the next flooding season soil moisture between non-flooded and flooded treatments diverged again (Figure 3).

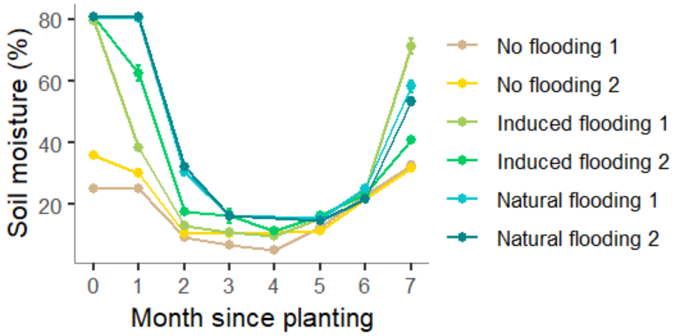

Figure 3 Mean soil moisture (± SE) measured at the base of each plant seedling (n = 45) in each of six plots. Each two plots belong to one of the three treatments: no flooding, induced flooding and natural flooding.

We estimated plant area index (PAI), the plant area per unit ground area, as a proxy for light availability within each plot using hemispherical photography and image analysis. Plots were divided into four quadrants and we took a photograph in the center of each of them. We fitted a generalised linear model using beta distribution (with PAI as response and treatment plot as predictor variable) to assess if canopy cover differed between the six treatment plots. There were no significant differences in PAI between plots (data not shown) indicating light availability did not need to be considered as predictor for the measured plant responses in this experiment.

2.4. Statistical analysis

For each species the difference in survival over time between treatments was assessed with the Kaplan-Meier estimate using the *survival* R package (Therneau, 2020). We calculated height growth and stem diameter growth for each plant as the difference between the height and diameter measurement at months 1–7 and month 13 since planting and the initial height or diameter at month 0. We then used gaussian linear mixed effects models, separately for each species, to assess the differences in height and diameter growth between treatments and over time. For all analyses, treatment and its interaction with time, represented as month after planting, were modelled as fixed factors, and plot and plant nested within plot as random factors. We fitted all generalized linear mixed models using the *glmmTMB* package (Brooks *et al.*, 2017). In all growth models the no flooding treatment was set as the intercept for comparison with induced and natural flooding treatments. Effects were inferred as significant if the 95% confidence intervals of the effect estimate did not span zero (or one for survival analysis), and significant differences were inferred when 95% confidence intervals of estimates did not overlap.

We used simple linear models to test the effects of soil moisture on total seedling height and diameter growth after one growing season (at seven months after planting). We assumed plant growth responses to soil moisture to be delayed. Therefore, we built models using the mean soil moisture of all eight months (0-7) as a predictor for total height and diameter growth, for each species separately.

All statistical analysis was performed in R version 3.5.0. (R Development Core Team, 2018).

3. Results

3.1 Seedling survival

Flooding treatments had different effects on the survival rates of the three species. All *E. camphora* seedlings survived when not flooded. Survival decreased ~30% under natural flooding but did not decrease significantly under induced flooding (Figure 5 A). When flooded (naturally or induced), *E. camphora* seedling survival rates decreased immediately after planting and then declined further slowly over time (Figure 4 A, Figure 5 A). *L. lanigerum* seedlings had the highest survival rates overall with no difference between treatments (Figure 4 D, Figure 5 D). The survival of *M. squarrosa* seedlings, in contrast, were ~50% higher with natural or induced flooding than without flooding (Figure 5 G). Without flooding, *M. squarrosa* survival rates dropped rapidly in summer, three months after planting, and then decreased gradually until the end of the experiment (Figure 4 G).

3.2 Seedling growth

3.2.1. Height growth

Height growth was greater with flooding than without flooding across all species (Figure 4 B, E, H). These differences became apparent after two months for *M. squarrosa*, 4 months for *L. leptospermum* and after 5 and 6 months for *E. camphora* seedlings subject to natural and induced flooding, respectively (Figure 5 B, E, H). Natural flooding resulted in slightly more height growth (9–25 cm after 7 months, 34–44 cm after 13 months) than induced flooding (9–13 cm after 7 months and 19–29 after 13 months) whereas height growth was lowest with no flooding (1–3 cm after 7 months and 4–10 cm after 13 months) across all species (Figure 4 B, E, H). Temporal growth patterns varied between species (Figure 4 B, E, H). *L.*

leptospermum and *M. squarrosa* seedling height growth commenced soon after planting but was negligible between 4–7 months (during dry summer conditions). *L. leptospermum height* growth was low in the first seven months but then increased between months 7–13. *E. camphora* seedling height growth started later, in month three, and remained steady from then on.

The variation in total height growth after 7 months explained by mean soil moisture during that period was 18 % for *E. camphora*, 8 % for *L. leptospermum* and 47% for *M. squarrosa* (Figure 6 A, C, E). Tip dieback of *E. camphora* seedlings at flooded sites and *M. squarrosa* seedlings at not flooded sites resulted in negative growth in some months.

3.2.2. Diameter growth

After seven months, natural flooding resulted in higher stem diameter growth than no flooding in all species (Figure 5 C, F, I). In the induced flooding treatment, *E. camphora* and *M. squarrosa* seedlings had higher stem diameters than without flooding after 13 months, and *L. leptospermum* seedlings after seven months (Figure 5 C, F, I). All species showed similar patterns in diameter growth (Figure 4 C, F, I). Thirteen months after planting, stem diameters increased with natural flooding (3–5 mm) and induced flooding (1 mm) but shrunk without flooding (-5– -3 mm). Diameters increased more during the second, longer, flooding season than in the first seven months of the experiment. The variation in diameter growth after 7 months explained by mean soil moisture in that period was 8% for *E. camphora*, 24% for *L. leptospermum* and 18% for *M. squarrosa* (Figure 6 B, D, F).

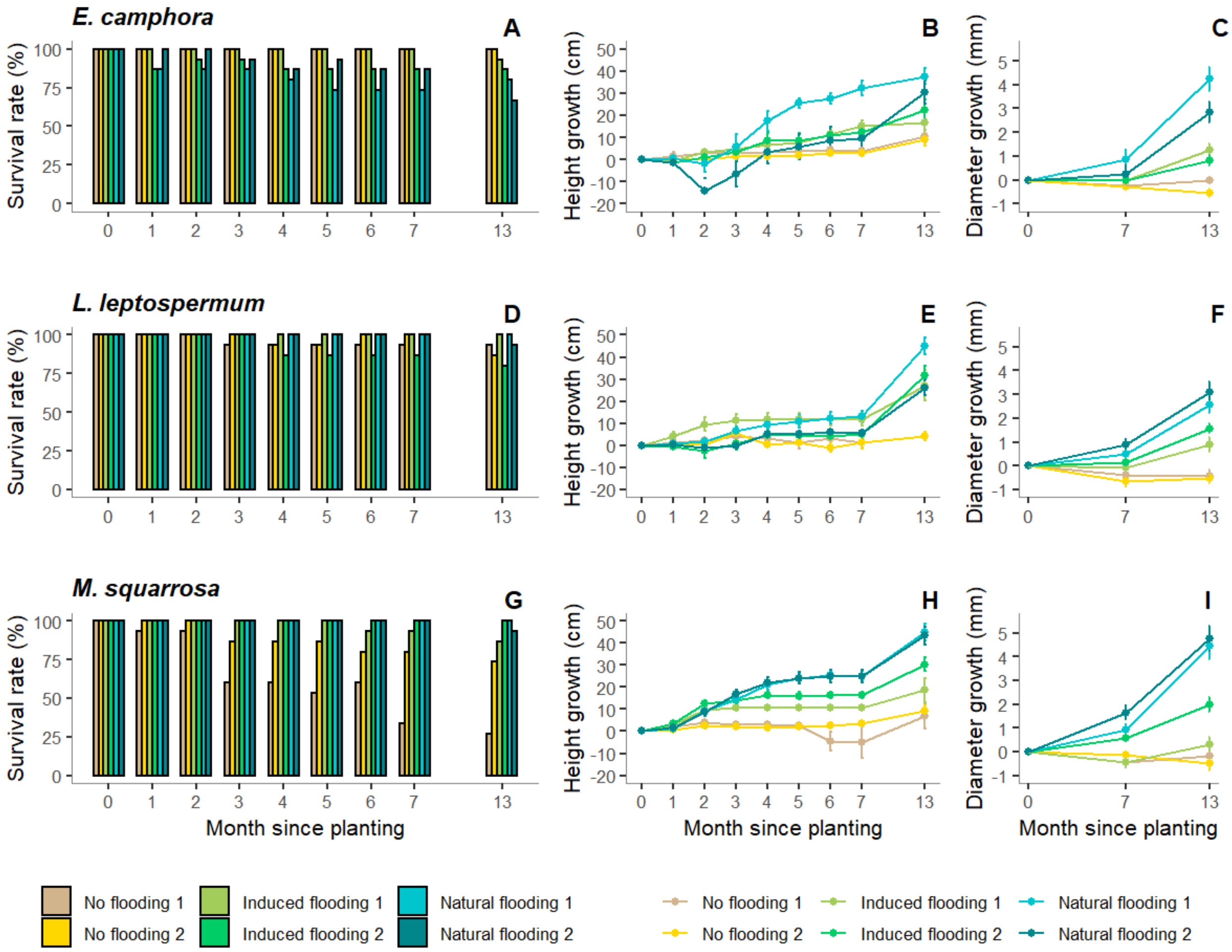

Figure 4 Survival rate, height growth and stem diameter growth for seedlings of the three studied plant species (n = 15) in each of six plots. Means ± SE of raw data presented for each experimental plot. Note statistical analysis was performed for treatments. There are two plots for each of the three treatments: no flooding, induced flooding and natural flooding. Seedlings where counted as dead if no green foliage was present at a monthly survey. However, some leafless seedlings resprouted later and were counted as alive in following months, which explains the drop and rise in survival rates in some cases. Surviving seedlings with top dieback explain negative height growth.

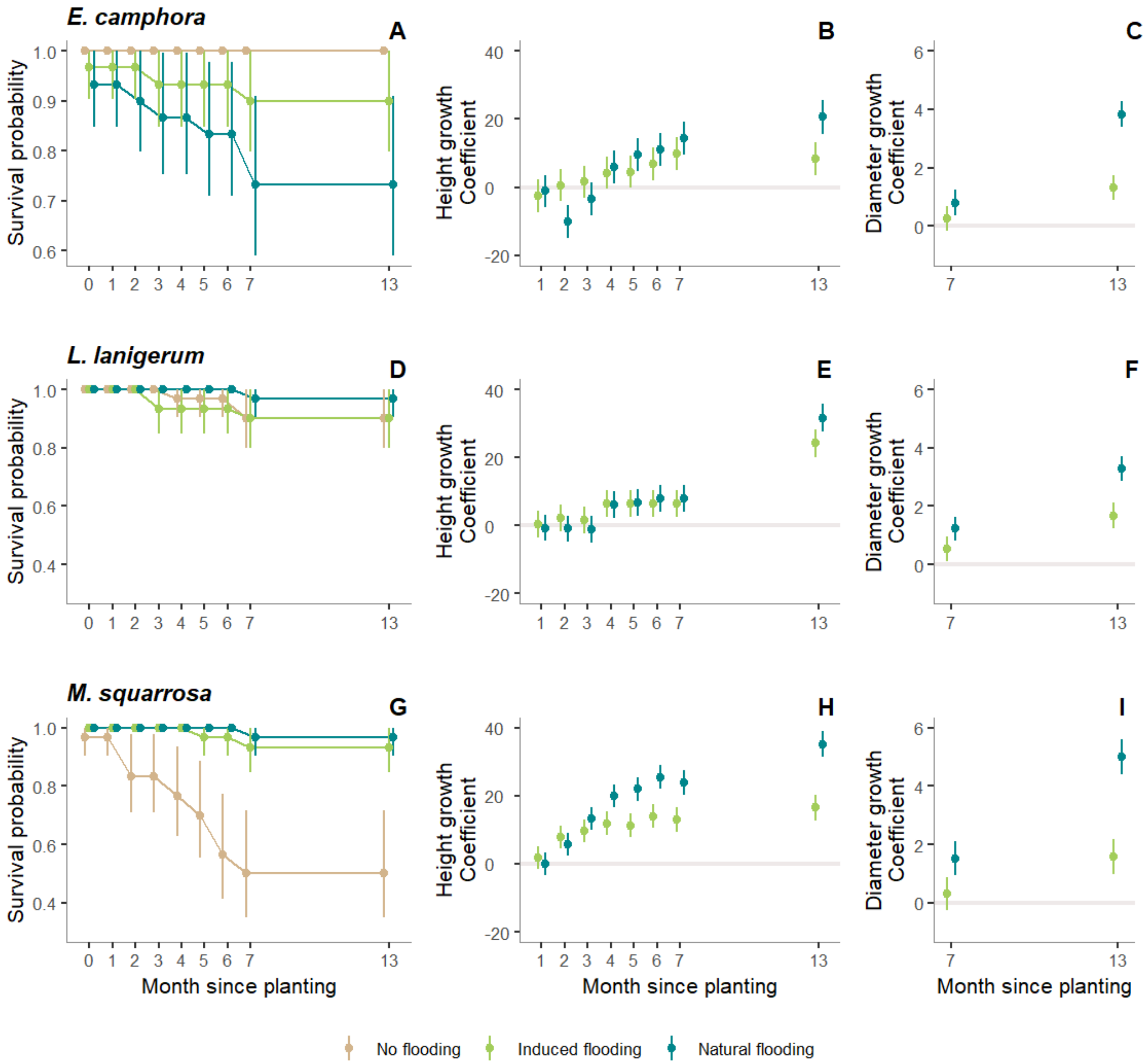

Figure 5 Estimated survival probability (± 95% confidence intervals) (A,D,G) and coefficient estimates (± 95% confidence intervals) of fixed effects (treatment and month since planting) for height growth (B, E, H) and diameter growth (C, F, I) models for each of the three studied species. Note points for each treatment have been slightly shifted horizontally to avoid overlapping of confidence interval lines.

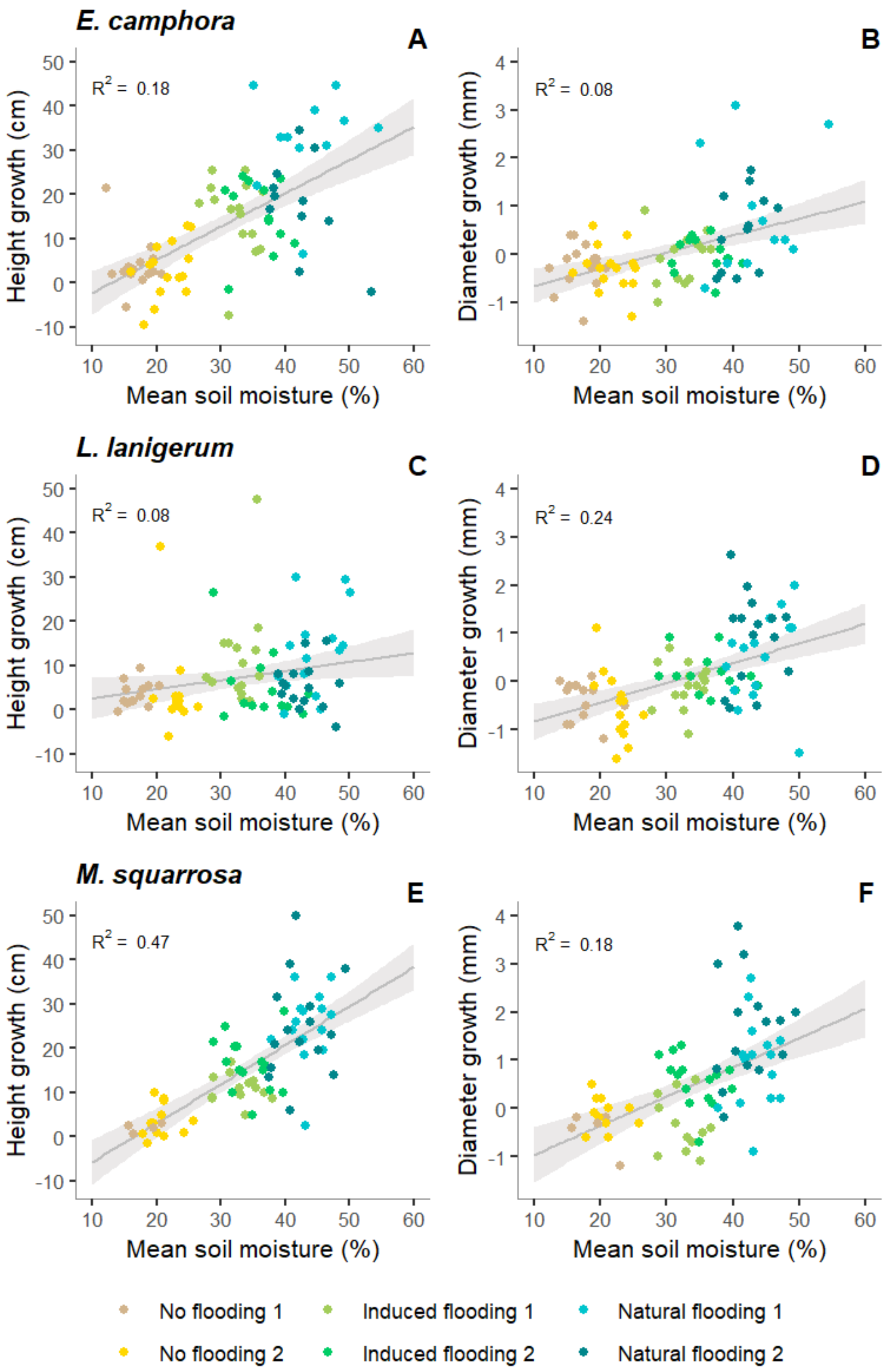

Figure 6 Relationship between mean soil moisture and total height and diameter growth over seven months after planting for the three studied plant species. Grey line and shading indicate regression lines and 95% confidence intervals.

4. Discussion

Our results highlight the suitability of two complementary restoration approaches – restoring hydrology and revegetation – for promoting the regeneration of riparian forests. In-stream weirs aided in laterally distributing water across the floodplain, with flooding of reengaged, disconnected sites resembling that of naturally flooded areas. We showed the importance of such flooding in facilitating the establishment of woody riparian plants. Planted seedlings had higher growth rates at both induced and naturally flooded than at non-flooded sites. However, survival rates and temporal growth patterns differed between species according to variation in flood duration and soil moisture, illustrating the different hydrological requirements of the coexisting species. This stresses that variable flooding and drying patterns are essential to create recruitment niches for different riparian plant species and demonstrates the importance of river-floodplain connectivity for providing adequate flooding regimes.

4.1. i) Flooding affects seedling growth and survival

Generally, planted seedings endured flooding for up to one month. Soil saturation can deplete oxygen in the root zone and hinder root respiration with consequent disruptions of water and nutrient uptake, internal coordination, photosynthesis and metabolism in flooded plants (Pezeshki, 2001; Sauter, 2013). However, in our field experiment floodwater was moving down historic distributary channels and therefore likely carried oxygen, which might have slowed the development of anerobic soil conditions (Kabrick *et al.*, 2012). Our three study species are known to be flood tolerant and displayed morphological adaptations to flooded conditions: increases in stem diameters of seedlings in flooded plots indicating the formation of aerenchyma, a spongy tissue enabling gas exchange between shoots and roots which aids in supplying oxygen to submerged roots (Seago Jr *et al.*, 2005). Nevertheless, in contrast to *L. leptospermum* and *M. squarrosa* seedlings, *E. camphora* survival rates reduced, and its seedlings experienced stress (as indicated by discoloration and tip dieback) when inundated or waterlogged (Norby and Kozlowski, 1983).

The lack of growth in some seedlings during inundation in the first weeks of the trial may be a stress response or survival strategy. Delaying growth reduces tissue maintenance cost in times of limited energy production during flooding (Pryor *et al.*, 2006). Stagnant height growth can further imply a shift in biomass allocation, that is favoring root growth over shoot growth (Gomes and Kozlowski, 1980). Plants might have developed adventitious roots, which form on the stem upon flooding and serve to colonize upper, more aerated and nutrient rich soil layers under flooding (Blom *et al.*, 1994). We did not quantify root growth but our studied species are known to quickly initiate adventitious root growth after becoming inundated (Greet, 2015; Zacks *et al.*, 2019), and we observed this in the field. The maintenance of positive growth of *M. squarrosa* during flooding suggests it is capable of maintaining physiological activity while flooded. Similarly, studies comparing the same genera as our study species found that flood tolerant *Melaleuca cajuputi* and *Leptospermum scoparium* species maintain photosynthesis, sustain assimilate transport to roots and alter metabolic pathways during flooding, whereas for *Eucalyptus camaludensis and Eucalyptus obliqua,* photosynthesis and growth ceases (Kogawara *et al.*, 2006; Pryor *et al.*, 2006).

The absent or negligible growth in seedlings that did not experience flooding suggests that rain water or other potential water sources were insufficient or unavailable to support biomass accumulation. In fact, decreasing stem diameters of seedlings in non-flooded plots provide evidence that seedlings experienced water stress (Ogigirigi *et al.*, 1970). Floodplain trees can obtain water from different sources for example groundwater, aquifers, rain or soil moisture (Mensforth *et al.*, 1994; Snyder and Williams, 2000; Andersen, 2005). However, seedlings with a sparse root system might have a limited ability to access distant water sources which stresses the importance of flood delivered soil moisture.

Seedlings previously exposed to flooding performed better during summer drawdown, which suggests lagged benefits of previous floods. Previously flooded *E. camphora* sustained height growth and *M. squarrosa* were able to survive in contrast to individuals planted in unflooded sites. One to two months after flood recession soil moisture approximated values critical for riparian tree seedling survival (i.e. soil moisture below 10%; Jensen 2008). When floodplains become too dry, seedlings experience difficulties in extracting soil water to replace water lost via transpiration. To avoid desiccation, plants reduce stomatal conductance, which consequently hinders photosynthetic activity and thus reduces carbon and energy supply for building structural biomass and maintaining metabolism (Sperry, 2000). Short periods of favourable growth conditions during or post flooding may not only have supported growth flushes in the planted seedlings but also allowed them to accumulate excess photosynthate in storage pools (Chapin III *et al.*, 1990). These stored reserves may have later fueled metabolism when the seedlings' energy inputs were low or absent due to dry conditions (O'Brien *et al.*, 2014).

4.2. ii) Co-occurring species respond differently to flooding

Different temporal growth patterns among our study species indicate their different hydrological requirements. *Eucalyptus camphora* is vulnerable to prolonged flooding and requires moist, well drained soils to initiate growth, which then remains steady and seems to quickly become independent of surface soil moisture. *E. camphora* typically develops vertically oriented sinker roots which might have grown sufficiently to stay in contact with the dropping water-table and given access to deeper, well-watered soil layers (Mahoney *et al.*, 1992). *M. squarrosa* in contrast tolerates inundation and its growth depends on high surface soil moisture. Likewise, rapid, substantial increases in *L. lanigerum* height during or directly after flooding (here observed during the second but not the first flooding period) suggests its growth is restricted to wet periods. Perhaps because plant parts grown in acclimatization to flooding such as surface roots or leaves anatomically designed for increased water release are poorly suited for dry post flood conditions (Capon *et al.*, 2009; Zúñiga-Feest *et al.*, 2017). This might explain cessation of *L. leptospermum* and *M. squarrosa* seedling growth with reduced soil moistures. Continuous low soil moistures even lead to *M. squarrosa* mortality.

Connected floodplains are hydrologically dynamic and we observed that both excess and scarcity of water can compromise growth and survival of different riparian tree and shrub species. Hydrological conditions suitable for growth, on the contrary, are short-lived. The onset as well as the duration of growth pulses differs between species according to their flooding and soil moisture tolerances. Such temporal differentiation of resource use, namely complementary timing of growth between *E. camphora* and *M. squarrosa* and *L. leptospermum*, may enable species coexistence (Terradas *et al.*, 2009). This stresses that flooding and drying patterns are essential to create recruitment niches for co-existing riparian plant species. Connectivity between floodplains and their streams contributes to the creation of natural flooding regimes. The timing of natural flooding likely also coincides with climatic patterns and phenological cycles of riparian plant species and thus optimize establishment.

4.3. iii) Induced flooding promotes plant establishment to a similar extent as natural flooding

In our study, floodplain reconnection increased site quality for seedling growth to similar levels as sites with natural flooding. We acknowledge that the duration of flooding differed between the restored sites with induced flooding. This within-treatment difference is an unavoidable limitation of field-based experiments. However, the fact that slightly longer flooding at one site with induced flooding was accompanied by slightly higher seedling growth emphasizes the importance of flooding duration for seedling establishment. The longer flooding duration in naturally flooded sites compared to sites with induced flooding appeared to achieve a higher and longer-lasting recharge of soil moisture, which likely explains the highest growth observed in seedlings receiving natural flooding. Higher growth rates of flooded (naturally or managed) than non-flooded seedlings may be further attributable to greater groundwater recharge, increased nutrient supply and the removal of competition by less flood tolerant species (Megonigal *et al.*, 1997; Walls *et al.*, 2005; Johns *et al.*, 2009).

4.4. Management implications

4.4.1. Hydrological restoration

Our experiment attests that reengaging the hydrology of disconnected floodplains by installing partial weirs in incised, channelized streams is an effective means to distribute water widely without requiring additional water resources or flow regulation. Naturally flooded sites with historically reoccurring floods supported highest seedling growth. Thus, the benefits of flooding might accumulate over time, which underlines the importance of reinstating flooding regimes (regular flooding and drying cycles over time) rather than managing for single events. Flow diversion structures should therefore be designed to be long-lasting and subject to regular maintenance. While this study focused primarily on flood duration, other aspects of the flooding regime such as depth, frequency and timing also influence seedling establishment. Restoration of all aspects of the natural flood regime are likely to be served by restoring river-floodplain connectivity. However, investigating and managing other constraints to riparian forest regeneration (such as competition and herbivory) may further help to initiate ecosystem recovery.

4.4.2. Revegetation

Although flooding is essential, its duration during the establishment process is likely to be critical. Therefore, timing of revegetation is important because it regulates flooding exposure. Planting early during the flooding period may expose seedlings to anoxic soil conditions longer than they can tolerate. Planting after water has drained away, in contrast, may make it impossible for seedlings to profit from recharged soil moistures which may dissipate quickly. Thus, planting of woody riparian species is best undertaken at the end of the flooding season to allow for optimal recruitment conditions. Furthermore, species-specific hydrological niches should guide revegetation strategies. For example, *L. leptospermum* and *M. squarrosa* may be planted earlier than *E. camphora* given their greater flood tolerance. Alternatively, considering the natural heterogeneity of the floodplain (i.e. mounds and swales) during planting may help account for species-specific ecological requirements and thus augment growth and survivorship of co-existing species. Accordingly, species that are more reliant on floods and high soil moisture (e.g. *M. squarrosa* and *L. leptospermum*) should be planted closer to the stream channel or in lower microsites, whereas species that are less tolerant of floods and droughts (*E. camphora*) are better placed on more elevated positions. Importantly, hydrological restoration of larger riparian areas will potentially accommodate a greater variety of species-specific microsites and therefore promote biodiversity (Fraaije *et al.*, 2015).

5. Conclusion

Restoring degraded riparian forests is a critical global challenge. Our study provides strong empirical support that flooding and associated soil moistening is essential to enable woody plant establishment. We contend that sequences of floods and droughts determine the window of opportunity for establishment and growth of different riparian woody plants. Here we provide an example that restoration outcomes can be enhanced by applying complementary restoration approaches which address both biotic and abiotic constraints (i.e. lack of regeneration and absent flooding) to riparian forest restoration. Revegetation should consider species-specific hydrological requirements and be complemented by reinstating appropriate flooding regimes. Re-establishing the connectivity between rivers and floodplains may facilitate such flooding regimes.

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