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RIPARIAN TREES RESPROUT REGARDLESS OF TIMING AND SEVERITY OF DISTURBANCE BY COPPICING

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Abstract

Human modification of waterways has reduced flooding in many river systems, leading to the decline of riparian forests, which rely on flooding for their regeneration. Coppicing may help to promote the persistence of riparian trees by triggering resprouting and vegetative regeneration. The vigour of resprouting plants can vary with timing and height of coppicing and may depend on stored non-structural carbohydrate reserves like starch, the availability of which can vary seasonally. However, starch storage dynamics and the resprouting potential of broad-leafed evergreen riparian trees is not well understood.

We coppiced two riparian tree species, *Eucalyptus camphora* and *Melaleuca squarrosa*, at two different times (autumn, spring) and at two different heights (0 cm and 90 cm). Over 52 weeks, we regularly quantified shoot growth and changes in the starch storage pool size, compared to uncoppiced control trees, in different tree organs (root and stem) and estimated the final shoot volume.

The final shoot volume did not differ significantly between coppice treatments. Trees coppiced in autumn had a greater reliance on stored starch while they remained leafless (without shoots) over winter. Trees

cut at 90 cm had more starch reserves due to remaining stems but also had higher biomass maintenance costs. Starch storage varied seasonally only in *E. camphora*, with starch concentrations in control trees increasing over winter and decreasing over summer.

Although coppice timing and height affected use of stored starch, resprouting in our study species was not limited by starch availability - both species regenerated vegetatively to recover from physical disturbance. Thus, coppicing may be an efficient means to promote rejuvenation and persistence of tree species where site and tree condition are degraded and no longer support recruitment.

Key words: forest restoration, non-structural carbohydrates, seasonality, shoot growth, tree felling, vegetative regeneration

Author declaration:

All authors conceived the study and developed the methodology. SF and JG conducted the fieldwork. SF conducted the lab work. SF, JG and CW analysed the data. SF wrote the main manuscript text; all other authors reviewed the manuscript and provided editorial advice.

1. Introduction

Poor or absent natural recruitment from seeds threatens the integrity of many forests (Dey et al. 2019), including riparian forests. Forest restoration via planting can be slow and prone to failure due to high vulnerability of seedlings to environmental stress (Greet et al. 2020a, Laub et al. 2020). Vegetative regeneration (i.e. regeneration via resprouting) is an alternative means of regeneration, but many species require disturbance to initiate resprouting (Meier et al. 2012). However, under increasing anthropogenic influence, disturbance regimes have changed substantially, and this is particularly true for riparian ecosystems (Kingsford 2000, Tonkin et al. 2018). Most of the world's rivers have been modified (e.g. through damming, water extraction or flow regulation) and many floodplains flood less frequently (Tonkin et al. 2018, Grill et al. 2019). Flood disturbance acts as a trigger for vegetative regeneration in riparian trees by causing stem leaning and tree injury which is typically followed by regrowth from resprouts, enabling tree rejuvenation and longevity (Fischer et al. 2021a). As a consequence of reduced or absent flood disturbance riparian species may senesce and be gradually replaced by terrestrial vegetation communities (Tockner and Stanford 2002, Greet et al. 2013, Foard et al. 2016).

The initiation of vegetative regeneration via coppicing may help to promote the persistence of riparian species and maintain species composition and forest structure (e.g. canopy closure). During the procedure of coppicing, trees are, sometimes repeatedly, cut to stimulate sprout production from stumps or stems (Del Tredici 2001). Coppicing has a long tradition in forest management and wood production, is presently of economic importance (e.g. in short-rotation plantations) and is also a relevant technique for conservation and restoration (Sjölund and Jump 2013, Müllerova et al. 2014, Spinelli et al. 2017, Schweier et al. 2019). Studies concerning tree resprouting potential are scarce for riparian ecosystems, especially those composed of broad-leafed, evergreen species in temperate climates. Resprouting has primarily been studied in response to fire but also in response to logging, hurricanes and landslides (Bellingham et al., 1996; Nzunda et al., 2007; Clarke et al., 2013; O'Hara et al., 2017). Investigations into the resprouting

responses of trees from different ecosystem types are needed to help refine our general knowledge of the resprouting trait, its diversity and the underlying mechanisms of resprouting. Given current and projected changes to disturbance regimes resulting from human-driven environmental change (Dale et al. 2001, Sommerfeld et al. 2018, O'Briain 2019), increased understanding of resprouting is critically important as it is central to understanding forest dynamics, predicting vegetation changes and informing forest management (Pausas et al. 2016, Stojanović et al. 2017).

A primary requirement for species survival and recovery after physical disturbance, including coppicing, is the ability to remobilize stored resources, mainly carbon in the form of non-structural carbohydrates (NSC), like starch (Bond and Midgley 2001, Wildy and Pate 2002, Klimešová and Klimeš 2007). Carbon is a major building block of structural biomass required to form initial resprouts (Dietze et al. 2014, Turnbull et al. 2014). In addition, NSC serve as respiratory substrate from which energy can be released and used to maintain non-autotrophic tree components (e.g. roots and stems) while trees are leafless and thus, are unable to assimilate carbon via photosynthesis (Kozlowski 1992, Chen et al. 2017).

The availability of stored NSC varies seasonally. The NSC pool is often depleted during sprouting, bud break, periods of rapid growth, reproduction or dormancy and replenished when growth declines while assimilation remains high (or when storage formation is prioritized over other functions) (Hoch et al. 2003, Dietze et al. 2014). Apart from phenological events, the occurrence of stress or disturbance causes a reliance on stored NSC for survival (Miller et al. 2019, Miranda et al. 2020). Therefore, resprouting may be driven by the interaction of seasonal dynamics of plant resource use and timing of disturbance (Peguero and Espelta 2011), which is why coppice timing can influence the resprouting response. Timing will determine the environmental growth conditions (Wright and Clarke 2007) and will regulate the time until resprouting is initiated and thus has implications for the period for which coppiced trees need to draw on stored NSC during the recovery process.

Plant NSC pool size and dynamics differ between biomes depending on the seasonality or disturbance regime (Hoch et al. 2003, Shibata et al. 2016). Likewise, the NSC allocation among plant tissues depends on the type of disturbance and the tissues' disturbance resistance (Clarke et al. 2013). For example, where disturbance is likely to kill above ground structures (e.g. severe fire), roots are often the primary NSC storage organ (Bell and Ojeda 1999, Knox and Clarke 2005). Where aboveground structures survive (e.g. in systems disturbed by wind or erosion) stems may be important storage organs to fuel regrowth (Myers and Kitajima 2007, Nzunda et al. 2008, Franklin et al. 2010). However, remaining stems may also consume large proportions of stored NSC for their maintenance, especially while they are leafless (Smith et al. 2018). Therefore, the disturbance severity or the copping height (i.e. the amount of remaining stem as a storage organ) may be an important determinant of the resprouting response.

The seasonality of NSC storage pool size and the importance of different tree organs as storage pools for riparian trees is unclear (i.e. the availability and requirement to draw on stored NSC from roots or stems to recover from damage). Furthermore, individual tree characteristics (e.g. size or condition) or environmental factors (e.g. light availability) have been documented to cause variation in resprouting (Casals and Rios 2018, Zhang et al. 2021).

Here we investigate resprouting response of temperate broad-leafed, evergreen riparian trees after artificial disturbance via coppicing (i.e. decapitation). We examine seasonal variability of resprouting and its dependency on stored NSC resources in the form of starch in above and belowground plant organs. Such knowledge will advance ecological understanding of resprouting and yield information on best practice for coppicing (i.e. timing and height of cutting). Specifically, we ask: 1) does timing (cut season) and severity (cut height) of coppicing influence recovery and resprouting (i.e shoot production and availability of stored starch in roots and shoots); 2) does resprouting depend on stored starch resources.

2. Methods

2. 1 Study site and study species

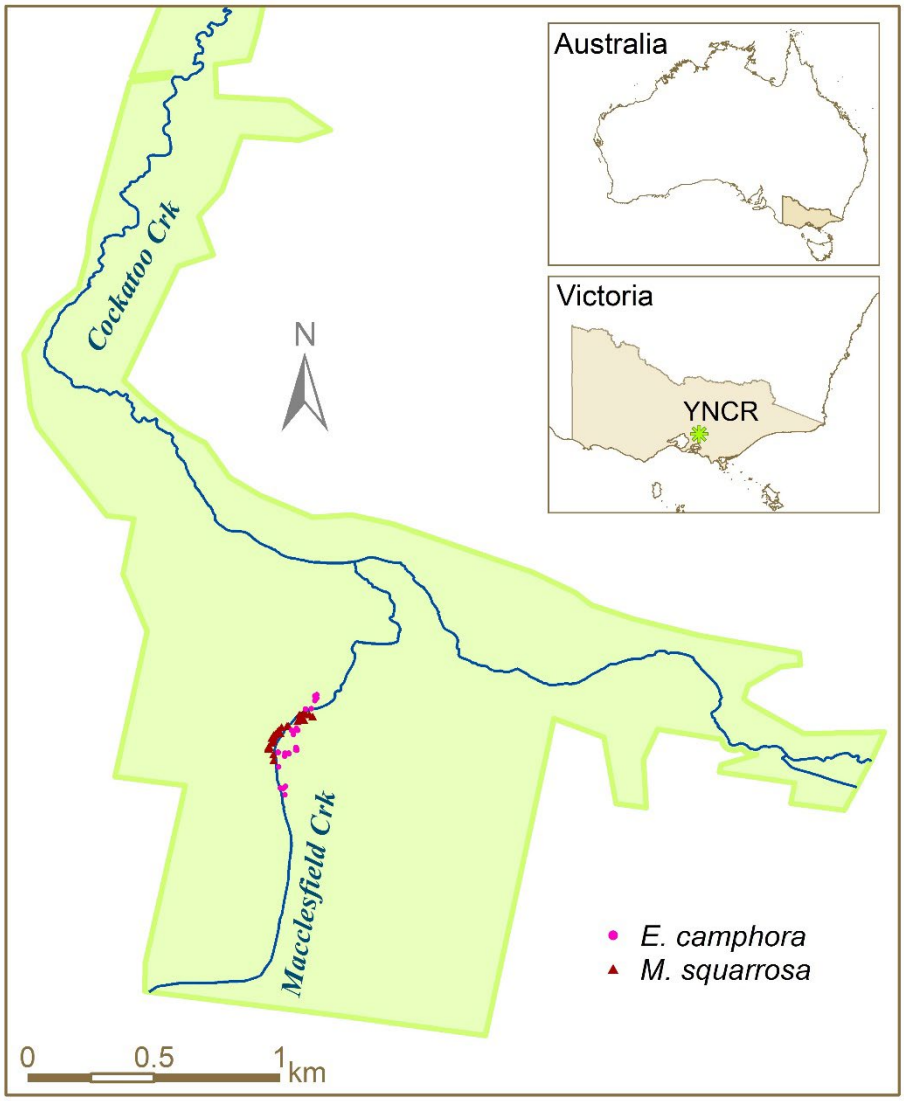


Figure 1 Map of the location of the coppiced trees within the Yellingbo Nature Conservation Reserve (YNCR, green polygon). Inset maps show the location of the reserve (green star) in relation to Victoria, Australia.

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 mean daily maximum temperatures of 13.6 °C in winter and 25.6 °C in summer and

receives ~1100 mm of rainfall annually. The reserve contains seasonally inundated riparian zones populated by threatened 'Sedge-rich *Eucalyptus camphora* swamp forest'. The structure of this vegetation community varies from open forest to woodland (canopy height 6–25 m) and features shrub thickets and a dense understorey comprising sedges, rushes, grasses and forbs (Turner 2003). Tree mortality, deteriorating tree condition and an absence of natural regeneration has resulted in the local decline of this globally unique vegetation community (Turner 2003). This degradation is, at least in part, attributable to reduced flooding as a result of past human modification of local watercourses, drainage and levee bank construction (Greet 2016, Harley 2016). Forest restoration efforts are being undertaken within the reserve as the last wild lowland population of the critically endangered Leadbeater's possum (*Gymnobelideus leadbeateri*) is found within Yellingbo (Harley 2016).

Figure 2 E. camphora (top row) and M. squrrosa (bottom row) stands in which coppicing was undertaken (A, D) and examples of resprouting high coppice trees (B, E) and low coppice trees (C, F), photographed in late spring.

Our experiment was set up on the Macclesfield creek floodplain (Figure 1). Owing to poor condition and growth form (i.e. small, upright, slender stems, Figure 2 A, D) the present vegetation structure consisting of mostly even-aged trees does not support Leadbeater's Possum foraging, moving and nesting (Greet et al. 2020b). Coppicing is a potential yet untested means to arrest further riparian swamp forest degradation and promote its recovery. Our two study species are broad-leafed, evergreen, flood-tolerant, woody species, pivotal to the overall physical structure of these swamp forests. *Eucalyptus camphora* R.T.Baker is the sole canopy species in this vegetation community. *Melaleuca squarrosa* Donn. ex Sm. (together with *Leptospermum lanigerum* (Aiton) Sm.) dominates the midstorey.

2. 2 Tree selection

Trees selected for the experiment were scattered over the Macclesfield creek floodplain over an area of ca. 2.4 ha so we could avoid clearing a larger forest patch (Figure 1). All trees were single-stemmed. *E. camphora* had a mean diameter at breast height (DBH) of 11 cm (range 8–16 cm) and *M. squarrosa* had a mean DBH of 9 cm (range 7–14 cm). Only subdominant trees were chosen for coppicing to prevent substantial alteration of the canopy cover and therefore microclimate and light conditions at the tree locations. Prior to the start of the experiment we assessed crown vigour, a proxy for tree condition, by visually estimating the proportion of the potential crown supporting live foliage to the nearest 5% (Cunningham et al. 2007, Salter et al. 2010). The mean crown vigor of the experimental trees was 50% (range 30–70%) for both species.

2. 3 Experimental treatments

We applied five treatments to 8 replicate trees per treatment of *E. camphora* and *M. squarrosa*: two different cutting heights, two different cutting seasons (high autumn, low autumn, high spring, low spring) and no cutting (control). All coppice trees were randomly allocated to the four different coppice treatments. Out of a total of 40 trees per species, 16 were cut at ground level (low) and 16 at height of ~90 cm (high) using a chain saw (Figure 2 B, C, E, F). Half of these low and high coppiced trees were cut in May 2018 (autumn) and the other half in October 2018 (spring). The remaining 8 trees per species were left uncut as controls. To prevent browsing of emerging sprouts, all coppiced plants were guarded with cylindrical guards ~90 cm in diameter and 1.8 m high made from chicken wire (5-cm mesh).

2. 4 Sampling protocol

2. 4. 1 Sprout measurements

We regularly checked stumps for the onset of resprouting. Once the first shoots emerged (in week 19 of the experiment in trees coppiced in autumn), the regrowth of shoots on all trees was monitored for one growing season from October 2018 to June 2019. In weeks 19, 22, 26, 28, 32, 35, 49 and 52 of the experiment we measured the length of the five longest resprouting shoots on each stump and calculated the mean resprout length at each week (Spinelli et al. 2017). At the conclusion of the experiment (52 weeks after first trees were coppiced in autumn) we also counted all living and dead shoots for each stump and estimated shoot volume as a proxy of differences in shoot biomass between treatments. The experimentally coppiced trees should improve the vegetation structure and habitat quality in the Yellingbo Nature Conservation Reserve in the long term, thus, we were unable to perform a final, destructive harvest for measuring shoot biomass. Hence, we measured the length and diameter at stem base of the five longest shoots, which are a good indicator of coppice shoot biomass (Matula et al. 2015).

Assuming a cone geometry for the shoots we used length and diameter measurements to calculate their volume ($r^2 \times \pi \times$ length/3).

Shoot growth can be influenced by light reaching the stump (Pelc et al. 2011, Casals and Rios 2018). To account for different light availability during resprouting we estimated canopy openness for each stump using hemispherical photography and image analysis. The photographs were taken on top of each stump after trees had been cut and as such comprised shading by understory vegetation as well as the canopy. The mean canopy openness was 27% (range 20–42%) for *E. camphora* and 26% (range 19–36%) for *M. squarrosa*.

2. 4. 2 Tissue sampling

We sampled tissue from roots and stems (potential storage organs) to assess the carbon pool dynamics following coppicing and during resprouting. Samples were taken four times: 1) in late autumn (early June 2018) prior to coppicing; 2) in spring (mid October 2018) when autumn coppice were still leafless and prior to spring coppicing; 3) in early summer (mid December 2018) after shoots emerged from both autumn and spring coppiced trees; and 4) in late autumn (early June 2019) at the end of the growing season when shoots were expanded. This sampling schedule corresponds to week 0 (autumn and control trees only), 19, 28 and 52 of the experiment. We assumed no differences in carbon pools between control and spring coppice trees in week 0 and thus only sampled control and autumn coppice trees at that time. Owing to the feasibility of the experiment and to reduce variability, we repeatedly sampled the same individuals. Stem wood was sampled on high coppice and control trees after removing the bark by drilling with a 4.5-mm drill 35 mm into the wood at a height of ~75 cm from two opposing sides (north and south) and collecting the shavings. Root samples were taken on all trees by digging out a part of the root system close to the stem and collecting tissue with the drill in the same manner. The drill was cleaned with a

196 sterilized cloth between samples. All tissues were immersed in liquid nitrogen directly after harvest and
197 subsequently kept at -80 °C until further processing to prevent enzymatic degradation of carbohydrates.
198 After being microwaved at 800 W for three minutes tissue samples were dried and ground to fine powder
199 using a bead mill (TissueLyser II, Qiagen, Hilden, Germany).

200

201 *2. 5 Chemical analysis*

202 Starch is the main non-structural carbohydrate compound from which carbon is remobilized to enable
203 resprouting (Smith et al. 2018). Thus, we focused on tissue starch concentration to relate resprouting
204 response to carbon storage. Starch was extracted and quantified following a modified version of Arndt et
205 al. (2008), described in Smith et al. (2018). Samples were washed with ethanol to remove soluble sugars
206 and then dried before being incubated with α-amylase (Sigma A4551, Castle Hill, Australia) and
207 amyloglucosidase (Sigma 10,115) to enzymatically convert starch into glucose molecules. Subsequently,
208 sample solution was incubated with hexokinase and glucose 6-phosphate dehydrogenase (Sigma G3293)
209 to convert glucose into glucose 6-phosphate and into 6-phosphogluconate. In the latter reaction oxidized
210 NAD (nicotinamide adenine dinucleotide) is reduced to NADH. The resulting change in absorbance at 340
211 nm is equivalent to the glucose concentration in the sample and was measured using a microplate
212 spectrophotometer (Multiskan GO, Thermo Fisher Scientific, Melbourne, Australia). We used a standard
213 curve (derived for each microplate) to calculate sample glucose concentration and expressed it as mg per
214 g dry weight. Each plate also included an internal lab starch standard to check for consistency of enzymatic
215 activity (Smith et al. 2018).

216

217 *2. 6 Statistical analysis*

We performed statistical analysis for each species separately.

Firstly, we evaluated if resprouting response (shoot growth, shoot number, shoot volume) differed between treatments (Q1). Using the *lme4* package (Bates et al. 2015), we fitted gaussian linear mixed effect models to assess the difference in shoot length between treatments and over time (shoot growth). The interaction between cut height, cut season and time (week of experiment) were modelled as fixed factors and tree was included as random factor. Further, we fitted two simple linear models to test for differences in the final shoot number and the final shoot volume, respectively, between cut-height and cut-season treatments. Shoot volume (cm^3) was ln(x + 1) transformed and shoot number was ln(x + 10) transformed to meet model assumptions of normality of residuals. Post-hoc contrasts between treatments were performed with a Tukey correction for multiple comparisons using the *emmeans* package (Lenth 2021). Since there was no interaction between cut height and cut season (high autumn, low autumn, high spring, low spring) in any model, we assessed the difference in shoot growth, shoot number and shoot volume between cut height (low, high) and cut season (autumn, spring) separately.

We performed additional regression analysis to test the effect of coppicing treatment on starch concentration in different tree organs (root and stem) (Q1). Using the *glmmTMB* package (Brooks et al. 2017), we fitted generalized linear mixed models separately for roots and stems to assess differences in starch concentration between treatments and over time. A single treatment effect with five levels (low-autumn, low-spring, high-autumn, high-spring, and control) was used instead of separate height and season effects because there was only a single control treatment that was not crossed with height and season treatments. All starch concentrations were square-root transformed to meet model assumptions. Treatment and its interaction with time (week of experiment) were modelled as fixed factors and tree was included as random factor. Only weeks 19, 28 and 52 were included in the models where data was available for all five treatments (starch concentrations in week 0 were only measured in autumn coppice and control trees). Surprisingly, by visual assessment, starch concentrations in *E. camphora* stems differed

242 in week 0 between the control and high autumn coppice trees (Figure 3 C). Therefore, we fitted one
243 additional model including all experimental weeks (0, 19, 28, 52) and control and high autumn coppice
244 treatment to assess whether the initial differences between stem starch concentrations were significant,
245 but they were not. Post-hoc contrasts between treatments were performed using the *emmeans* package
246 (Lenth 2021).

247 We tested if starch concentrations at the start of resprouting (week 19) and after resprouting (week 52)
248 were related to final shoot volume (Q2). Therefore, we fitted simple linear models (separately for each
249 tree organ) with starch concentration in week 19 and in week 52, respectively, as the predictor variable
250 and shoot volume as the response variable. Treatment was initially included as an interaction term but
251 was removed as the interaction between treatment and starch concentration was not significant. Shoot
252 volume (cm^3) was ln(x + 1) transformed and starch concentrations were square root transformed to
253 reduce leverage of high values, and to be consistent with earlier analyses.

254 Finally, we tested if tree size, tree condition and light availability influenced coppice resprouting (Q2), as
255 tree factors and growth conditions may affect resprouting. To do this, we fitted general linear models with
256 crown extent, DBH and canopy openness as predictor variables and shoot volume (ln(x+1) transformed)
257 as the response variable.

258 All statistical analysis was performed in R version 3.5.0. (R Development Core Team 2018). Differences
259 were inferred if $P < 0.05$.

3. Results

3. 1 Treatment effects on resprouting (Q1)

3. 1. 1 Shoot production

All 64 coppiced trees except one *M. squarrosa* tree in the low autumn treatment resprouted. For both species, autumn coppice remained leafless for ~19 weeks before resprouting and shoots became readily apparent shortly after the spring coppice treatment was applied (Week 22). Spring coppice resprouted in 3–6 weeks (Week 26-28).

In *E. camphora* spring coppice shoots grew faster than those of trees coppiced in autumn. Shoot lengths were significantly longer in autumn coppice trees than in spring coppice trees in weeks 26 (mean shoot length ± SE of 36 ± 5 cm versus 5 ± 1 cm) and week 28 (mean shoot length of 46 ± 7 cm versus 23 ± 4 cm), but not thereafter (Figure 3 A, Appendix 1 Table A1). Shoot growth did not differ between high and low coppice at any time in *E. camphora* (Appendix 1 Table A1).

In *M. squarrosa* autumn coppice trees had longer shoots than spring coppice trees from week 26 onward (autumn shoots were 9–19 cm longer than spring shoots) (Figure 3 B, Appendix 1 Table A1). This difference between autumn and spring coppice was significant in weeks 26, 28, 32, 35 and 52 but not in week 49 (Appendix 1 Table A1). *M. squarrosa* shoots of high coppice were significantly longer than those of low coppice in the later weeks (mean shoot length of 65 ± 6 cm versus 54 ± 7 cm in week 49 and mean shoot length of 66 ± 5 cm versus 54 ± 5 cm in week 52). In both species, resprout growth slowed in all treatments after week 35.

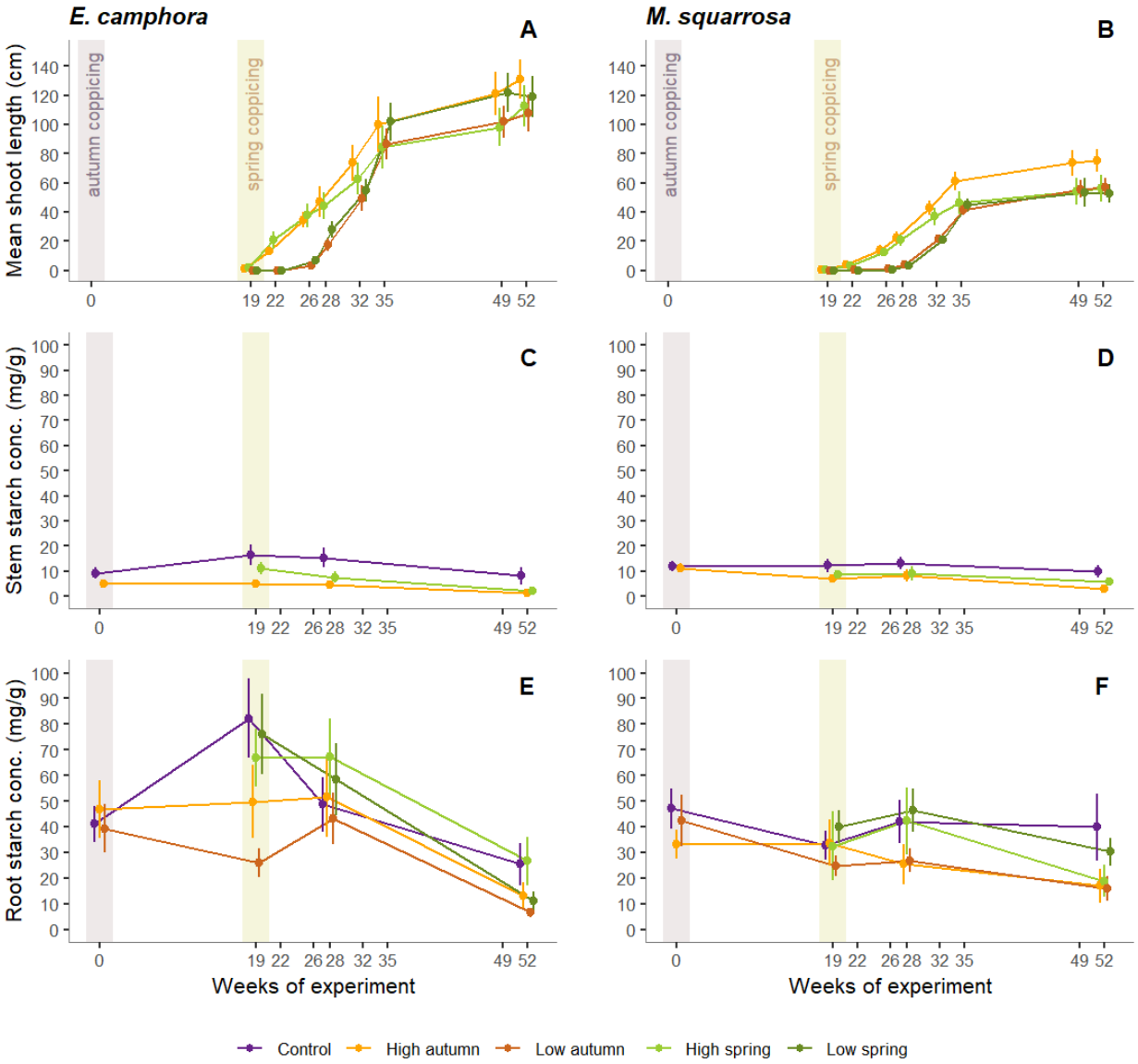
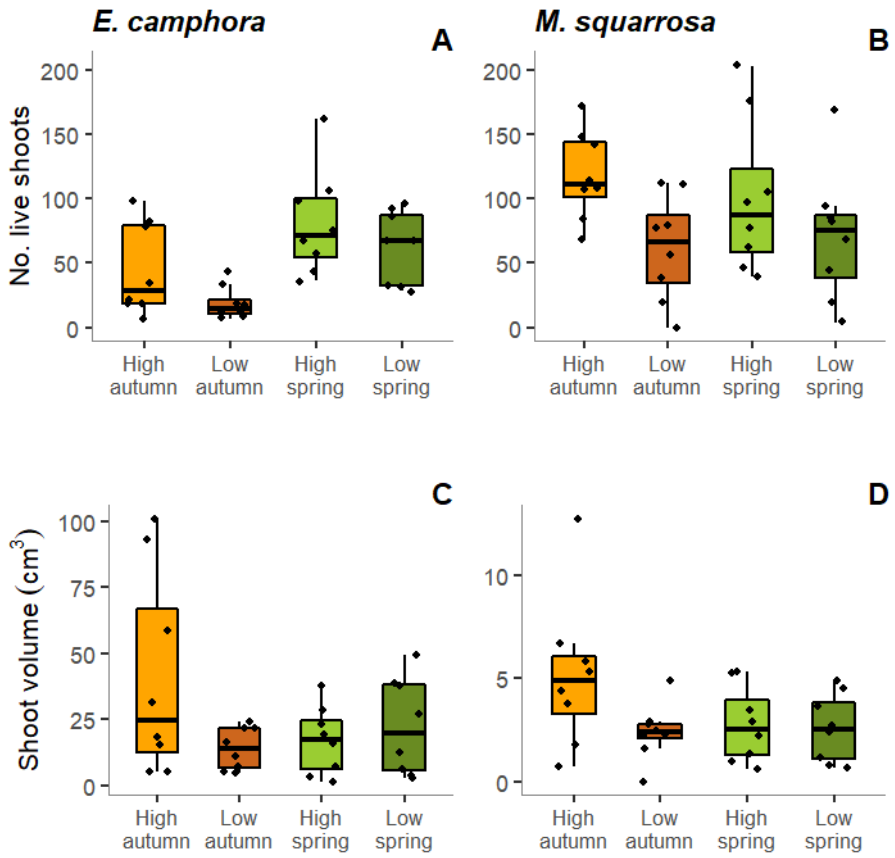


Figure 3 Mean length of the five longest shoots (means ± SE of raw data) (A, B) for trees of the four coppice treatments (n=8) and starch concentrations in stems (C,D) and roots (E,F) for both study species. Means ± SE of raw data presented for each of five different coppicing treatments (control, high autumn, low autumn, high spring, low spring). Note figures for mean resprout length (A, B) show raw data for crossed treatments whereas statistical analysis was performed with cut height and cut season as separate factors. Statistical analysis on starch concentrations (C, D, E, F) were performed on square root transformed data for crossed treatments. Note that low coppice treatments did not have stems and starch concentrations in week 0 were only measured on

autumn coppice and control trees. Points for each treatment have been slightly shifted horizontally to avoid overlapping of confidence interval lines. Gray and beige shading indicate time of autumn and spring coppice treatment application, respectively.

Generally, coppiced *M. squarrosa* tended to produce more shoots than coppiced *E. camphora* but *E. camphora* shoot volume was on average ~5 times greater than that of *M. squarrosa* (Figure 4). In both species high coppice trees had significantly more alive shoots than low coppice trees (mean of 63 versus 41 shoots in *E. camphora* and mean of 109 versus 66 shoots in *M. squarrosa* high and low coppice, respectively) at the end of the experiment (week 52) and in *E. camphora* spring coppice trees had significantly more alive shoots than autumn coppice trees (mean of 72 versus 32 shots) (Figure 4 A, B; Appendix 2 Table A2). Shoot volume at the end of the experiment did not differ between high and low or between spring and autumn coppice in either species (Figure 4 C, D; Appendix 2 Table A2). However, on average, high autumn coppice trees produced the highest shoot volume (Figure 4 C, D).



299

300 *Figure 4 Boxplots of number of live shoots (A, B) and shoot volume (C, D) for trees in four different coppice treatments (n=8) for*
301 *the two study species. Points indicate raw data. No. = number. Note figures show raw data for crossed treatments whereas*
302 *statistical analysis was performed on log transformed data with cut height and cut season as separate factors. Note the*
303 *different scales on the y-axis in C and D.*

304

305 *3. 1. 2 Starch concentrations*

306 In both species starch concentrations were higher in roots (~4 times) than in stems (Figure 3 C vs 3E, 3D
307 vs 3F). Starch dynamics within a year, as observed in control trees across the 52 weeks of the experiment,
308 differed between the study species. In control trees of *E. camphora* starch concentrations of both stems
309 and roots increased during winter between week 0 and week 19 of the experiment and subsequently

decreased over spring and summer between week 19 and week 52 of the experiment (Figure 3 C, E). Starch concentration dynamics in all treatments of *M. squarrosa* were less pronounced and remained relatively stable throughout the year (Figure 3 D, F).

Coppicing treatment affected the starch concentrations in autumn coppice trees in *E. camphora*. Stem starch concentrations in trees coppiced in autumn (high autumn treatment) were significantly lower than control trees: at week 19 prior to the onset of resprouting; at week 28 during resprouting; and at week 52 after resprouting (Figure 3 C; Appendix 3 Table A3). Likewise, the starch concentrations in roots of low autumn coppice trees were significantly lower than those in uncoppiced trees (control and low spring but not high spring and high autumn) at week 19 at the time of spring coppice implementation, prior to the onset of resprouting (Figure 3 E; Appendix 3 Table A3).

In *M. squarrosa*, stem starch concentrations of autumn coppice trees were significantly lower than those of control trees at the end of the experiment in week 52 (Figure 3 D; Appendix 3 Table A3). There were no significant differences in starch concentrations between treatments at any other time in *M. squarrosa* (Appendix 3 Table A3).

3. 2 Importance of storage, tree factors and growth conditions for resprouting (Q2)

The variability in final shoot volume was not explained by the starch concentrations in roots or stems in week 19 (prior to resprouting) or week 52 (after resprouting) in either species (Appendix 4 Figure A1 A, B, C, D; Appendix 5 Table A4).

Pre-coppice tree DBH had a significant positive effect on shoot volume in *E. camphora* but not *M. squarrosa* (Figure 5 A, B). Pre-coppice tree crown extent or canopy openness did not affect final shoot volume in either species.

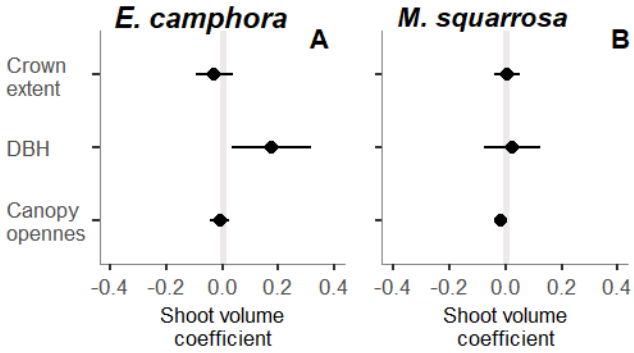


Figure 5 Coefficient estimates (±95% confidence intervals) of fixed effects (pre-coppice crown extent, pre-coppice DBH, canopy openness) for shoot volume in week 52 of the experiment for both study species. DBH = diameter at breast height.

4. Discussion

Both riparian tree species resprouted successfully after coppicing, regardless of coppice timing or severity. Although coppice timing and height affected the availability and use of stored starch in some coppiced trees, these treatments did not affect the shoot volume produced over the course of a year (Q1), indicating that resprouting is not limited by resource storage (Q2). Our findings indicate that *E. camphora* and *M. squarrosa* can regenerate vegetatively following physical disturbance such that coppicing may provide a practical means to promote riparian forest regeneration.

As observed in other temperate, evergreen trees, resprouting coincided with seasonal growth flushes rather than subsequent to disturbance via coppicing (Smith et al. 2018). Although evergreen trees have the potential to grow all year (Griebel et al. 2017), bud burst in temperate climates typically requires seasonal environmental stimuli, for example increases in temperature or solar radiation (Klimešová and Klimeš 2007, Masaka et al. 2015). Therefore, the autumn coppice trees were dormant and remained leafless for ~19 weeks. Spring conditions (i.e. warmer temperatures and moist, but well aerated, soils after flood recession) were favorable for resprout emergence and growth. As such, spring coppice trees resprouted relatively quickly after cutting (within ~3 weeks) and resprouted more vigorously (i.e. shoots grew faster) than trees coppiced in autumn.

Coppice timing did not affect the shoot volume of resprouts which was produced by our study species at week 52. In contrast, resprout biomass has been shown to vary with coppice timing in other species, which can be attributed to the extent of seasonal fluctuation of resources stored within stumps and roots, which can be crucial for resprouting success (Wildy and Pate 2002, Pelc et al. 2011, Hmielowski et al. 2014). Only one of our study species, *E. camphora*, displayed substantial seasonal variation of starch concentrations between the two coppice times in autumn and spring. Starch concentrations increased considerably in roots and stems of control *E. camphora* trees over winter. Typically, winter flooding occurs

in our study area and *E. camphora* ceases shoot expansion when flooded (Fischer et al. 2021b). Since *E. camphora* is flood tolerant, and photosynthesis likely did not cease in the evergreen tree, the slow growth in winter might have allowed plants to accumulate starch in storage pools. *M. squarrosa,* in contrast, maintains growth during flooding in winter and thus may not prioritize starch storage formation, which might explain why starch concentrations remained relatively stable.

Coppicing altered storage use as the starch dynamics in coppiced trees differed from those of control trees during the leafless period. Unlike in uncoppiced *E. camphora* trees, starch decreased in roots of low coppiced trees and starch did not accumulate in stems of high-coppiced trees. Starch was also depleted in stems of autumn-coppiced *M. squarrosa* over winter, however not to significantly lower levels than in control trees. Stored starch was likely consumed for tissue maintenance respiration in coppiced trees while carbon assimilation remained absent (Smith et al. 2018).

There was no relationship between stem/root starch concentrations and the shoot volume in our study species. In contrast, trees in other ecosystems have been shown to either not survive or resprout poorly when coppiced or disturbed at a time of low carbon storage levels (e.g. after drought or at the end of the growing season) (Von Fircks and Sennerby-Forsse 1998, Hmielowski et al. 2014). Among all treatments high autumn coppice would have had the highest starch demands since these trees had a larger biomass to maintain than low coppice and for an extended period without photosynthetic input, unlike spring coppice. The fact that the high-autumn treatment also produced the highest shoot volume in both species provides further evidence that starch reserves are not limiting for resprouting, potentially because starch is stored in excess (Cruz et al. 2003, Moreira et al. 2012, Wiley et al. 2019). Stored reserves in riparian trees may satisfy the demands for both maintaining biomass after disturbance and for restoring biomass.

The high site productivity (i.e. nutrient richness, moisture availability)of riparian zones (Naiman and and Decamps 1997) might have been conducive for resprout growth (Clarke et al. 2005) and thus alleviated

coppiced trees' dependency on stored resources for resprouting. Unlike temperate *Eucalyptus* growing in upland areas, riparian species seem not to experience drought stress during dry summer months which induces a storage depletion (Smith et al. 2018). Root groundwater access might have allowed for continued photosynthesis throughout the resprouting period. Being photosynthetically active, newly formed shoots likely self-supported their own growth with freshly assimilated carbon (Landhäusser 2011, Wiley et al. 2019). Light conditions, a key determinant for photosynthesis, can be highly influential on resprouting responses in trees (Pelc et al. 2011, Casals and Rios 2018). In our study canopy openness was not related to the shoot volume of resprouting trees, which suggests similar light availability across our experimental trees. This is not surprising given all experimental trees were subdominant.

Stem diameter can influence resprouting response (Matula et al. 2019, Zhang et al. 2021) and accordingly we found larger diameter *E. camphora* stumps to produce a higher shoot volume. Given the absence of a correlation between resource availability and resprouting in this study, higher shoot volume in larger trees or stumps might have been due to better moisture and nutrient access because of larger root systems, rather than due to a greater amount of stored reserves.

Where stems remained, below and above ground starch reserves were reduced following coppicing in our study trees. Storage and remobilization of stem resources is common in trees which resprout epicormically after disturbance which leaves stems intact (Clarke et al. 2013). The fact that root starch depletion and shoot volume did not differ between high and low coppice implies that the presence of stems and the availability of stored starch therein does not translate into better resprouting. The overall higher starch depletion (in roots and stems combined) of high coppice trees indicates that their higher biomass entails higher maintenance cost which in turn requires more starch remobilization (Salomón et al. 2018, Smith et al. 2018).

405 The ability to resprout from stems and to remobilize stored stem resources mirrors allocation patterns
406 from other disturbance prone ecosystems where stems are retained (Nzunda et al. 2008, Franklin et al.
407 2010, Smith et al. 2018). Where disturbance types and severities vary the diversification of storage across
408 above and belowground organs may allow for flexible response to disturbance (Nzunda et al. 2008,
409 Franklin et al. 2010). Coppicing poses a more severe disturbance than damage from seasonal flooding.
410 The ability to resprout both epicormically and from stumps indicates that resprouting is not purely an
411 adaptation to regular flooding, but rather that these riparian trees are well equipped to survive more
412 destructive disturbance such as fire, which also occurs at our study site (Pearce 2000).

413 Physical disturbance has the potential to promote tree longevity by inducing rejuvenation and reversing
414 senescence. Since human impacts often reduce or eliminate flooding in riparian ecosystems (Kingsford
415 2000, Grill et al. 2019), coppicing may help to preserve native tree species at degraded sites which no
416 longer support recruitment (i.e. natural regeneration from seed). Altered flooding regimes can preclude
417 germination and establishment of riparian trees due to altered dispersal vectors, increased understory
418 competition and lack of soil moisture (Fischer et al. 2021b, Greet et al. 2022). Besides, deteriorated health
419 of adult trees, caused by inadequate flooding regimes, can reduce the production and release of seeds
420 (Jensen et al. 2008, Greet et al. 2022). Our study suggests that reduced tree condition does not, however,
421 impair the ability of trees to regenerate vegetatively following disturbance by coppicing. Coppiced trees
422 are likely also less vulnerable to environmental stresses (e.g. water limitation) than tree seedlings and
423 thus require less specific site conditions, which highlights the advantage of coppice management (Pietras
424 et al. 2016). However, the long-term development of coppiced riparian trees (including potential
425 consequences for genetic diversity of forest stands) requires further investigation.

426

5. Conclusion

Given the good ability of *E. camphora* and *M. squarrosa* to resprout regardless of coppice timing and severity, it is more likely that their mortality will occur sooner due to the absence rather than the occurrence of physical disturbance. Coppicing alters tree architecture, changes tree physiology and increases tree growth rates (Drake et al. 2009, Nolan et al. 2014). Therefore, trees may be better suited for persisting at a site which has undergone degradation if they are coppiced rather than left untreated. Nonetheless, stress and disturbance history as well as tree phenology should be considered when undertaking coppicing. Based on our observations, coppicing of temperate evergreen riparian trees may be undertaken in autumn or spring. Coppicing immediately before the seasonal growth flush may be favorable as trees are less likely to deplete their carbon storage, which will increase resilience to potential subsequent disturbances or stress such as browsing, drought or waterlogging. Cut height can be chosen to optimize vegetation structure outcomes. For example, coppicing at greater height will potentially reduce browsing of new shoots which often emerge on the upper parts of the remaining stem (Pyttel et al. 2013, Smith et al. 2018) and thus potentially out of reach of browsers. Copping at ground level, in contrast, leads to basal resprouting which more likely results in multi-stemmed trees. Regardless of cut height, coppiced trees within existing, even-aged forest stands may then form an additional forest storey and increase structural complexity and vegetation density.

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