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*Communication*

# Early Differential Responses of Co-dominant Canopy Species to Sudden and Severe Drought in a Mediterranean-climate Type Forest

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**Abstract:** Globally, drought and heat-induced forest disturbance is garnering increasing concern. Species from Mediterranean forests have resistance and resilience mechanisms to cope with drought and differences in these ecological strategies will profoundly influence vegetation composition in response to drought. Our aim was to contrast the early response of two co-occurring forest species, *Eucalyptus marginata* and *Corymbia calophylla*, in the Northern Jarrah Forest of southwestern Australia, following a sudden and severe drought event. Forest plots were monitored for health and response, three and 16 months following the drought. *Eucalyptus marginata* was more susceptible to partial and complete crown dieback compared to *C. calophylla*, three months after the drought. However, resprouting among trees exhibiting complete crown dieback was similar between species. Overall, *E. marginata* trees were more likely to die from the impacts of drought, assessed at 16 months. These short-term differential responses to drought may lead to compositional shifts with increases in frequency of drought events in the future.

**Keywords:** forest die-off; forest mortality; climate change; epicormic response; *Eucalyptus marginata*; *Corymbia calophylla*

## 1. Introduction

Climatic changes are expected to drastically modify growing conditions for forest trees in the coming decades [1], primarily driven by changes in the frequency, intensity and duration of extreme events [2]. Reports of forest dieback associated with drought and heat events are becoming increasingly common and have been reported from a wide variety of forest types [3]. Further examples of drought-induced forest dieback have recently emerged from southwestern United States [4,5], the Mediterranean Basin [6] and from southwestern Australia [7,8]. Water-limited forest environments (e.g., Mediterranean-climate ecosystems, MCEs) are thought to be particularly prone to dieback due to projected reductions in rainfall and increasing temperatures [2,9]. In fact, assessing the impacts of drought-induced mortality has been recently recognized as a research priority for Mediterranean ecosystems [10].

Extreme drought and heat waves have the potential to cause catastrophic ecosystem type changes, transforming forest composition, structure and ecosystem functioning on a sub-decadal timescale [11] (although see discussion on existence of stabilizing processes minimizing and counteracting the effects of these events [12]). Differential species-specific susceptibility to drought can favor more tolerant species, thus shifting forest composition [13,14]. For example, a rapid (<5 year) landscape-scale shift of a woody ecotone between semiarid ponderosa pine forest and piñon-juniper woodland in response to a severe drought in northern New Mexico was reported by Allen and Breshears [15] and has persisted for more than 40 years. Such ecosystem responses will be determined by the intrinsic traits of species to withstand drought (resistance traits), respond to drought (resilience traits), or the ability to adapt or migrate [16]. Compositional shifts in ecosystems are expected in the coming decades with climatic changes [17].

In contrast to many temperate species, those from MCEs are recognized as being highly resilient to disturbances through a wide range of morphological, ecological and phenological adaptations [18,19]. After disturbance, resprouting is a common trait in many trees and shrubs in MCEs and allows for the persistence of many perennial plant species [20]. Australian Myrtaceae (especially *Eucalyptus* and its allies) are well known as successful epicormic and basal resprouters [21], as well as *Quercus* and *Adenostoma* in California, North America [22,23] and *Acacia* and *Olea* in South Africa [24]. However, little is known about the response of these species to drought and the role of drought in driving shifts in composition.

There are several studies that have investigated the susceptibility and response of Mediterranean species following drought events, for example, in mixed conifer forests in the western United States [25], in woody vegetation in central and Southern Spain [26], and in pine forests in France [6]. Determining the relative susceptibility of co-occurring tree species to drought, and their recovery, is particularly important for determining the potential for compositional changes and ecosystem shifts with continued climate change. Here, we aim to determine the susceptibility and response pattern of the two co-occurring dominant overstory tree species *Eucalyptus marginata* Donn ex Sm. and *Corymbia calophylla* R. Br. K.D. Hill and L.A.S. Johnson, to extreme drought in a Mediterranean-type forest in southwestern Australia. Specifically, we examine their relative probability of experiencing: (a) partial crown dieback, (b) complete crown dieback; (c) resprouting; and (d) tree mortality, assessed 16 months following the drought.

## 2. Experimental Section

### *2.1. Study Area*

The Northern Jarrah Forest (NJF), in the Southwest Botanical Province of Western Australia, covers an area of 1,127,600 ha [27] (see map in Brouwers *et al.* [28]), and ranges in form from an open and dry sclerophyll forest in the north to a tall, closed forest in the south [29]. This study is focused on upland areas, which are dominated by *Eucalyptus marginata* (jarrah) and *Corymbia calophylla* (marri). The NJF overlies Archaean granite and metamorphic rocks capped by an extensive lateritic duricrust, which is interrupted by occasional granite outcrops in the form of isolated hills [30]. The lateritic plateau has an average elevation of 300 meters. The climate of the NJF is a Mediterranean-type, with most (~80%) rainfall falling between April and October (winter) [9] and a seasonal drought (summer) that may last from four to seven months [31]. There is a strong west-east rainfall gradient across the forest, ranging from >1100 mm/year on its western edge (The Darling Scarp) to ~700 mm/year in the north east [31].

### *2.2. The 2011 Drought Event in the Northern Jarrah Forest*

Beginning in February 2011, in the midst of a decade's-long precipitation downturn, after one of the driest years since comparable records began [32] and, following nine days over 35 °C [33], tree crowns in the NJF began to rapidly discolor and die. This process continued through May 2011, resulting in discrete patches of nearly complete forest canopy loss (Figure 1). An estimated 16,500 ha of the NJF was severely affected with greater than 70% tree crown dieback [8]. The dominant forest tree species were impacted, in addition to associated midstory species such as *Banksia grandis* R. Br. [8]. The site [28], and stand [8] factors associated with the drought event have been determined previously. The winter rainfall period following the drought was marked by above-average precipitation (Figure 2).

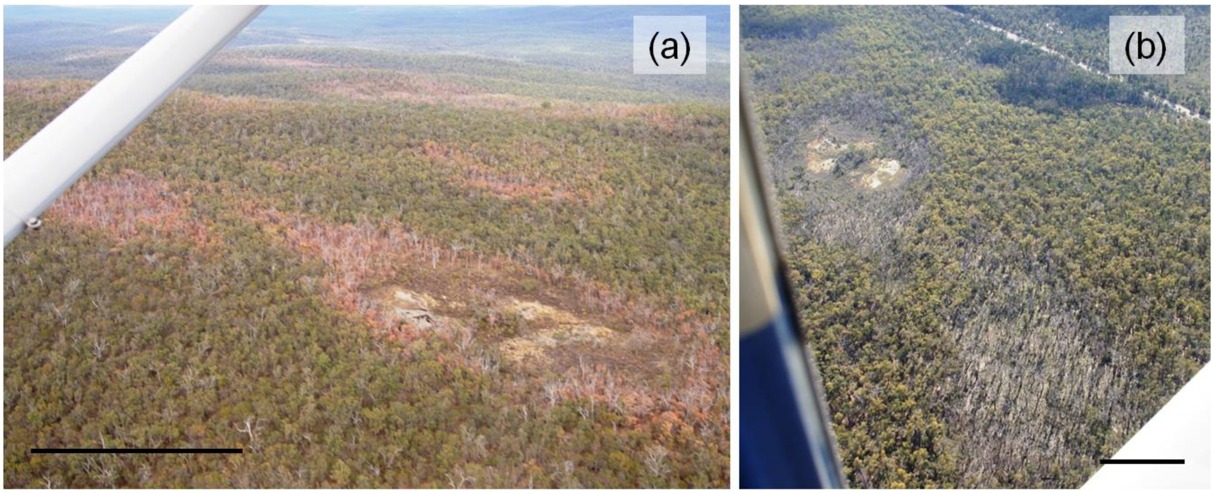


**Figure 1.** Aerial photo of an area of the Northern Jarrah (*Eucalyptus marginata*) Forest, Western Australia (Site 74), at (**a**) three and (**b**) 16 months following drought. Scale bar represents approximately 200 metres.

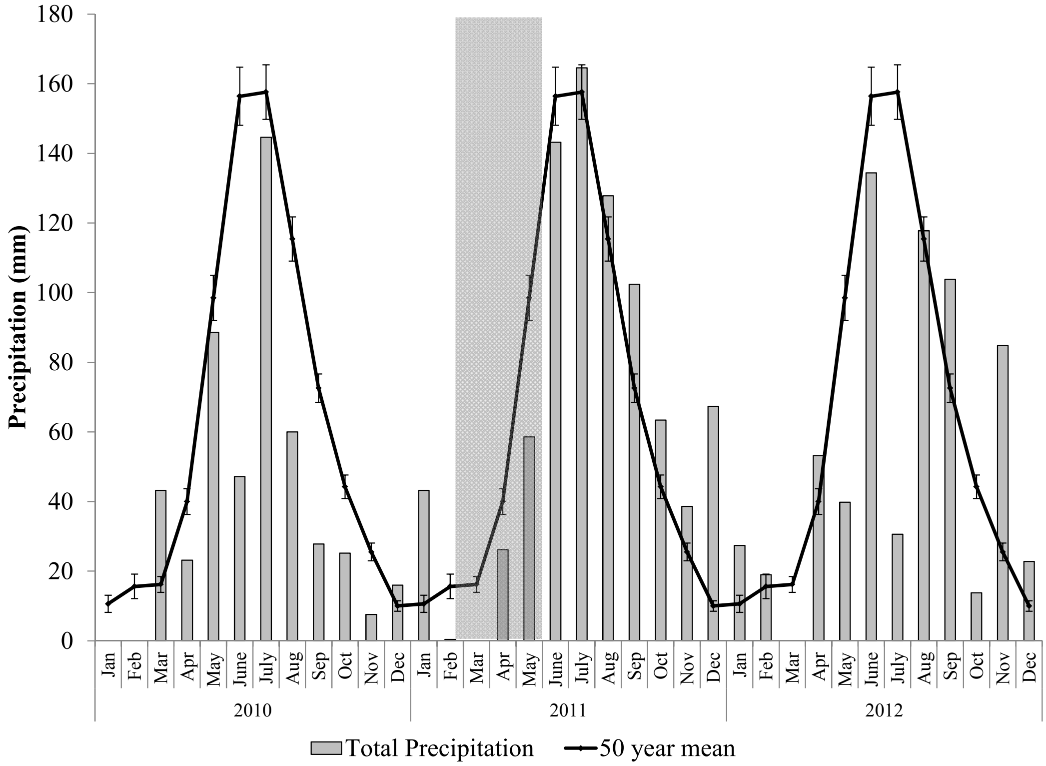


**Figure 2.** Monthly precipitation and fifty-year mean monthly precipitation (mm) for Perth, Western Australia (± standard error). Light shading denotes the period of forest disturbance in the Northern Jarrah Forest. Data reported is for Perth Airport, Station number 9021, Latitude 31.93°, Longitude 115.98°.

### *2.3. Site Selection*

Twenty forest patches affected by the drought were selected randomly from a population of 235 affected patches identified during an aerial survey conducted at the cessation of the drought period (May 2011). Affected patches that were deemed inaccessible were discounted for field investigations, including those restricted to private property and those more than 3 km from roads. From the remaining population, 28 were chosen for ground delineation and a random subsample of 20 were chosen for field investigations [8]. Sites were visited at three (June/July 2011) and 16 months (July 2012) following the drought event.

### *2.4. Sampling*

The affected forest patches, defined as >70% tree crown response (presence of dry and red foliage), was delineated accurately using a differential GPS (Pathfinder Pro XRS receiver, Trimble Navigation Ltd., Sunnyvale, CA, USA). Three 6 m circular radius plots (0.01 ha) were randomly established within the affected forest patches using FGIS forestry cruise software (Wisconsin DNR-Division of Forestry). Paired control plots were located approximately 20 m outside the affected site boundary at the shortest straight-line distance from each affected plot [8]. However, these plots were not considered here for the analysis of drought recovery as their condition did not change significantly. The relative abundance of the study species were similar in the affected and control plots (die-off plots: *E. marginata* = 66.8, *C. calophylla* = 20.4, Control: *E. marginata* = 74.2, *C. calophylla* = 18.4) [8].

For the purposes of this analysis, the health of all *E. marginata* and *C. calophylla* greater than or equal to 1 cm diameter at breast height (DBH) were categorized into one of three crown health categories during plot measurement at three months: (1) unaffected crowns, which showed either no or minimal evidence of stress; (2) moderately affected crowns which had predominately dry and discoloured leaves, but still retained green foliage; and, (3) severely affected crowns, which experienced complete crown dieback. Thus, trees that were moderately affected experienced partial crown dieback, while severely affected suffered complete crown dieback.

Since the primary survival mechanism in drought-affected trees was resprouting from the tree or below-ground tissue [8], the presence or absence of resprouts, number of resprouts and resprout height were determined at 16 months in all trees in all plots. Trees were considered dead if they had failed to resprout above breast height at 16 months.

### *2.5. Data Analysis*

For testing the relative susceptibility and response of *E. marginata* and *C. calophylla* to the drought, only those affected patches with both species present were used ($n = 17$). Each of the four primary assessment variables (partial crown dieback, complete crown dieback, resprouting, tree mortality) was analyzed for tree species differences using a generalized mixed model using the logit function in the GLIMMIX procedure in SAS statistical software (SAS Institute, version 9.3, Cary, NC, USA), including tree species as the fixed factor and site as the random intercept. Measurements assessing the strength of resprouting, including resprout height and sprout number, were used in a similar model using GLIMMIX with no link function. Resprouting was assessed in trees experiencing crown dieback only.

## 3. Results and Discussion

*Eucalyptus marginata* had a higher probability of experiencing both partial ($F = 4.11$, $p = 0.0431$) and complete crown dieback ($F = 28.33$, $p < 0.0001$) compared to *C. calophylla* (Figure 3). Of those trees experiencing dieback, both species had an equal probability of being able to resprout following dieback ($F = 0.35$, $p = 0.5554$), despite *E. marginata* having significantly taller sprout heights (3.3m *vs.* 2.3m, $F = 4.30$, $p = 0.0389$) compared to *C. calophylla* by 16 months following drought. Overall, *E. marginata* had a higher probability of tree mortality after 16 months ($F = 7.53$, $p = 0.0063$) as more of this species experienced dieback at the outset.

This study has highlighted contrasting strategies and thresholds to a sudden and severe drought by co-occurring species in a Mediterranean-climate type forest. We have shown that after 16 months *E. marginata* had a higher probability of being affected by the drought, and a lower probability of surviving the drought compared with *C. calophylla*. These findings after 16 months are different from recent work [8] that found at six months there was no difference between these species in terms of the percentage of trees that remained alive. Thus, it seems that longer term shifts in composition may develop at these sites. Such shifts in composition have been noted elsewhere following drought events, such as in semiarid ponderosa pine forest and pinyon-juniper woodland in northern New Mexico [15] and in pinyon-juniper woodland in northern Arizona [34]. Nonetheless, although such drought events have the potential to induce changes in forest composition directly by altering species-specific tree survival patterns, as seen here, permanent vegetation change will occur only if recruitment patterns are also affected [14]. This will be the focus of future research.

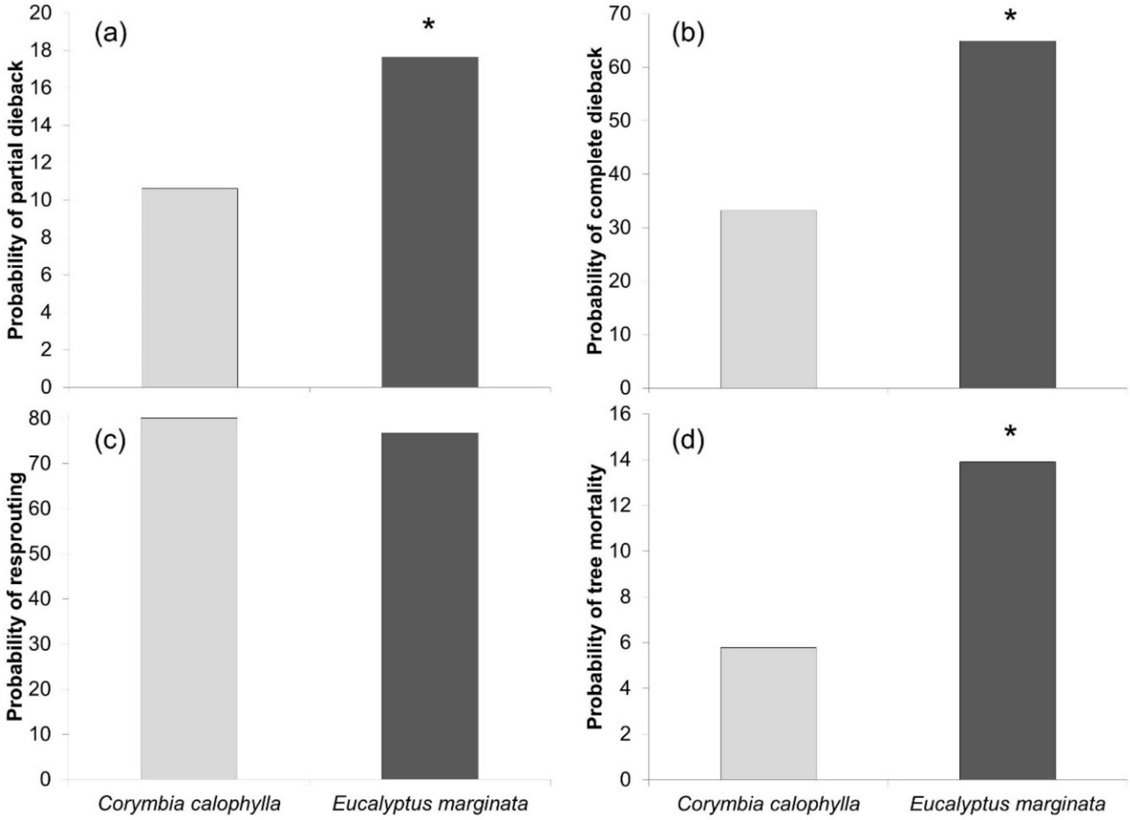


**Figure 3.** The probability of *Corymbia calophylla* and *Eucalyptus marginata* trees experiencing: (**a**) partial crown dieback; (**b**) complete crown dieback; (**c**) resprouting (of trees that experienced dieback); and (**d**) overall tree mortality, following drought in the Northern Jarrah Forest, Western Australia. An asterisks indicates significantly higher probabilities from generalized mixed models at alpha = 0.05.

There are clear differences in drought resistance among co-occurring species, which can originate from different physiological responses to drought [34,35] and species-site interactions [36]. The hydraulic framework proposed by McDowell *et al.* [11] suggests that trees are more likely to die via hydraulic failure under sudden and intense droughts, however, strict control of stomata closure under those conditions is predicted to be beneficial. Although both species in this study are able to tolerate drought by closing stomata early in the drought cycle, *C. calophylla* seems to have a greater capacity to do this than *E. marginata* [37]. This might explain the lower mortality in *C. calophylla* during the sudden and severe drought event in this study. A more detailed investigation of the differential physiological characteristics of the co-occurring species at the study sites is needed.

*Eucalyptus marginata* is known to maintain relatively high transpiration rates during summer [38], owing to its deep root system accessing stored water [39]. These high transpiration rates may make this species more vulnerable on shallow soils that have limited connection to groundwater during extended periods of drought [40]. Given that the drought-affected sites in this study are associated with sites at high elevations, on steep slopes, and close to rock outcrops [28], this event illustrates the site-driven vulnerability of *E. marginata* during drought. Site-driven responses have also been observed in a mixed hardwood-loblolly pine forest in Georgia, in terms of a soil moisture and transpiration interaction. The study showed that in the upslope section, which had shallower soils, transpiration became limited by soil moisture [41]. This is because more water is stored in deeper soils, and removing the same amount of water from a section of deep soil and from a shallow soil results in a faster depletion of moisture in the shallow soil [41].

Given the patterns outlined above, one could suggest that *C. calophylla* has strong resistance traits to drought (e.g., osmotic adjustment), and, since there was no difference in the level of resprouting between the species, both species have equally strong resilience traits following drought. It is currently unknown whether these differential responses will lead to longer term changes in co-dominance within drought-affected patches. If *C. calophylla* is able to maintain functioning crowns, produce flowers, attract pollinators to such a contracted resource and set viable seed more quickly than *E. marginata*, it has the potential to drive longer term compositional changes. Further research will offer critical information on longer-term health trajectories, canopy seed bank dynamics, natural recruitment, the drought-fire interactions that are likely to occur in this system, and the implications of shifting forest composition on faunal species that are reliant on these canopy species.

## 4. Conclusions

Our results have important implications for forest dynamics under predicted climatic conditions; the length and severity of drought is expected to increase in Mediterranean and semi-arid regions such as southwestern Australia [9], the southwestern United States [42] including California [43], and the Mediterranean Basin [44]. Thus, drought-induced forest die-off and mortality events, and associated shifts in forest composition, may become more frequent and severe.

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## Author Contributions

Katinka X. Ruthrof assisted with designing the experiment and running of the experiment, undertook field work, supervised field assistants and co-wrote the manuscript. George Matusick designed the original study, undertook field work, analysed data and co-wrote the manuscript. Giles E. St. J. Hardy undertook field work and carried out manuscript editing.

## Conflicts of Interest

The authors declare no conflict of interest.

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