The Impacts of Drought Stress and *Phytophthora cinnamomi* Infection on Short-Term Water Relations in Two Year-Old *Eucalyptus obliqua*

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**Abstract:** The effects of drought stress, *Phytophthora cinnamomi* infection and their interaction on water relations and growth were examined for 28 days on two year-old potted trees of *Eucalyptus obliqua* (L'Hér.). There were significant effects of drought stress on plant photosynthesis, stomatal conductance, biomass accumulation, plant water potential at turgor loss point and the bulk modulus of elasticity. *E. obliqua* was successfully infected but the trees showed only mild symptoms. Infection with *P. cinnamomi* led to a significant reduction in the root biomass and root-to-shoot ratio in well-watered and droughted plants but did not impact water relations. There was no observable cumulative effect of drought and *P. cinnamomi* infection. There are multiple potential reasons why *P. cinnamomi* infection did not lead to drought-like symptoms in *E. obliqua*, including short experimental duration, delayed infection symptoms, potential resistance of *E. obliqua* and a possible lower aggressiveness of the *P. cinnamomi* strain. Hence, our results indicate that *P. cinnamomi* infection will not always lead to immediate short-term symptoms, and that plants that are mildly symptomatic respond very similar to drought stress compared to non-infected trees.

**Keywords:** drought; *Phytophthora*; *Eucalyptus*; dieback; plant water relations

1. Introduction

Drought stress is one of the major factors leading to the degradation of forests worldwide [1–4]. Biotic agents such as pathogens can also contribute to tree mortality and potentially exacerbate the impact of drought stress [5]. The presence of plant pathogens has been correlated to tree dieback in a range of forest ecosystems [6,7]. Furthermore, the interaction between drought and disease could influence deterioration of tree health status [8,9].

*Phytophthora* species are some of the most invasive fungal pathogens in the world [10–12]. They have been associated with tree decline in many ecosystems, including native forests and urban environments in a large variety of tree species across the world [13–20]. In Australia, *Phytophthora* has been strongly linked to many cases of tree dieback in both native and urban ecosystems [21,22], in Victoria [23], Northern Queensland [24] and Western Australia [25,26]. *Phytophthora* has a wide range of host plants, including many Australian native plant species [27], e.g., members of the genus *Eucalyptus* [20,21]. This pathogen is considered as a major threat to the Australian biodiversity under the Environmental Protection and Biodiversity Conservation Act 1999 [28,29].

The major stress of *Phytophthora* infection is associated with the impairment of the plants root system [24]. Zoospores are attracted to root exudates, germinate in the root cap cell zone, and develop mycelium in the cortical cells, phloem and xylem of the infected fine roots [27,30,31]. The infection then leads to the formation of necrotic lesions and eventually damages the roots, leading to inefficiency of water and nutrient uptake [28]. Accordingly, the infected host plants could develop symptoms similar to those under drought stress,
including leaf chlorosis, canopy dieback and the development of epicormic shoots and mortality [19,21].

In natural ecosystems, especially in Mediterranean ecosystems, Phytophthora infections often occur in wet and warm winters. The infected plants are subsequently exposed to hot and dry summers, and the compromised root system may be unable to supply the plants with sufficient water [30]. However, there is conflicting evidence if Phytophthora-infected plants actually experience water deficit, similar to those under drought-induced stress. It has been reported that Phytophthora infection leads to the presence of drought stress symptoms due to the inefficiency of water and nutrient uptake and thus causes water deficit in plants [15,27]. This has been confirmed in some studies where significant differences in water potential, stomatal conductance, and photosynthesis occurred following P. cinnamomi infection [32,33]. However, other studies did not find a significant effect of P. cinnamomi infection on plant water relations [34–36]. Furthermore, it has been suggested that drought events might worsen the impacts of Phytophthora infection on plants by lowering the plant resistance [28] or increasing the inoculum production and infection rate [37,38]. Consequently, drought events that frequently occur in Australia potentially exacerbate tree decline due the drought-induced water deficit on infected plants. The effects of climate change might also result in changes in the distribution of forest pathogens such as Phytophthora with some areas becoming more or less likely to support the species depending on temperature and water availability [39]. Nevertheless, there is insufficient evidence that the Phytophthora infection leads to more severe symptoms in a plant that initially has undergone water deficits during a drought event. Since the symptoms of Phytophthora infection resemble drought symptoms, it is often challenging to identify Phytophthora infection in the field [13]. As a consequence, the pathogens’ contribution to tree mortality is often overlooked, thus highlighting the importance of understanding the relationship between drought stress and Phytophthora infection on tree mortality.

This study investigated the effects of drought, P. cinnamomi infection, and the interaction of both factors on the water relations and gas exchange in Eucalyptus obliqua. Three hypotheses were examined: (1) Drought stress significantly decreases plant water potential, gas exchange, and biomass accumulation due to limited soil water availability; (2) P. cinnamomi infection results in plant water deficit which leads to drought stress symptoms described above; (3) The interaction between drought stress and P. cinnamomi infection will increase drought stress symptoms due to the additive impacts of both factors on limiting water uptake through the roots.

2. Materials and Methods

2.1. Plant Material

Eucalyptus obliqua (L’Her.) seedlings for this study were sourced as tube stock from a commercial nursery (Bushland Flora, Mt. Evelyn, VI, Australia) in winter and grown in a shade house at the Burnley campus of The University of Melbourne, Victoria, Australia. In October 2018, the four months-old seedlings were about 0.3 m tall and transplanted into 9-L pots containing a mix of 50:30:20 medium, comprising pine bark (3–5 mm), expanded coir (fine grade: 0–6 mm), and coarse horticultural sand in 6-L pots. In addition, 4 kg Macracote Coloniser fertiliser plus (Fertool, Dandenong, VIC, Australia), consisting of 8–9 moths, N, P, K (15, 13, 9), and trace elements were added as the supply of macro and micronutrients. The plants were grown for a further four months in an open area in the nursery and watered once daily to soil capacity before the start of the experiment. In February 2019, the plants were transferred to a rainout shelter with open side walls where the experiment took place and were between 1.2–1.4 m tall at the start of the experiment.

2.2. Experimental Design

The experiment was conducted in a completely randomized design with two main factors; Drought and Disease (pathogen inoculation with P. cinnamomi). The combination of the two factors resulted in four treatments: Control (Con) (well-watered and non-inoculated),
Drought (Dro) (deficit irrigation and non-inoculated), Disease (Phy) (well-watered and inoculated), and combination of Drought and Disease (DroPhy) (deficit irrigation and inoculated). Due to an uneven number of trees, we allocated six replicate trees for Con and seven replicates for each of other three treatments (Dro, Phy, and DroPhy).

During the experiment, two pots of the same disease factor were placed in 60-L black plastic containers to prevent cross contamination between inoculated and non-inoculated plants. The pots were placed on a raised mesh within the plastic containers so that pots could drain freely and no cross contamination between the pots in the same container would occur. The trays were distributed randomly in the experimental area to eliminate bias due to potential differences in microclimatic conditions in the rainout shelter. The climatic conditions under the rainout shelter were similar to the outside conditions, with small reductions (5%–10%) of the level of photosynthetic active radiation due to the plastic cover of the shelter (GroTuff greenhouse plastic 180UM, Sage Horticultural, Hallam, VIC, Australia) and no rainfall.

2.3. Inoculation with Phytophthora and Re-Isolation

In December 2018, we conducted a preliminary study using four pots of E. obliqua seedlings to determine the time required for P. cinnamomi to infect the seedlings roots. The P. cinnamomi inoculum was isolated from soil samples collected from field sites in Eastfield Park, Maroondah Melbourne, where tree decline and the presence of P. cinnamomi had been observed. P. cinnamomi was isolated from soil by baiting using Eucalyptus sieberi cotyledons floated on water on the soil [40]. After five days the cotyledons were then removed from the water and placed on potato dextrose agar (PDA) plates [41]. The agar plates were stored in a cool environment to provide suitable environment for Phytophthora to grow for ten days [10].

The seedlings were inoculated with P. cinnamomi by pouring 100 mL of the Phytophthora inoculum solution into each pot. The suspension was prepared by suspending half of a 90 mm diameter PDA-cultured inoculum in 1000 mL water. The solution was stored in dark and cool environment for five days to promote the growth of active sporangia [42]. Four weeks after inoculation, the infection of roots was evaluated by collecting roots from plants in infected pots with a small cork borer and plating of root samples in PDA medium. Prior to the plating, the root samples were cleaned under distilled running water and placed in distilled water in a shallow container. After 24 h, the roots were sterilized using 70% ethanol for 20 sec and rinsed in demineralized water prior to the plating to suppress the presence of contaminants [43]. The P. cinnamomi species was evaluated with microscopy and identified based on the colony growth pattern on PDA after 5–7 days, as described and illustrated in [10] and its morphological characteristic was examined as described and illustrated in [44].

In the preliminary study, Phytophthora was successfully re-isolated from the roots four weeks after inoculation. Dieback symptoms such as leaf chlorosis and wilting were also observed, and symptoms gradually worsened until the end of the trial. However, no tree mortality occurred during the experiment. Results of this trial were used to estimate the time for Phytophthora inoculation prior to the main experiment.

In late February 2019, plants subjected to Phy and DroPhy treatments were inoculated using the same method outlined above. Four weeks after inoculation, however, there were no visible symptoms of the infection on aboveground organs of the infected plants.

In March 2019, all disease treatment plants were re-inoculated using a second P. cinnamomi inoculum sourced from infected soil samples taken from field where P. cinnamomi symptoms were observed. P. cinnamomi in the soil was again baited by using fresh Rhododendron spp. leaves [45] sourced from the Burnley gardens. The infected leaf was cut into 5 mm × 5 mm pieces, placed in PDA media and grown for 7 d [10]. The inoculum was made of 90 mm diameter section of the pure culture of P. cinnamomi diluted in 1400 mL of deionized sterile water. Each pot was given 100 mL of liquid inoculum and in addition five pieces of 0.5 mm × 0.5 mm block of agar containing P. cinnamomi mycelium.
The *P. cinnamomi* was re-isolated from roots as described above after 14 d confirming successful inoculation.

### 2.4. Watering

Before the start of the study, all plants were hand watered to field capacity in the afternoon every two days. A week before the experiment, the weights of every pot were recorded before and after watering to estimate daily plant water use to determine the level of irrigation for Dro and DroPhy treatments. The irrigation requirements were calculated based on the average daily water use of each plant, which was gradually decreased by 10% every week for the plants in both drought treatments. Plants in the Dro and DroPhy treatments showed signs of rapid drought stress after the first observation. To prevent excessive plant stress, the irrigation level was increased from 80% of the estimated daily evapotranspiration to 80% of saturated pot weight. Subsequently, the irrigation requirements for the drought treatment were calculated based on the soil water capacity instead of daily evapotranspiration. The irrigation level of drought treatment was decreased by 10% every week (Figure 1), whereas the well-watered plants received water at field capacity (3L) at the same time.

![Figure 1](image-url)

**Figure 1.** Relative pot weight as a percentage of the initial pot weight of *E. obliqua* seedlings subjected to Control (Con), Drought (Dro), Phytophthora (Phy), and Drought-Phytophthora (DroPhy) treatments. Bars indicate ± standard errors of the mean values. Where no error bars are visible, the values are smaller than the size of the symbol.

### 2.5. Data Collection

#### 2.5.1. Water Relations

Pre-dawn (Ψ<sub>pd</sub>) and midday (Ψ<sub(md)</sub>) leaf water potential of all trees were measured once a week using a pressure chamber (3000 Series Plant Water Status Console, Soilmoiture Equipment Corp. Goleta, CA, USA) [46]. A fully expanded leaf with long petiole was cut from each tree. Ψ<sub>pd</sub> samples were collected 30 min before sunrise and Ψ<sub>md</sub> samples were collected at 13:00 h. Leaf samples were stored in ziplocked polyethylene bags inside a non-transparent box with an icepack to prevent water loss due to transpiration during the transportation from the nursery to the laboratory [47]. The samples were measured within one hour of collection.

#### 2.5.2. Gas Exchange

Gas exchange of leaves was measured with an infrared gas analyzer (LI6400, Licor, Lincoln, NE, USA) once every week between 10:00 and 13:00 h on the same day as the water relations measurements on fully expanded leaves of each plant with two to three replicates per plant. This method was non-destructive to the leaves. Irradiance was set...
at 1800 µmol m\(^{-2}\) s\(^{-1}\), block temperature was set at 25 °C, and air flow rate through
the chamber was 400 mL min\(^{-1}\). Readings were taken after steady state was achieved,
usually after three minutes for each measurement. Light-saturated photosynthesis (\(A_{\text{sat}}\))
and stomatal conductance (\(g_s\)) were used as the key measurements for gas exchange.

2.5.3. Pressure-Volume (PV) Curves

Pressure volume (PV) curves were determined using the same pressure chamber
described above. Two fully expanded leaves were collected from each plant at 08:00 h.
The samples were rehydrated via the petiole in 50 mL Sarstedt tubes filled with 15 mL
of distilled water inside a non-transparent box for about three hours. This is usually a
sufficient amount of time to achieve rehydration of leaves of eucalypts [48]. One leaf
sample per plant was used in the PV analysis. The leaf was weighed to determine its
fresh weight and then the water potential was determined in the pressure chamber. The
leaf was then allowed to dry out on a bench at room temperature and the process of
leaf weighing and water potential measurement was repeated. Each leaf was measured
approximately 12–15 times until 4–5 water potential measurements were collected that
were more negative than the water potential at turgor loss point. Upon completion of the
measurements, the leaf was oven-dried at 80 °C until constant weight and the dry weight
obtained. The data were then processed to determine the osmotic potential at full turgor
(\(\pi_{100}\)), water potential at Turgor Loss Point (\(\Psi_{\text{TLP}}\)), relative water content at turgor loss
point (\(\text{RWC}_{\text{TLP}}\)), apoplastic water fraction (\(R_a\)), and bulk modulus of elasticity (\(\varepsilon\)) based on
Schulte and Hinckley [49] using an Excel spreadsheet downloaded from Landflux webpage:
http://landflux.org/Tools.php.

2.5.4. Final Harvest Biomass Assessment

All trees were harvested after four weeks. Leaves, branches, and stems were separated
and stored in a weighed paper bag and oven-dried to constant weight at 80 °C. Roots were
separated from potting mix in a root washing bay, bagged and also dried at 80 °C. The dry
weight of each sample was recorded. Above ground biomass was determined from the
combined dry weights of leaves, branches, and the stem (g). Below ground biomass was
equal to the dry weight of root samples (g). The root-to-shoot ratio was calculated as the
ratio of above ground biomass to below ground biomass.

2.6. Statistical Analysis

All data were analysed using one-way analysis of variance (ANOVA) to examine the
effect of the treatments. Fisher’s least significant difference (LSD) test was performed to
determine the significant differences (\(p \leq 0.05\)) between treatments using Minitab version
17 statistical software (Minitab, LLC, State College, PA, USA).

3. Results

3.1. Phenotypic Symptoms of Drought and Pathogen

Well-watered plants had no drought-like symptoms (leaf necrosis or chlorosis, leaf
wilting, leaf rolling) after four weeks, regardless of inoculation (Phy or Con). Leaf chlorosis
and wilting were observed in the droughted plants; however, there were no differences
between inoculated (DroPhy) and non-inoculated (Dro) treatments. Seedlings in both
well-watered treatments (Phy and Con) had healthier-looking leaves that were greener in
colour compared to the plants in both drought treatments.

Root necroses was not visible in any of the inoculated plants (Phy and DroPhy).
Control plants appeared to have more vigorously growing roots compared to the other
treatments and had more fine roots with a brighter colour. No visual differences were ob-
served for roots of plants in drought (Dro) and drought-Phytophthora (DroPhy) treatments.

Despite the absence of root necroses, \(P.\ cinnamomi\) was re-isolated from most of the
root samples that were collected randomly from the infected plants, indicating that the
inoculation treatments were successful. In addition, \(P.\ cinnamomi\) was not recovered from
the root samples of non-inoculated plants (Con and Dro) indicating there was no cross-contamination between inoculation and no-inoculation treatments.

3.2. Water Relations

The pre-dawn (Ψ<sub>pd</sub>) and mid-day (Ψ<sub>md</sub>) water potentials of the <i>E. obliqua</i> indicated that there were significant effects of the drought treatments but no effects of <i>P. cinnamomi</i> inoculation treatments. Both Ψ<sub>pd</sub> and Ψ<sub>md</sub> were statistically different between well-watered and drought treatments by the end of the experiment, regardless of <i>Phytophthora</i> inoculation (Figure 2).

Both the Ψ<sub>pd</sub> and Ψ<sub>md</sub> of well-watered (Con and Phy) plants were relatively constant, with Ψ<sub>pd</sub> ranging from −0.05 to −0.24 MPa and Ψ<sub>md</sub> ranging from −0.60 to −0.99 MPa. There were no significant differences between Con and Phy treatments by the end of the experiment. The Ψ<sub>pd</sub> and Ψ<sub>md</sub> of plants in drought treatments (Dro and DroPhy) gradually decreased, and by the end of the experiment Ψ<sub>pd</sub> were around −3.70 MPa and Ψ<sub>md</sub> ranged from −3.76 to −3.99 MPa. There were no statistically significant differences between Dro and DroPhy plants. On a few occasions, however, significant differences between Dro and

Figure 2. (A) Pre-dawn (Ψ<sub>pd</sub>) and (B) midday (Ψ<sub>md</sub>) water potentials (MPa) of <i>E. obliqua</i> seedlings subjected to Control (Con), Drought (Dro), <i>Phytophthora</i> (Phy), and Drought-<i>Phytophthora</i> (DroPhy) treatments for five weeks. Error bars indicate ± standard error of the mean values; where no error bars are visible, the values are smaller than the symbol. Means with different letters are significantly different at <i>p</i> ≤ 0.05, after ANOVA and LSD test.
DroPhy occurred as on the fifth observation of $\Psi_{pd}$ and fourth and fifth observations of $\Psi_{md}$, which were primarily driven by few individual plants with lower water potential in the Dro treatment.

3.3. Gas Exchange

Light-saturated photosynthesis ($A_{sat}$) and stomatal conductance ($g_s$) was significantly reduced in both drought treatments (Figure 3). The $g_s$ of well-watered treatments (Con and Phy) showed some fluctuation and ranged from 0.14 to 0.38 mol H$_2$O m$^{-2}$ s$^{-1}$, but there were no statistically significant differences between Con and Phy treatments. The $g_s$ of the two drought treatments (Dro and DroPhy) were always lower compared to the well-watered treatments, and decreased considerably with increasing drought. In the last three weeks of the experiment stomata were almost completely closed in both drought treatments. There were no significant differences for $g_s$ between Dro and DroPhy treatments (Figure 3).

![Figure 3. (A) Stomatal conductance ($g_s$) and (B) light-saturated photosynthesis rate ($A_{sat}$) of E. obliqua seedlings subjected to Control (Con), Drought (Dro), Phytophthora (Phy), and Drought-Phytophthora (DroPhy) after ANOVA and LSD test.](image)

The light saturated photosynthesis ($A_{sat}$) of well-watered treatments (Con and Phy) fluctuated and ranged from 10 to 17 mmol CO$_2$ m$^{-2}$ s$^{-1}$. There were no significant differences between the Con and Phy treatments at the end of the experiment. The $A_{sat}$ of the two drought treatments (Dro and DroPhy) significantly decreased on the fourth observation and at the end of the experiment where $A_{sat}$ was close to zero (around 1 mmol
CO₂ m⁻² s⁻¹). There were no significant differences between Dro and DroPhy treatments (Figure 3).

3.4. Biomass

The aboveground biomass of E. obliqua plants subjected drought treatments (Dro and DroPhy) was significantly lower than both well-watered treatment plants (Con and Phy) (Figure 4). However, inoculation had no significant effect on aboveground biomass in well-watered or droughted plants.

![Figure 4](https://example.com/figure4.png)

**Figure 4.** (A) Final above- and belowground biomass and (B) root-to-shoot ratio of E. obliqua seedlings subjected to Control (Con), Drought (Dro), Phytophthora (Phy), and Drought-Phytophthora (DroPhy) treatments. Error bars indicate ± standard error of the mean values. Means with different letters are significantly different at p ≤ 0.05, after ANOVA and LSD test.

There were significant differences in below-ground biomass with well-watered (Con) plants having a greater root biomass than all other treatments, and well-watered inoculated (Phy) plants having significantly lower root biomass compared to the control treatment (Figure 4). Phy plants also had the lowest root:shoot ratio and there were significant differences between Phy and Con, but no differences between Phy, Dro, and DroPhy.

3.5. Pressure-Volume (PV) Analysis

Pressure-volume (PV) analysis showed no significant differences between treatments of the osmotic potential at full turgor (π₁₀₀) or leaf relative water content at turgor loss point (RWCₜₐₖ) (Table 1). However, plants in the two drought treatments (Dro and DroPhy) had significantly lower water potential at turgor loss point (TLP) and decreased bulk modulus of elasticity (ε) compared to both well-watered treatments (Con and Phy) (Table 1).

| Treatment | π₁₀₀   | Ψₜₐₖ  | RWCₜₐₖ | ε       |
|-----------|--------|--------|---------|---------|
| Con       | -1.48 ± 0.05 | -1.63 ± 0.05 | 0.91 ± 0.01 | 16.60 ± 2.25 ab |
| Phy       | -1.52 ± 0.13 | -1.67 ± 0.09 a | 0.91 ± 0.01 | 20.47 ± 7.65 a  |
| Dro       | -1.75 ± 0.26 | -2.18 ± 0.60 b  | 0.87 ± 0.07 | 12.14 ± 4.77 b  |
| DroPhy    | -1.65 ± 0.13 | -1.93 ± 0.35 b  | 0.87 ± 0.03 | 12.38 ± 4.96 b  |

4. Discussion

The first hypothesis was confirmed as drought stress significantly decrease plant water potential (Figure 2), stomatal conductance (Figure 3A), photosynthesis (Figure 3B) and above-ground biomass (Figure 4A) in both drought treatment plants. Moreover, we observed drought symptoms such as leaf wilting and chlorosis, consistent with previous
studies [50–52]. Limited soil water availability can lead to plant water deficit and therefore, substantially reduce plant water potential in most plant species [53]. Furthermore, many plants species, including Eucalyptus species, tend to close their stomata to reduce water loss following the onset of initial drought stress, which leads to a decrease in photosynthesis and ultimately limits plant growth [52].

Drought stress also affected longer-term water relation traits in E. obliqua as both $\Psi_{TLP}$ and $\varepsilon$ were reduced in plants of both drought treatments compared to plants in the well-watered treatments (Table 1). This decrease of the $\Psi_{TLP}$ of plants subjected to drought supports previous studies, as many plants species under drought stress adjust their turgor loss point to maintain physiological activity with declining leaf water content [54,55]. This adjustment is often achieved by osmotic adjustment, or the increase in leaf solutes, which in turn leads to a decrease in the $\pi_{100}$ which is seen as the main mechanism of turgor maintenance [56]. However, while the $\pi_{100}$ was lower in both the drought treatments (Table 1) the change was not significant compared to the well-watered treatments, indicating that leaf solute accumulation alone did not lead to turgor maintenance. This is unusual because osmotic adjustment is a common response of Eucalyptus species to drought stress [56,57]. Instead, turgor maintenance was achieved by means of elastic adjustment. The cell walls of the E. obliqua leaves became more elastic in plants under drought stress, which is indicated by the significantly lower $\varepsilon$ in both the Dro and DroPhy treatment plants (Table 1). These plants also had a lower (but not significantly different) relative water content at turgor loss point. Hence, more elastic cell walls allowed for more water to be lost before turgor was lost. Elastic adjustment is not often observed, but is recognized as a mechanism for turgor maintenance under water deficit conditions [58].

The second hypothesis was that P. cinnamomi infection would result in water deficit through reduced root water uptake, which then would lead to drought stress symptoms. However, our results did not confirm this hypothesis. P. cinnamomi infection often results in root necroses, which eventually damages the root system, and reduces plant water uptake [59,60]. The reduction of plant water uptake could cause water deficit in the plant and thus potentially decreases plant water potential and stomatal conductance [61,62]. This can also limit plant growth and often leads to the development of drought-like symptoms [19,21,60]. In this experiment, P. cinnamomi infection did not lead to root necroses and the development of drought-like symptoms. In addition, it did not significantly affect plant water relations (Figure 2, Table 1), photosynthesis (Figure 3B), stomatal conductance (Figure 3A), aboveground biomass (Figure 4A), and other drought tolerance traits. Nevertheless, P. cinnamomi infection significantly reduced average root biomass in well-watered inoculated plants (Phy) compared to control, and the root:shoot ratio of Phy was the lowest among all treatments (Figure 4B). In other studies, Phytophthora infection decreased root biomass by inhibiting the growth of new fine roots [35,61,62]. The absence of primary or secondary symptoms of Phytophthora inoculation, such as root necrotic and drought-like symptoms, is in contrast to previous studies [19,21,60,63]. However, our results are similar to Turco et al. [36], who observed no symptoms in Quercus ilex and Q. cerris that were inoculated by P. cinnamomi in a full irrigation treatment, although root necrosis was eventually observed after 11 weeks. The occurrence of secondary symptoms following the P. cinnamomi infection might be latent depending on the pathogen aggressiveness, host susceptibility and environmental condition [22,61]. A time lag of 6 to 18 months can occur during Phytophthora infection until drought-like symptoms are observed in field studies [22,35,61].

The decrease of plant water potential in some species following P. cinnamomi infection often causes severe root damage which limits plant water uptake to the point that the remaining roots are insufficient to meet plant water demand [60,64]. Similarly, the reduction in root mass could have contributed to the reduction of stomatal conductance, which tends to lower photosynthesis and eventually limits carbon gain for plant growth, as the trees adjusted their water balance following the reduction in plant water uptake by avoiding water loss from transpiration [59,61,62]. Some studies also reported that
although _P. cinnamomi_ infection did not significantly affect plant water potential, the root loss following the infection is more likely to reduce stomatal conductance as it is more sensitive to root loss compared to water potential [59,60]. Additionally, _Phytophthora_ infection can affect the cytokinin and phenolics which can be responsible for controlling stomata closure [65]. In our experiment, severe root damage was not observed in the infected plants, although lower root biomass was observed in the infected trees with full irrigation, suggesting that _P. cinnamomi_ did not cause water deficit in _E. obliqua_ as the plants still had sufficient roots to meet their water demand over the experiment period. These results are consistent with some previous studies such as Maurel et al. [61] and Turco et al. [36] which reported that _Phytophthora_ infection does not always cause plant water deficit. Maurel et al. [61] suggested that _Phytophthora_ infection will potentially lower plant water relations if more than 90% of the plants roots are damaged. This conclusion was also confirmed by Crombie et al. [66] that showed plant water potential was not affected until more than 80% of roots were removed.

Other factors could have contributed to the lack of effects of _P. cinnamomi_ infection on plant water relations in this experiment including the relative short duration of the experiment, resistance of plants to the pathogen, delayed response of the plants to the infection and unexpected adaptation to the stress. A lack of effects of _P. cinnamomi_ on plant water potential despite the development of root necrosis can be caused by high tolerance of the trees to the infection and delayed response of the trees to the infection [36]. This was previously observed in species with higher resistance to _P. cinnamomi_ [67]. _P. cinnamomi_ infection can affect resistant species; however, the progression of the symptoms is slower than in more susceptible species [68]. Differences in infection symptoms can be caused by differences in the defense response between susceptible and resistant species to _P. cinnamomi_ [69].

The third hypothesis was that the interaction between drought stress and _P. cinnamomi_ infection would increase the drought stress symptoms in plants due to the additive impacts of both factors on limiting plant water uptake. However, we observed no additional effects of _P. cinnamomi_ infection under drought treatment, indicating that there were no cumulative effects of the interaction of both factors. It has been suggested that drought conditions could ameliorate the effect of _Phytophthora_ on plants [64,68]. Soil drought can limit _Phytophthora_ growth, which can inhibit the build-up of the inoculum and thus also reduce the rate of _Phytophthora_ infection [70]. This was reported for _Eucalyptus marginata_ where drought was impacted the growth of _P. cinnamomnic_ [71]. Consequently, more significant effects of _Phytophthora_ infection were mostly observed in wet soils compare to dry soils [62,72,73]. Similarly, greater root loss was observed in infected plants with full irrigation compared to deficit irrigation [62]. Weste and Ruppin [70] also suggest that ecosystem devastation caused by _Phytophthora_ was greater in areas with frequent waterlogging and poor drainage.

In our experiment, the soil of the plants was kept moist after inoculation, thus favoring _P. cinnamomi_ growth. But the soil in the drought treatments was very dry. The effects of _P. cinnamomi_ infection on root conditions were more apparent in the inoculated plants with full irrigation rather than the droughted plants. Although plant water potential, photosynthesis, stomatal conductance, and above ground biomass accumulation of the plants in the DroPhy treatment were similar to those in the drought treatment, this was likely due to limited soil water availability rather than _P. cinnamomi_ infection.

The absence of effects of _Phytophthora_ infection on _E. obliqua_ water relations, gas exchange and biomass accumulation in this study could also be due to other factors: First, it could be related to the low pathogenicity of the _Phytophthora_ species used for inoculation. Zentmyer and Guillemet [42] reported that more than 300 _P. cinnamomi_ isolates were distributed in the world and that each of them has different pathogenicity. However, we did not examine the strain and pathogenicity of _P. cinnamomi_ used and its aggressiveness is unknown. This strain was isolated from soil in parks in Maroondah, Melbourne, where many heavily declined and dead eucalypt trees are present, including _E. obliqua_. The pathogen was isolated from the soil, was present in roots of eucalypts in the parks, and
it led to canopy decline and tree death, so it has had some pathogenicity. Several other *Phytophthora* were also isolated from the reserves and future investigations that examine the pathogenicity of each of these *Phytophthora* would help to understand its aggressiveness and the species that are susceptible [74]. It is also possible that *P. cinnamomi* may have lost its virulence after subculturing in *vitro*.

Second, it is also possible that this population of *E. obliqua* has a greater resistance to *P. cinnamomi*. A study by Stukely and Crane [75] demonstrated that some resistant trees were discovered among 16 *E. marginata* provenances, which are known as one of the most susceptible *Eucalyptus* species to *P. cinnamomi*. This *Phytophthora* resistance was strongly controlled by genetic factors, and the resistance of provenances was based on the mortality rate and lesion length following stem inoculation [75]. Since resistant trees have a lower probability of being severely affected by *P. cinnamomi* infection [67], future studies on intra-species variation of susceptibility to *P. cinnamomi* would also be useful. Should this particular *E. obliqua* provenance be more resistant to *P. cinnamomi*, it could be selected for breeding for rehabilitation projects in *P. cinnamomi* declined areas.

Third, it is also possible that our experimental period was too short, as *P. cinnamomi* could take a longer time to affect the trees [22,35,61]. The effects of *Phytophthora* infection can develop slowly, depending on the aggressiveness of the pathogen, the plant condition and the growth condition. In other studies, it could take one to two years of observation before the impacts of *P. cinnamomi* infection on plants were apparent [35,60]. Accordingly, a longer duration of the experiment is recommended for future studies.

5. Conclusions

In this study *P. cinnamomi* infection did not affect plant water relations, gas exchange and above ground biomass despite its effects on root biomass, and there were no cumulative effects with drought stress. While *Phytophthora* infection of roots was confirmed by the re-isolation from the root samples it is possible that the effects of the infection on plant physiology were delayed or other factors, including pathogen aggressiveness and plant condition could have contributed. As *P. cinnamomi* is a water-based pathogen, the drought conditions in our experiment could have reduced its pathogenicity. However, it is also possible that the links between drought stress symptoms and *Phytophthora* infection are not as common as previously proposed.

**Author Contributions:** S.K.A. conceived and designed the study, participated in the collecting of data, supervised data analysis and wrote and edited the manuscript; M.U. designed the study, collected the data, performed the data analysis and wrote the manuscript; L.M.P. collected data, performed some analyses and edited the manuscript. All authors have read and agreed to the published version of the manuscript.

**Funding:** This research was funded by the Maroondah City Council as part of research into tree health in urban green spaces in Maroondah City Council.

**Acknowledgments:** The authors are very grateful for the support by Rowan Berry, Brett Hough and Sascha Andrusiak of the Burnley nursery in assisting with the preparation and maintenance of plants.

**Conflicts of Interest:** The authors declare no conflict of interest.

**References**

1. Adams, H.D.; Guardiola-Claramonte, M.; Barron-Gafford, G.A.; Villegas, J.C.; Breshears, D.D.; Zou, C.B.; Troch, P.A.; Huxman, T.E.; Mooney, H.A. Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global-change-type drought. *Proc. Natl. Acad. Sci. USA* **2009**, *106*, 7063–7066. [CrossRef] [PubMed]
2. Allen, C.D.; Breshears, D.D.; McDowell, N.G. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere* **2015**, *6*, 1–55. [CrossRef]
3. Anderegg, W.R.; Kane, J.M.; Anderegg, L.D. Consequences of widespread tree mortality triggered by drought and temperature stress. *Nat. Clim. Chang.* **2013**, *3*, 30. [CrossRef]
4. Matusick, G.; Ruthrof, K.K.; Brouwers, N.C.; Dell, B.; Hardy, G.S.J. Sudden forest canopy collapse corresponding with extreme drought and heat in a mediterranean-type eucalypt forest in southwestern Australia. *Eur. J. For. Res.* **2013**, *132*, 497–510. [CrossRef]
5. McDowell, N.; Pockman, W.T.; Allen, C.D.; Breshears, D.D.; Cobb, N.; Kolb, T.; Plaut, J.; Sperry, J.; West, A.; Williams, D.G.; et al. Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought? *New Phytol.* 2008, 178, 719–739. [CrossRef]

6. Camarero, J.J.; Gazol, A.; Sangüesa-Barreda, G.; Oliva, J.; Vicente-Serrano, S.M. To die or not to die: Early warnings of tree dieback in response to a severe drought. *J. Ecol.* 2015, 103, 44–57. [CrossRef]

7. Waller, M. Drought, disease, defoliation and death: Forest pathogens as agents of past vegetation change. *J. Quat. Sci.* 2013, 28, 336–342. [CrossRef]

8. Desprez-Loustau, M.L.; Marçais, B.; Nagelesen, L.M.; Piou, D.; Vannini, A. Interactive effects of drought and pathogens in forest ecosystems. *Ann. For. Sci.* 2006, 63, 597–612. [CrossRef]

9. Garrett, K.A.; Dendy, S.P.; Frank, E.E.; Rouse, M.N.; Travers, S.E. Climate change effects on plant disease: Genomes to ecosystems. *Annu. Rev. Phytopathol.* 2006, 44, 489–509. [CrossRef]

10. Erwin, D.C.; Ribeiro, O.K. *Phytophthora Diseases Worldwide*; American Phytopathological Society (APS Press): St. Paul, MN, USA, 1996.

11. Hansen, E.M. *Phytophthora Species Emerging as Pathogens of Forest Trees*. Curr. For. Rep. 2015, 1, 16–24. [CrossRef]

12. Dunstan, W.A.; Howard, K.; Hardy, G.S.J.; Burgess, T.I. An overview of Australia’s *Phytophthora* species assemblage in natural ecosystems recovered from a survey in Victoria. *IMA Fungus* 2016, 7, 47–58. [CrossRef] [PubMed]

13. Sena, K.; Crocker, E.; Vincelli, P.; Barton, C. *Phytophthora cinnamomi* as a driver of forest change: Implications for conservation and management. *For. Ecol. Manag.* 2018, 409, 799–807. [CrossRef]

14. Vettraino, A.M.; Morel, O.; Perlerou, C.; Robin, C.; Diamandis, S.; Vannini, A. Occurrence and distribution of *Phytophthora* species in European chestnut stands, and their association with Ink Disease and crown decline. *Eur. J. Plant Pathol.* 2005, 111, 169. [CrossRef]

15. Corcobado, T.; Cubera, E.; Moreno, G.; Solla, A. *Quercus ilex* forests are influenced by annual variations in water table, soil water deficit and fine root loss caused by *Phytophthora cinnamomi*. *Agric. For. Meteorol.* 2015, 169, 92–99. [CrossRef]

16. Liebhold, A.M.; Brockerhoff, E.G.; Garrett, L.J.; Parke, J.L.; Britton, K.O. Live plant imports: The major pathway for forest insect and pathogen invasions of the US. *Front. Ecol. Environ.* 2012, 10, 135–143. [CrossRef]

17. Arentz, F.; Simpson, J.A. Distribution of *Phytophthora cinnamomi* in Papua New Guinea and notes on its origin. *Trans. Br. Mycol. Soc.* 1986, 87, 289–295. [CrossRef]

18. Von Broembsen, S.; Kruger, F. *Phytophthora cinnamomi* associated with mortality of native vegetation in South Africa. *Plant Dis.* 1985, 69, 715–717. [CrossRef]

19. Weste, G.M.; Taylor, P. The invasion of native forest by *Phytophthora cinnamomi*. I. Brisbane Ranges, Victoria. *Aust. J. Bot.* 1971, 19, 281. [CrossRef]

20. Podger, F. *Phytophthora cinnamomi* a cause of lethal disease of indigenous plant communities. *Phytopathology* 1978, 62, 972–981. [CrossRef]

21. Pratt, B.H.; Heather, W.A. The origin and distribution of *Phytophthora cinnamomi* Rands in Australian native plant communities and its association with particular plant species. *Aust. J. Biol. Sci.* 1973, 26, 559. [CrossRef]

22. Davison, E.M. Relative importance of site, weather and *Phytophthora cinnamomi* in the decline and death of *Eucalyptus marginata*—jarrah dieback investigations in the 1970s to 1990s. *Australas. Plant Pathol.* 2018, 47, 245–257. [CrossRef]

23. Weste, G. The changing status of disease caused by *Phytophthora cinnamomi* in Victorian open forests, woodlands and heathlands. *Australas. Plant Pathol.* 1997, 26, 1–9. [CrossRef]

24. Weste, G.; Marks, G.C. The biology of *Phytophthora cinnamomi* in Australasian Forests. *Annu. Rev. Phytopathol.* 1987, 25, 207–229. [CrossRef]

25. Shearer, B.L.; Crane, C.E.; Barrett, S.; Cochrane, A. *Phytophthora cinnamomi* invasion, a major threatening process to conservation of flora diversity in the South-west Botanical Province of Western Australia. *Aust. J. Bot.* 2007, 55, 225–238. [CrossRef]

26. Anderson, P.; Brundrett, M.; Griersson, P.; Robinson, R. Impact of severe forest dieback caused by *Phytophthora cinnamomi* on macrofungal diversity in the northern jarrah forest of Western Australia. *Forest Ecol. Manag.* 2010, 259, 1033–1040. [CrossRef]

27. Hardham, A.R.; Blackman, L.M. *Phytophthora cinnamomi*. Mol. Plant Pathol. 2018, 19, 260–285. [CrossRef] [PubMed]

28. Cahill, D.M.; Rookes, J.E.; Wilson, B.A.; Gibson, L.; McDougall, K.L. *Phytophthora cinnamomi* and Australias biodiversity: Impacts, predictions and progress towards control. *Aust. J. Bot.* 2008, 56, 279–310. [CrossRef]

29. Kueh, K.H.; McKay, S.F.; Facelli, E.; Facelli, J.M.; Velzeboer, R.M.A.; Able, A.J.; Scott, E.S. Response of selected South Australian native plant species to *Phytophthora cinnamomi*. *Plant Pathol.* 2012, 61, 1165–1178. [CrossRef]

30. O’Meara, W.; Fleischmann, R.; Rigling, D.; Coelho, A.C.; Cravador, A.; Diez, J.; Dalio, R.J.; Horta Jung, M.; Pfanz, H.; Robin, C.; et al. Strategies of attack and defence in woody plant–*Phytophthora* interactions. *For. Pathol.* 2014, 44, 169–190. [CrossRef]

31. Hardham, A.R. *Phytophthora cinnamomi*. *Mol. Plant Pathol.* 2005, 6, 589–604. [CrossRef]

32. Corcobado, T.; Cubera, E.; Juárez, E.; Moreno, G.; Solla, A. Drought events determine performance of *Quercus ilex* seedlings and increase their susceptibility to *Phytophthora cinnamomi*. *Agric. For. Meteorol.* 2014, 192–193, 1–8. [CrossRef]

33. Sghaier-Hammami, B.; Valero-Galván, J.; Romero-Rodriguez, M.C.; Navarro-Cerrillo, R.M.; Abdelly, C.; Jorrín-Navo, J. Physiological and proteomes analyses of Holm oak (*Quercus ilex* subsp. *ballota* [Desf.] Samp.) responses to *Phytophthora cinnamomi*. *Plant Physiol. Biochem.* 2013, 71, 191–202. [CrossRef] [PubMed]
34. León, I.; García, J.J.; Fernández, M.; Vázquez-Piqué, J.; Tapías, R. Differences in root growth of Quercus ilex and Quercus suber seedlings infected with Phytophthora cinnamomi. Silva Fenn. 2017, 51. [CrossRef]

35. Maurel, M.; Robin, C.; Capron, G.; Desprez-Loustau, M.-L. Effects of root damage associated with Phytophthora cinnamomi on water relations, biomass accumulation, mineral nutrition and vulnerability to water deficit of five oak and chestnut species. For. Pathol. 2001, 31, 353–369. [CrossRef]

36. Turco, E.; Close, T.J.; Fenton, R.D.; Ragazzi, A. Synthesis of dehydridin-like proteins in Quercus ilex L. and Quercus cerris L. seedlings subjected to water stress and infection with Phytophthora cinnamomi. Physiol. Mol. Plant Pathol. 2004, 65, 137–144. [CrossRef]

37. Brasier, C.M.; Scott, J.K. European oak declines and global warming: A theoretical assessment with special reference to the activity of Phytophthora cinnamomi. EPPO Bull. 1994, 24, 221–232. [CrossRef]

38. Burgess, T.J.; Scott, J.K.; McDougall, K.L.; Stukely, M.J.C.; Crane, C.; Dunstan, W.A.; Briggs, F.; Andijé, V.; White, D.; Rudman, T.; et al. Current and projected global distribution of Phytophthora cinnamomi, one of the world’s worst plant pathogens. Glob. Chang. Biol. 2017, 23, 1661–1674. [CrossRef]

39. Home, P.; Gonzalez, M.; Matías, L.; Godoy, O.; Pérez-Ramos, I.M.; García, L.V.; Gomez-Aparicio, L. Exploring interactive effects of climate change and exotic pathogens on Quercus suber performance: Damage caused by Phytophthora cinnamomi varies across contrasting scenarios of soil moisture. Agric. For. Meteorol. 2019, 276–277, 107605. [CrossRef]

40. Marks, G.C.; Kassab, F.Y. Detection of Phytophthora cinnamomi in Soils. Aust. For. 1972, 36, 198–203. [CrossRef]

41. Masago, H.; Yoshikawa, M.; Fukada, M.; Nakashima, N. Selective inhibition of Phytophthora spp. on a medium for direct isolation of Phytophthora spp. from soils and plants. Plant Pathology 1977, 67, 425–428. [CrossRef]

42. Zentmyer, G.A.; Guillemet, F.B. Evidence for strains of Phytophthora cinnamomi [Avocados, Camellia japonica, California]. Plant Dis. 1981, 65, 475–477. [CrossRef]

43. Drenth, A.; Sendall, B. Practical Guide to Detection and Identification of Phytophthora; CRC for Tropical Plant Protection: Brisbane, Australia, 2001; pp. 1–41.

44. Gallegly, M.E. Phytophthora: Identifying Species by Morphology and DNA Fingerprints; American Phytopathological Society (APS Press): St. Paul, MN, USA, 2008.

45. Vettraino, A.M.; Natili, G.; Anselmi, N.; Vannini, A. Recovery and pathogenicity of Phytophthora species associated with a resurgence of ink disease in Castanea sativa in Italy. Plant Pathol. 2001, 50, 90–96. [CrossRef]

46. Scholander, P.F.; Hammel, H.T.; Bradstreet, E.D.; Hemmingsen, E.A. Sap pressure in vascular plants. Science 1965, 148, 339–346. [CrossRef] [PubMed]

47. Arndt, S.K.; Clifford, S.C.; Wanek, W.; Jones, H.G.; Popp, M. Physiological and morphological adaptations of the fruit tree Ziziphus rotundifolia in response to progressive drought stress. Tree Physiol. 2001, 21, 705–715. [CrossRef]

48. Callister, A.N.; Arndt, S.K.; Adams, M.A. Comparison of four methods for measuring osmotic potential of tree leaves. Physiol. Plant. 2006, 127, 383–392. [CrossRef]

49. Schulte, P.J.; Hinckley, T.M. A comparison of pressure—volume curve data analysis techniques. J. Exp. Bot. 1985, 36, 1590–1602. [CrossRef]

50. Davidson, N.J.; Reid, J.B. Response of eucalypt species to drought. Aust. J. Ecol. 1989, 14, 139–156. [CrossRef]

51. Rice, K.; Matzner, S.L.; Byer, W.; Brown, J.R. Patterns of tree dieback in Queensland, Australia: The importance of drought stress and the role of resistance to cavitation. Oecologia 2004, 139, 190–198. [CrossRef]

52. Sinclair, R. Water potential and stomatal conductance of three Eucalyptus species subjected to water deficit and the role of resistance to cavitation. Oecologia 2000, 127, 276–277. [CrossRef] [PubMed]

53. Merchant, A.; Callister, A.; Arndt, S.; Tausz, M.; Adams, M. Comparing the physiological responses of six Eucalyptus species to water stress. Ann. Bot. 2007, 100, 1507–1515. [CrossRef]

54. Farrell, C.; Szota, C.; Arndt, S.K. Does the turgor loss point characterize drought response in dryland plants? Plant Cell Environ. 2017, 40, 1500–1511. [CrossRef] [PubMed]

55. Guarnaschelli, A.B.; Lemcoff, J.H.; Prystupa, P.; Basci, S.O. Responses to drought preconditioning in Eucalyptus globulus Labill. provenances. Trees 2003, 17, 501–509. [CrossRef]

56. Sanders, G.; Arndt, S.K. Osmotic adjustment under drought conditions. In Plant Responses to Drought Stress; Aroca Alvarez, R., Ed.; Springer: Berlin/Heidelberg, Germany, 2012; pp. 199–229.

57. Roberts, S.W.; Strain, B.R.; Kenneth, R.K. Seasonal patterns of leaf water relations in four co-occurring forest tree species: Parameters from pressure-volume curves. Oecologia 1980, 46, 330–337. [CrossRef] [PubMed]

58. Saito, T.; Terashima, I. Reversible decreases in the bulk elastic modulus of mature leaves of deciduous Quercus species subjected to two drought treatments. Plant Cell Environ. 2004, 27, 863–875. [CrossRef]

59. Cromptie, D.S.; Tippett, J.T. A comparison of water relations, visual symptoms, and changes in stem girth for evaluating impact of Phytophthora cinnamomi dieback on Eucalyptus marginata. Can. J. For. Res. 1990, 20, 233–240. [CrossRef]

60. Sterné, R.E. Effect of Phytophthora root rot on water relations of avocado: Interpretation with a water transport model. Phytopathology 1978, 68, 595. [CrossRef]

61. Maurel, M.; Robin, C.; Capdevielle, X.; Loustau, D.; Desprez-Loustau, M.L. Effects of variable root damage caused by Phytophthora cinnamomi on water relations of chestnut saplings. Ann. For. Sci. 2001, 58, 639–651. [CrossRef]

62. Robin, C.; Capron, G.; Desprez-Loustau, M.L. Root infection by Phytophthora cinnamomi in seedlings of three oak species. Plant Pathol. 2001, 50, 708–716. [CrossRef]
63. Ruiz Gomez, F.J.; Perez de Luque, R.; Sanchez-Cuesta, R.; Quero, J.L.; Navarro Cerillo, R.M. Differences in the response to acute drought and Phytophthora cinnamomi Rands infection in Quercus ilex L. seedlings. Forests 2018, 9, 634. [CrossRef]
64. Tippett, J.; McGrath, J.; Hill, T. Site and seasonal effects on susceptibility of Eucalyptus marginata to Phytophthora cinnamomi. Aust. J. Bot. 1989, 37, 481–490. [CrossRef]
65. David, M.C.; Gretna, M.W.; Bruce, R.G. Changes in cytokinin concentrations in xylem extrudate following Infection of Eucalyptus marginata Donn ex Sm with Phytophthora cinnamomi Rands. Plant Physiol. 1986, 81, 1103–1109.
66. Crombie, D.; Tippett, J.; Gorrddard, D. Water relations of root-pruned jarrah Eucalyptus marginata (Donn ex Smith) saplings. Aust. J. Bot. 1987, 35, 653–663. [CrossRef]
67. Cahill, D.; Grant, B.; Weste, G. How does Phytophthora cinnamomi kill a susceptible eucalypt? Australas. Plant Pathol. 1985, 14, 59–60. [CrossRef]
68. Tippett, J.; Hill, T.; Shearer, B. Resistance of Eucalyptus spp. to Invasion by Phytophthora cinnamomi. Aust. J. Bot. 1985, 33, 409–418. [CrossRef]
69. Naidoo, S.; Külheim, C.; Zwart, L.; Mangwanda, R.; Oates, C.N.; Visser, E.A.; Wilken, F.E.; Mamni, T.B.; Myburg, A.A. Uncovering the defence responses of Eucalyptus to pests and pathogens in the genomics age. Tree Physiol. 2014, 34, 931–943. [CrossRef]
70. Weste, G.; Ruppin, P. Factors affecting the population density of Phytophthora cinnamomi in native forests of the Brisbane Ranges, Victoria. Aust. J. Bot. 1975, 23, 77–85. [CrossRef]
71. Lucas, A. Water Stress and Disease Development in Eucalyptus marginata (jarrah) Infected with Phytophthora cinnamomi. Ph.D. Thesis, Murdoch University, Perth, Australia, 2003.
72. Brasier, C.M. Phytophthora cinnamomi and oak decline in southern Europe. Environmental constraints including climate change. Ann. Sci. For. 1996, 53, 347–358. [CrossRef]
73. Shearer, B.L. Jarrah Dieback: The Dynamics and Management of Phytophthora Cinnamomi in the Jarrah (Eucalyptus Marginata) Forest of South-Western Australia; Department of Conservation and Land Management: Como, WA, USA, 1989.
74. Robin, C.; Desprez-Loustau, M.-L. Testing variability in pathogenicity of Phytophthora cinnamomi. Eur. J. Plant Pathol. 1998, 104, 465–475. [CrossRef]
75. Stukely, M.; Crane, C. Genetically based resistance of Eucalyptus marginata to Phytophthora cinnamomi. Phytopathology 1994, 84, 650–656. [CrossRef]