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Topography influences the distribution of autumn frost damage on trees in a Mediterranean-type *Eucalyptus* forest

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Abstract

Key message

Extreme temperatures are causing forest dieback in a Mediterranean-type forest. Topography and cold-air pooling explain the geographic distribution of frost dieback in susceptible tree species.

Abstract

Alterations to the frequency and intensity of extreme temperatures, predicted with climate change, pose a threat to the health of many forests. Some Mediterranean climate regions are experiencing higher temperature variability, including more extreme low and high temperature events. Following one such low-temperature event in autumn 2012, we conducted landscape- and site-level studies to examine the impact of frost on trees and the interaction between topography, temperature, and dieback in a forest ecosystem in the Mediterranean climate region of southwest Australia. Canopy damage was widespread across the survey area and occurred in distinct patches, with sizes ranging between 4.1 and 2,518.0 ha. In affected forest, *Eucalyptus marginata* and *Corymbia calophylla* experienced nearly complete crown dieback, while E. patens and E. wandoo were undamaged. Canopy damage was found more frequently in valleys and lower to mid-slope positions, and site-level studies confirmed that crown dieback generally increased with decreasing elevation. Low temperatures were strongly correlated with elevation along damaged forest transects and cold-air pooling explained the pattern of forest damage. By regressing temperatures from damaged sites against those collected from the nearest meteorological station, projected minimum air temperatures ranged from −0.1 to −2.7 °C at valley bottom when the dieback occurred. Insufficient tissue hardening is suspected to have predisposed trees to this autumn frost. The interaction between shifting temperature regimes with climate change and frost damage is discussed. With continued increases in temperature variability, we can expect to see more temperature-driven disturbance events and associated reductions in forest health.

Keywords: Climate change, Temperature, Dieback, Frost pocket, Jarrah, Marri

Introduction

Alterations to the frequency and intensity of extreme temperature events, predicted with climate change, pose a threat to the health of forest trees in many areas of the world (Allen et al. 2010; Williams et al. 2012). Mediterranean climate regions are predicted to be especially sensitive to shifts in extreme temperatures (Diffenbaugh et al. 2007; Giorgi and Lionello 2008). Since these regions represent many of the world's biodiversity hotspots (Mittermeier et al. 2011), they are disproportionally susceptible to biodiversity loss (Klausmeyer and Shaw

2009). Recently, periods of extreme high temperatures (5+ days of >5 °C above average monthly maximum temperature), coupled with drought, have been implicated in severe forest disturbances in Mediterranean climate regions (Carnicer et al. 2011; Matusick et al. 2013). Indeed, some Mediterranean climate areas are experiencing a greater frequency of extreme high temperatures during summer (Schär et al. 2004), and average temperatures are expected to increase in the future (Giorgi and Lionello 2008). However, with increased temperature variability, the potential for changes in the frequency, intensity, and timing of extreme cold events leading to frost damage in trees is also likely (Jönsson et al. 2004; Woldendorp et al. 2008).

Frost can be a serious disturbance agent in forest ecosystems (Kullman 1989; Cambours et al. 2005; Auclair et al. 2010), directly leading to reductions in tree growth (Thomson et al. 2001; Davidson et al. 2004; Dittmar et al. 2006), changes in growth form (Nigre and Colin 2007), increased susceptibility to pests (Thomson et al. 2001; La Spina et al. 2012) and even tree mortality (Paton 1988). Shifts in temperature regimes can also affect trees indirectly, through interactions with tree phenology, by causing premature de-hardening in spring (Jönsson et al. 2004). Indeed, some forests are experiencing long-term increases in frost risks from warming trends and increased temperature variability associated with climate change (Gu et al. 2008; Augspurger 2013). Finally, increases in atmospheric CO2 concentrations and increased temperature during the warm season may also make certain trees more susceptible to frost damage during periods of cold, by delaying frost acclimation (Loveys et al. 2006) and compromising protective mechanisms (Wayne et al. 1998). These multiple effects of frost on trees have significant implications for forest development and productivity with predicted climate change (Hufkins et al. 2012).

The regional climate of southwest Australia, one of the five Mediterranean climate regions, is characterised by hot, dry summers (December–February) [mean maximum temperatures of ~32 °C for the hottest month (Perth, WA, Australia)] and cool, moist winters (June–August) [mean minimum temperature of 8 °C for the coolest month (Perth, WA, Australia)]. The region has experienced significant shifts in temperature and precipitation patterns over the past three decades, with average annual precipitation falling by 14 % and average temperature increasing by 0.15 °C per decade (Bates et al. 2008). These changes have contributed to severe declines in tree, forest, and woodland health (Auclair 1992; Archibald et al. 2005; Matusick et al. 2013). For instance, periods of extremely high temperatures, coupled with the most severe droughts on record, resulted in rapid forest canopy dieback and tree mortality in 2006 and 2011 (Batini 2007; Matusick et al. 2012, 2013). Despite rising average annual temperatures, this region experienced record cold temperatures in the winter preceding both drought-induced dieback events, including the lowest minimum air temperatures on record in 2006 and a record 15 days below 2 °C in 2010 at Perth Airport (Australian Bureau of Meteorology). Evans and Lyons (2013), in scrutinising the long-term climatic trends in southwest Australia, found that winter mean minimum temperatures have decreased correspondingly with increasing summer mean and maximum temperatures. In other words, while summer (warmer) months are getting hotter, winter (cooler) months have become colder in the last decade.

Little is known about the effects of frost in the Mediterranean-type forests of southwest Australia (Abbott and Loneragan 1986) which limits our ability to account for and predict climate change-driven shifts in the frost. The occurrence of frost in these forests is relatively rare (Gentilli 1989). In an effort to understand the impacts of frost events on forest trees, a study was initiated following the first period of frost in 2012. This study addressed the following objectives: (1) to examine the geographic distribution of frost damage at the landscape level, (2) to determine the topographic associations with frost damage at both the landscape and site levels, (3) to describe the frost damage observed on affected tree species, (4) to determine the temperature–elevation relationship in frost-affected forest, and (5) to estimate the temperature conditions which led to frost damage in 2012.

Materials and methods

Study area

The study was conducted in the Northern Jarrah Forest (NJF), a broadleaved evergreen Mediterranean-type forest, which covers an estimated 1,127,600 ha (Havel 1975) in southwest Australia. The dry sclerophyll forest ranges from open forest in the north to tall forest in the south (Specht et al. 1974). The overstory of NJF is dominated by *E. marginata* Donn ex Sm. and *C. calophylla* (R. Br.) K.D.Hill & L.A.S.Johnson in the uplands, and commonly mixes with *E. wandoo* Blakely, *E. patens* Benth., and *E. megacarpa* F. Muell. in the drainages. A strong precipitation gradient occurs in the NJF, from 635 mm annual precipitation in East to 1200 mm per annum in the West (Boddington to Pinjarra [~64 km], Gentilli 1989). Mean summer high temperatures range from ~27.6 °C (Mundaring) in the North to ~30.6 °C (Dwellingup) in the South, while mean winter lows range from ~8.5 °C (north) to ~6 °C (south). The NJF occupies the Darling Plateau, which has rolling topography with crests ranging in altitude from 280 to 320 m. However, several prominent summits rise above the plateau, reaching a maximum height of 582 m (e.g. Mt. Cooke). Moving from east to west, the terrain becomes increasingly dissected, with the deepest valleys occurring at the Darling Scarp on the far western edge of the plateau (Churchward and Dimmock 1989). Field sites were located in the Monadnocks Conservation Park, which is located approximately in the centre of the NJF (Fig. 1). The topography of the Monadnocks Conservation Park region is characterised by high peaks, including Mt. Cooke and broad, deep valleys.

Aerial survey

To determine the geographic extent of frost damage across the northern Jarrah Forest in 2012, a 370 km long aerial survey was conducted in mid-July 2012 using a Cessna 172 fixed-wing aircraft. The flight attempted to maximise coverage of the NJF by taking a zigzag pattern (Fig. 1). The flight path was recorded using a Garmin GPS (GPSMAP 92 s, Garmin International Inc., Missouri, USA). Two DSLR digital cameras (Nikon D90, Nikon Corporation, Tokyo, Japan and Sony A55, Sony Corporation, Tokyo, Japan) were used to capture oblique, geo-referenced aerial photos of affected forest patches. The affected areas, captured by the digital images, were translated to GIS using a manual digitisation technique following Matusick et al. (2013). Landform, roads, cleared areas, and other landmarks were used to match oblique images with vertical orthorectified images. Delineation and digitization of the affected areas were completed using OxiExplorer GIS mapping software (version 3.95.5, Brisbane, Australia).

Topographic landscape analysis

To investigate the position of the frost-affected areas in relation to the surrounding landscape, a 10-m spatial resolution digital elevation model (DEM) was used to calculate the topographical position index (TPI) (Weiss 2001). The TPI is a useful index to characterise the position of individual locations within the wider landscape. Topographical Position Index values centre around 0 (mid-slope), where the low (minus) values indicate valleys and lower slopes, running uphill towards the high positive TPI values, indicating ridges. The TPI is computed by comparing the elevation of each grid cell of the DEM with the elevation of the surrounding grid cells in a geographical information system (GIS) environment (Weiss 2001; Jenness et al. 2011). In this case, the Land Facet Corridor Tools extension for ArcMap (ArcGIS 10, ESRI, California, USA) was used (Jenness et al. 2011). Multiple TPI layers were generated using various neighbour distances (100–500 m). Using the DEM and slope layer of the landscape for reference, a circular neighbour distance of 500 m around each individual cell was used to develop the TPI layer, which was found to most accurately characterise landscape positions in the NJF.

The delineations of the affected areas and the surrounding unaffected areas were used to generate a presence/absence sample (300 points randomly distributed in each) using ArcGIS Data Management tools. These points were then used to extract values from the TPI raster layer using the bilinear interpolation option in ArcGIS Spatial Analyst tools, and for further statistical analysis (see below).

Plot establishment and tree measurements

At two sites in the Monadnocks Conservation Park (Albany Hwy and Millars Log Rd.), three parallel altitudinal transects were established, spanning from flat drainage areas to upper slope positions. Each transect was composed of six sample points (totalling 18 sample points for each site), with points established every 4 m in elevation, starting at 275 m and 271 m at the Albany Hwy and Millars Log Rd. sites, respectively. Elevation was determined using a wrist-top computer altimeter (Suunto Core, Suunto, Finland).

At each sample point, the damage to trees in each of three forest strata [i.e. understory, midstory, and overstory, based on definitions outlined by the USDA, forest inventory and analysis program (USDA 2011)] was assessed separately (midstory was not assessed at the 271 m point at Millars Log Rd. since it was not present). The trees to be sampled for each stratum were selected based on the point-centered quarter method of sampling (Mitchell 2010). The area surrounding each sample point was split into four quadrants by extending a plane perpendicular to the central transects, running through the sample point. The tree from each stratum in each quadrant located closest to the sample point was selected for sampling, totalling 28 sample trees for each stratum and transect. The distance from each sample point to the nearest tree, species, and DBH (for midstory and overstory strata only) was recorded for each quadrat. The incidence and severity (%) of crown foliage damage for each tree were assessed based on the definitions stated in Stone et al. (2003). The crown damage index (CDI), established for assessment of eucalypt crown damage (Stone et al. 2003), was used to estimate crown damage on each sampled individual. Each crown with affected foliage was placed into one of four damage categories based on predominate colour of the affected foliage, including purple, pink, orange, or brown (ordered from least to most damage). In addition, the relative location of the foliage damage, either at the periphery, interior, or throughout crown was noted.

Temperature measurements

At the Albany Hwy site, 18 temperature/relative humidity data loggers (EL-USB-2, Datataq® Instruments) were installed along the sampling transects to determine the temperature–elevation relationships. Each logger was fixed to the closest tree (>10 cm DBH), at each sample point along the three transects, at 1 m above the ground, and facing north on 13 June, 2012. The temperature (±0.3 °C), relative humidity (%), and dew point temperature (°C) were recorded every 30 min until 15 July 2012. In addition, temperature data were collected from the nearest climate station (Wungong Brook, Lat: −32.252777, Long: 116.141436), located approximately 18 kilometres from the field site, for the period spanning from 1 May 2012 (prior to onset of symptoms) to 15 July 2012 (through the site measurement period). Combining both datasets allowed for development of a predictive model to calculate site temperatures at the time of damage.

Statistical analysis

To examine frost damage at the landscape level, including the topographic associations with the observed damage, the presence/absence (i.e. frost affected vs. not affected) dataset (n = 600) was used. First, normality was checked by generating histograms and performing Shapiro–Wilk tests in R (Version 2.12.0, R Core Team 2012). For further statistical analyses, the data analysis tool in Microsoft Excel was used. To test for differences in landscape position (i.e. TPI) between frost-affected and unaffected sites, first a two-sample F-Test to determine the potential difference in variance between the two samples was performed, followed by a two-sample t test assuming unequal variances.

In examining frost damage at the site level, all analyses were conducted separately for each forest strata and site. Following testing of assumptions, mixed models in the MIXED procedure in SAS statistical software (SAS Institute, version 9.3, Cary, NC) were used to inspect relationships between tree health, strata, and elevation. The influence of elevation on tree health (CDI) was analysed using elevation as the fixed and transect as a random factor in the mixed model.

To determine the temperature–elevation relationship in frost-affected forest at the Albany Hwy site, correlation analysis (Spearman rank) in the CORR procedure in SAS was used to examine the relationship between mean half-hourly minimum temperatures and elevation, with the analysis restricted to the cool hours of the day (0:00–07:30). In addition, the mean daily minimum temperatures for each elevation were compared using a mixed linear model in the MIXED procedure in SAS, including elevation as the fixed factor and transect as the random factor.

To estimate minimum temperatures at each sample elevation during the period when the damage occurred (prior to the study), a simple linear regression equation was developed for each elevation point separately using minimum daily observed temperatures (field sample points) and corresponding records from the nearby climate station. This set of equations (one for each elevation) was used to predict minimum temperatures in the month preceding the field study to provide an estimated minimum temperature at each elevation when the damage occurred.

Results

Aerial Survey

Affected forest extended across large areas of the NJF (Fig. 2). Affected sites occurred in distinct patches within the landscape with sizes ranging between 4.1 and 2518.1 ha. These sites were generally found more frequently in valleys and lower to mid-slope positions compared to unaffected sites, which were generally found on higher locations within the landscape (Fig. 3). This pattern was confirmed by the t test for TPI, where frost-affected sites were found at lower landscape positions (i.e. lower TPI) than unaffected sites (mean (SE) TPI: −3.715 (0.307) vs. −0.373 (0.421), respectively; *t* test: $t = 6.411$, d$f = 547$, $P = < 0.001$).

Field observations

Observations of foliage damage in overstory trees in the NJF were made in the first week of June 2012, approximately two weeks following the first frost event of the year (May 25 and 26, 2012). In the most severely affected areas, *E. marginata* and *C. calophylla* crowns were nearly completely discoloured (Fig. 2). Within frost-affected leaves, damage appeared to spread from the leaf tip towards the base. In *E. marginata*, foliage discoloration spanned a wide gradient from deep purple (least affected) (23 % of stems) to bright pink (68 %), orange (28 %), and light brown (most affected) (8 %). In contrast, affected *C. calophylla* foliage was consistently dry, dark brown, and desiccated, with little variation at the time of measurement. On 27 % of affected *E. marginata* and 31 % of *C. calophylla,* discoloration was isolated to the outside of the crown, with interior leaves showing little or no evidence of damage. The remaining crowns that were measured were completely discoloured. *E. wandoo* and *E. patens* were found in low numbers and limited to the low-lying valley bottoms within the landscape

(271 and 275 m), while *E. macrocarpa* was not present on either of the study sites (Table 1). Both *E. wandoo* and *E. patens* lacked evidence of foliage discolouration or other evidence of frost-related damage at sample points or elsewhere in the study area.

Tree health

Crown damage from frost varied by elevation for all strata levels and at both measurement sites, however, lower levels of damage could be observed with increasing elevation (Fig. 4). The level of damage generally decreased with increasing elevation in all strata levels at the Albany Hwy site, with statistically similar high crown damage observed at the two lowest slope positions (275 and 279 m). In contrast, no crown damage was found at the two highest elevations (291 and 295 m) in both understory and midstory trees and no damage was found in overstory trees at the three highest elevations. A similar damage pattern was observed at the second field site (Millars Log Rd.) at middle to upper slope positions (279–295 m). However, for understory trees at the lowest elevation (271 m), CDI levels were significantly lower than observed at 279 m. The curve also failed to hold true for overstory trees at the lowest elevation (271 m), which had significantly less damage than 275 m.

Temperature

Clear stratification of average temperatures was recorded among the six elevations during the cooler hours of the day (00:00–07:00 am), showing a decreasing trend with time and increasing mean temperatures with elevation (Fig. 5). Elevation was strongly correlated with mean half-hourly minimum temperature (Spearman's rank correlation, rho = 0.92, $P < 0.0001$) in frost-affected forest. Daily minimum temperature was significantly different between elevations (*F* = 7.04, *P* < 0.0001), with the lowest temperatures observed at the two lowest elevations (275 and 279 m) (Fig. 6). Statistically significant (alpha = 0.05) simple linear regression equations were developed using plot temperature data for each elevation and data from the nearest weather station (Fig. 7). These regression equations were used to predict the timing of the frost event and the temperature range that caused the observed damage. By projecting minimum site temperatures over the month preceding the study period, we predict the damage occurred during the first cold period of the year (May 25/26) and minimum air temperatures averaged −1.4 °C (−0.1 °C to −2.7 °C) at the lowest sample point (275 m) during the frost event (Fig. 8).

Discussion

The canopy disturbance event described here represents a critical step towards understanding the current and future potential impact of extreme cold temperatures on the Mediterranean-type NJF in southwest Australia. The widespread damage is similar to frost events documented in southeast Australia (O’Brien 1989), where severe frost events occur every 10–20 years (Banks and Paton 1993). These frost events signify an ecologically significant disturbance, influencing species composition (Paton 1988) and ecosystem structure (Davidson and Reid 1985). Frost, however, has not previously been regarded as an important disturbance factor in the Mediterranean-type forests of southwest Australia. Although some anecdotal observations of frost damage have been made in the NJF previously during cold years (Abbott and Loneragan 1986; Gentilli 1989), this study is the first formal investigation of the phenomenon, including (1) a characterization of the damage in dominant tree species at both the landscape and site-scales, (2) the influence of topography on temperature and the observed level of damage, and (3) estimates of projected air temperatures experienced by trees at the time of damage.

Even though forest damage from frost was widespread in 2012, most was concentrated in the central portion of the NJF in a region known for its density of relatively tall peaks and deep valleys (e.g. Monadnocks Conservation Park). The landscape-level analysis shows that low-lying topographic positions, including low and middle slopes, were the most susceptible to frost damage. Low-lying areas in hilly topography act as cold-air drainages and are prone to cold-air pooling when dense cold air sinks and becomes trapped beneath an inversion layer on clear, windless nights (Gustavsson et al. 1998), which often results in the formation of frost pockets (i.e. frost hollows) (Paton 1988). Frost pockets develop in a wide variety of natural ecosystems (Hough 1945; Paton 1988; Motzkin et al. 2002), including those in other Mediterranean regions (Waco 1968; Daly et al. 2010). Since valley depth influences the magnitude of cooling during frost pocket formation (Vosper and Brown 2009), the geographic distribution of frost damage reported here, including the concentration of forest damage in the Monadnocks Conservation Park, is likely explained, in part, by its unusually deep valleys compared to the remainder of the NJF.

The relationship between topography, low temperatures, and forest damage observed in the NJF may help explain larger scale forest patterning. While a strong positive correlation was found between elevation and minimum daily temperatures, generally forest damage and elevation were inversely related. The exception was at the Millars Log Rd. site where the lowest elevation had substantially less damage than higher elevations. This could be explained by the higher proportion of *E. patens* within the low-elevation drainage area, which was largely resistant to the disturbance during field studies (as were *E. wandoo* at the Albany Hwy site). These findings support previous observations during frost events that found *E. patens* and *E. wandoo* less affected than *E. marginata* and *C. calophylla* (Quain 1964; McChesney et al. 1995). *Eucalyptus patens* and *E. wandoo* are generally confined to valley bottoms, which, combined with their observed tolerance to frost, helps explain the findings from the landscape-level study that showed valley bottoms are less likely to experience damage. Since minimum temperatures in frost pockets can reach tens of degrees less than the surrounding area (Waco 1968), climatic conditions conducive to frost pocket formation can be ecologically important in shaping the vegetation communities (Davidson and Reid 1985; Dy and Payette 2007). Although no formal follow-up investigation was conducted, observations made in the period following frost suggest foliage damage resulted in dieback and resprouting in established trees. Based on these and other observations (Abbott and Loneragan 1986), mortality of established trees from frost is thought to be limited. However, frost in the NJF is thought to limit seedling emergence of *E. marginata* and *C. calophylla* at low elevations (McChesney et al. 1995) and may kill seedlings and coppice regrowth (Abbott and Loneragan 1986), especially if affected repeatedly. Tree composition within the lowest elevations in the NJF has always been thought to be driven by soil type and moisture availability (Bell and Heddle 1989). In light of our observations, however, additional research is needed to determine the potential ecological significance of frost events in influencing tree composition and structure in these frost-prone areas.

Contrasting physiology may help to explain the relative resistance to frost among tree species in the NJF. Osmotic adjustment can be an important physiological response to both drought and cold temperature stress in eucalypts (Callister et al. 2008). During recent physiological studies in Western Australia, *E. wandoo* exhibited greater potential for osmotic adjustment compared to *E. marginata* and *C. calophylla*, which is thought to be an adaptation to drought (Poot and Veneklaas 2013). However, this trait may also help to explain differential resistance to frost among the same co-occurring eucalypts observed in this study, where *E. wandoo* was better able to withstand cold-temperature stress in lower elevation sites in the NJF. Future work should investigate the relative importance of osmotic adjustment in response to drought and frost to help determine the factor driving species distribution, as done elsewhere (Callister et al. 2008).

The frost-triggered discoloration patterns at the leaf level characterised in this study support patterns of freezing (Ball et al. 2002) and pigmentation change (Nicotra et al. 2003) when *Eucalyptus* leaves pass critically low temperature thresholds. The notably dry leaves of *C. calophylla* are consistent with frost-induced dehydration following cell rupture (Ball et al. 2002). Though these results show that *E. marginata* and *C. calophylla* are both highly susceptible to damage from cold temperatures, contrasting leaf-level symptom patterns may be indicative of differing tolerance to the stressor (Boorse et al. 1998). Many *Eucalyptus* are sensitive to low-temperature stress (King and Krugman 1980); however, species grown in the same environment can have different susceptibilities to frost damage (Davidson and Reid 1985). While frost-damaged *C. calophylla* leaves showed little variation, *E. marginata* leaves spanned a large colour and severity gradient. Variation in the pigmentation among frost-affected *E. marginata* leaves may indicate an attempt at photo protection (García-Plazaola et al. 2003) through the accumulation of carotenoids (Larcher 2000) or anthocyanin (Close et al. 2002). Alternatively, differing discoloration patterns between *E. marginata* and *C. calophylla* may simply reflect differences in the relative speed of symptom development. For instance, damaged *C. calophylla* leaves may be prone to relatively higher rates of dehydration following damage due to the relative thickness of its leaf cuticle or density of stomata (Ridge et al. 1984). Formal resistance studies are needed to conclusively determine the relative frost tolerances among NJF species and the rate of symptom development.

Although the frost damage described here in the NJF occurred at marginally low air temperatures (−0.1 to −2.7 °C), experimental studies have shown that temperatures at the leaf surface can be an additional 1–3 °C colder than the ambient air temperature (Leuning and Cremer 1988). It is therefore likely that the actual temperatures experienced at the leaf level in the valley bottoms when the damage occurred were lower (−3.1 to −5.7 °C) than our estimated air temperatures. Field studies have shown that many *Eucalyptus* species are highly susceptible to frost damage when experiencing temperatures below −10 °C (King and Krugman 1980). Given that the tree damage occurred following the first frost event of the year, it could be explained, in part, by insufficient cold acclimation (i.e. hardening), which is an important protective mechanism eucalypts use to avoid frost damage (Davidson and Reid 1987; Almeida et al. 1994). For example, with sufficient hardening, Harwood (1980) found that leaf damage thresholds were lowered by up to 4 °C (from −6 °C in unhardened trees to −10 °C in hardened) in subalpine *Eucalyptus* species. The frost event which resulted in the observed damage (May 25, 2012) is considered early for the region. For instance, it was the third earliest frost (below 0 °C air temperature) in the 56-year temperature record at Dwellingup, Western Australia, which is south of the study area but experiences an average 4 days below 0 °C per year (Australian Bureau of Meteorology). Evergreen trees are especially sensitive to damage from autumn frosts (Redfern and Cannell 1982; Cannell et al. 1985). Though climate warming can interact with phenology to predispose trees to spring frost in certain regions (Gu et al. 2008; Hufkens et al. 2012), its impact on hardening and autumn frost is less well understood. It is conceivable that by lengthening the growing season and delaying cold hardening, which is expected with climate change (Morin et al. 2010;

Gunderson et al. 2012), evergreen trees may become more susceptible to sudden and severe autumn frost events.

Increasing average temperatures and decreasing precipitation in southwest Australia in the last decade have also been accompanied by decreasing winter minimum temperatures (Evans and Lyons 2013). Winter conditions for two of the driest years on record in southwest Australia (2006/2007 and 2010/2011) resulted in some of the lowest temperatures on record (2006/2007) and record numbers of days below 2 °C for the Perth area (Australian Bureau of Meteorology). An analogous sequence of events occurred in northeast Victoria (Australia) in 1982 (O'Brien 1989), where the most severe frosts recorded in the region occurred in a year where the annual rainfall was 30 % of the annual average. Given that the NJF has historically experienced seasonal droughts during the summer period (December–February, Gentilli 1989), extreme dry years have been driven by below-average winter precipitation (Li et al. 2005). Dry winters are dominated by calm, clear conditions necessary to facilitate development of cold-air pooling, inversion layer development, and frost events in low-lying areas (Gustavsson et al. 1998), suggesting a relationship between these climate phenomena. In addition, the magnitude of radiative cooling is more pronounced under dry conditions, since moisture increases the thermal conductivity of soil, which leads to greater radiation absorption during the day and retention at night (Geiger et al. 2003). Most global circulation models predict increasing average temperatures and decreasing incidence of severe cold spells for southwest Australia (Suppiah et al. 2007). However, due to the spatial resolution of the datasets used, these models fail to consider the influence of local factors, including topography, on fine-scale climatological processes, such as the incidence of localised frost events. Recent studies have shown that since cold-air drainages are decoupled from the free atmosphere, they fail to follow synoptic circulation patterns and predicted regional climate patterns (Daly et al. 2010). The cold temperature-induced disturbance described here, during a period of warming and drying, highlights the need for additional research into the connection between regional climate changes and its interaction with local factors (e.g. topography) that help to govern temperature extremes.

Conclusion

The southwest Australia has shown significant changes in climate in the last decades, and the NJF is one of the first ecosystems to show substantial effects and changes in vegetation health (Batini 2007; Brouwers et al. 2013; Matusick et al. 2013). The region of the NJF that was most affected by frost in this study (2012) was also highly affected by drought and multiple heat waves in 2010/2011 (Brouwers et al. 2013; Matusick et al. 2013). Although the likelihood of the two disturbances impacting the same trees is likely to be low, considering that drought effects occurred at higher landscape positions (Brouwers et al. 2013), the two disturbances have combined to cause extensive damage throughout the forest over a short time scale. This combination of disturbances (frost and drought) has caused extensive defoliation and canopy dieback across all landscape positions, with likely negative flow-on effects on the associated flora and fauna that rely on an intact forest canopy. With increasing temperature variability in southwest Australia and elsewhere, an increased frequency and severity of extreme temperature events are expected. Identification of the short- and long-term impacts of these events on forest ecosystems is therefore critical, along with the development of accurate methods of mapping and modelling forest damage, to ensure sustainable forest management. This research highlights frost as an important canopy disturbance factor in the NJF, the critical influence of topography on frost distribution within the forest, as well as the relative susceptibilities of co-occurring eucalypts to low-temperature events.

Author contribution statement

G. Matusick served as the primary researcher on the project by collecting much of the field and aerial survey data, conducting data analysis, and preparing the manuscript for submission. K. Ruthrof made significant contributions to data collection and manuscript preparation. N. Brouwers contributed by analysing aerial survey data and manuscript preparation. G. Hardy was instrumental in attracting research funding for the project and made significant contributions to data collection and manuscript preparation.

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Conflict of interest

The authors declare that they have no conflict of interest.

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Fig. 1. The flight path (black line) from an aerial survey of the Northern Jarrah Forest (medium grey) in southwest (Western) Australia following the onset of frost damage in July 2012. Significant overstory tree damage from frost (black polygons) occurred in the Monadnocks Conservation Park (dark grey), where two study sites were established. White and light grey areas represent cleared and intact native vegetation, respectively, outside the NJF

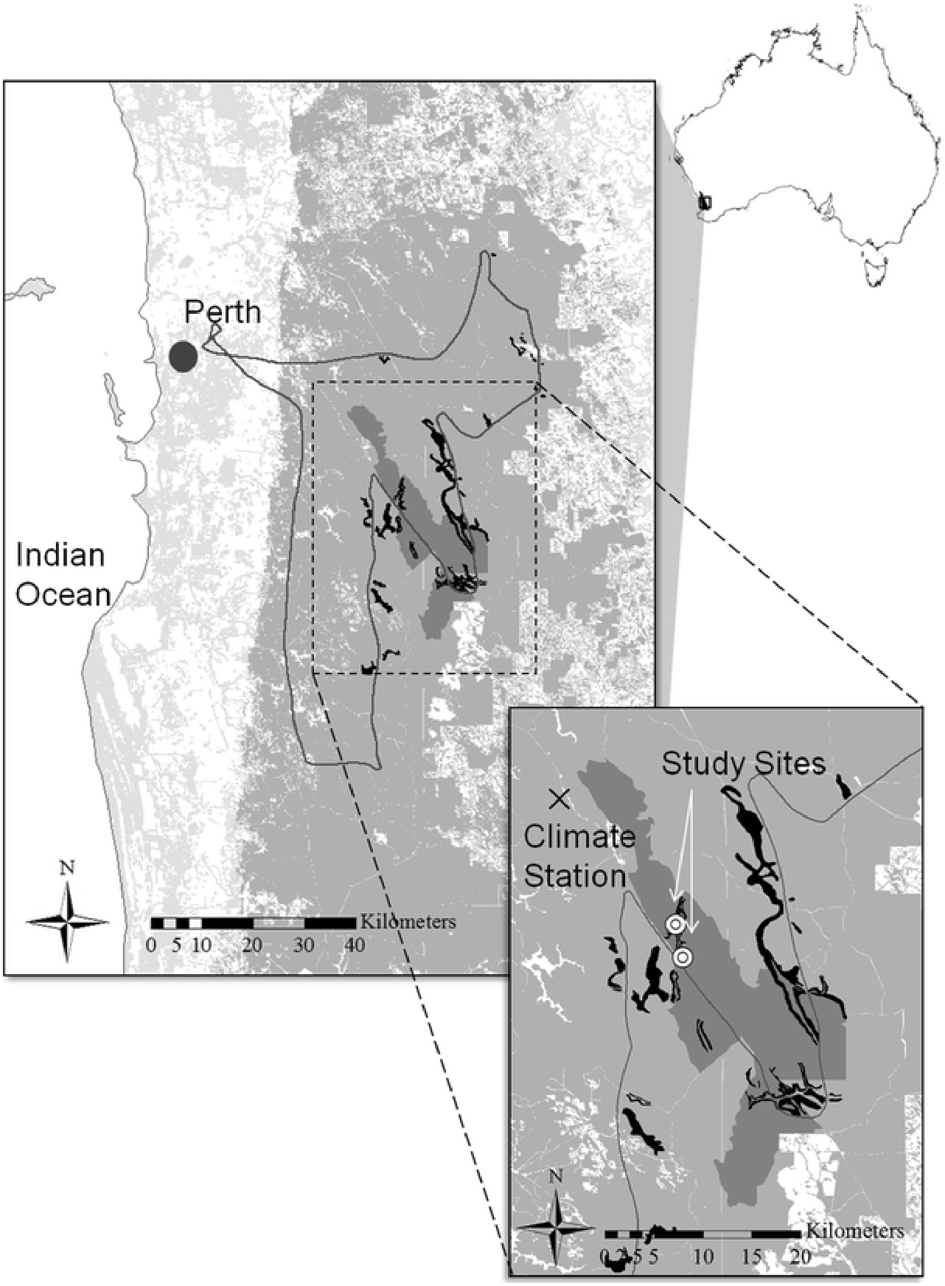

Fig. 2. a Discoloration in frost-affected forest extending across large areas of the Northern Jarrah Forest, southwest Australia. Photo taken during aerial survey, 13 July 2012. b Foliage discolouration in affected trees in the Northern Jarrah Forest, southwest Australia, observed on 20 June, 2012

Fig. 3. Frequency distribution of topographic position index (TPI) values for sample points selected within frost-affected (*black bars*) and unaffected (*white bars*) forest observed in 2012 in the Northern Jarrah Forest, southwest Australia. Topographic position index values range from valley to ridge (−30 to +30), with values between −8 and 0 occurring on lower slope positions

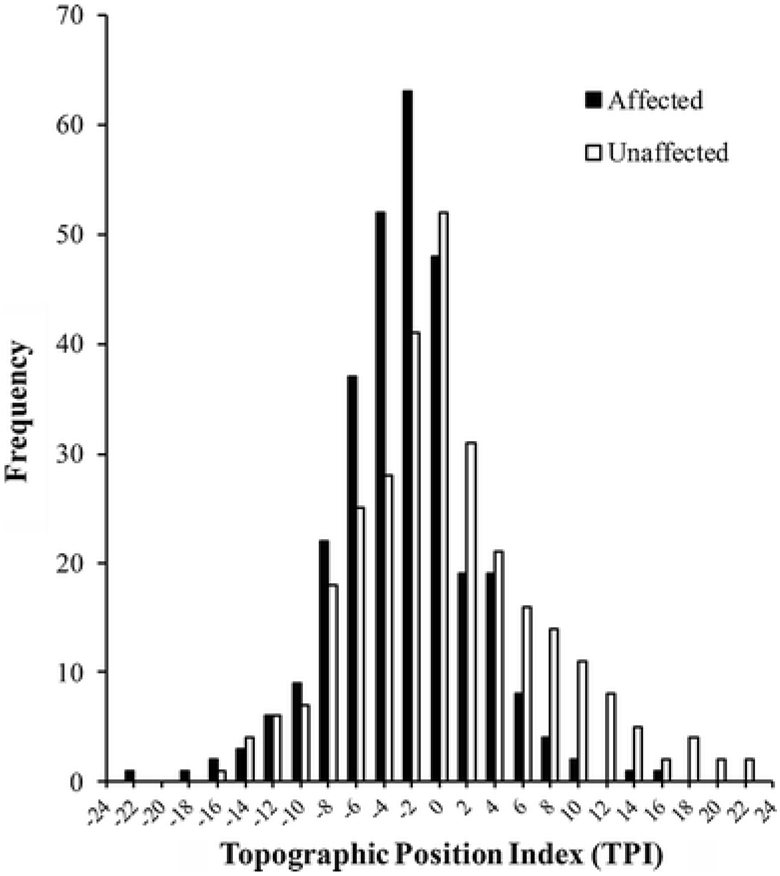

Fig. 4. Average crown damage index (CDI) in understory (a), midstory (b), and overstory (c) trees measured at six elevations in the Northern Jarrah Forest at two sites (Albany Hwy and Millars Log Rd.). Statistical significance is indicated by different letters (normal for Millars Log Rd. and CAPS for Albany Hwy) and was obtained from mixed model analyses at alpha = 0.05, followed by Tukey’s multiple comparison tests. Error bars represent the standard error of the means

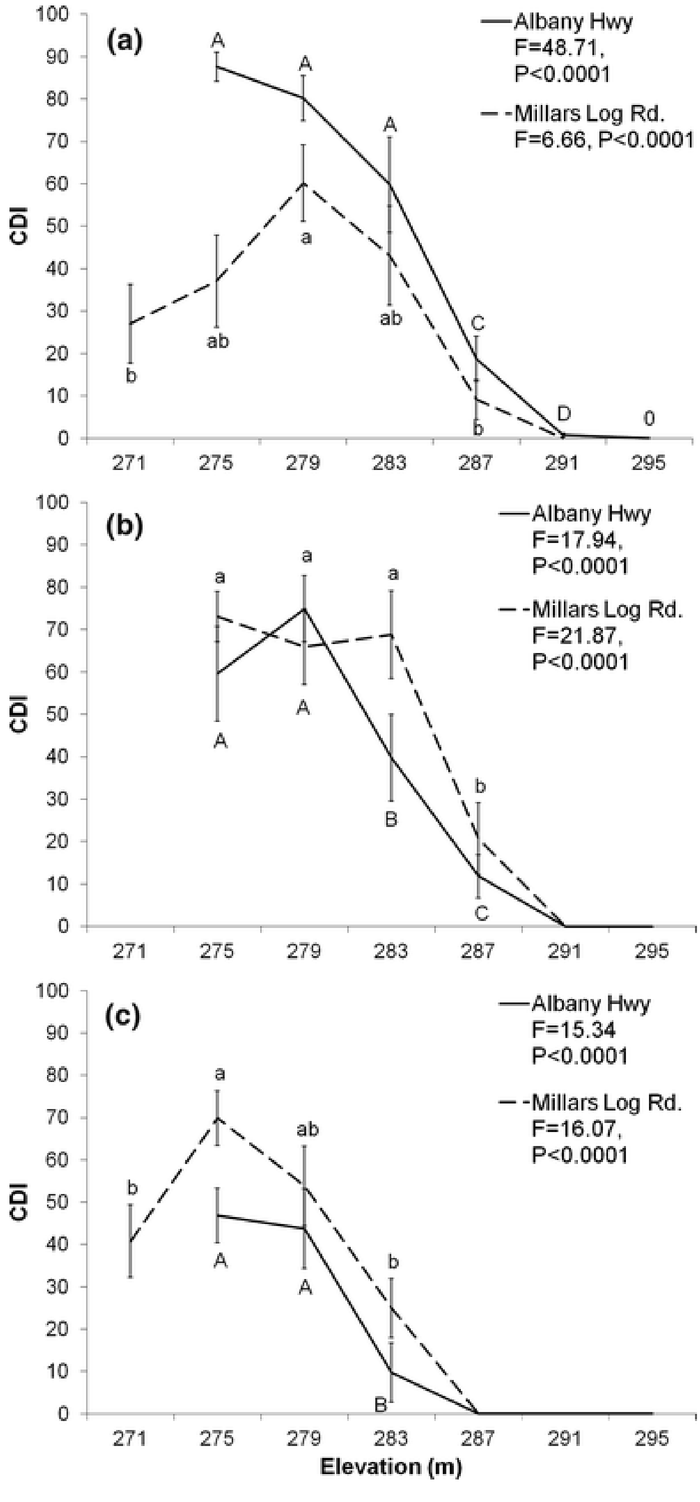

Fig. 5. Average temperatures during the coolest hours of the night from three transects at the Albany Hwy site in the Northern Jarrah Forest. Transects consisted of six elevation points from drainage to upper slope. *Error bars* represent the standard error of the mean

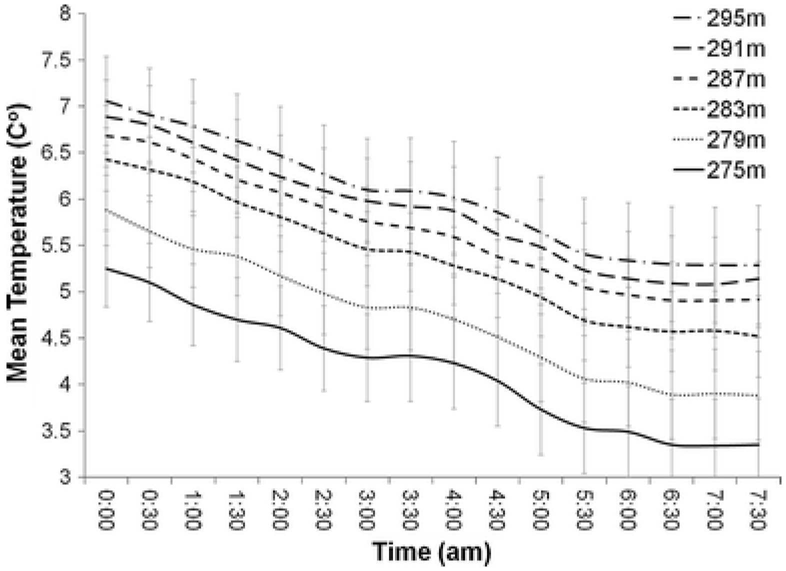

Fig. 6. Daily mean minimum temperature observed at six elevations along three transects in the Northern Jarrah Forest. *Error bars* represent the standard error of the mean. Columns with the same letter indicate no statistical difference based on mixed linear model and Tukey's multiple comparison test, alpha = 0.05

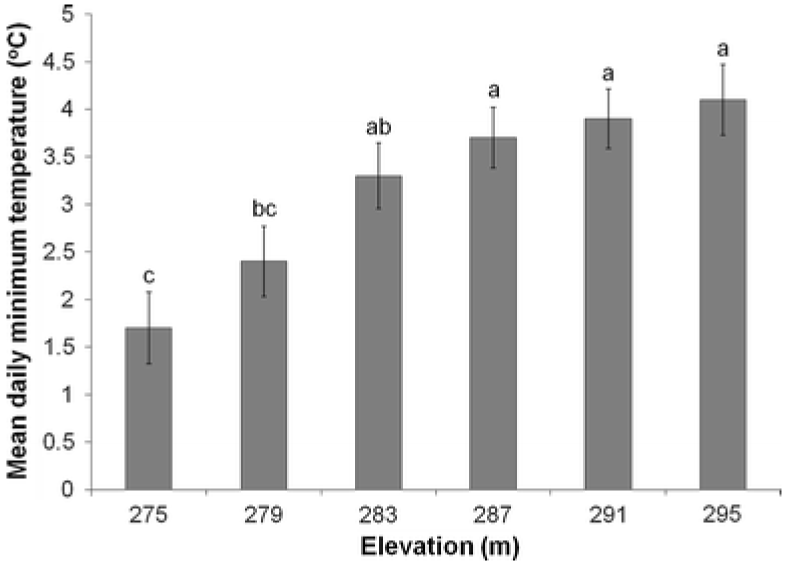

Fig. 7. Simple linear regression equations for site temperature at 275 m (a), 279 m (b), 283 m (c), 287 m (d), 291 m (e), and 295 m (f) elevation at the Albany Hwy site in the Northern Jarrah Forest, where x = Weather Station daily minimum temperature (Wungong Brook, Lat: −32.25277, Long: 116.14143)

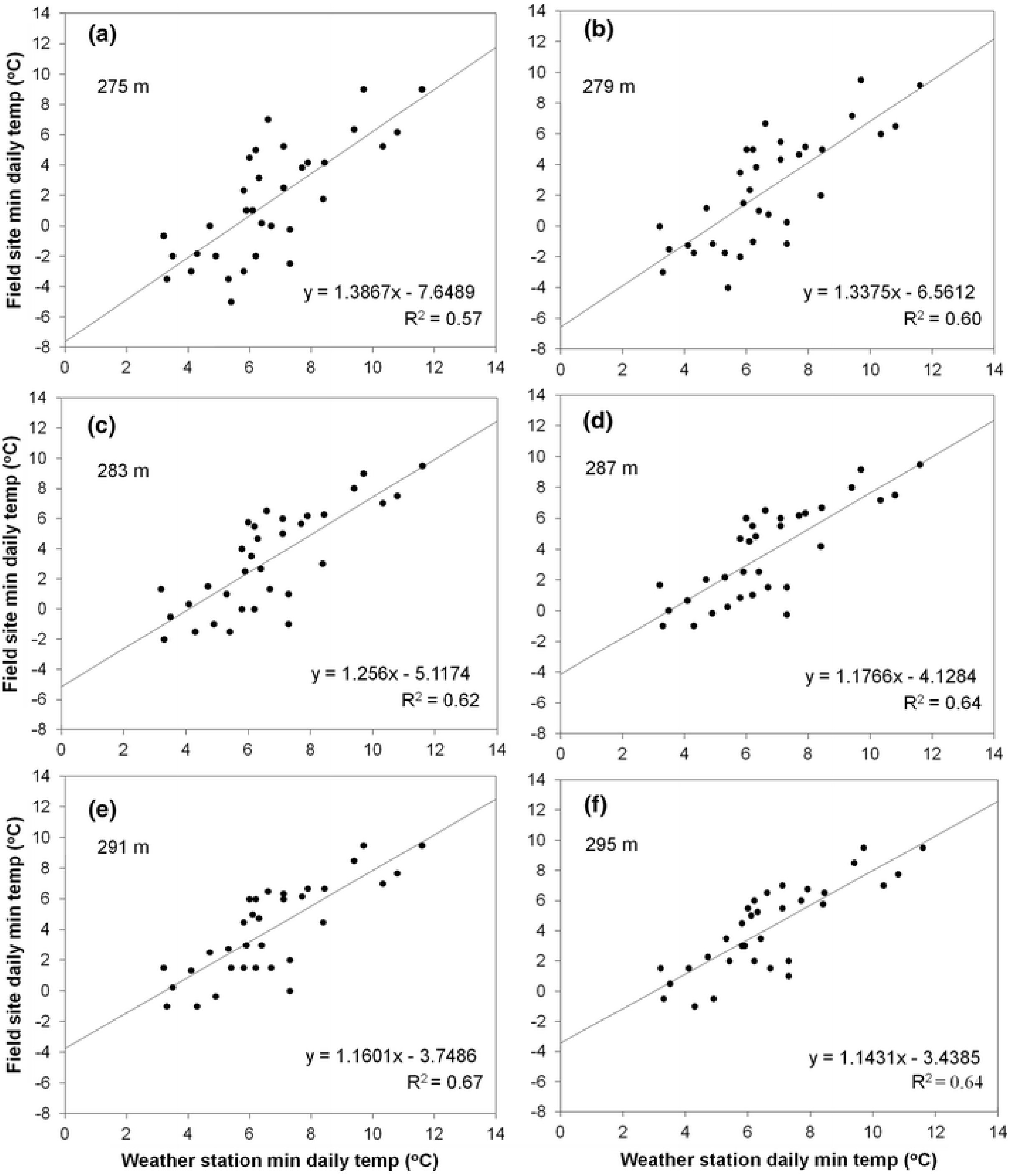

Fig. 8. Modelled minimum temperature for 275, 279, 283, 287, 291, and 295 m in elevation at the Albany Hwy site in the Northern Jarrah Forest from regression equations developed from site temperature and those experienced at nearest weather station (Wungong Brook, Lat: −32.25277, Long: 116.14143) Modelled data cover the period in which severe damage was sustained by tree crowns

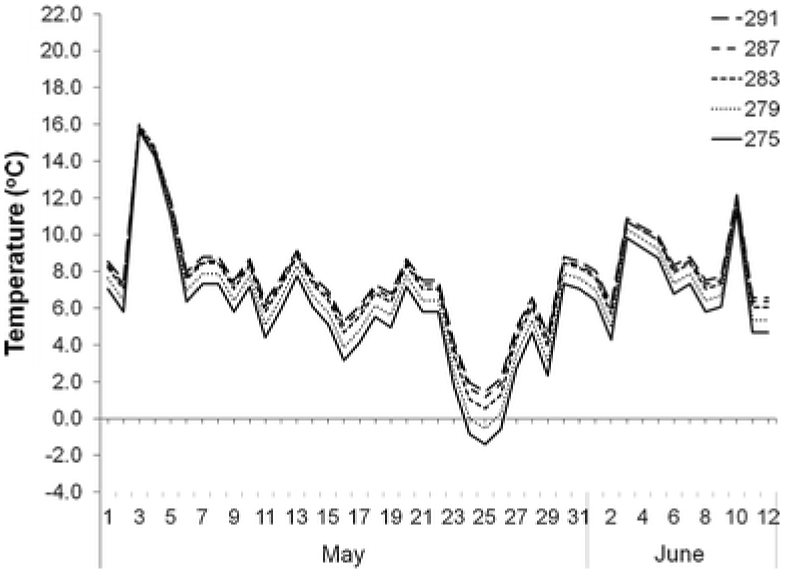

Table 1. Tree species composition (%) in three strata levels from plots at six elevations along transects at two sites in the Northern Jarrah Forest impacted by frost damage in 2012. Data obtained using Point Centered Quarter method of tree sampling

Site	**Strata**	**Elevation (m)**	**Eucalyptus marginata**	**Corymbia calophylla**	**Eucalyptus patens**	**Eucalyptus wandoo**
Albany Hwy	Understory	275	67	33	0	0
		279	100	0	0	0
		283	92	8	0	0
		287	100	0	0	0
		291	100	0	0	0
		295	67	33	0	0
	Midstory	275	60	40	0	0
		279	93	7	0	0
		283	94	6	0	0
		287	100	0	0	0
		291	100	0	0	0
		295	100	0	0	0
	Overstory	275	73	13	7	7
		279	100	0	0	0
		283	100	0	0	0
		287	100	0	0	0
		291	100	0	0	0
		295	100	0	0	0
Millars Log Rd.	Understory	271	8	17	75	0
		275	100	0	0	0
		279	100	0	0	0
		283	100	0	0	0
		287	92	8	0	0
		291	75	25	0	0
	Midstory	271	na	na	na	na
		275	100	0	0	0
		279	100	0	0	0
		283	100	0	0	0
		287	83	17	0	0
		291	86	14	0	0
	Overstory	271	6	17	78	0
		275	100	0	0	0
		279	100	0	0	0
		283	92	8	0	0
		287	100	0	0	0
		291	93	7	0	0