Disturbance history and stand dynamics in tall open forest and riparian rainforest in the Central Highlands of Victoria

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Abstract Spatial heterogeneity in the intensity of past disturbances has directly influenced the structure and composition of present-day forests around the world. In south-eastern Australia infrequent, high-intensity wildfires are a major part of the historical disturbance regime. While these fires are often assumed to produce even-aged stands, spatial heterogeneity in fire intensity due to highly variable topography may lead to more complex forest age structures. Our study describes the influence of disturbance on the age structure and dynamics of a mosaic of tall, open eucalypt forest, cool temperate rainforest and mixed species forest surrounding Bellel Creek in the Central Highlands of Victoria using dendrochronological techniques. We were particularly interested in the impacts of the 1939 Black Friday fire and its effects on forest age structure and subsequent stand development patterns. Within our study site tall open forest displayed two distinct age cohorts: (i) trees that established immediately after the 1939 fire and accounted for the majority of individuals in the forest, and (ii) scattered groups of older trees estimated to be approximately 200–250 years old. Cool temperate rainforest and mixed forest were also dominated by the post-1939 fire age cohort. However, a greater proportion of trees in these forest types survived the 1939 fire relative to the tall open forest. The impact of the 1939 fire on the growth of surviving trees was highly variable but generally short-lived. In most cases growth decreased after the 1939 fire, but generally returned to prefire levels within 1–3 years. Non-fire disturbances were limited to small-scale branch- and tree-fall events, although the extreme snowstorm of 1977 appears to have caused extensive damage to rainforest communities. Our study demonstrates the opportunities for dendroecological studies to reconstruct historical dynamics and disturbance patterns in Australian forests and provides important insights into variation in landscape-scale fire impacts and their effect on subsequent forest development patterns.

Key words: dendrochronology, eucalypts, growth release, mountain ash, multiple-age cohorts.

INTRODUCTION

Past disturbances are an important source of variation in contemporary forest structure at the stand and landscape scales (Baker 1992; Attiwill 1994a; Turner & Romme 1994). The intensity of individual disturbance events is rarely homogeneous even at small spatial scales (Attiwill 1994a; Mackey et al. 2002). Over decades and centuries variation in the frequency, intensity and location of multiple disturbance events across a landscape creates a complex mosaic of forest patches that vary in species composition and stand structure (Baker 1992; Williams et al. 1994). In the absence of long-term, historical records of forest change, dendroecology has been widely used to investigate forest stand dynamics and the role of disturbance in shaping the structure and composition of forests, particularly in the northern temperate zone. Dendroecological studies, which use tree rings to reconstruct the age structure and growth dynamics of forests, have been used to describe the influence of fire, windstorms, heavy snowfalls, pathogens and insect outbreaks on forest dynamics (e.g. Readshaw & Mazanec 1969; Foster 1988; Cho & Boerner 1995; Abrams & Orwig 1996; Oliver & Larson 1996; Nowacki & Abrams 1997; Abrams et al. 1999; Bergeron et al. 2002; Pollmann 2003).

Dendroecology has received limited attention in Australia owing to the widely held belief that most Australian tree species do not form distinct annual growth rings (Ogden 1978; Dunwiddie & LaMarche 1980; Pearson & Searson 2002). In addition, the few tree ring studies that have been conducted in Australian forests have rarely applied rigorous cross-dating techniques to ensure strict dating control (Brookhouse 2006). Cross-dating is the matching of ring widths across all samples from a given site or region to assign the correct year to each ring and to guarantee a correct temporal sequence. In the absence of cross-dating, it is impossible to determine the correct dates of disturbance events, tree ages and timing of abrupt growth increases or decreases.

The forests of south-eastern Australia are subject to a variety of disturbance types and intensities.
High-intensity wildfires are an important component of the long-term disturbance regime in many of these forests, but the long-term impacts of such fires on individual tree growth and stand dynamics are poorly understood owing to the lack of detailed historical data. In the Central Highlands of Victoria infrequent high intensity fires have been a major force shaping contemporary forest communities and their dynamics (Ashton 1981). The Central Highlands region is dominated by tall open forests (sensu Specht 1970), but cool temperate rainforest is commonly found in the gullies and riparian zones that dissect the landscape. The tall open forests produce substantial amounts of leaf and bark litter that, when combined with the prolonged hot and dry conditions seasonally experienced in the region, can create highly flammable conditions (Ashton & Attiwill 1994; McCarthy et al. 1999; Ashton 2000). The extreme flammability of these forests was demonstrated on 13 January 1939, Black Friday, when hot north winds caused a string of small fire fronts to join and burn across 1380 000 ha of mountain forests in Victoria (approx. 13.5% of the total Victorian land area), including large tracts of forest in the Central Highlands (Noble 1977; Griffiths 2001). The high mortality rates caused by such extreme fire events have led to a general consensus among Australian foresters and forest scientists that such events are stand-replacing and that the current forests are primarily even aged (Ashton 1976; Squire et al. 1991; Ashton & Attiwill 1994; Attiwill 1994a; McCarthy & Lindenmayer 1998; Lindenmayer et al. 2000a).

Fire, as a form of disturbance, is notoriously variable in the severity of its effects across large areas owing to the influence of topography on a wide range of variables, including evaporation rates, soil moisture, primary productivity, species distribution, decomposition rates, fuel loads and fuel wetness (Chandler et al. 1983; Nelson 2001). In areas where the terrain is highly variable, such as the Central Highlands, fire intensity and spread rate will vary across a range of spatial scales (Flannigan & Wotton 2001; Taylor & Skinner 2003). As a consequence, localized portions of the landscape may experience much less severe fire effects and thus allow for the survival of remnant pockets of forest within the greater landscape. These forest remnants may serve important functions in the recolonization of adjacent areas that have experienced higher mortality rates from the fires. They may also develop into more complex, multi-aged stands as a consequence of the more moderate mortality and regeneration associated with the locally less intense fire.

A variety of approaches have been used to assess the presence and relative abundance of multi-aged stands in the Central Highlands of Victoria. Analyses of aerial photographs after the 1983 Ash Wednesday fires demonstrated that most trees survived in approximately 70% of the forest that was burnt, and that canopy leaf scorch was extremely variable within any given burnt area (Smith & Woodgate 1985). Other studies have inferred the presence of multi-aged stands from stem diameter distributions, where stem diameter is used as a proxy measure of tree age. For example, Lindenmayer et al. (2000a) looked at 625 sites across the Central Highlands and found seven different naturally occurring ‘age’ classes of mountain ash forest. However, stem diameter is often a poor substitute for age owing to the indeterminate nature of tree growth and the importance of local environmental conditions on short-term growth rates (Baker 2003). The difficulties associated with this method can be overcome using dendroecology, which provides accurate age estimates for individual trees and forest stands.

In this study we used dendroecological techniques to investigate the stand development history of several interdigitated forest types in an area of forest adjacent to Bellel Creek near Marysville, Victoria. We were particularly interested in identifying the role of the 1939 Black Friday fires on tree recruitment and growth dynamics in each of the forest types. We hypothesized that variation in topography and forest type within our study site would be associated with distinctly different post-fire dynamics within each forest type. We tested this hypothesis by reconstructing the age structure and growth dynamics of most of the dominant tree species within the site. Together these data allowed us to determine the role that disturbances have played in shaping the present-day forest and to reconstruct the historical stand development patterns of these mixed-species forests in the aftermath of one of the most destructive wildfires of the past century.

METHODS

Study site

Our study was conducted in an area of forest near Lake Mountain in the Central Highlands of Victoria (37°33′33″S, 145°50′00″E; Fig. 1). The study site was located in the upper regions of the O’Shannassy water catchment in the Yarra Ranges National Park, an area that has been protected from human disturbances (e.g. logging) since 1888 (Griffiths 2001). We sampled across an edaphic gradient along a 700 m section of Bellel Creek, which ran east to west, giving slopes northerly and southerly aspects. The edaphic gradient ranged from a low-lying riparian zone along the creek dominated by cool temperate rainforest, up the slopes through a section of mixed species forest to upland sites supporting tall open forest. The tall open forests are typical of those described by Specht (1970) and are characterized by a tall overstory of Eucalyptus, a
mid-story dominated by *Acacia* species and a dense understory of small trees and ferns. The cool temperate rainforest was characterized by a dense canopy of myrtle beech (*Nothofagus cunninghamii*) and southern sassafras (*Atherosperma moschatum*), creating a shaded and moist forest environment with a sparse understory. In most cases it was restricted to the flat floodplain of the creek with the transition to steeper
slopes marking its boundaries. In the mid-slope zone between the tall open forest and cool temperate rainforest communities, mixed forest occurred. This forest type was characterized by a closed canopy of myrtle beech and the presence in small numbers of Acacia, Eucalyptus and other species characteristic of tall open forests.

**Field survey**

We sampled a total of 132 trees in a study site of approximately 30 ha between July 2005 and January 2006. Trees were selected using random stratified sampling. We divided the study site into five separate sampling zones that reflected obvious differences in vegetation structure and composition: an upper-slope zone dominated by tall open forest and mid-slope zone dominated by mixed species forest on each side of the valley, and a single central riparian zone containing cool temperate rainforest. Within the upper and mid-slope zones we randomly selected six sample points. In the riparian zone we selected seven sample points to increase the number of samples from the cool temperate rainforest. At each sample point we quantified forest composition by recording the species and diameter at breast height (d.b.h.; 1.3 m) of each living stem >6.5 cm d.b.h. located within a 200 m² circular plot. We then used the point-centred quarter (PCQ) method to select four trees for coring. When the closest tree within a given quarter was not suitable for coring owing to its physical condition (e.g. significant stem rot), we selected the next closest tree within the same quarter. From each sample tree two cores were removed from a height of 1 m on the stem using a Suunto increment corer. The species and d.b.h. of each sample tree were also recorded. Our sampling of mountain ash (Eucalyptus regnans) was limited to four trees because preliminary assessment of the growth rings indicated that reliable cross-dating was not possible. We also selected a small number of additional sample points where trees of potential interest in the study site were not selected for sampling using the PCQ method. This included uncommon tree species or trees that appeared to be particularly old. A total of eight trees was sampled in this way.

**Data and radial growth analysis**

The mean basal area and mean number of individuals per hectare were calculated for species in each sampling zone. The sum of the relative density, cover and frequency of each species was calculated to yield an importance value for that species, providing an indication of the relative dominance of each species in our study area. All tree core samples were mounted on wooden trays and sanded using progressively finer grades of sandpaper (from 100 to 800 grit). Sanded cores were then scanned at high resolution (1600 dpi) using a digital scanner (Epson 4870 photo) and ring counts and measurements were made using an image analysis program. Where the tree core missed the pith of the tree, we used Duncan’s (1989) geometric method to estimate the number of missed rings. In brief, this method estimates the missing distance to the pith based on the curvature of the innermost ring. This distance is then divided by the mean ring width value for the core to calculate the number of missing rings. To ensure correct dating of the time series we used an iterative cross-dating procedure. The first step involved visually cross-dating each pair of cores taken from the same tree. We then used the program COFECHA to develop a mean chronology from all of the dated tree ring series (Holmes 1983). COFECHA generates mean interseries correlation (MIC) values by comparing each individual tree ring series to the mean chronology. This allows obvious dating errors to be identified and the appropriate corrections to be made. The redated cores were then re submitted to COFECHA and the procedure repeated until all dating errors were reconciled (Grissino-Mayer 2001). To facilitate this procedure we subdivided the cores into groups based on species, topographic position (upper slope, mid-slope or riparian zone) and whether the tree established before or after the 1939 fire (based on preliminary ring counts). Where an individual tree ring series was poorly correlated with the mean chronology and the dating anomaly could not be rectified, the tree ring series was excluded from further analysis.

We used the cross-dated tree ring series to construct age distributions for the study site and to identify periods of sudden growth increase (release) or decrease (suppression). Release and suppression events were identified using the per cent growth change method described by Nowacki and Abrams (1997). We calculated per cent growth change for each tree using the mean ring width series of the two cores from each tree. In calculating per cent growth change, we used a 10-year window for comparison to avoid the influence of short-term climatic fluctuations and to enhance detection of abrupt and sustained radial-growth changes characteristic of canopy disturbance (Nowacki & Abrams 1997). We defined two arbitrary threshold values based on previous studies of growth releases in other tree taxa. When an individual tree showed a growth increase of >100% (i.e. doubled growth over consecutive decades) we considered this to be a major growth release. When an individual showed a growth increase of 50–100%, we defined this as a moderate growth release. We used the same, but negative, threshold values to define growth suppression.

RESULTS

Forest composition and structure

The riparian zone was dominated by myrtle beech (*N. cunninghamii*) and to a lesser extent southern sassafras (*A. moschatum*). Silver wattle (*Acacia dealbata*) was sparsely distributed through the riparian zone, often extending above surrounding myrtle beech. Only one large individual of mountain ash (*E. regnans*) was found in the riparian zone. Like the riparian zone, the mid-slope zone was also dominated by myrtle beech, although only two individuals of southern sassafras were found in this zone (both on the north-facing slope). The mid-slope zone also included alpine ash (*Eucalyptus delegatensis*) and mountain ash and silver wattle were more prominent (Table 1). The upper slopes were dominated by the two canopy eucalypt species: mountain ash, which dominated the south-facing slope, and alpine ash, which dominated the north-facing slope. Silver wattle was common in the upper slope zone and was the dominant mid-story tree. Myrtle beech was present on the upper slopes, but sparsely distributed (Table 1). The open canopy of the tall eucalypt forest allowed more diverse mid- and understory vegetation to exist. Several species of small tree were found in the upper slopes including *Lomatia fraseri, Phebalium wilsonii* and, to a lesser extent, *Acacia obliquinervia, Pittosporum bicolour* and *Tasmania lanceolata* (Table 1).

Cross-dating

Twenty-two of the 132 sampled trees were removed from the analyses because, for several reasons, they could not be cross-dated. Out of the 22 trees removed from analysis seven were removed because the species could not be cross-dated owing to poorly formed growth rings. These included the species *L. fraseri* and *E. regnans*. A further four trees were removed owing to errors in the mounting and sanding process of cores that made their use impossible. The remaining 11 trees were removed because they did not correlate well with the bulk of trees sampled. Eight of these trees contained highly abnormal growth rings in the sample caused by branch traces and other growth anomalies and three were removed because the rings were simply too poorly formed and difficult to see for the tree to be accurately dated. Thus, trees from cross-dateable species that could not be cross-dated represent only 8.3% of the total sample population, which is similar to exclusion rates from other dendroecological studies (e.g. Bergeron 2000; Brown & Wu 2005).

Cross-dating with COFECHA was most effective for trees that established after 1939. High MIC values

### Table 1. Characteristics of species found within survey plots in the riparian, mid and upper zones

<table>
<thead>
<tr>
<th>Species</th>
<th>Upper slope</th>
<th>Mid-slope</th>
<th>Riparian</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Acacia dealbata</em></td>
<td>8.6 (2.8)</td>
<td>5.0 (4.0)</td>
<td></td>
</tr>
<tr>
<td><em>Acacia obliquinervia</em></td>
<td>0.1 (0.08)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Allophylus moschatum</em></td>
<td>0.1 (0.08)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Eucalyptus delegatensis</em></td>
<td>48.4 (19.7)</td>
<td>90.0 (25.0)</td>
<td></td>
</tr>
<tr>
<td><em>Eucalyptus regnans</em></td>
<td>61.5 (30.1)</td>
<td>90.0 (25.0)</td>
<td></td>
</tr>
<tr>
<td><em>Lomatia fraseri</em></td>
<td>0.6 (0.35)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Nothofagus cunninghamii</em></td>
<td>10.1 (3.6)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Phebalium wilsonii</em></td>
<td>0.1 (0.08)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Pittosporum bicolour</em></td>
<td>0.1 (0.08)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Tasmania lanceolata</em></td>
<td>0.6 (0.35)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Basal area (m²) and number of individuals are expressed as mean values per hectare with standard errors in parentheses. BA, mean basal area (m² ha⁻¹); IV, importance values; N, mean number of individuals per hectare.

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were obtained for the post-1939 cohorts of silver wattle and myrtle beech (Table 2). Older myrtle beech and southern sassafras were more difficult to cross-date owing to the large amount of within-core ring width variation (Table 2). The high MIC values for groups of trees analysed with COFECHA indicate that there was consistency in the growth rate of trees within each group. Such high MIC values could not be obtained when analysing all trees together, suggesting some differences in growth trends among the species and topographic groups.

Of the two sampled eucalypt species only alpine ash was successfully cross-dated. Tree rings in alpine ash were not as clearly defined as those in myrtle beech or silver wattle though cross-dating was still effective. Mountain ash were not cross-dated with COFECHA owing to an inability to obtain accurate ring-counts from three of the four trees sampled. Cores from the same tree rarely showed consistent growth patterns. Figure 2a displays ring widths from two cores taken from a single mountain ash and is typical of the highly varied ring width series displayed by this species. We found one tree core that showed a major release in the 1940 ring (the year being based on simple ring counts, not cross-dating), the year after the Black Friday fire (Fig. 2b). While the timing of the growth release might be taken as support for simple ring counting, there is a lack of consistency with and high variability among the other mountain ash tree ring series. This raises important questions about the quality of the ring-counting and any conclusions made from mountain ash ring width series. In the absence of cross-dating, it is not possible to determine if the lack of a common pattern was real or whether it was due to dating errors.

### Age distributions

We used a total of 93 trees for which at least one core passed close enough to the pith to allow accurate age estimates to develop the stand age distribution (Fig. 3). The ages represent the time at which the trees reached sampling height (1 m) and not the exact year of establishment. The stand age distribution is dominated by myrtle beech, silver wattle, alpine ash and southern sassafras, but also includes an *A. obliquinervia* and two *P. wilsonii*. The stand age distribution is dominated by a single distinct peak in establishment from 1940 to 1955, after which recruitment decreased until approximately 1980. The lack of trees establishing after 1980 is primarily an artefact of the minimum diameter that we used when coring trees. The stand age distribution also shows that there was consistent establishment during the period from

![Ring width measurements from two Mountain ash (Eucalyptus regnans) trees. (a) Displays ring width measurements of two cores from the same tree. It demonstrates the typically high variability in ring widths within each tree that made cross-dating impossible for this species. (b) Shows ring width measurements from a Mountain ash that displayed evidence of growth release immediately following the 1939 fire. While this tree ring series was not cross-dated, the sudden growth release in 1940 suggests that the dating in the outer section of the tree was relatively accurate.](image)

### Table 2. Mean series intercorrelation values for groups of trees analysed using COFECHA

<table>
<thead>
<tr>
<th>Species</th>
<th>Upper-zone Pre 1939</th>
<th>Upper-zone Post 1939</th>
<th>Mid-zone Pre 1939</th>
<th>Mid-zone Post 1939</th>
<th>Riparian Pre 1939</th>
<th>Riparian Post 1939</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Nothofagus cunninghamii</em></td>
<td>–</td>
<td>0.449</td>
<td>0.245</td>
<td>0.412</td>
<td>0.245</td>
<td>0.406</td>
</tr>
<tr>
<td><em>Acacia dealbata</em></td>
<td>–</td>
<td>0.372</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>0.473</td>
</tr>
<tr>
<td><em>Atherosperma moschatum</em></td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>0.307</td>
</tr>
<tr>
<td><em>Eucalyptus delegansensis</em></td>
<td>0.257</td>
<td>0.316</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
</tbody>
</table>

Because of small numbers of trees establishing before 1939 in the mid-slope zone, we grouped pre-1939 trees from the mid-slope and riparian zones.

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1850 to 1920. Only three of the sampled trees, all myrtle beech, established before 1850 (Fig. 3). The lack of trees establishing before 1850 is not necessarily indicative of low recruitment during that period. More likely it reflects a bias in sampling towards younger trees because the majority of the largest, and presumably oldest (based on stem physiognomy), trees had severe rot in their trunks. This problem was most pronounced in myrtle beech for which nearly every individual >50 cm d.b.h. was rotten or hollow.

Age distributions of individual species differed somewhat. The majority of myrtle beech establishment occurred from 1940 to 45 in the wake of the 1939 fire. Establishment continued after this peak until the 1970s, but at a much slower rate (Fig. 3). Alpine ash also showed a distinct pulse of establishment immediately following the 1939 fire (Fig. 3). Only one of the alpine ash trees predated the 1939 fire. The age distribution of alpine ash was also biased towards younger individuals owing to the large size of the trees, many of which were too large for our 50 cm tree corer to reach the tree centre. Incomplete ring counts in five alpine ash with d.b.h. of 80–130 cm showed 67–96 years of growth (i.e. dating back to 1938 and 1906). Two large mountain ash (d.b.h. = 157 and 160 cm) had incomplete ring counts dating back to 1821 and 1859, respectively. Cores from these trees display only the outermost 40–50 cm of the tree ring record and most likely represent <50% of the entire record. While growth rates may be higher during the early stages of stand development, age estimates based on the number of observed rings and total d.b.h. indicate that these trees may have established in the mid- to late-1700s.

The age distribution of silver wattle was restricted to individuals that established after 1939 (Fig. 3). Curiously, however, the peak of silver wattle establishment lagged behind those of the other species by 10–15 years. The single *A. obliquinervia* that was sampled established at the same time as the silver wattle. The seven southern sassafras recruited between 1855 and 1955 and showed no evidence of episodic recruitment. Indeed, no more than one sampled sassafras established in any given 5-year period (Fig. 3). Southern sassafras was unique among the study species in showing no evidence of heightened recruitment after the 1939 fire.

**Disturbance history**

Ring widths varied considerably within and among trees of the same species, and among trees of different species (Fig. 4). Measures of per cent growth change in the tree ring series provided evidence of release and suppression in each species in most decades. Growth releases were more common than growth suppressions; indeed, we found no evidence of major suppression events in any species. Sample sizes of old myrtle beech and southern sassafras were sufficient to enable the reconstruction of release and suppression events before the 1939 fire. Prior to 1900 myrtle beech and southern sassafras exhibited consistent low levels of suppression and release. Because of the small sample sizes prior to the 1850s, we place little value on interpretations of the two peaks (one of release and one of suppression) during that period.

There is little evidence that the 1939 fire had a consistent or sustained impact on radial growth among the surviving myrtle beech, southern sassafras and alpine ash trees (Fig. 5). Twenty-three trees (six southern sassafras, three alpine ash and 14 myrtle beech) were old enough to allow comparisons of pre- and post-fire growth rates. The growth patterns were highly individualistic and showed the full range of potential growth.

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**Fig. 3.** The distribution of estimated years of establishment for trees sampled at Bellel Creek. Dates are grouped into 5-year intervals. The vertical dotted line indicates the 1939 fire. Establishment dates indicate the year that trees reached the sampling height of 1 m.
responses to the fire. The most common response to fire was a short-term decrease in growth (52% of the trees; Fig. 6). However, the growth suppression was short-lived, lasting only 1–3 years, after which growth rates returned to approximately prefire levels. The remaining trees were approximately evenly split into two groups: those that showed no obvious change in growth following 1939 and those that showed a marked growth increase after the 1939 fire.

In the decades following the 1939 fire growth releases and suppression occurred at low frequency in all species. The only exceptions were myrtle beech, in which 24% of sampled trees showed growth releases during the 1970s and southern sassafras in which 57% of sampled trees showed growth releases during the 1980s (Fig. 5). Silver wattle experienced few growth releases. Moderate suppression was common throughout stand development, with nearly half of all trees showing suppression in any given decade (Fig. 5). Alpine ash showed remarkably consistent growth – only two release events and 11 suppression events were detected in the growth records of all sampled individuals. There were no releases or suppressions detected prior to 1950 in alpine ash (Fig. 5).

**DISCUSSION**

We used dendroecological analyses to reconstruct nearly 150 years of the disturbance history and stand development patterns of mixed-species forest stands at Bellel Creek in the Central Highlands of Victoria. The tree ring analyses allowed us to examine critically two key aspects of the forest community response to the recent disturbance history. First, by reconstructing the age distribution of sampled trees we can identify periods of peak recruitment throughout the stand. We can use these data to investigate the role that disturbances play in abetting seedling recruitment and stand regeneration and how these patterns are influenced by topographic position within the stand. Second, the analysis of abrupt increases and decreases in inter-annual growth rates allowed us to investigate the severity of disturbance events and differences among species and across topographic gradients in their response to disturbances of varying intensity. These dendroecological data provided new insights into the recent disturbance history of a mosaic of forest types in the Central Highlands and, in particular, their different responses to one of the most severe wildfires of the past century – the 1939 Black Friday fire.

**Age distributions**

**Tall open forests**

Regeneration in tall open mountain ash forest is controlled almost entirely by fire (Ashton 1981). The two eucalypt species found at Bellel Creek, mountain ash and alpine ash, depend on high intensity fires for reproduction, as the fires desiccate the seed capsules which then release masses of seeds (up to 14 million per hectare; Attiwill 1994b; Bell & Williams 1997). Mountain ash seedlings are intolerant of shade and rarely establish in mature forest (Ashton & Attiwill 1994; Attiwill 1994b). When a fire kills most of the adult trees, the dramatic increase in understorey light levels and the creation of a nitrogen-rich ash bed leads to profuse seed germination and seedling establishment after the fire (Ashton & Martin 1996). While mountain ash and alpine ash rely on fire to regenerate, they are considered to be fire-sensitive species because they lack the ability to reproduce vegetatively and are killed by the high-intensity fires characteristic of the region (McCarthy & Lindenmayer 1998; Florence 2004).
lished forest trees with seedlings following crown fire in these forests has led to the assumption that eucalypt stands in the Central Highlands of Victoria are generally even aged (McCarthy & Lindenmayer 1998).

When the intensity of a fire is insufficient to kill all of the trees, but sufficiently high to kill some, a mixture of age classes occurs within the forest. Several studies have suggested that mountain ash forests may have multiple age classes. However, these assessments have been based on either diameter distributions, used as a proxy for age distributions (McCarthy & Lindenmayer 1998; Lindenmayer et al. 2000a; Florence 2004) or on qualitative assessments of forest structure and composition (Squire et al. 1991; Ashton & Attiwill 1994; Attiwill 1994a). In this study we used tree ring evidence to demonstrate that most of the trees in the tall open forest at Belle Creek established soon after the 1939 fire. However, the fire did not eliminate all of the trees that were on the site in 1939. Several scattered clumps of eucalypt trees were clearly older than the majority of trees that had established post 1939. Previous studies have noted that in most stands of moun-

**Fig. 5.** Percentage of sampled trees displaying release events (above x-axis) and suppression events (below x-axis) per decade. Stacked bars represent the proportion of major and moderate releases per decade. Sample size is plotted on secondary y-axis (right).

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tain ash there are individuals that had established following an earlier fire and then survived the more recent fire (e.g. McCarthy & Lindenmayer 1998; Lindenmayer et al. 2000a). Age estimates based on incomplete tree cores and the large diameters of the remnant trees at Bellel Creek indicate some may be >250 years old and that there are at least two distinct age cohorts in the forest. The presence of small patches of older, remnant mountain and alpine ash within the matrix of post-1939 regrowth suggests that the effects of the 1939 fire were not uniformly severe across the study area.

In contrast, silver wattle showed no evidence of having survived the 1939 fire. All of the silver wattle that were on the plot established after the fire. The mid-canopy position of silver wattle crowns and their thinner, less protective bark makes them more susceptible to fire-induced mortality than the tall, thick-barked eucalypts. Silver wattle is one of the few species in the tall open forest that produces hard seeds that can remain viable in the soil for long periods of time, awaiting fire to stimulate germination (Adams & Attiwill 1984; Attiwill 1994b). As such, the pulse of silver wattle recruitment would be expected to occur directly after the 1939 fire, synchronous with the recruitment of the alpine and mountain ash. While the fire must have been less intense as it passed over the riparian zone, the tree ring evidence for growth releases in the years following 1939 suggest that some trees were killed. This mortality created large canopy gaps, which led to extensive recruitment of myrtle beech in the years immediately after the fire. Seedling regeneration of myrtle beech after the fire would have been restricted to the seed of lightly damaged or undamaged trees (Howard 1973). The individuals establishing most rapidly after the fire would have been coppicing from dormant epicormic buds in basal stem burls, a pattern common to Victorian populations of myrtle beech and one that often leads to distinctive multi-stemmed individuals (Howard 1973; Read & Brown 1996; Lindenmayer et al. 2000b).

The relatively small number of riparian myrtle beech establishing prior to the 1939 fire made large-scale recruitment events prior to 1939 difficult to identify. It is likely that past fires similar to the 1939 fire would have created similar opportunities for seedlings and coppice growth, and generated comparable pulses of establishment and growth release. Recruitment of myrtle beech between intense fire events would likely have occurred in the small-scale canopy gaps created regularly by individual tree falls, but at a slower rate than in areas that experienced stand-replacing fires. It is important to note that the number of remnant trees in the forest was substantially greater than the number presented here. Large myrtle beech trees with

Cool temperate rainforest and mixed forest

The many older myrtle beech and southern sassafras found in the riparian and mid-slope zones of the study site indicate that the 1939 fire did not burn through this forest type with the same intensity as it did in the tall open forest. Fires in the Central Highlands of Victoria are not uniform across the landscape and may pass over gullies with relatively little impact on the vegetation (Ashton 1981). At Bellel Creek where the 1939 fire would have moved swiftly through the crowns of the eucalypts on the upper slopes, the number of trees that survived in the riparian zone suggests that the fire jumped from the crowns of the ash on one side of the gully to those on the other side. While the fire must have been less intense as it passed over the riparian zone, the tree ring evidence for growth releases in the years following 1939 suggest that some trees were killed. This mortality created large canopy gaps, which led to extensive recruitment of myrtle beech in the years immediately after the fire. Seedling regeneration of myrtle beech after the fire would have been restricted to the seed of lightly damaged or undamaged trees (Howard 1973). The individuals establishing most rapidly after the fire would have been coppicing from dormant epicormic buds in basal stem burls, a pattern common to Victorian populations of myrtle beech and one that often leads to distinctive multi-stemmed individuals (Howard 1973; Read & Brown 1996; Lindenmayer et al. 2000b).

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Fig. 6. Ring width measurements for myrtle beech (*Nothofagus cunninghamii*) and southern sassafras (*Atherosperma moschatum*) trees showing a sharp decrease in growth, marked by a circle, after the 1939 fire. Vertical dotted line marks the 1939 fire.

complex, reiterated crown structures accounted for nearly 20% of the myrtle trees in our vegetation survey. Most of these large trees had rotten centres and could not be used for dendroecological analyses in this study; however, all such individuals that we cored and that did have solid centres were >100 years old.

Southern sassafras was the only species that did not show a pulse of recruitment after the 1939 fire. In closed forests it rarely establishes from seed owing to its low germinative capacity (Hickey et al. 1982) and its susceptibility to browsing (Read & Brown 1996). While little is known of southern sassafras’s ability to regenerate after wildfire, it is known to regenerate from basal sprouts after logging and in undisturbed forest (Read & Brown 1996). This allows it to maintain its presence in the canopy, but limits its ability to utilize canopy gaps other than by crown extension from the edge of the gap (Read & Brown 1996). Our sample of southern sassafras was limited to seven trees and, as such, any conclusions should be considered tentative. However, the uniform distribution of its establishment suggests strongly that in the relatively protected riparian environment where it is found sassafras regeneration has not been significantly influenced by fire.

Disturbance history

Fire

In the tall open forests of the Central Highlands of Victoria infrequent, high-intensity crown-killing fires dominate the disturbance regime (Ashton 1981). The 1939 fire was one of the most destructive on record in the region and hundreds of thousands of hectares of forest were impacted by the fire. In many places the fire led to complete mortality of the trees in the forest. In other cases, some or all of the canopy and mid-story trees survived. Where trees did survive, the effects of the 1939 fire were varied and in most cases short-lived. Most surviving trees recovered to their prefire growth rates within 1–3 years (Fig. 6) and many others were seemingly unaffected. We sampled sufficient numbers of old myrtle beech and southern sassafras to allow comparisons of pre- and post-fire growth rates of surviving trees of these species. Neither species showed evidence of any long-term impact on individual trees as a result of the 1939 fire. The lack of a substantial impact from the fire on these individuals is likely due to their location in the cool, moist environment in the riparian zone along Bellel Creek.

In contrast to the myrtle beech and southern sassafras, we only had a small number of tree cores from eucalypts that established prior to 1939 for comparing pre- and post-fire growth. There were only three cross-dated alpine ash cores that extended beyond 1939 and none of these showed evidence of sustained release or suppression, although, one showed a substantial decrease in growth for 1–3 years after the 1939 fire. The lack of eucalypts older than the 1939 fires and the single-age cohort of mountain and alpine ash establishing immediately after the fire suggest that, in contrast to the cool temperate rainforest in the riparian zone, most trees on the upper slopes were killed by the fire. For those trees that were able to survive in the upper slope sites, the period following the fire would have presented a local environment free of competition from neighbours. That at least some of the eucalypts survived the 1939 fire without a sustained change in growth while most of their neighbours were killed, further exemplifies the heterogeneous impacts of the 1939 fire on the forest at Bellel Creek.

Post-fire stand development patterns in the forest surrounding Bellel Creek follow the general model of single-cohort, multi-species stand dynamics described by Oliver and Larson (1996) and more specifically for mountain ash stands by Ashton (1975). These models describe the dynamic vertical stratification of forests that occurs as species with fast height growth rates quickly dominate the canopy, while slower growing, shade tolerant species are overtopped and relegated to the middle or lower strata of the forest. At Bellel Creek seedlings established synchronously after the 1939 fire, but as the forest developed the fast initial growth rates of mountain ash and alpine ash (Squire et al. 1991) enabled them to overtop slower growing competitors such as silver wattle. The ability of these eucalypt species to reach canopy dominance so early in stand development is reflected in the lack of suppression and release events in their radial growth patterns. Consequently, the primary controls on the growth of these eucalypts come from competition with neighbouring conspecific trees and subsequent disturbances such as windstorms, snowstorms or insect attacks. In contrast, silver wattle, which most likely establishes synchronously with the eucalypts, would grow in a suppressed state throughout ontogeny unless an overtopping eucalypt neighbour was killed. This would release the silver wattle from direct growth suppression, allowing it to grow more vigorously in the large canopy gap created by the mortality of the ash tree(s).

Non-fire disturbance

The lack of synchronous release or suppression among large numbers of trees at Bellel Creek suggests that non-fire disturbances in the forest have been dominated by small-scale, localized events. In the tall open forests, such disturbances often come in the form of tree or branch falls that occur during windstorms or heavy snowfalls. Formation of small canopy gaps between larger-scale disturbances may also be a

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natural consequence of the mortality associated with forest development (Ashton 2000). As an even-aged stand develops, trees self-prune and stands self-thin. Self-pruning occurs as branches that become increasingly shaded as the forest canopy grows in height, begin to die and fall to the ground. Self-thinning occurs as individual trees that have been outcompeted, die and fall. In mountain ash forests of the Central Highlands Lindenmayer et al. (1997) observed >1000 large hollow-bearing eucalypt trees over a 10-year period. They found an annual collapse rate of approximately 3–4% among these trees. At Bellel Creek the abundance of large logs on the forest floor indicated that such small-scale disturbance events were quite common. The fall of a fully grown mountain ash (>60 m) would create a large-gap in the canopy and damage or destroy any mid-story trees below it. The great height of the mountain ash and alpine ash trees means that the damage created by their falling may extend well beyond the tall open forest into the cool temperate and mixed species forests. This would create opportunities for growth release among individuals experiencing higher light levels along the gap edge, as well as growth suppression for those individuals damaged by the falling tree.

The tree ring data demonstrate that small-scale canopy gap formation has occurred at a consistently low level for at least 100 years. The sole exceptions to this pattern are the peaks in moderate releases of myrtle beech in the 1970s and southern sassafras in the 1980s (Fig. 5), suggesting the occurrence of a widespread, but low-intensity disturbance, in these forests. In 1977 a particularly heavy snowfall caused extensive damage to forests at Wallaby Creek in the Central Highlands of Victoria (Ashton 2000). It is possible that this same snowstorm caused heavy snow-laden eucalypt branches to break and fall into the forest canopy of the riparian zone at Bellel Creek, which is at higher elevation than Wallaby Creek and receives more snowfall. The thinning of the upper canopy by heavy snow loads would have increased subcanopy light levels, which may have benefited trees undamaged by the snowstorm and led to moderate growth releases.

CONCLUSIONS

High intensity crown fires are the dominant disturbance type in the tall open forests of the Central Highlands of Victoria. However, the impacts of such fires vary across the landscape and are not uniformly destructive. In such topographically diverse areas, site conditions are variable over small spatial scales, leading to variation in forest structure and composition, and in local fire conditions. As a consequence, the intensity of the fire and its impacts on the forest are heterogeneous within the landscape. This heterogeneity may generate multiple age cohorts of canopy trees and distinct changes in forest structure over small spatial scales — structures that may have significant conservation values in the aftermath of large, landscape-scale fires. Dendroecological studies can provide important insights into the historical dynamics of forests and disturbances that influence them. Our study has demonstrated the utility of dendroecology in providing high-resolution age and growth data from Australian forests to better understand long-term forest stand dynamics and the consequences of disturbances on forest development. More specifically, we have shown that myrtle beech, southern sassafras, silver wattle and alpine ash are particularly well suited to dendroecological studies in the Central Highlands. Further dendroecological studies in Australia should provide valuable insights into the dynamics of many of Australia’s unique forest ecosystems and provide a strong foundation for developing conservation and management strategies for them.

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REFERENCES


