Eucalyptus regnans (Myrtaceae): A fire-sensitive eucalypt with a resproouter epicormic structure

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Determining the location of buds and bud-forming meristems and hence the level of protection from heat is essential to understanding plant response to fire. Most eucalypts resprout readily from the stem (epicormic resprouting) and the base after felling or high intensity fire. In contrast, Eucalyptus regnans is one of the few eastern Australian fire-sensitive, obligate seeder eucalypts. Some authors have suggested that the relatively weak epicormic resprouting is due to a lack of bud-forming structures. Epicormic strands from the bark and outer xylem of three very large trees and two saplings were examined anatomically. Epicormic bud-forming structures were found in all samples examined. The bud-forming capacity consisted of narrow, radially elongated strips of cells of meristematic appearance. These strips were continuous from the outermost secondary xylem through to the outer bark. Bark was relatively thick at the base of the large trees, but remarkably thin above this basal skirt. Eucalyptus regnans was found to possess the apparently fire-adapted epicormic strands previously described in other eucalypts, thus showing its fire-adapted lineage. However, this fire-sensitive species apparently directs much of its resources to rapid height-growth rates in younger trees, rather than to vegetative fire survival.

Key words: accessory meristems; epicormic; eucalypts; Eucalyptus regnans; fire; leaf axil; meristematic; mountain ash; Myrtaceae; resprouting.

Understanding how plants regenerate after fire depends on establishing what tissues are killed by the heat of a fire. In this respect, the most important tissues are probably the vascular cambium and the various buds (apical, axillary, epicormic, lignotuber). While the protection given to the vascular cambium by various thicknesses and types of bark has received considerable research attention (e.g., Gill and Ashton, 1968; Jones et al., 2006), the effect of heat on buds has received less attention. In general terms, this study is intended to show the importance of determining the location of bud meristems or bud-forming tissues and hence the degree of protection provided from the heat of a fire. This is just as important in rhizomatous grasses (e.g., Choczynska and Johnson, 2009), northern hemisphere conifers and angiosperms (e.g., Hanson and North, 2009; Peter et al., 2009) or, the subject of this study, a southern hemisphere hardwood species, Eucalyptus regnans.

Plant species are generally divided into resproouter (regenerating from buds on existing plants) or seeder (recruiting new individuals from a seed bank) categories based on their postfire response, with the resproouters further divided into basal (from buds at or just below soil level) or epicormic (from dormant buds on aboveground branches and stems) categories. Epicormic shoots are generally considered to originate from buds on woody stems, not from terminal buds or the axillary buds of leafy shoots. In woody plants, basal resproouting after disturbance from a lignotuber or the root collar is very common (Del Tredici, 2001). In contrast, epicormic resprouting, after moderate or high intensity fire, is very rare (e.g., Pausas, 1997; Burrows, 2008). In fire-prone environments, resprouting is generally considered the ancestral trait, with the obligate seeder strategy an evolved characteristic (Bond and van Wilgen, 1996; Lloret et al., 1999; Bond and Midgley, 2003; Vesk and Westoby, 2004).

While postfire epicormic sprouting is rare, the eucalypts (species of Angophora, Corymbia, and Eucalyptus) are regarded as excellent epicormic resproouters (Florence, 1996; Gill, 1997; Wardell-Johnson, 2000; Burrows, 2002). This epicormic capability could provide a competitive advantage over basal resproouters and seeders through the rapid re-establishment of a large, elevated photosynthetic area (Hodgkinson, 1998; Burrows, 2008). Epicormic resprouting of eucalypts after intense fire has been associated with specialized meristem structures in woody stems (Jacobs, 1955; Burrows, 2000, 2002, 2008). A wide diversity of eucalypt species have epicormic strands with bud-forming potential across the full thickness of the bark and even in the outer wood (Burrows, 2000, 2002). With this unusual epicormic structure, at least the innermost cells of the epicormic meristem strips, located close to the vascular cambium, can be protected from the heat of a fire by the total bark thickness.

Less than 10% of the more than 900 eucalypt taxa have been classified as obligate seeders (a lignotuber is absent, and no vegetative regrowth follows crown destruction by fire) (Nicolle, 2006). Most of these are smaller Western Australian species that have a relatively short life-span due to the absence of a lignotuber and the high intensity fire regime of their habitats, but about 10 taller eastern Australian species, including E. regnans, are also regarded as obligate seeders (Nicolle, 2006).

Eucalyptus regnans F. Muell., in the subgenus Eucalyptus (Brooker, 2000), is often given the title of the world’s tallest flowering plant and may attain heights of up to 100 m and reach 350 to 400 years of age (Ashton, 1981a; Banks, 1993; Gill, 1993).
It is an important component of the tall open forests (wet sclerophyll forests) in the mountainous areas of Tasmania and Victoria and is highly valued for its timber and used in construction and for furniture and wood pulp (Squire et al., 1991). It is one of the small percentage of eucalypts that are reported not to produce a lignotuber (Nicolle, 2006). Within the eucalypts, it is regarded as a weak resprouter, both basally and epicormically, both after high intensity fire and after being felled in forestry operations (Cremer, 1962; Ashton, 1981a; Gill, 1997). Favorable environmental conditions of high, reliable rainfall (Cremer, 1962; Ashton, 1981a; Gill, 1997) are a strong indication of the subsequent epicormic potential. Our anatomical examination of the epicormic structure of mature E. regnans saplings 5–6 yr old, there has been no anatomical examination of the epicormic structure of mature E. regnans. In this study, we describe the regenerative structures in the medium- and large-diameter stems of E. regnans. It is known that epicormic strands originate from axillary buds on leafy shoots (Jacobs, 1955; Cremer, 1972). Therefore, we also examined leaf axil structure to provide an indication of the subsequent epicormic potential. Our anatomical analysis was used to determine whether the epicormic structures were of the eucalypt fire-adapted type (e.g., Burrows, 2000, 2002), the “typical” surface-level buds of either seeders or basal resprouter species (e.g., Fink, 1983 and 1999) or were completely absent.

**MATERIALS AND METHODS**

Samples were primarily collected from three E. regnans trees in a lowland (400 m above sea level) forest in the Powelltown area of Victoria, 90 km east of Melbourne. Samples were also obtained from two E. regnans saplings in a wet sclerophyll forest in southern Tasmania. The Victorian forest was part of the fire regeneration after Black Friday on 13 January 1939, and the 67-yr-old (when sampled) trees ranged from 50 to 60 m tall. Sampling included leaf axils from the upper canopy, and epicormic structures from two zones: on the main trunk at the base of the smooth bark (50–70 cm diameter, just above the basal skirt of rough bark), and from branches (~10 cm diameter) in the canopy of each tree. The leaf axils were collected from small-diameter branchlets in the upper canopy and included material with both intact and abscised primary axillary buds (naked buds) (Fig. 1). They are termed naked because bud scales are not present, while the first-formed (outermost) leaf primordia can expand and develop into photosynthetic leaves. Tree diameter at the sample zones and at 1.5 m above ground, bark thickness at the sample zones and at 1.5 m above ground, and height of the basal skirt of rough bark were measured (Table 1). For the Tasmanian trees, only epicormic samples were collected, and these came from stems with diameters of 7 cm and 15 cm, and a bark thickness of 2–3 mm. Eight replicates were cut from each of the three sample zones on the Victorian trees and the single sampling zone of the Tasmanian trees.

Locating the epicormic structures on the branches and trunk was relatively difficult, but they were usually visible on the surface of the smooth, pale gray bark as small protrusions or depressions (Fig. 2A, C) and were excised with some supporting bark tissues. Small protrusions were often observed projecting from the cambial surface of the wood once the bark tissues were excised (Fig. 2B, D). These “wood spikes” were a clear indicator of an epicormic strand, with a corresponding depression in the back of the bark, and they were sampled by cutting into the wood to a depth of 3–4 mm.

In general terms, the accessory buds and meristems in a eucalypt leaf axil will give rise to a single epicormic strand (Cremer, 1972). This strand would have a radial orientation in the stem or branch, would extend from the outer pith to the bark surface and would be several millimeters in height and width. An epicormic strand may be divided into several substrands (Fig. 2A, B), but together the substrands would be considered a single strand. Each strand (or sub-strand) may have several meristem strips embedded within it (Burrows, 2002). These meristem strips also have a radial orientation but have a much smaller height and width than the strand and are usually only present in that part of the strand embedded in the outermost xylem and the bark.

It was not possible to locate epicormic structures in the basal skirt of rough bark of the Victorian trees. As noted, it was difficult to locate the small surface irregularities of the strands even on the smooth bark and impossible on the rough bark. In this situation, it is sometimes possible to peel away the bark in a single sheet to the level of the cambium, then look for the strands as irregularities on the cambial side of the bark (Burrows, 2002, 2008). Unfortunately, at the time the sampling was conducted (to coincide with commercial logging operations), the rough basal bark was not “slipping” freely, and this technique could not be employed.

At least four leaf axils from each Victorian tree were examined in radial longitudinal section (RLS). The bark epicormic strands were sectioned in transverse and longitudinal section, while transverse sections (TS) were made of the wood spikes. It should be noted that a TS of an epicormic strand was a tangential longitudinal section (TLS) of the stem or branch. A RLS of a stem also produced a RLS of the epicormic strand, while a TS of a stem also produced a longitudinal section of the strand. At least four (and as many as eight) epicormic strands were sectioned from both the trunk and branch sampling locations of the three Victorian trees, and the stem sampling location of the two Tasmanian saplings.

Material was fixed in FAA (5% formalin : 5% acetic acid : 90% ethanol (50%)) dehydrated through a graded ethanol series and infiltrated with Leica Historesin (Leica Microsystems, Heidelberg, Germany) under a slight vacuum for a minimum of 7 d. The samples were placed in pharmaceutical gelatin capsules containing Historesin and polymerized overnight at 60°C. They were then sectioned at 5 µm using tungsten-carbide-tipped steel blades fitted to a motorized retraction microtome (Leica RM 2265). Sections were stained with 0.5% toluidine blue and observed with bright field microscopy.

**RESULTS**

**Leaf axils**—The E. regnans trees had alternate lanceolate leaves with blades that were approximately 15–30 mm wide and 100–200 mm long and petioles up to 50 mm long. Initially, all the E. regnans leaf axils would have possessed a naked bud (Fig. 1A). Some of these developed into a branch (Fig. 1B), but the naked buds had abscised in most of the leaf axils collected (Fig. 1C), and externally, the leaf axil appeared to have no remaining regenerative potential (Fig. 1C). In the small percentage of leaf axils with intact naked buds, an accessory bud was found on the petiole (abaxial) side of the naked bud (Fig. 3A, B). A primary accessory bud usually consisted of an apical dome and a pair of leaf primordia and ranged from 75 to 150 µm in height. A secondary accessory bud was usually located on the abaxial side of the primary accessory bud (Fig. 3B) and consisted of a small mound of tissue of meristematic appearance. In the leaf axils where the naked bud had abscised, a well-developed primary accessory bud was located on the abaxial side of the naked bud scar (Figs. 3C–F). These buds consisted of an apical meristem with several leaf primordia arched over the apical dome (Fig. 3D), and the buds ranged from 350–550 µm high. Less-developed secondary accessory meristems were present at the base of the first accessory bud (Fig. 3D, F), usually on the petiole side. Most axils had only one secondary accessory meristem,
observations of the strands at the bark and cambial surfaces (Fig. 2A, B). The epicormic strands consisted of a matrix of mainly parenchymatous cells, many with darkly staining phenolic compounds (Figs. 4A, 6A), in which were embedded radial strips of cells that were considered to possess a meristematic appearance because they were small, isodiametric, compactly arranged, and thin-walled, with large nuclei and dense cytoplasm (e.g., Figs. 4C, 5B, 6C). In TS, the meristem strips generally appeared as small domes 100–200 µm wide and 25–100 µm high (e.g., Figs. 5A, B, 6B–D), with their outer surfaces varying in shape from convex to concave (Fig. 5B, 6D) and always adjacent to narrow lacunae. Within the strands of the large-diameter stems, there were usually 6–15 meristem strips. The radially elongated structure of the strips was best observed in RLS, with the strips usually continuous from the innermost bark, and even the outer xylem, to the outer bark (Fig. 4A). Few distinct buds were observed (Fig. 5D). Other structures, which appeared to be leaf primordia, because they were more lobed than a typical meristem strip, were more commonly present (Figs. 5A, B, 6B–D), with their outer surfaces varying in shape from convex to concave (Figs. 5B, 6D) and always adjacent to narrow lacunae. Within the strands of the large-diameter stems, there were usually 6–15 meristem strips. The radially elongated structure of the strips was best observed in RLS, with the strips usually continuous from the innermost bark, and even the outer xylem, to the outer bark (Fig. 4A). Few distinct buds were observed (Fig. 5D). Other structures, which appeared to be leaf primordia, because they were more lobed than a typical meristem strip, were more commonly present (Figs. 5B, 6B). In the smaller-diameter branches, the epicormic strands were generally slightly smaller in TS (0.5–1.0 mm wide and 1.0–2.0 mm high) and with fewer meristem strips (2–7).

Although a few had secondary accessory meristems on both sides of the primary accessory bud (Fig. 3D).

The accessory buds were usually located approximately 150–700 µm in from or below the externally visible base of the axil (Fig. 3C, E). In all axils, an axillary pocket (a crack or slit extending down from the externally visible base of the leaf axil) was visible and extended part or, in most cases, all the way from the apparent base of the axil to the primary accessory bud (Fig. 3). The axillary pockets and accessory buds and meristems were not externally visible (Figs. 1A–C).

Epicormic strands in the bark—In general, the epicormic structures in the smaller (7, 10, and 15 cm diameter) and larger (50–70 cm diameter) stems were very similar (Figs. 4–6). The strands from the larger stems were approximately elliptical (1.0–3.0 mm wide and 2.0–4.0 mm high) in transverse section (Figs. 2B, D, 6A) and clearly distinct from the surrounding bark tissue. Most strands were divided into two substrands with typical bark tissue in between, correlating with the macroscopic observations of the strands at the bark and cambial surfaces (Fig. 2A, B). The epicormic strands consisted of a matrix of mainly parenchymatous cells, many with darkly staining phenolic compounds (Figs. 4A, 6A), in which were embedded radial strips of cells that were considered to possess a meristematic appearance because they were small, isodiametric, compactly arranged, and thin-walled, with large nuclei and dense cytoplasm (e.g., Figs. 4C, 5B, 6C). In TS, the meristem strips generally appeared as small domes 100–200 µm wide and 25–100 µm high (e.g., Figs. 5A, B, 6B–D), with their outer surfaces varying in shape from convex to concave (Figs. 5B, 6D) and always adjacent to narrow lacunae. Within the strands of the large-diameter stems, there were usually 6–15 meristem strips. The radially elongated structure of the strips was best observed in RLS, with the strips usually continuous from the innermost bark, and even the outer xylem, to the outer bark (Fig. 4A). Few distinct buds were observed (Fig. 5D). Other structures, which appeared to be leaf primordia, because they were more lobed than a typical meristem strip, were more commonly present (Figs. 5B, 6B). In the smaller-diameter branches, the epicormic strands were generally slightly smaller in TS (0.5–1.0 mm wide and 1.0–2.0 mm high) and with fewer meristem strips (2–7).

When viewed in TS, a meristem strip was often associated with a roughly circular structure (e.g., Fig. 6A, B, D) that formed from the differentiation of procambial strands at the flanks of the meristem strips. Occasionally the procambium differentiated into a cambium that produced a limited amount of secondary phloem to the outside, and some secondary xylem (mainly fibers and parenchyma) to the inside (Fig. 6A, B, D). These structures become very small-diameter vascular cylinders that are perpendicular to the stem they were formed within.
is essential to understand how plants will respond to fires of differing intensities. This approach is applicable to plants of widely differing growth forms and taxonomy. For example, in a study of postfire regeneration of three species of American rhizomatous grasses Choczynska and Johnson (2009) emphasized the importance of knowing the shapes of belowground bud distribution. Understanding epicormic resprouting requires a knowledge of aboveground bud distribution and protection. Given their taxonomic differences, some European (Fernandes et al., 2008) and North American pines (Hanson and North, 2009) share some similar fire responses with E. regnans. These trees are usually killed by crown fire, but E. regnans and some of these pines may flush or produce epicormic buds after crown scorch from lower intensity fires. They also share some morphological similarities. The bark at the base of the bole of at least some of these trees is proportionally thicker than higher up (Fernandes et al., 2008), and in tall trees there is generally a greater degree of physical separation between a surface fire and the crown. The main difference occurs in bud structure. In the pines, a higher resprouting capacity appears to be associated with large buds that possess numerous overlapping scales (Fernandes et al., 2008) (see also Peter et al., 2009), while in E. regnans at least some of the cells that produce epicormic shoots are protected by a 3–7 mm thick layer of bark.

Most eucalypt species are excellent resprouters, either epicormic and/or basal, after fire or other disturbance (e.g., Jacobs, 1955; Benson and McDougall, 1998; Wardell-Johnson, 2000). However, a small percentage of species, including E. regnans, are considered to have a relatively weak vegetative regenerative capacity, either after intense fire (Ashton, 1981a) or after being cut down (Cremer, 1973) and are classified as obligate seeders (Nicolle, 2006). This weak resprouting capacity has led some to suggest that E. regnans has no buds in the stems or in specific parts of the stems (Cremer, 1973; Mackey et al., 2002). The results of the current study demonstrate that, while it is considered an obligate seeder, E. regnans has the typical (for a eucalypt) complex array of naked and accessory buds in the leaf axils, and the typical eucalypt, fire-adapted epicormic structure of multiple meristem strips in the inner bark and outermost wood. However, as discussed later, bark thickness may be critical to an individual’s survival and resprouting success after fire.

DISCUSSION

Determining the location of buds and bud-forming meristems is essential to understand how plants will respond to fires of differing intensities. This approach is applicable to plants of widely differing growth forms and taxonomy. For example, in a study of postfire regeneration of three species of American rhizomatous grasses Choczynska and Johnson (2009) emphasized the importance of knowing the shapes of belowground bud distribution. Understanding epicormic resprouting requires a knowledge of aboveground bud distribution and protection. Given their taxonomic differences, some European (Fernandes et al., 2008) and North American pines (Hanson and North, 2009) share some similar fire responses with E. regnans. These trees are usually killed by crown fire, but E. regnans and some of these pines may flush or produce epicormic buds after crown scorch from lower intensity fires. They also share some morphological similarities. The bark at the base of the bole of at least some of these trees is proportionally thicker than higher up (Fernandes et al., 2008), and in tall trees there is generally a greater degree of physical separation between a surface fire and the crown. The main difference occurs in bud structure. In the pines, a higher resprouting capacity appears to be associated with large buds that possess numerous overlapping scales (Fernandes et al., 2008) (see also Peter et al., 2009), while in E. regnans at least some of the cells that produce epicormic shoots are protected by a 3–7 mm thick layer of bark.

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Fig. 3. Radial longitudinal sections of leaf axils from the crown of 67-yr-old *Eucalyptus regnans* trees. (A) Axil with a young branch (b) and accessory bud on its abaxial side (arrow). Scale bar = 1000 µm. (B) Detail of (A) showing the narrow groove or slit that extends down to the accessory bud, with an additional meristem at its base (arrowed). Scale bar = 500 µm. (C) Axil showing the scar of the abscised naked bud (short arrow) and the accessory bud (long arrow) located about 700 µm in from the surface of the axil. Scale bar = 1000 µm. (D) Detail of the axil shown in (C). Note the narrow groove above the accessory bud and the two smaller meristems (arrowed) at the base of the accessory bud. Scale bar = 500 µm. (E, F) Similar to (C) and (D) but from a different tree. Scale bars = 1000 and 200 µm, respectively.
Fig. 4. Longitudinal sections of the epicormic strands of *Eucalyptus regnans*. (A) and (B) are from a 50-cm diameter stem and (C) is from a 10-cm diameter stem. (A) Radial longitudinal section of the outer part of the epicormic strand in the bark, with the right hand side adjacent to the cambial surface. Two meristem strips are arrowed at the top of the image. Several other meristem strips are partially shown below these two. Scale bar = 2000 µm. (B) Detail of a meristem strip (arrowed) from similar material to that shown in (A). Scale bar = 200 µm. (C) Longitudinal section of the strand but a transverse section of the tree (see the fibers and small diameter vessel elements in the top half of the image). This image is of the outermost wood where the parenchymatous part of the epicormic strand extends into the wood for a short distance (see Fig. 2B, D). Note the meristem strip (arrowed) with its surface layer and adja-}
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Accessory bud usually develops into a dome of tissue up to 1 mm high, often with several leaf primordia (Cremer, 1972; Burrows, 2000). The primary accessory bud in the leaf axils of *E. regnans* was comparatively smaller (up to 350 µm), but of similar structural development and position within the leaf axil. Several species of Northern Territory eucalypts appear to have more deeply buried and complex accessory buds than *E. regnans*, and in about half of these species accessory buds were found both abaxial and adaxial to the naked bud or its scar (Burrows et al., 2008).

(Fig. 1C), but all investigated eucalypt species had an array of "buried" accessory buds. Thus, descriptions of eucalypt leaf axil structure have mainly concentrated on the "concealed" accessory buds (Chattaway, 1958; Cremer, 1972; Burrows, 2000; Burrows et al., 2008), which are usually located between the naked bud (or its scar) and the leaf petiole (abaxial or lower side of the naked bud). These buds are mostly exogenous (of surface origin), with a narrow slit (the axillary pocket) of epidermal origin that links the surface of the axil with the accessory bud. The first-formed accessory bud usually develops into a dome of tissue up to 1 mm high, often with several leaf primordia (Cremer, 1972; Burrows, 2000). The primary accessory bud in the leaf axils of *E. regnans* was comparatively smaller (up to 350 µm), but of similar structural development and position within the leaf axil. Several species of Northern Territory eucalypts appear to have more deeply buried and complex accessory buds than *E. regnans*, and in about half of these species accessory buds were found both abaxial and adaxial to the naked bud or its scar (Burrows et al., 2008).
Fig. 6. Transverse sections of the epicormic strands of *Eucalyptus regnans* (tangential longitudinal sections of the stem). These sections were from near the base (diameter 50–70 cm) of all three Victorian trees. All sections were of strands in the innermost bark or surrounded by the outermost xylem. (A) This image shows a whole epicormic strand. Note its narrow elliptical shape and about eight meristem strips (arrowed). Scale = 500 µm. (B) Part of an epicormic strand within the uppermost region of the basal skirt of rough bark, showing five well-developed meristem strips, with one showing evidence of development into a bud primordium (arrowed). Scale = 200 µm. (C) Detail of a meristem strip showing the small, compactly arranged cells and large nuclei of the meristem, the lacuna at the meristem’s surface and the procambial development on the flanks of the meristem. Scale = 100 µm. (D) Two meristem strips (arrowed), both with associated procambial development. In the lower example, the procambial cells make an almost complete circle. Scale = 200 µm.

Many plants worldwide possess leaf axils with only a single well-developed axillary bud, and this bud is usually long-lived and externally visible in the axil (Evert, 2006). Accessory buds have been found in anatomical studies of other species in the Myrtaceae (Carey, 1931; Shah and Unnikrishnan, 1969; Burrows, 2008; Burrows et al., 2008), but not in some mor-
phological studies (Lee and Rao, 1984). Accessory buds have also been found in a wide range of other families (Bell et al., 1999; Fink 1999). Eucalypt leaf axils appear to be unique as the naked bud is delicate, unprotected and usually abscises shortly after formation, while the accessory buds are long-lived and buried relatively deeply within the axillary tissues. This study has shown that *E. regnans* has a plentiful reserve of axillary buds and meristems, which allow trees to recover from minor canopy damage.

The developmental progression from axillary buds and meristems to preventious epicormic buds and strands is well established for eucalypts (e.g., Jacobs, 1955; Cremer, 1972; Burrows, 2000) and many other tree species (e.g., Fink, 1999). However, the anatomical steps in this progression are poorly understood. In the eucalypts, the change from accessory buds in a leaf axil to radially elongated meristem strips in the bark appears particularly complex and has not been described. Likewise, the way the epicormic strand integrates with the vascular cambium, leaving an epicormic trace in the secondary xylem, should be investigated.

**Epicormic strands in the bark**—The first detailed examination of epicormic structure of any eucalypt was by Cremer (1972), who examined “intermediate accessory buds” from 4–6 cm diameter stems of 5–6-yr-old *E. regnans* saplings. While a clear picture was not obtained (only five samples were examined), he noted that the epicormic structure in the stem exhibited a greatly reduced complexity compared with that of the leaf axils. He described the persistence of “primitive” but distinct buds embedded within the bark, which is consistent with the small-diameter branch epicormic structures described by Baranova (1960) in *E. calophylla* and *E. cinerea*. Burrows (2000) described the epicormic strand structure in the bark of small-diameter stems (0.5–4.5 cm) of *E. cladocalyx*. He noted the presence of 2–4 buds with limited vascular development in the mid to outer bark. To the rear of these buds was a largely parenchymatous epicormic strand containing 3–13 strips of radially orientated meristem tissue that traversed the inner to mid bark. Strips of cells of meristematic appearance were the main feature of the small-diameter branches in this study, but buds were still present in some samples. The descriptions from this and previous studies suggest that the epicormic structure of small-diameter eucalypt stems are in transition from axillary buds and meristems to fully developed epicormic strands. The epicormic strand structure in the large-diameter stems of *E. regnans* was very similar to that described by Cremer (1972) and Burrows (2000, 2002, 2008) for other species in the Myrtaceae. The *E. regnans* strands were generally smaller in height and width but similarly shaped in TS, contained similar numbers of meristem strips, and the meristem strips were similar in structure (radially elongated with a narrow lacuna adjoining the surface of the meristem). This study and that of Burrows (2002) describe the division of the strands into substrands, separated by normal bark tissue. A circular to elliptically shaped ring of procambial tissues described in previous studies was also observed. Burrows (2002) noted the progressive simplification of the strand structure across the bark, compared to a more constant structure from inner to outer bark in this study and Cremer (1972). Burrows (2002) also noted the presence of bud primordia in some samples of some species, in positions ranging from the inner to outer bark. Bud primordia were occasionally noted in this study, but were not recorded for the epicormic strands of the large-diameter stems of *E. viminalis* (Cremer, 1972).

Given the range in morphological (e.g., bark types ranged from gum, stringy, iron-bark), geographical, and taxonomic diversity of the eucalypts examined in the above studies (Cremer, 1972; Burrows, 2000, 2002), as well as in this study of *E. regnans*, there is a remarkable consistency in eucalypt epicormic structure.

**Epicormic strands in the outer wood**—Anatomical observations of bud-forming tissues in epicormic strands in the wood, rather than bark, of eucalypts have been recorded in only two other studies (Burrows, 2000, 2002). Burrows noted that the strands had the greatest number of meristem strips close to the cambial level, and there was an overall reduction in strand size (in terms of nonlignified cells) and number of meristem strips as the strand was followed a few millimeters toward the pith from the level of the cambium. *Eucalyptus regnans* was similar, in that the meristem strips reduced in size and complexity as they progressed several millimeters toward the pith. There was an associated increase in thick-walled, lignified cells, but some tissue of meristematic appearance was still observable 3 mm into the wood. The presence of tissues of meristematic appearance in the outer wood of *E. cladocalyx* (Burrows, 2000), in *E. nicholii* (Burrows, 2002) and *E. regnans* in this study provides substantive evidence for the eucalypts’ ability to resprout from bare wood. Jacobs (1955) documented and illustrated this remarkable phenomenon, and the presence of tissues with the potential to produce buds within the outer secondary xylem has only been recorded for two other genera (*Syncarpia* and *Tristaniopsis*), also members of the Myrtaceae (Burrows, 2008).

**Fire**—Burrows (2002, 2008) has indicated that radially orientated meristem strips extending across all or most of the bark is a type of epicormic structure that has not been recorded outside the Myrtaceae. The advantage of this type of epicormic structure is that at least some of the bud-forming cells are protected from the heat of a fire by the total bark thickness. Epicormic resprouting after fire could provide a competitive advantage compared to basal resprouters and seeders through the rapid re-establishment of leaf area over the full extent of the stem and branches, with more efficient sunlight interception and the consequent shading of competitors (Hodgkinson, 1998; Burrows, 2008; Dietze and Clark, 2008).

While high-intensity canopy fires are generally regarded as fatal to *E. regnans*, recent studies of the ecology of *E. regnans* forests have found that the existence of multiaged stands is more common than previously thought (McCarthy and Lindenmayer, 1998; Lindenmayer et al., 2000; Simkin and Baker, 2008). Cremer (1962) noted that many *E. regnans* trees resprouted epicormically after complete defoliation caused by fire. It has also been reported that a majority of *E. regnans* trees survived in 70% of the area affected by the 1983 Ash Wednesday fires in Victoria (Squire et al., 1991), and some mature *E. regnans* trees have survived and recovered from several fires (McCarthy and Lindenmayer, 1998). While the variation in fire intensity is probably a factor behind the survival of some *E. regnans* stands (Simkin and Baker, 2008), the recovery of some older trees from fire would suggest that the resprouting ability of this species persists with age and that the bark of mature-aged trees (>100 yr old) can sometimes provide adequate insulation against certain fires. This last point and the existence of the *E. regnans* epicormic strand structure described in this study counter the claim made by Cremer...
found that for E. oreades, another of the eastern Australian obligate seeder species, basal bark thickness in trees with a basal diameter of about 100 cm was ~30–40 mm (Table 2), but was only ~6 mm thick at 7 m above the ground.

The nine eastern Australian obligate seeder eucalypt taxa share some interesting features (Nicolle, 2006). All are members of Eucalyptus subgenus Eucalyptus (a group of more than 120 taxa), all are trees (no mallee or mallet growth forms), none have a lignotuber, all occur in higher rainfall zones, and most have a basal skirt of rough, thicker bark. On the basis of several lines of evidence, Nicolle (2006) considers that the obligate seeder regeneration strategy is likely to be derived for the relatively numerous western species, but ancestral and relicual in the eastern species.

It was unfortunate that epicormic strand structure could not be sampled in the rough basal bark of E. regnans. Nevertheless, confirming the presence or absence of bud-forming tissues in this region does not preclude our understanding the anatomical aspects of the species’ fire ecology. In the typical stand-replacing (crown) fires the fire intensity is so high that all of the aboveground vascular cambium is killed. With no lignotuber, the trees are killed, and no resprouting occurs. In lower intensity fires, the basal skirt can afford the lower vascular cambium sufficient protection from direct fire contact. A pulse of hot air will cause leaf scorch but not death of the epicormic meristems in the inner bark. In this case, the tree may resprout from its upper half (Cremer, 1962).

**Age and resprouting**—Cremer (1973, p. 21) noted the lack of shoots on coppiced 15- and 30-yr-old E. regnans may have been related to a “lack of potential buds”. Several authors have noted a decline in resprouting ability as plants age or in large-diameter stems, both in natural systems (Bellingham and Sparrow, 2000; Barton, 2005; Dietze and Clark, 2008) and after coppicing (Blake, 1983; Del Tredici, 2001). The reasons for this decrease are not well known, but are generally suggested to be related to genetic, physiological, and/or anatomical reasons (Del Tredici, 2001). The anatomical reasons are not well researched, but it appears the buds may senesce over time (Fontaine et al., 2001; Vesk, 2006), be overgrown by secondary xylem (Mohamed and Gimingham, 1970; Hobbs and Mooney, 1985), be cut off by initial bark formation (Fink, 1984), or be overgrown by bark (Gill and Tomlinson, 1971; Vesk, 2006). Interestingly, Verdaguer and Ojeda (2005) noted atrophied buds in the cotyledonal axils of a seeder Erica species. It has also been suggested that the buds can be viable, but they do not form a functioning connection with the vascular system of the supporting branch or trunk (Del Tredici, 2001).

**Conclusions**—In summary, in fire-prone environments, resprouting is often considered the ancestral trait, with reseeding a more recent characteristic. Although E. regnans possesses the typical fire-adapted eucalypt epicormic structure, its rapid height growth, especially in younger trees, at the expense of increasing bark thickness generates insufficient protection over much of the tree for the cambium and epicormic meristems in higher intensity fires. In short, E. regnans is in most situations an obligate seeder eucalypt, but shows its fire-adapted lineage through its epicormic structure. Future research on this topic should concentrate on elucidating the progression from accessory buds to epicormic strands and the structure of epicormic strands in the basal skirt of thick bark and measuring changes in bark thickness over time for the full tree height.

<table>
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<tr>
<th>Reference</th>
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<th>Bark thickness (cm) at BH</th>
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LITERATURE CITED


