Eucalypt naked buds – expansion or abscission?

A comment on Schoonderwoerd & Friedman (2021) ‘Naked resting bud morphologies and their taxonomic and geographic distributions in temperate, woody floras’

In a recent issue of New Phytologist, Schoonderwoerd & Friedman (2021) indicated that woody angiosperms with naked buds (buds that lack cataphylls) that can survive freezing temperatures are more common than was previously thought. A commentary on this paper titled ‘... we really don’t know [buds] at all …’ was also published in the same issue (Jones, 2021).

Naked buds in temperate areas (i.e. exposed to freezing temperatures) were found in at least 87 genera in 42 angiosperm families (Schoonderwoerd & Friedman, 2021). Included in these 87 genera was Eucalyptus (Myrtaceae). The eucalypts are composed of c. 800 species, in three closely related genera, Angophora, Corymbia and Eucalyptus (González-Orozco et al., 2014). Probably all eucalypts have naked buds (e.g. Jacobs, 1955; Chattaway, 1958a; Cremer, 1972; Burrows, 2013), but before considering how the buds of this group were classified by Schoonderwoerd & Friedman, the structure and function of these axillary buds needs to be reviewed.

There are three main features of these buds. First, the buds do not look particularly bud-like. Before expanding into a shoot, they consist of a very slender structure with very few leaf

Fig. 1 Shoot system of Eucalyptus cladocalyx. (a) Shoot system showing older mature leaves (from the stem in the top half of the image) and recently initiated leaves below. Note the naked buds (small arrows) and where the naked buds (large arrows) have abscised. The asterisk indicates where a naked bud had developed into a branch but was removed to make the scan clearer. The scale shown is in mm. (b) Recently formed leaf axil with a naked bud (nb) consisting of a proximal stem (st) and distal leaf primordia (lp) that surround the shoot apical meristem. p, petiole; s, stem of main shoot. Bar, 1000 µm. (c) Older leaf axil. Note the scar created from the abscission of the naked bud (large arrow). The smaller arrow indicates where the accessory buds would emerge. Bar, 1000 µm.

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primordia (see Cremer, 1972 and Figs 1–3). The shoot apical meristem is located at the tip of an elongated stem (Fig. 1b), thus the meristem receives no protection from the base of the petiole, as occurs in some Myrtaceae genera (Burrows et al., 2008). Second, under favourable conditions the naked buds can allow for rapid expansion of the shoot system (see the large arrow in Fig. 2a); however, nearly all naked buds are abscised shortly after formation (Jacobs, 1955; Chattaway, 1958a; Cremer, 1972; Carr, 1998; Burrows, 2013). This leaves a circular scar in the leaf axil (Figs 1c, 2c,d, 3b,f). For example, Chattaway (1958a) examined the leaf nodes of 44 eucalypt species and recorded that naked buds occurred in every axil, but most were shed in the first hot dry spell. Third, while many plant species have only a single bud in a leaf axil, the eucalypts have additional buds (accessory buds) at the base of the naked bud. After naked bud abscission, it appears externally that the axil no longer possesses any regeneration potential, but these well-protected accessory buds and meristems (Fig. 2d; Burrows, 2000: figs 2–5, 2013: fig. 3; Burrows et al., 2008: figs 1–4; Waters et al., 2010: figs 1, 3) allow regeneration after minor damage (e.g. fire scorch, low-level drought, insect herbivory, severe frost). They are also the progenitors of the eucalypts’ epicormic strands, which have remarkable resprouting capacity after crown fire (Burrows, 2013). Cremer (1972, p. 185) noted of 20 eucalypt species from the Australian Capital Territory (within the Southern Tablelands of New South Wales (NSW) and one of the colder parts of Australia) ‘… very few primary buds had survived the winter and a large proportion of the shoots growing in spring had come from accessory buds located on the previous year’s shoots.’ This would also be my general observation of c. 20 eucalypt species from around Wagga Wagga, NSW. Thus, in the eucalypts the naked buds can lead to a rapid expansion of the shoot system but in the main are ‘expendable’, while the important bud reserve is the accessory buds. The three monotypic genera (Arillastrum, Allosyncarpia, Stockwellia) closest to the eucalypts have compact, long-lived primary buds and a series of accessory buds at surface level (Burrows et al., 2008).

While the above is a general description of eucalypt naked buds, some variation has been recorded. Cremer (1972) notes that for Eucalyptus regnans in Tasmania, shoot growth in spring mainly came from primary buds that survived the winter. Cremer also noted that the overwintering primary buds of Eucalyptus pauciflora (snow gum, often found lining the runs in Australian ski fields) were covered by a single pair of cataphylls. Combined with my observations of what appear to be bud scales for one Angophora species (Fig. 3d,e; see also Carey, 1931) there is some variability in the structure and behaviour of eucalypt primary buds. With c. 800 eucalypt species, it is possible that further variation is yet to be described.
Schoonderwoerd & Friedman classified naked buds into six morphological categories, four with exposed buds (archetypal, heteroblastic, nonenveloping, caducous) and two with unexposed buds (recessed, stipular). They indicated that *Eucalyptus* had archetypal naked buds. Archetypal buds have three main features: ‘… outermost preformed leaves in the resting bud are exposed directly to the aerial environment during summer, autumn and winter.’ (p. 526); ‘… considerable preformation of foliage leaves …’ occurs (p. 526); and no scale leaves are formed, not even those that are nonenveloping or caducous. While eucalypts definitely have naked buds, two issues exist with classifying eucalypt naked buds as archetypal. First, as noted, eucalypt naked buds are usually slender, delicate structures with few leaf primordia (Figs 1b, 2b, 3a,f). A ‘considerable preformation of leaves’ does not occur. Second, if the eucalypt naked buds do not immediately develop into a branch they will be abscised; thus, primary resting buds are not exposed to freezing temperatures (although see Cremer’s comments on *E. regnans*). Schoonderwoerd & Friedman did not have access to living eucalypt material (pers. comm.), and herbarium specimens might not show the developmental sequence illustrated in Figs 1(a) and 2(a). Over 60 years ago, Chattaway (1958b, p. 45) noted that the regenerative powers of the eucalypts were ‘distinctive and unique’, with the structure and function of the naked and concealed (accessory) buds not as well-known as they should be.

It is not stated how many eucalypt species Schoonderwoerd & Friedman included in their study. For the climate and tree height analyses, they note (p. 525) ‘… *Eucalyptus* spp. were excluded to avoid phylogenetic biases introduced by a single species-rich clade …’ and ‘… when the species-rich *Eucalyptus* radiation in Australia is excluded …’ (p. 529). Combining the data of González-Orozco et al. (2014) on spatial patterns of eucalypt richness with the Australian Bureau of Meteorology’s map of potential frost days, it appears that several hundred eucalypt species in southern Australia would be exposed to freezing temperatures. The area where the inclusion of eucalypts as having archetypal naked buds might have the greatest influence on their paper is their fig. 4(a,b), where it appears that the coastal and tableland regions of southeast Australia have the world’s greatest number and relative richness of species with exposed naked buds (among freezing-tolerant woody angiosperms). Much of this richness might be from the inclusion of eucalypt species. As the eucalypt naked buds are probably not present when frosts occur, this figure could be considered misleading. Also, many of the darkly coloured cells in...
their fig. 4a,b are in southeast Queensland, where frosts rarely occur, and some coloured cells extend well into the tropics, where frosts would never occur.

Carey (1930), from a study of 140 woody species of NSW, recorded naked buds in several families not listed by Schoonderwoerd & Friedman. Carey recorded 22 families with naked buds, 11 of which were in Schoonderwoerd & Friedman’s study, while the remaining 11 were not included. In short, there may be still more to be discovered about naked buds, especially away from the well described European and North American woody floras. Jones (2021) considered that the recent study of naked buds and cold was perhaps somewhat prophetic?

In summary, the eucalypts are possibly the largest group of woody plants that form naked buds. They are probably the only group of woody plants in which most primary buds are abscised soon after formation and deeply buried accessory buds form the resprouting reserve. This unusual combination of axillary structures is apparently quite consistent across this large and diverse group. While the eucalypts have naked buds they are not archetypal and possibly require an expansion of Schoonderwoerd & Friedman’s classification system. It could be argued that eucalypts have two types of naked bud – exposed and nonexposed. The accessory buds could be an extreme form of naked recessed bud, although their initial leaf primordia (Fig. 2d) may be cataphylls to protect the bud as it pushes through the overlying tissues. These two very different axillary buds give the eucalypts the ability to rapidly expand shoots whenever the conditions are suitable, while also having an excellent protected bud reserve.

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Data availability

All new data are available in the three figures.

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