Root-suckering and Clonality in a Blue Mountains *Banksia* Taxon (Proteaceae)

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We report novel observations of widespread root-suckering from shallow lateral roots, and clonal morphology in 29 populations of plants ascribed to *Banksia paludosa* subsp. *paludosa* in the upper Blue Mountains, NSW, and differing from southern populations (Southern Highlands and Woronora Plateau) which are lignotuberous resprouters.

Following fire, Blue Mountains populations can resprout to form multi-stemmed shrubs appearing to be lignotuberous resprouters, but form root connected populations of sometimes closely spaced ramets in discrete areas. New single- or multiple-shoot root suckers frequently arise following fire from lateral roots at varying distances from the nearest established ramets. No lignotubers (developed on seed-grown plants) were observed, but multi-stemmed ramets which survive multiple fires may develop small, swollen, woody underground structures where they originate from lateral roots, but these are also frequently killed by fire and thus not reliably persistent regenerative organs. Cone development is rare, compared with southern populations, and no seedling recruitment was observed in any population.

Such geographically widespread and ubiquitous root-suckering has not previously been reported in *Banksia* species in eastern Australia, though it has been reported in southwestern Australian species and in an ecotype of *Banksia marginata* from western Victoria and South Australia. We suggest that Blue Mountains populations of this species may represent a distinct taxon with a different post-glacial history and recommend genetic and taxonomic studies to better understand the relationships with related species, including the identity and placement of the Blue Mountains root-suckering taxon reported here.

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INTRODUCTION

Banksia species (Proteaceae) are characteristic components of woodland and heath vegetation on low nutrient sand and sandstone soils in eastern and south-western Australia and are prominent in Sydney area vegetation where fire is a prominent part of the ecology (e.g., Hammill & Tasker, 2010; Myerscough et al., 2000). Because of their abundance in shrubby sclerophyll vegetation, *Banksia* species are often important markers in post-fire recovery studies where counts of annual growth spurts can indicate post-fire ages (Cowling & Lamont, 1985; Wills, 2003), and loss of fire sensitive species can demonstrate the impact of fires at short time intervals (Bradstock & O'Connell, 1988; Bradstock et al., 1997; Gallagher et al., 2021).

For some *Banksia* species mature individuals respond to fire by resprouting from basal lignotubers and/or stem epicormic shoots (resprouters); in other species (fire-sensitive seeders), individuals are killed by fire (Gill, 1981; Myerscough et al., 2000), to be replaced by seedling recruitment from seed released post-fire from canopy stored woody infructescences (*Banksia* cones), a condition known as serotiny (Lamont et al., 2020). In low nutrient sandy soils of southwestern Australia, some *Banksia* species have evolved additional vegetative regenerative strategies, including rhizomatous habits, with new shoots developing from near surface woody rhizomes, e.g., the non-lignotuberous *Banksia goodii* (Witkowski & Lamont, 1997), and root suckering from shallow lateral roots originating from lignotubers (He et al., 2011; Lamont, 1988). *Banksia elegans*, a lignotuberous species, produces an extensive network of suckering shoots arising from lateral roots (Lamont, 1988), and *Banksia gardneri*, a lignotuberous species produces rhizomes with shoots, which die back to a lignotuber following fire and do not form ramets (clonal plants) (Witkowski & Lamont, 1997).

In the case of root-suckering species, root suckering networks are then able to extend themselves over time to form potentially long-lived colonies of ramets (Pate et al., 2020). Root-suckering is well represented in Western Australian banksias and is widely understood to be an evolutionary response to fire in fire-prone ecosystems (He et al., 2019). Merwin et al. (2012) reported a potential lifespan of at least 1000 years in study populations of the rhizomatous, clonal suckering species, *Banksia candolleana*. Where ramets with multiple suckering shoots arise from lateral roots the development over time of small swollen woody structures where suckers arise from lateral roots has also been reported (Lamont, 1988). Clonal species may have reduced capacity for long distance dispersal by seed, as demonstrated in *Banksia candolleana* from sand dune habitats in fire-prone sclerophyll shrublands in southwestern Australia, where suitable dune habitat is separated by broad swales of unsuitable habitat. This species co-occurs with metapopulations of non-clonal resprouter and non-resprouter *Banksia* species in the same patchy dune habitats (Merwin et al., 2012). Based on regenerative strategies, intra-specific population divergence between old (OCBIL; Old Climatically Buffered Infertile Landscapes) and young (YODFEL; Young, Often Disturbed, Fertile Landscapes) landscapes, has been reported in *Banksia seminuda* in southwestern Australia (Robins et al., 2021), and in the rare Western Australian *Banksia ionthocarpa*, with extensive clonality and low genetic diversity in the lignotuberous subsp. *chrysophoenix*, and no observed clonality and high genetic diversity in the non-lignotuberous fire-sensitive subsp. *ionthocarpa* (Millar et al., 2010). Similarly, *Banksia ashbyi* is reportedly a small tree in the southern part of its range in Western Australia (south of Shark Bay), and a lignotuberous shrub north of Carnarvon to Exmouth (Liber, 2005).

Root-suckering from lateral roots has also been reported in *Banksia marginata* (the most widely distributed *Banksia* species) from the semi-arid Eyre Peninsula in South Australia (Specht & Rayson, 1957), and from western Victoria, where the species is reportedly found as a large (~10 m) seeding tree, or as a small (1 m), suckering, non-seeding shrub in the Colac region and in the Grampians (Liber, 2005). Specht et al. (1958) noted that in Eyre Peninsula populations, parent plants could resprout from lignotubers following fire, but that ramets developed from root-suckers could also outlive their parent plants. In these populations fire does not stimulate root suckering, which is not initiated until 15 years post-fire (Specht et al., 1958). Some root-suckering has been reported in NSW coastal populations of *Banksia integrifolia* subsp. *integrifolia*, as a result of non-fire-related disturbance, and for an isolated hinterland population at Elderslie (near Camden, NSW) where it was evidently "important for recruitment in dry sandy scrub" (Benson & McDougall, 2000). Stephen Bell (pers. comm.) reported some root-suckering in *Banksia conferta* north of Taree on the mid-North Coast of NSW, in addition to the presence of lignotubers on some plants (Bell, 2017). To the best of our knowledge, widespread root suckering and clonal networks of root connected ramets have not otherwise been reported in any eastern Australian *Banksia* species.

While undertaking field surveys for a population ecology study of *Banksia penicillata* in the Blue Mountains and *Banksia paludosa* subsp. *astrolux* in the Southern Highlands (Baird & Benson, 2021), we encountered medium-sized, shrub *Banksia* plants in the Blue Mountains consistent with descriptions of *Banksia paludosa* subsp. *paludosa* (floral specimens confirmed by the National Herbarium of NSW), but with a pattern of post-fire root-suckering rather than lignotuberous resprouting previously reported in the literature. *Banksia* taxa in the Blue Mountains include the fire sensitive, non-lignotuberous species - *Banksia cunninghamii* subsp. *cunninghamii*, *B. ericifolia* var. *ericifolia*, *B. integrifolia* subsp. *monticola*, *B. marginata* and *B. penicillata,* and lignotuberous or stem resprouters - *Banksia serrata*, *B. oblongifolia*, *B. spinulosa* var. *spinulosa*, *B. spinulosa* var. *collina* and *B. paludosa* subsp. *paludosa*.

Although originally coined to describe the woody swellings at the base of stems of many Australian eucalypts and angophoras (Kerr, 1925), the term 'lignotuber' is now commonly used to describe any conspicuous woody swelling at the base of stems, at or below ground-level, which bears dormant buds (Debenham, 1970) and has been applied to a range of underground woody regenerative structures (Pausas et al., 2018). In different parts of the world, additional terms are used, including 'burls' and 'xylopodia'. Such structures occur in at least half of all *Banksia* species (Mibus & Sedgley, 2000; Thiele & Ladiges, 1996). They are persistent woody regenerative organs from which new shoots arise from dormant buds, usually post-fire or otherwise through removal or loss of above ground parts, and developed on seed-grown plants only; they are widely understood to be a response to frequent fire (e.g., He et al., 2019; Lamont et al., 2020; Pausas et al., 2018). For want of a better term and to avoid confusion with other perhaps inappropriate terms, 'pseudolignotuber' is used in this paper to refer to swollen, woody, underground regenerative structures formed at the base of suckering shoots or shoot clusters where they arise from lateral roots connecting clonal populations (genets) of ramets. These are thus not developed on seed grown plants and do not have tap roots.

Banksia paludosa* subsp. *paludosa

Banksia paludosa subsp. *paludosa* R. Brown is considered a medium-sized, serotinous, lignotuberous, resprouter shrub, occurring in sandy loam or loam in woodland, often near swamps, and in rocky (sandstone) loam near creeks or on ridges, in woodland or low shrubland (Harden, 2002; https://plantnet.rbgsyd.nsw.gov.au/). It occurs from the northern Blue Mountains, south along the Woronora Plateau and Southern Highlands to Nowra, and inland to the Budawangs, with a disjunct population at Eden. Blue Mountains occurrences form a disjunct cluster at its northern limit (Figure 1). We refer to this population as *Banksia paludosa* subsp. *paludosa* (Blue Mtns) in this paper.

Superficially, *Banksia paludosa* subsp. *paludosa* may be confused with *Banksia oblongifolia*, a similar-sized shrub of broadly similar appearance, which is conspicuously lignotuberous, and frequently, but not exclusively associated with swampy areas or areas of impeded drainage, with perianth yellowish-green, and densely and persistently rusty villose on new stem growth (Benson & McDougall, 2000; Harden, 2002). It is a mostly northern species (with most AVH records north of Maddens Plains), with its southern limit near Batemans Bay and western limit in the mid Blue Mountains, where it may overlap with *Banksia paludosa* subsp. *paludosa*.

Banksia paludosa subsp. *astrolux* A. George is restricted to a relatively small area in dry sclerophyll woodland and open forest near Hilltop in the Southern Highlands and, is a large, non-lignotuberous, fire sensitive, serotinous shrub (Baird & Benson, 2021; George, 1999).

This paper reports our field investigations of root-suckering populations of *Banksia paludosa* subsp. *paludosa* (Blue Mtns), compared with resprouting populations of *Banksia paludosa* subsp. *paludosa* elsewhere in the Sydney Basin, and raises questions around its distinctiveness in the context of the widespread occurrence of vegetative regenerative strategies in banksias in southwestern Australia (e.g., Merwin et al., 2012).

METHODS

Field observations of *Banksia paludosa* subsp. *paludosa* (Blue Mtns)

During 2020 and 2021 we surveyed 29 of 42 *Banksia paludosa* subsp. *paludosa* (Blue Mtns) sites in the upper Blue Mountains (including Australian Virtual Herbarium records (AVH) and additional newly recorded sites). For a minimum of 3 plants per site (but often many more), we recorded evidence of lignotubers and/or root suckering and ramet development. Sites included those burnt in the late 2019 Gospers Mountain Fire and Grose Valley Fire (almost all populations), and some unburnt sites. We confirmed fire histories using NSW National Parks and Wildlife Service fire history maps, which identify boundaries of individual fires; however, due to a range of topographic and other factors, this does not mean that all areas within individual fire boundaries were burnt.

For a detailed investigation of the root-suckering habit, we selected a site near Mt Victoria, burnt in 2019, where a high density of plants of different sizes, or number of resprouting branches were evident, with soil suitable for shallow excavation. At this site, on 7–10 September 2021, we marked out a 5 m^2 area containing numerous apparently individual plants with similar vegetative characteristics to other populations observed (though the density of plants in this study quadrat was greater than normally observed). At the base of each plant, we carefully scraped the soil away using a garden trowel to identify and expose any evidence of root-suckering or lignotuber formation. Where root-suckering was identified we followed the typically shallow lateral roots horizontally, exposing them wherever possible in each direction, and continued this across the study quadrat until all plants and all root connections between plants had been identified where possible.

The resulting network was mapped and photographed to accurately depict the relative locations of all plants (which we term ramets) and root connections. The number of suckering branches (live and dead, including bases of identifiable dead suckers only) at each ramet, the depth below ground level and diameter of roots where suckers were arising, the distance between each ramet, whether

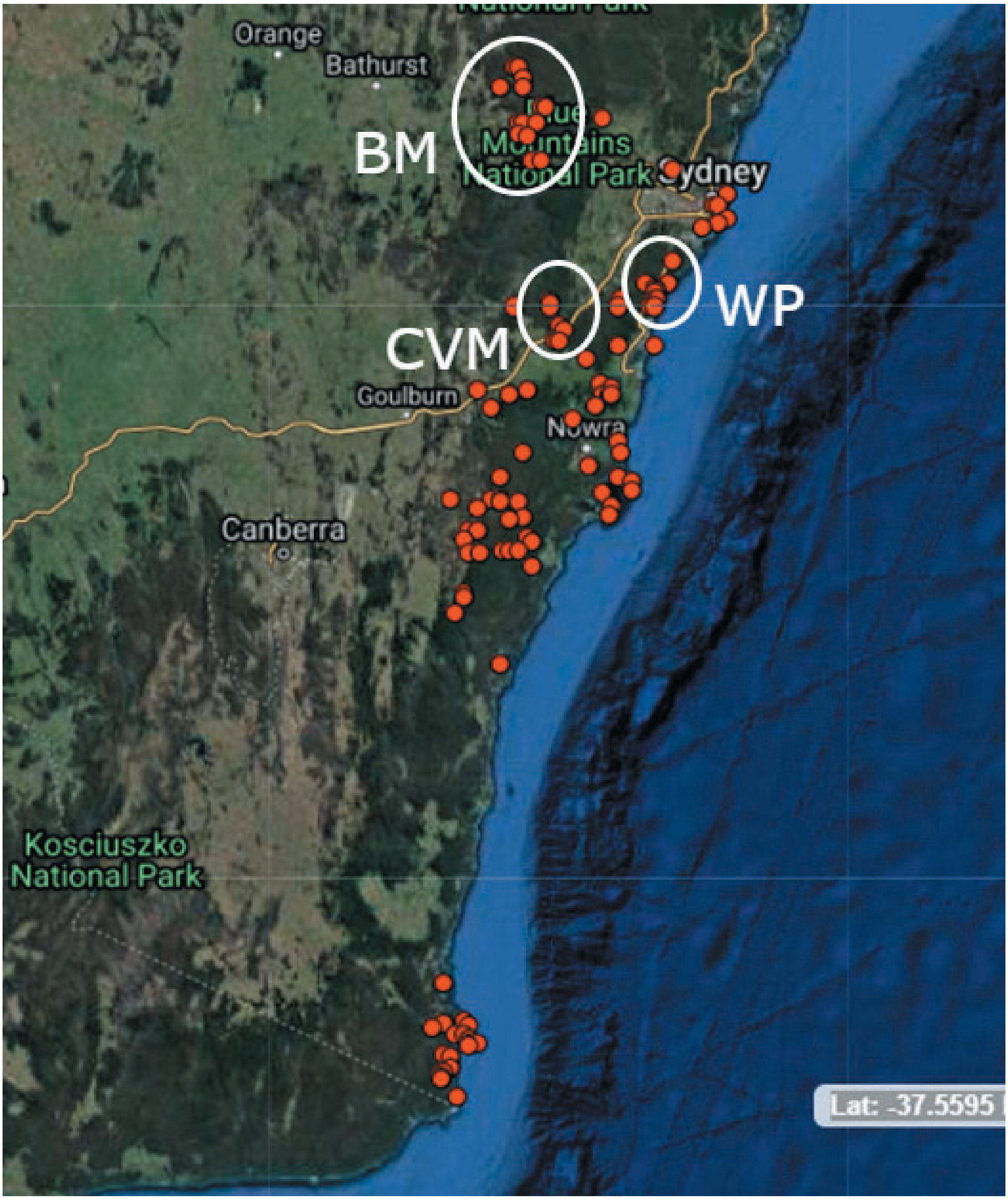

Figure 1. Distribution of *Banksia paludosa* subsp. *paludosa* showing Blue Mountains (BM), Colo Vale-Mittagong (CVM) and Woronora Plateau (WP) study areas. Note Blue Mountains occurrences as disjunct cluster at northern range limit (source AVH).

ramets were alive or dead following the recent fires, evidence of lignotubers or other woody regenerative organs, and discontinuities in lateral root connections, were recorded. Plants with no clearly identifiable suckering from lateral roots were identified, and additional vegetative features were recorded. After survey, excavated soil and litter were replaced around exposed roots and plant bases.

To compare the relative proportions of resprouting versus fire-killed and unburnt pre-fire ramets, and the number of new single stem ramets originating as root suckers post-fire across populations, three populations along the Ikara Head walking trail near Mt Victoria (IHT1, ~50 m^2; IHT2, ~100 m^2; IHT3, ~1000 m^2) and five populations in close proximity to each other in the Mt Hay Range (MHR1–MHR5) (all burnt in 2019) were surveyed in August 2021. All dead plants, resprouting plants, unburnt plants, and new, post-fire, single-stem, root-sucker ramets were counted. Additional opportunistic shallow excavations were undertaken at various sites to confirm results from the Mt Victoria and Mt Hay Range sites. Across all populations, observations of inflorescences, cone development and seedlings were recorded.

Comparison with *Banksia paludosa* subsp. *paludosa* southern populations

To compare *Banksia paludosa* subsp. *paludosa* (Blue Mtns) populations with the closest southern populations, we investigated four sites in coastal upland habitats on the Woronora Plateau (Stanwell Tops, Darkes Forest, Maddens Plain) and four sites in the Southern Highlands (Colo Vale-Mittagong) using AVH and Atlas of Living Australia records (Figure 1). We recorded whether these populations were lignotuberous (as stated in the literature) or also included root-sucker responses. At Colo Vale-Mittagong we measured lignotuber diameters for a subset of plants. During fieldwork on the Woronora Plateau, we compared lignotuber development and post-fire seedling recruitment in co-occurring and nearby populations of *Banksia oblongifolia*.

RESULTS

Distribution of recorded *Banksia paludosa* subsp. *paludosa* (Blue Mtns)

The localised populations of *Banksia paludosa* subsp. *paludosa* (Blue Mtns) we recorded are distributed across the Mt Hay Range north of Leura; along ridgelines in the Medlow Bath, Blackheath, Mt Victoria, and Mt Wilson areas; and along Waratah Ridge on the eastern side of the Newnes Plateau. All 42 recorded populations occurred between 780–1040 m elevation. Populations, or spatially discrete colonies of ramets, ranged in area from <50 m^2 to ~1 ha.

Of the 42 populations, 40 were on ridgetops in variably rocky terrain, and 2 were in similar habitat, but on slopes, lower down on valley sides. Soils ranged from sandy loams to loams. All but 3 populations were in *Eucalyptus*-dominated (frequently *Eucalyptus piperita, E. racemosa* and *E. sieberi*), dry sclerophyll woodland or open forest with a mixed herbaceous and shrubby understorey (Figure 2), with two of these extending onto a small rocky knoll in montane heath (Figure 3); three populations were restricted to montane heath on a ridgetop. None was associated with swampy or obviously impeded drainage areas typical of *Banksia oblongifolia* habitat in the Blue Mountains.

Root-suckering extent and morphology

Root-suckering and shallow lateral root connections between ramets were found to be the typical form of post-fire regeneration in all 29 populations examined in the field. No true lignotubers (developed on seed-grown plants) were observed. The age of post-fire stem growth was counted using the annual growth bursts count method and was consistent with time since previous fire. Generally, new suckers arise within 1 year of fire, but it is possible that some suckers arise from lateral roots at other times.

The true nature of the vegetative regeneration is only revealed through careful subsurface investigation. The study quadrat at Mt Victoria revealed a complex network of root-connected ramets (Figure 4). The details of the network are summarized in Table 1. Fire induced mortality of older multi-stemmed ramets connected to live lateral roots was frequently observed; live lateral roots also supported new suckers regenerating from pre-fire ramets and new, single shoot, post-fire suckers at new locations on the roots (Figure 5). Lateral roots supporting suckering shoots varied in diameter from <0.3–3 cm (Figure 5–9). Frequently, single suckers arising post-2019 fire were already thicker than their thin supporting lateral root (Table 1). New single shoot post-fire suckers generally arise from the top of the lateral root but may also develop from the sides.

All lateral roots giving rise to suckers were shallow (up to 7 cm depth to top of root), with the exception of roots that encountered rocks in the soil; in these cases, roots typically burrowed deeper and were not able to be readily traced. Sometimes, ramet development was associated with rock fractures or from beneath a rock where a root had descended. Lateral roots also disappeared among the root systems of other shrubs or graminoids and were unable to be readily followed. Lateral roots which give rise to new ramets also have scattered, fine, shallow feeder roots and sometimes branch to form new lateral roots which terminate in networks of finer feeder roots. New ramets may develop at junctions where a lateral root divides or from an unbranched length of lateral root. New lateral roots also develop from locations of existing ramets or independent of the locations of a ramet. Woody descending roots sometimes

Figure 2. Fire-killed, single-stem *Banksia paludosa* subsp. *paludosa* (Blue Mtns) ramet with 16 years of growth in woodland on the Mt Hay Range (site MHR1), and multiple, single post-2019-fire suckers growing from lateral roots within 30 cm each side (arrowed) of the dead main stem. A series of new suckers (not shown) were spaced out on a lateral root 3 m away. 26 July 2021 (Photo: Ian Baird).

develop from undersides of woody lateral roots and presumably provide access to deeper soil moisture. They can develop independent of the presence of a ramet and ramets do not have tap roots. There was no sign of any apparent proteoid roots as have been reported for various taxa, including many Western Australian banksias (Pate et al., 2020).

Small lignotuber-like woody structures (hereafter termed 'pseudolignotuber') at the base of suckering shoots, where they arise from the lateral root, were present at 33% of ramet locations (n=36), with a maximum 7 cm diameter recorded (Figures 5 & 7). Depending on the size or age of the pre-fire ramet and size of the associated pseudolignotuber, the number of new post-fire suckers at individual ramet locations varied from 1–14, and the number of dead suckering branches (or burnt stem bases) at locations of dead ramets varied from 1–11.

Lateral roots connecting a series of ramets were often overlain by apparently unconnected lateral roots with their own ramets, forming complex multi-layered networks of root connected ramets, with lateral roots of different diameters and ages (Figures 5 & 8). In terms of connectivity within this lateral root network, we identified up to 10 apparently separate root systems in the 5 m^2 area, but it is possible that most or all apparently separate root sections are connected within or outside the study area boundary and cannot discount past connections subsequently broken.

Characteristics of the network of root connected ramets in the study quadrat were confirmed across all our study populations with the exception of the high density of ramets. Though it was not uncommon to record at least 10 live ramets within a 5 m^2 area, ramet spacing varies considerably and ramets may be metres apart. Lateral root connections between ramets were sometimes discontinuous, but typically the presence of a former connection was evident (Figure 9). Across all sites, fire appeared to be the only identifiable cause of mortality and subsequent decay of a length of the shallow lateral root connectors. Sometimes, old multi-stemmed ramets had a thick, live, lateral root

Figure 3. Resprouting *Banksia paludosa* subsp. *paludosa* (Blue Mtns) ramets (arrowed) on rocky knoll near Hat Hill, Blackheath (Mt Banks in background). Dead pre-2019-fire branches evident. Tracing lateral root connections in this rocky habitat is impossible, but lateral root connections were evident for some ramets.13 July 2021 (Photo: Ian Baird).

connection (up to ~3 cm diameter) on one side and none on the other (Figure 10), but close examination generally revealed the presence of an old scar or rotted root remnant where the original lateral root previously continued on that side of the plant but had now died and rotted away (Figure 9, 10). Through this process, clonal populations can be physically broken up into groups of connected clonal ramets. In the case of some of the thickest, woody lateral roots, they were sometimes exposed on the surface due to erosion of the covering soil and progressive thickening of the root towards the surface (Figure 9); in these situations, they are more vulnerable to fire.

No true lignotubers (i.e., developed on plants derived from seed) were observed in any population, but pseudolignotuber development was identified in association with the bases of many older multi-stemmed ramets, where they originated as suckers from large lateral roots (Figures 5, 7 & 10). The swollen woody structure does not appear to form directly from the root but is more a gradual thickening of the base of a sucker, or merging of the bases of multiple root suckers, where they arise from the same area on the root, and where they have survived and resprouted following repeated fires. Pseudolignotubers ranged up to ~12 cm diameter. Sometimes, young, single shoot suckers have a small pea-sized swelling at their base where they arise from the top of the lateral root (Figure 5, 7 & 9), presumably forming the foundation for development of a pseudolignotuber; however, this is frequently not the case and many new single shoot suckers show no evidence of such basal swellings. These structures do not appear to continue to grow laterally with age as in lignotuberous banksias (e.g., *Banksia spinulosa* and *Banksia oblongifolia* which can form large lignotubers to >50 cm diameter). They also do not reliably act as persistent regenerative organs through fire events, as evidenced by the frequent mortality of older multi-stemmed ramets (Table 2), even though the dead ramets were still frequently

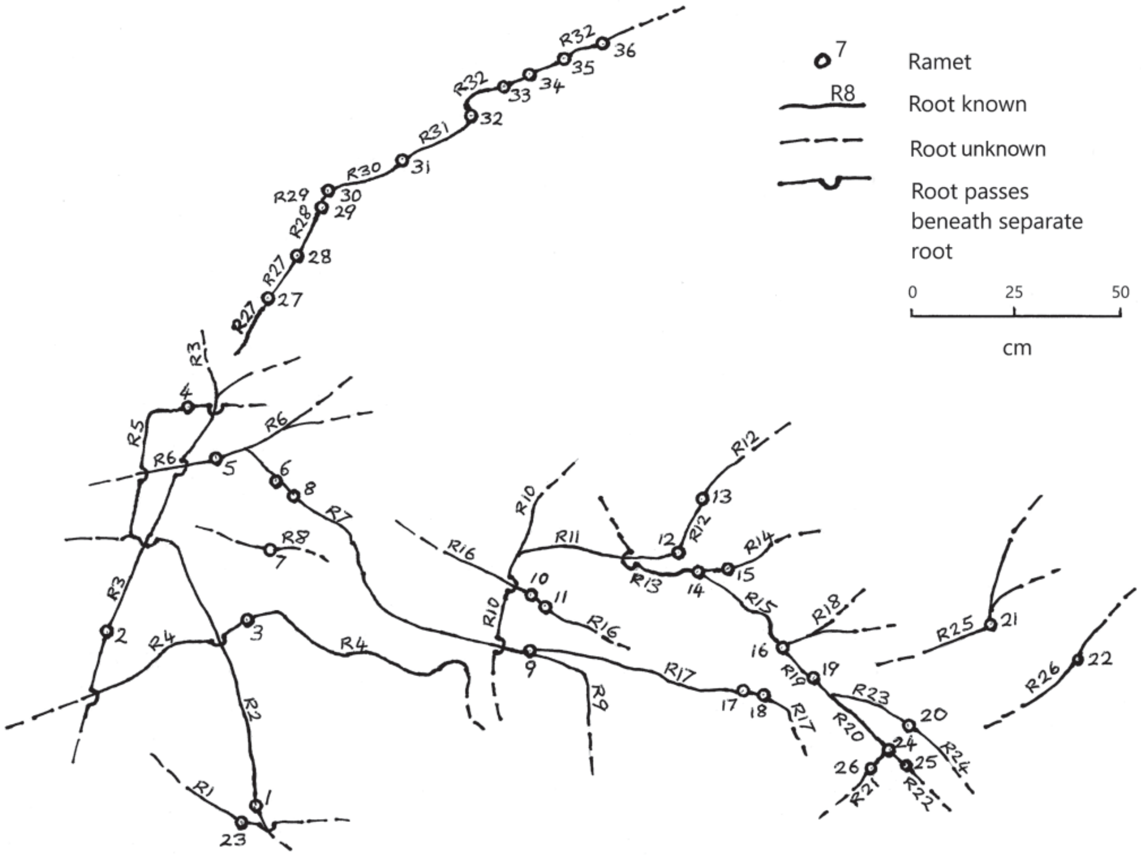

Figure 4. Map of *Banksia paludosa* subsp. *paludosa* (Blue Mtns) 5 m^2 study site near Mt Victoria (to scale) showing locations of ramets and connecting lateral roots. Branching pattern of roots shown (where known) suggests the likely direction of root extension. "Root unknown" refers to identified root sections which were not followed because they either extended beyond the study area, did not have any live or identifiable dead ramets in that direction, or were unable to be followed. See Table 1 for details.

connected to a live, lateral root system, often on both sides (or below) of the dead ramet. Where ramets develop from lateral roots among rocks or within rock fissures, they may be provided with extra protection from fire and sometimes develop irregular-shaped pseudolignotubers, with many suckering branches developed across multiple fire events.

In some cases, there was evidence of an old fire-killed, decaying pseudolignotuber next to, or contiguous with, a live section of pseudolignotuber, which was still connected to the original woody root on one side, but with only the rotting scar from the old root evident on the far side (Figure 10). Sometimes, these complex arrangements also included single new root suckers arising from additional lateral roots. New lateral roots can arise from old pseudolignotubers, and on one occasion we observed a root originating from the top of a buried pseudolignotuber from amongst the bases of suckering shoots, and then growing downwards into the adjoining soil, before growing laterally below the surface, giving the appearance of a rhizome, although we do not suggest that that is what it was. In other situations, there were strings of closely spaced root-suckers distributed along a single lateral root at varying distances from an established multi- or single-stemmed ramet (alive or dead) (Figure 6). We did not identify any old multi-stemmed plants with no lateral root connections to other ramets, but it is likely that such occurrences could occur due to fire severing connections.

New suckering shoots on existing ramets appear to originate from buds at the base of existing suckering stems, just above the lateral root; they also appear to arise from buds which develop on established pseudolignotubers (typically from the sides), where multiple suckering shoots have previously developed, and as new suckers, directly from the lateral root, immediately next to existing suckers; thus, contributing to expansion of the pseudolignotuber. Clusters of new post-fire suckers often only develop

Table 1. Details of lateral root connections and ramet development in the 5 m² study population (Figure 4) of *Banksia paludosa* subsp. *paludosa* (Blue Mtns) near Mt Victoria (burnt December 2019, recorded September 2021).

Ramet number	Dead (D) or Alive (A)	Live stems (n)	Pseudolignotuber present (Y/N)	Diameter of pseudo-lignotuber (cm)	Bases of dead stems evident (Y/N), (n), U = Unknown number	Lateral root number	Diameter of lateral roots (cm)	Root Alive (A) or Dead (D)
01	A	2	N	-	N	R01	0.3	A
02	A	14	N	-	N	R02	0.8	A
03	A	7	N	-	N	R03	1	A
04	A	2	N	-	N	R04	0.5	A
05	D	0	N	-	Y (1)	R05	0.6	A
06	A	1	N	-	N	R06	1	A
07	A	2	Y	1	N	R07	0.8	A
08	A	2	N	-	N	R08	0.4	A
09	A	3	Y	1	N	R09	1.1	A
10	A	1	N	-	Y (1)	R10	0.9	A
11	A	1	N	-	N	R11	0.9	A
12	D	0	Y	4	Y (9)	R12	0.5	A
13	A	1	N	-	N	R13	1.2	A
14	D	0	Y	7	Y (11)	R14	1.5	A
15	A	3	N	-	N	R15	3.5	A
16	A	1	N	-	Y (1)	R16	0.4	A
17	A	1	Y	0.8	N	R17	1.1	A
18	A	1	Y	0.8	N	R18	0.8	A
19	D	0	N	-	Y (1)	R19	1.5	A
20	A	10	Y	2	N	R20	1.8	A
21	A	1	Y	0.6	N	R21	0.6	A
22	A	2	Y	1	N	R22	0.6	A
23	A	1	Y	0.6	N	R23	1.2	A
24	A	2	Y	0.6	N	R24	1.2	A
25	A	2	N	-	N	R25	2.6	A
26	A	1	N	-	N	R26	0.5	D
27	D	0	Y	5	Y (U)	R27	2.3	D
28	D	0	N	1.5	Y (2)	R28	2	D
29	D	0	Y	4	Y (U)	R29	2.2	D
30	D	0	N	-	Y (1)	R30	2.2	D
31	D	0	N	-	Y (2)	R31	2	A
32	D	0	Y	3	N	R32	2	A
33	A	1	N	-	N			
34	A	1	N	-	N			
35	A	1	N	-	N			
36	A	2	N	-	N			

Figure 5. *Banksia paludosa* subsp. *paludosa* (Blue Mtns), Mt Victoria study site, showing two 2019-fire-killed ramets with pseudolignotubers (largest 7 cm diameter) and multiple dead stem bases; also new post-fire suckers on lateral roots each connected to a dead ramet. Note the variation in sizes of the lateral roots and beginning of a pseudolignotuber swelling at the base of the sucker in left foreground. Both dead ramets were on apparently separate lateral root systems crossing each other, with no evident connection. 7 September 2021 (Photo: Ian Baird).

from one side of an established pseudolignotuber, because the rest of the structure has been killed by fire (Figure 6).

Flowering and fruiting

Inflorescences were identified on resprouting stems a minimum of two years after fire. Plants in one large population (MHR1) of ramets on the Mt Hay Range (burnt in 2002-2003), with up to 16 annual growth spurts (branches subsequently killed in the 2019 fire), and in another population near Mt Victoria (unburnt for many years and surveyed August 2021, but not included in Table 2), both had old inflorescences of various ages, but no cones, indicating that, regardless of the abundance of inflorescences, subsequent cone development is rare.

We recorded multiple plants with cones in only one small site (MHR4), which was in a rocky, but fire exposed area on the end of a spur. Interestingly, 15 of these older fire-killed plants bore some old cones with some open follicles, but no seedlings were observed, regardless of good rainfall since the fire and abundant seedling recruitment observed in other co-occurring *Banksia* species, including fire-sensitive and resprouter species. This was the only observation of such a level of fruiting in any population. Across all except this one population (MHR4), only 1 cone with few filled out follicles (at a Mt Victoria site) was observed, out of hundreds of plants with a wide range of fire histories and years since previous fire. Rarity of fruit set could be due to a combination of sexual self-incompatability and the presence of only a single clone at a site. Goldingay and Whelan (1990) investigated the breeding systems of *Banksia paludosa* subsp. *paludosa* and *Banksia spinulosa* and found “self-pollination and autogamy treatments failed to produce any fruit in *Banksia spinulosa* and produced very few fruit in *Banksia paludosa*.”

No seedlings were observed at any site, regardless of the above average rainfall following the late 2019 fires, while seedlings of other co-occurring, fire-sensitive *Banksia cunninghamii* and *Banksia ericifolia*, and resprouter *Banksia serrata* and *Banksia spinulosa*, were abundant.

Fire impacts

Most populations were burnt in the 2019 Wollemi Complex Fire or associated Grose Valley Fire, and above ground stems killed. Unburnt plants were either growing in protected rocky refugia or next to roads which provided some fire protection. Across the Ikara Head trail (near Mt Victoria) and Mt Hay Range sites (Table 2), percentage of burnt ramets surviving and resprouting ranged from 24–98%. It is likely that some ramets in all populations, including older multi-stemmed ramets, died as a result of the drought leading into early 2020, as evidenced by the large number of old established individuals of resprouter and fire-sensitive *Banksia* species which died as a result of drought elsewhere across the Blue Mountains in 2019. The total population of ramets recorded in 2021 showed a marked impact of the 2019 fire, with reductions in total ramet populations varying from 11–71% in 6 of 7 populations, and an increase of 52% in one population (IHT3). It is very likely that some or many smaller pre-fire ramets with one or few stems only were burnt leaving no evidence of their pre-fire presence.

Mt Hay Range population MHR1, burnt in a back-burn associated with the 2019 Grose Valley Fire, had dead stems up to ~2.5 m high with up to 16 annual growth spurts (growth since the previous 2002-2003 fire), and new post-fire shoots resprouting either from below-ground bases of some established ramets, or as multiple, single, closely spaced suckers aligned along a lateral root at varying distances from the nearest old ramet (Figure 2); for some, the nearest live root suckers were at least 2 m from pre-fire plants (recorded

Figure 6. *Banksia paludosa* subsp. *paludosa* (Blue Mtns), Mt Hay Range. Large, near surface, lateral root with numerous new single stem suckers following the 2019 fire. Second large branching lateral root with suckers behind and dead smaller root with dead ramet base in front. No old dead pseudolignotubers present in this photo. Large shallow lateral roots are often vulnerable to fire. Scale ruler 13 cm, 31 July 2021 (Photo: Ian Baird).

Figure 7. *Banksia paludosa* subsp. *paludosa* (Blue Mtns), Mt Victoria study site, showing two apparently unconnected lateral roots which cross each other, with 2 suckering shoots on one and one sucker on the other. Note presence of small swellings at the base of suckers associated with potential pseudolignotuber development. Scale ruler 13 cm, 7 September 2021 (Photo: Ian Baird).

August 2021). Of 208 multi-stemmed and single stem ramets, with up to 16 years of pre-fire growth, only 80 had live resprouts, the rest were dead (Table 2). Dead ramets included many old single stem ramets without pseudolignotubers, presumably originating from single, new, lateral root-suckers after the 2002-2003 fire, and giving the superficial appearance of having originated from seed. This population will now be dominated by multi-stemmed ramets suckering from bases of surviving old ramets, plus new single-stem root-suckers (at varying distances from established ramets).

Part of MHR1 population (separated by a vehicle track and not included as part of MHR1 in Table 2 due to different recent fire history) was not burnt in the 2019 fire but was burnt in a hazard reduction burn in 2015; some plants in a rocky refuge were also unburnt. In the area burnt in 2015, all established ramets which survived the fire had resprouted to form multi-stemmed plants, in contrast to the older single stem cohort of plants on the other side of the road.

In Mt Hay Range population MHR5, also burnt in 2019, 60% of 86 multi-stemmed pre-fire plants were killed by the fire (some possibly by drought); the remainder resprouting from their bases with one or more new shoots (Table 2). New root-suckers at varying distances from the nearest fire-killed and resprouting ramets were evident across the population, confirming that death of individual ramets does not necessarily mean that the associated lateral root system is also killed.

In MHR4, in contrast to the pattern observed in other populations, all pre-fire multi-stemmed plants were killed, and all resprouting ramets were small and relatively young with few shoots.

Comparison with *Banksia paludosa* subsp. *paludosa* southern populations

All plants investigated in the populations of *Banksia paludosa* subsp. *paludosa* in the Southern Highlands (Colo Vale-Mittagong; 580–700 m elev.) and on the Woronora Plateau (Stanwell Tops-

Maddens Plains-Darkes Forest; 245–370 m elev.) were exclusively lignotuberous. Lignotubers at Colo Vale averaged 10–15 cm diameter and were up to 40 cm (Table 3). Some lignotubers showed evidence of fire damage and recovery indicative of considerable longevity. We found no evidence of widespread suckering from lateral roots, though two plants at Colo Vale had a single-stemmed sucker at the end of a 1.5–2 cm diameter root, 30–40 cm distant from a lignotuberous plant. These are likely to have developed from some past root damage or exposure, as is common in *Banksia integrifolia* subsp. *integrifolia*. We recorded lignotuber death in 5 of 17 plants burnt in a recent (<1 year) fire at Colo Vale 3 (with lignotubers from 4–13 cm diameter), and ~20% recent death in a long unburnt site at Mittagong, presumably from previous drought, not fire. All plants, unless recently burnt, had abundant cone development. In one Maddens Plains population we found one established seedling next to a mature plant, and some juvenile plants were found at Colo Vale and Mittagong. Some plants at Colo Vale 1 (burnt <16 yr ago), were in poor condition, likely due to competitive canopy shading from trees and tall shrubs.

None of the *Banksia paludosa* subsp. *paludosa* we observed on the Woronora Plateau were associated with swampy areas and were restricted to dry-sclerophyll eucalypt woodland. One population near Colo Vale included plants on the margins of a swampy area, but most plants occurred on sandy soils in adjoining dry-sclerophyll, eucalypt woodland, similar to the other sites nearby at Colo Vale and Mittagong.

Possible confusion with *Banksia oblongifolia*

There may be some identification confusion with *Banksia oblongifolia.* One site at Stanwell Tops and one at Maddens Plains, which according to AVH records were localities of *Banksia paludosa* subsp. *paludosa*, appeared to consist entirely of *Banksia oblongifolia*, although it is possible that further searching may have identified some *Banksia paludosa*

Figure 8. *Banksia paludosa* subsp. *paludosa* (Blue Mtns), Mt Victoria study site, showing a complex network of apparently unconnected and overlying lateral root systems with new post-2019-fire root suckers. Base of a dead single-stem, pre-fire ramet arrowed. Note that lateral roots have branched independent of the location of ramets. Scale ruler 13 cm, 7 September 2021 (Photo: Ian Baird).

Figure 9. *Banksia paludosa* subsp. *paludosa* (Blue Mtns), Mt Hay Range site MHR5. Two well-established new ramets suckering from a now disconnected lateral root with remains of former connecting lateral root arrowed at each end. Cause of mortality of this root section unknown. Note the presence of a small swelling at base of the stem of the right-hand ramet. Right-hand ramet also has a second smaller continuous lateral root below the damaged root. Scale ruler 13 cm, 26 July 2021 (Photo: Ian Baird).

subsp. *paludosa* nearby. Neither of these sites had AVH records for *Banksia oblongifolia*. One site at Maddens Plains included adjoining patches of both of these lignotuberous species with a sympatric zone in between. A site of *Banksia paludosa* subsp. *paludosa* (based on AVH records) in dry sclerophyll woodland at Darkes Forest was confirmed, but a large population (with no AVH record) which we found in moister open forest within 1 km, adjacent to the Darkes Forest Road, was exclusively of *Banksia oblongifolia*. In the other Maddens Plains population, which we found to be exclusively *Banksia oblongifolia*, and burnt recently, we observed numerous seedlings established post-fire beneath and adjacent to numerous resprouting lignotuberous plants in an area of Coastal Upland Swamp. Numerous additional plants of *Banksia oblongifolia* were also observed in adjacent unburnt open forest with a moist understorey. Typically, it appeared that *Banksia oblongifolia* is capable of attaining greater lignotuber sizes (>50 cm diameter, similar to *Banksia spinulosa*) than *Banksia paludosa* subsp. *paludosa*.

DISCUSSION

Root-suckering and clonality of populations

Despite the superficial appearance of lignotuberous clusters of branches, *Banksia paludosa* subsp. *paludosa* (Blue Mtns) clearly occurs as small, localised populations that recover from fire (and possibly to some extent drought) by resprouting from shallow lateral roots, generally within 1 year of fire (as occurs with lignotuberous resprouters), at varying distances from established ramets. With time, bases of suckers or clusters of suckers may develop small swollen woody structures (which we refer to as pseudolignotubers) from which, or adjacent to which, new suckers can subsequently arise post-fire. These pseudolignotubers, however, are not

Figure 10. ***Banksia paludosa*** **subsp.** ***paludosa*** **(Blue Mtns), Mt Hay Range, showing large old pseudolignotuber (right) connected to the top of a large lateral root and branching root network, independent of ramet location. One living branch (this plant was not totally burnt in the 2019 fire) and one fire-killed branch evident on top of pseudolignotuber and numerous new post-fire suckers on living part of the old pseudolignotuber. Bases of fire-killed old suckers shown (black arrows), one on the side of the pseudolignotuber and one independent of it. Any evidence of former lateral root connection on dead rotten side of old pseudolignotuber (red arrow) has rotted away. Single new post-fire sucker on smaller, possibly unconnected root at left. 11 August 2021 (Photo: Ian Baird).**

necessarily persistent regenerative organs, being frequently killed by fire (and potentially drought); the connecting lateral root system, however, is more likely to survive to produce new single stem suckers, post-fire. As a result, these lateral root systems form extensive, complex networks of ramets consisting of one-to-many shoots, and although we found evidence of lateral root systems broken up as a result of root sections between some ramets being killed by fire, we suggest the possibility that all of these root sections have at some time in the past originated from the same (or few) clone(s); thus now part of a larger clonal network (genet) of connected and disconnected sections (e.g., Robins et al., 2021). A similar post-fire suckering response is reported for Western Australian *Banksia elegans* (Cowling & Lamont, 1987), though root suckering in a South Australian *Banksia marginata* ecotype was apparently inhibited by fire (Specht et al., 1958). Both species, however, apparently include seed-grown lignotuberous plants in their clonal networks, whereas *Banksia paludosa* subsp. *paludosa* (Blue Mtns) does not appear to.

Our observations of inflorescences, but very infrequent fruiting, and no seedling recruitment, despite two years of above average rainfall since the 2019 fires, and abundant seedling recruitment in other sympatric fire sensitive and resprouter *Banksia* species, is consistent with observations that resprouters generally have lower seed set and viability, smaller seedbanks, and fewer seedlings compared with fire sensitive species (Bond & Midgley, 2001; Lamont & Wiens, 2003). No seed grown parent plants were identified.

Table 2. Counts (August 2021) of dead, post-fire resprouting, new single-shoot ramets, and alive and unburnt *Banksia paludosa* subsp. *paludosa* (Blue Mtns) ramets in populations along the Ikara Head trail near Mt Victoria (IHT) and in the Mt Hay Range (MHR), burnt 2019. New single post-fire suckers were not counted across MHR5. Burnt and dead ramets counted likely to underestimate pre-fire population as some small ramets probably burnt completely leaving no evidence in 2021.

Population code	Burnt and dead ramets (n)	Burnt and resprouting ramets (n)	**TOTAL burnt-dead and burnt-resprouting ramets**	**% of total pre-fire ramets resprouting**	New single shoot ramets (n)	Alive and unburnt ramets (n)	% of new single shoot ramets in 2021 population	Total ramet population 2021 excluding unburnt
IHT1	18	45	**63**	**71**	9	5	16	54
IHT2	12	51	**63**	**81**	5	0	9	56
IHT3	3	133	**136**	**98**	74	0	36	207
MHR1	128	80	**208**	**38**	30	0	27	110
MHR2	12	54	**66**	**82**	2	2	4	56
MHR3	3	11	**14**	**79**	0	0	0	11
MHR4	32	10	**42**	**24**	2	0	17	12
MHR5	48	38	**86**	**40**	-	0	-	-
TOTAL	**256**	**422**	**678**					
% of total burnt ramets	**38**	**62**						

Table 3. Comparison of pseudolignotuber diameters at the Mt Victoria study site (see Table 1) with lignotuber diameters of *Banksia paludosa* subsp. *paludosa* in Colo Vale-Mittagong populations (over ~8 km), show Mt Victoria plants have significantly smaller diameter structures, by a degree of magnitude.

Site	Pseudolignotuber* or lignotuber diameter (cm)				Total plants (n)
	Smallest	Largest	Average	Median	
Mt Victoria*	0.6	7	2.2	1	14
Colo Vale 1	2	40	15.6	10	18
Colo Vale 2	5	16	10.5	10	13
Colo Vale 3	4	40	12.7	10	17
Mittagong	4	25	9.8	6	16

Examples of similar vegetative regenerative systems, either lacking, or with low seedling recruitment, have been reported for populations of the root suckering ecotype of *Banksia marginata* from South Australia and western Victoria (Liber, 2005; Specht & Rayson, 1957; Specht et al., 1958), and the Western Australian *Banksia candolleana* (Merwin et al., 2012), *Banksia goodii* (Witkowski & Lamont, 1997), and *Banksia ionthocarpa* subsp. *chrysophoenix* (Millar et al., 2010).

Relict nature of these populations

Banksia paludosa subsp. *paludosa* (Blue Mtns) occurs in localised but spatially discrete populations, with populations surviving and perhaps spreading, primarily through vegetative, clonal, root-suckering networks with a predominantly (or exclusively) asexual reproductive system. The age of these clonal populations is a matter of conjecture, but it is likely, considering the extent of some populations, to be of the order of >1000 years old, as in Western Australian *Banksia candolleana* (Merwin et al., 2012).

Populations are typically associated with ridges, occurring with heath and woodland species, and restricted to very low nutrient soils of Triassic Narrabeen sandstone, clearly an OCBIL (Old Climatically Buffered Infertile Landscape) habitat; the taxon has OCBIL characteristics, including long-term persistence, limited propagule dispersal and high site fidelity (Hopper, 2009; Hopper, 2021). The distribution of these populations therefore is more likely to be the result of past historical events than current ecological processes, i.e., they persist in current conditions as relict populations.

Persistence in localized refugia through climate oscillations of the Pleistocene has been hypothesized to have been responsible for identified patterns of high levels of genetic diversity and structure in various species (e.g., Byrne, 2007; Byrne et al., 2019; Rix et al., 2015). Climatic oscillations of the Pleistocene, and the cold, windy, and relatively dry conditions of the Last Glacial Maximum (LGM; ~21,000 yrs BP) are likely to have resulted in geographic and genetic isolation of *Banksia paludosa* subsp. *paludosa* (Blue Mtns) from southern and coastal populations of *Banksia paludosa* subsp. *paludosa,* and subsequent development of root-suckering morphology, rather than lignotubers.

Genomic and paleoclimatic studies suggest that the quick-growing lignotuberous shrub, *Telopea speciosissima* (Proteaceae), which often occurs with *Banksia paludosa* subsp. *paludosa* (Blue Mtns), was reduced to refugial populations during the LGM but subsequently expanded from these refugia in the warmer Holocene as conditions became more suitable (Rossetto et al., 2012). In contrast, it is possible that due to its relatively slow growth, and especially, its root suckering habit, *Banksia paludosa* subsp. *paludosa* (Blue Mtns) may have been advantaged, particularly during the LGM, which would have favoured heath vegetation in the upper Blue Mountains (Hesse et al., 2003). Its current fragmented distribution, however, suggests it may have been disadvantaged in the warmer Holocene, possibly outcompeted by quicker-growing trees and tall shrubs. However, root suckering would have allowed continued persistence in the higher fire frequencies of the late Holocene, at the same time compensating for any developing limitations in its sexual reproduction (studies of its breeding system would be interesting in this context). Subjected to the same past climatic conditions, populations of the rare root-suckering shrub, *Zieria covenyi* (Rutaceae) in the upper Blue Mountains, for example, have been reduced to just two known sites characterised by extensive clonality, with high genetic disparity between them, presumably as a result of paleo-historical isolation (Australian Institute for Botanical Science, 2020). Similarly, Millar et al. (2010) suggested that the rare *Banksia ionthocarpa* subsp. *chrysophoenix* is a derived lineage and that clonality developed in association with its more marginal environment and recurrent fires.

We recommend further genomic, taxonomic, and reproductive studies of *Banksia paludosa* subsp. *paludosa* and related taxa. Based on its root-suckering and clonal morphology, *Banksia paludosa* subsp. *paludosa* (Blue Mtns) may represent a distinct taxon. Identifying the extent of clonality within and among populations of *Banksia paludosa* subsp. *paludosa* (Blue Mtns) could also potentially inform our understanding of the history of this taxon within its current range.

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