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# Observations on root-suckering in *Hakea decurrens* subsp. *decurrens* (Proteaceae) in central west NSW, and its ecological implications for historical persistence in other *Hakea* taxa

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## Abstract

The nature and extent of root-suckering in the poorly-known shrub *Hakea decurrens* subsp. *decurrens* (Proteaceae) in central west NSW is described for the first time. We surveyed 15 groups of plants in fire-prone, eucalypt-dominated, dry sclerophyll woodland in two geographically separate areas. Root-suckering from shallow lateral roots was recorded across all populations, forming complex networks of variably connected clonal shrubs (ramets). Low intensity fire generally killed suckering plants back to the lateral roots, but depending on depth of soil coverage, lateral roots generally survived fire with evidence of subsequent resprouting from roots. While plants flower, fruit and produce viable seeds, we found no evidence of seedlings across our recently burnt or unburnt study populations.

Stress tolerator traits of root-suckering or basal resprouting occur in about a quarter of Sydney region *Hakea* species and are currently associated with localized fire persistence rather than expansion; these species occur across a range of soil and base-rock types and are likely to have coped well with the cold, Last Glacial Maximum conditions, and been more widely distributed. However, in the warmer, wetter Holocene Climatic Optimum conditions (6 000 yrs BP), and subsequently increasing fire conditions associated with ENSO, the distributions of these species are likely to have become more restricted, compared with fire sensitive seeders, which appear to be currently more successful competitively (particularly in new or disturbed environments). Geographic distributions and vigorous seedling recruitment suggest seeders currently have greater potential expansion capabilities. Therefore, as climate has changed over millennia, the relative abundances in the landscape of species with these alternative survival traits is likely to have fluctuated.

**Keywords**: persistence traits, stress tolerators, seeders, clonality, *Hakea* taxa, climate change, Holocene Climatic Optimum, ENSO influence

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## Introduction

Scientific interest in rooting systems in the Proteaceae family began with the investigation of cluster or Proteoid roots and their role (nonmycorrhizal) in the uptake of nutrients in low nutrient soils (e.g. Grierson and Attiwill 1989). In the 1970s fire ecology studies drew attention to morphological traits associated with fire recovery by basal sprouting in some species. This led to the recognition of lignotuberous responses in particular shrub taxa (particularly *Banksia*), analogous to that recognized in some eucalypt species, and implying a large, woody, underground regenerative organ capable of resprouting. The term *resprouter*, adopted from the then-expanding eucalypt fire ecology (Gill et al. 1981), was applied to species with this trait which was generally found to be consistent across its range. Species with resprouter morphology contrasted with *seeders*, species with no morphological adaptions to prevent individuals from death in fires, but with ecological traits associated with strong post-fire recruitment. Some 'species' with populations showing both response characteristics have been subsequently recognized as including separate species (e.g. *Hakea dactyloides* and *Hakea laevipes*; PlantNet 2026), although the expression of the two responses in other species may be related to the operation of differing degrees of fire intensity on different populations, and unrelated to taxonomy. Fire response traits in most resprouter Proteaceae have been reported as basal sprouting from existing plants. More careful observations have, however, recognized root-suckering or suckering from rhizomes (i.e. remote from the central base) in various West Australian *Banksia* (He et al. 2011, 2019; Lamont 1988; Witkowski and Lamont 1997) and in *Banksia marginata* in South Australia (Specht and Rayson 1957). Populations of *Banksia paludosa* subsp. *paludosa* in the Blue Mountains (NSW) only occur as obligate root-suckering populations; there is apparently no viable seed production, although some flowering and rare cone formation does occur (Baird and Benson 2022). These populations are geographically separated from southern populations of the typical lignotuberous *Banksia paludosa* subsp. *paludosa* and fire sensitive *Banksia paludosa* subsp. *astrolux*.

The remote-suckering form of resprouting occurs in *Grevillea* (either in conjunction with seed reproduction or infrequently in absence of seed production) in numerous species scattered across the major infrageneric groups (sensu Makinson 2000). *Grevillea obtusiflora* includes rhizomatous and sterile subsp. *obtusiflora* restricted to the Clandulla area in the Cudgegong River catchment, and rhizomatous but fertile subsp. *fecunda,* restricted to the adjoining, but east-flowing Capertee Valley. The ecological and conservation implications of the vegetative reproduction mode have only been analysed in depth for *Grevillea renwickiana* (James and McDougall 2014) and *Grevillea rhizomatosa* for which Gross et al. (2012) hypothesized that frequent fires drive selection for clonal reproduction at the cost of flowering; sexual functions are not maintained through selection, and the build-up of somatic mutations in meristems results in high genotype diversity at the cost of pollen and ovule fertilities.

Root-suckering has also been recognized in *Hakea*. The very restricted *Hakea asperma* persists vegetatively in East Gippsland by ramet production in the absence of seed production (Molyneux and Forrester 2009). Our interest in the occurrence of root-suckering in Proteaceae led to chance observations that revealed an interesting root-suckering network in the relatively little-known shrub *Hakea decurrens* subsp. *decurrens* in central west NSW. A point of interest is that a related subspecies, *Hakea decurrens* subsp. *physocarpa* is a seeder and has spread as a significant weed in southern Europe. Here we describe our field investigations and likely ecological significance of the rooting system of *Hakea decurrens* subsp. *decurrens* and consider the ecological implications of resprouter and seeder traits in various *Hakea* taxa.

## Methods

*Hakea decurrens* is widespread in southeast Australia occurring as three allopatric subspecies (Table 1). We searched AVH herbarium records of the three subspecies for any references to fire sensitivity or resprouting. *Hakea decurrens* subsp. *decurrens* was the only subspecies where root or rhizome suckering, resprouting, or clustering of plants suggestive of root or rhizome suckering, was noted in collection records.

We surveyed populations of *Hakea decurrens* subsp. *decurrens* in Wambool Nature Reserve and Clandulla State Forest (Central Tablelands, NSW), both locations with AVH records, in August and September 2025 to determine the extent of root-suckering, characteristics of the connecting root system, any evidence of basal resprouting from possible lignotubers, and the extent of flowering and fruiting. Root system investigations involved use of a trowel to carefully expose lateral roots associated with established living or dead plants, and tracing these roots to identify their extent, branching habit and presence of suckers. Any excavation was limited to about 5-8 cm of litter and surface soil. Following our investigations any excavated soil and covering litter was replaced.




**Figure 1.** Distribution of *Hakea decurrens* subsp. *decurrens* across central NSW (AVH records 2026).

**Table 1.** *Hakea decurrens* occurs as three allopatric subspecies with the following general distributions (from Australian Virtual Herbarium AVH 15/8/2025)

| |
|---|
| ***Hakea decurrens* subsp. *decurrens*** (see Figure 1)<br>Distribution: Restricted to NSW. Pilliga scrub south to Braidwood and Canberra,<br>Notes: Variable soils though low nutrients, upper slopes, sandy to clay, well drained. |
| ***Hakea decurrens* subsp. *platytaenia***<br>Distribution: Far South Coast in Nadgee NP and coastal heath in Ben Boyd NP (NSW), Wilsons Promontory (Victoria) and Flinders Island (Tasmania). |
| ***Hakea decurrens* subsp. *physocarpa***<br>Distribution: Victoria and Tasmania – widespread,<br>Notes: Confused with *Hakea sericea* in Europe where it is an invader. Fire sensitive. Barker et al. (1996) do not mention lignotuberous forms for either of the two Victorian occurring subspecies. |

## Results

### *Specimen information and informant responses*

Of 122 AVH specimen records of subsp. *decurrens*, root-suckers were only recorded on two occasions: Giles in 1953 from Mt Canobolas (Federal Falls) - *Shrub to 3 feet, often forming clumps due to suckering from roots. Rather rare*. There is no mention of subsp. *decurrens* in Hunter's (2002) description of the surrounding vegetation of Mt Canobolas State Recreation Area. The second record is by Rosemary Purdie in 2016 from Black Mountain, Canberra - *Species forms clumps through suckering/ shooting from exposed roots. Locally common. Shrub*.

Eight specimens included descriptive notes describing plants *as clumped or occasional*, consistent with localized root-suckering patches. For example: Hosking 2014 - *Two large clumps and over 30 smaller plants near clumps. Highest plants in clumps to 2m high*; McRaild 2022 - *Shrub. Patches of several plants to 2m tall, 1m diameter, short lived and dense, often much dead wood. Flowers and fruit profusely, young plants often evident*; Hadobas 1993 - *Shrub to 60cm x 60cm. Occasional populations of about 10 plants*. Two small discrete patches recorded near the junction of the Coxs River and Blackheath Creek in the Blue Mountains (Baird AVH record, 2004) had a high density of plant stems suggesting possible root-suckering (I. Baird, unpubl. obs.).

There are no references to fire impacts and no information on the fire response for this taxon in the official NSW Flora Response Database according to Liz Tasker (pers. comm. 9/10/25) but she had observed resprouting 2–12 months after fire in the Pilliga Scrub at all three field sites where she encountered it. It was noted that it may have been resprouting not only from the base but also from "rhizomes".

### *Field observations of populations in Wambool Nature Reserve and Clandulla State Forest*

Twelve groups of *Hakea decurrens* subsp. *decurrens* plants were examined in Wambool Nature Reserve near Bathurst and three groups of plants in Clandulla State Forest near Kandos. The Clandulla State Forest site was burnt in a low intensity prescribed burn in mid-2025 whereas the Wambool site was long unburnt. Observed patterns of growth were similar across all groups of plants. Plants occur in patches up to a radius of ~10m, but usually much less, separated by 100–500 m. In several cases, groups of plants were separated by vehicle tracks, suggesting that they were previously contiguous. All groups of plants occurred on ridges, slopes or elevated undulating terrain in fire-prone, dry sclerophyll open forest dominated by eucalypts, with an open understorey. Plants observed were growing in stony, clay-loam, sandy loam or sandy soils, and on metasedimentary geology.

Mature plants were up to ~2 m high, mostly <1.2 m, often with a single vertical stem (but sometimes multiple) arising from a lateral root and branching at various angles (Figures 2, 3). In many cases there were also multiple young suckers arising next to others from the same location on a lateral root (Figure 4). These plants were recorded with mature fruits and flowers in August and September 2025. Fruiting was limited, with large plants having 10–20 fruits and smaller plants <10. Some mature fruits had opened on dead broken branches, but fruits remained closed on live branches. Plants with flowers only were generally from 0.5–1 m high, plants <~0.5 m were non-fertile. European Honeybees were observed visiting flowers. No seedlings were identified at either site, regardless of fire history, but our survey at Clandulla was probably too soon after the fire for any seedlings to be evident. Small plants were all suckers from shallow lateral roots.



**Figure 2.** *Hakea decurrens* subsp. *decurrens* - Three single-stem shrub ramets (arrowed) growing from shallow lateral roots in dry sclerophyll woodland, Wambool NR August 14th 2025 (30 cm scale ruler).



**Figure 3.** *Hakea decurrens* subsp. *decurrens* - Older multi-stemmed shrub in flower (centre), with younger shrub ramets growing from lateral roots (arrowed), Wambool NR August 14th 2025.




**Figure 4.** *Hakea decurrens* subsp. *decurrens* - lateral root (R1) with very young sucker (S1) and branching root (R2) with multiple sucker shoots (S2) growing from the side and underside of R2. Apparently separate lateral root (R3) crosses over R2, has a single-stem sucker (S3) growing from next to the decaying stub of former continuing lateral root (R4), with two descending roots (R5) below. Wambool NR August 14th 2025 (30 cm scale ruler).

### *Rooting system in* Hakea decurrens *subsp.* decurrens

Investigation of horizontal roots revealed suckers along most of them and some branching of the roots in most, forming a complex network of variably connected shallow roots < 5cm diameter across the site, many <1cm, with suckering stems of different heights and thickness distributed along them (Figures 4, 5), including roots as small as 3mm diameter (Figure 6). Suckers generally arose from the upper root surface but also arose from the sides and undersides (Figure 4). Many root and sucker networks overlapped with each other, and it was difficult to discern the origin of individual networks or to extrapolate their complex developmental history (Figures 4, 7, 8). Lateral roots were consistently dark red when scraped, whereas stems when scraped were green/white, enabling differentiation between them.

Lateral roots were usually <3cm below the soil surface, often <1cm below, and covered with variable, although often thin layers of plant litter, and sometimes bare soil. Some larger roots had their upper surface exposed at the soil surface or with a litter layer covering only and thus more vulnerable to direct fire impacts. These roots, notably, gave the impression of being rhizomes rather than shallow lateral roots, and whole lateral root sections, or at least the apparently terminal section, with one or more stems arising from them, could often be lifted from one end without resistance from feeder roots or taproots (Figure 9).

Some lateral roots were dead and connected plants which had arisen as suckers from the root were also dead. In some cases, the terminal end of a lateral root was dead with a mature dead plant which had arisen as a sucker from it, but the root was still alive with living suckers of varying sizes occurring further back towards its apparent point of origin. Some large shrub stems had been burnt back almost to the top of a thick lateral root, but the root was still alive where it maintained some soil coverage. Some thick lateral roots had living stems at their end and elsewhere but also had a dead stem(s) which had developed as suckers in between (Figure 8).

In several cases we followed relatively thick lateral roots to where they terminated with a mature living shrub which had developed as a sucker. In some of these cases, there was evidence of a scar at the base of the stem on the opposite side from where the root was still connected, suggesting that the lateral root had previously continued but had subsequently died and rotted off back to the base of the surviving end sucker (Figures 4, 8). Evidence of a scar, however, was not always present. It is likely that the lateral roots with the least soil cover are the most vulnerable to fire impacts and we saw evidence of sections of lateral root networks which were dead, probably because of fire, as observed at Clandulla following recent fire. At Wambool we observed that resprouting from surviving lateral roots (from an earlier fire) occurs from new locations on the roots and from around the base of fire-killed stems where they originated from lateral roots.

In several cases, the end of the lateral root where it joined the last sucker (with no existing continuation of the root) formed a bend rather than a typical right-angled junction as occurs from a continuing lateral root, suggesting that the sucker itself was an extension of the root (Figures 8, 9). It is also possible that the sucker developed on a young root, that the continuing root subsequently died leaving no persistent scar, and with time, the connection from root to end sucker developed into a bend as the most efficient growth habit. Sometimes, these plants developing from the end of a lateral root and with a single stem would become top heavy and rollover to the ground, twisting and lifting the lateral root above soil level with no resistance from any secondary rooting system or taproots (Figures 8, 9). Rarely, what

appeared to possibly be the original plant from which a lateral root originated, or an established shrub from which it extended, had died, but the network of suckering plants arising from that plant's lateral root system were persisting to varying degrees at a distance from the root's point of origin. In one site at Wambool there was a cluster of old ~2m high plants (which had survived fire in a very small patch) with progressively smaller plants suckering from progressively finer roots radiating out from it, indicating that the cluster was expanding or reoccupying former area (Figure 10).

Larger plants often do not have any additional lateral roots (or apparent descending roots) branching from where they have developed initially as suckers, but in other cases they do and may have several additional smaller roots arising from the same location, either as secondary lateral roots or as possible descending feeder roots (Figure 11). These branching roots can also occur on lateral roots independent of the location of a sucker. Small suckers may also have additional smaller lateral root(s) originating from the point of connection, though one is usually dominant, suggesting a tendency to single directional root dominance. In some cases, lateral roots are divided into similar diameter roots and continued as such. We did observe lateral roots of different sizes with associated rootlets, larger feeder roots which did not appear to be typical lateral roots from which suckers arise, or larger descending roots, and in some cases a lateral root with suckers became a descending woody root which disappeared immediately or shortly after the last sucker (Figures 8, 11). Some larger shrubs arising from thicker lateral roots were well anchored in the ground with additional descending roots (Figures 7, 8, 11). In one case, we followed a thick lateral root for >0.5m from the base of a large plant before the root turned down and disappeared under rocks, perhaps becoming a sort of taproot or simply following the path of least resistance.

Death of individual plants arising from lateral roots is presumably associated with moisture conditions (drought), fire, mechanical damage, or perhaps just age. In the absence of recent fire, probably less than 10% of plants in any patch at Wambool were dead or dying.

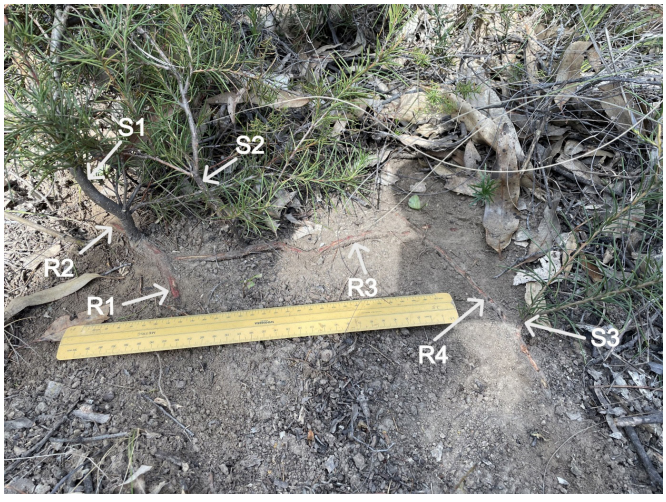



**Figure 5.** *Hakea decurrens* subsp. *decurrens* - Single stem shrub sucker (S1) from primary lateral root (R1) with smaller continuing root (R2), and lateral root branch (R3) with single-stem shrub sucker (S2). Separate lateral root (R4) crosses R3 and has a smaller branching single stem sucker (S3). Wambool NR August 14th 2025 (30 cm scale ruler).



**Figure 6.** *Hakea decurrens* subsp. *decurrens* - Small suckering stem growing from the top of a 3mm diameter shallow lateral root, showing no anchoring root connections. Wambool NR August 14th 2025.

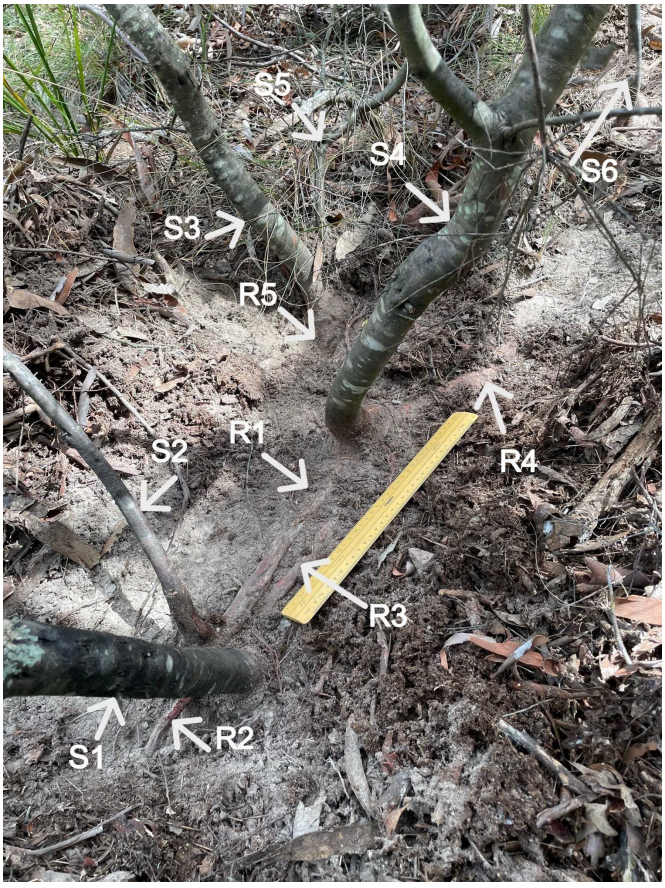



**Figure 7.** *Hakea decurrens* subsp. *decurrens* - Older group (see Figure 10) of connected single-stem shrubs (S1–S6) originating as suckers from lateral roots (R1–R5). This goup of stems were securely anchored with descending roots. Wambool NR August 14th 2025 (30 cm scale ruler).




**Figure 8.** *Hakea decurrens* subsp. *decurrens* - Complex network of suckers and lateral roots. Stem S1 (with evidence of former continuing lateral root) growing semi-upright at end of large lateral root (R1). Smaller lateral root (R2) from separate network crossing R1, with multiple young suckers (S2) in cluster, single sucker (S3) and smaller branching lateral root (R3). Live shrub S5, which has fallen over, apparently originated at the end of separate lateral root R5 where two large descending roots (R4) occur, has two dead ascending shrub branches (S4). Wambool NR August 14th 2025 (30 cm scale ruler).

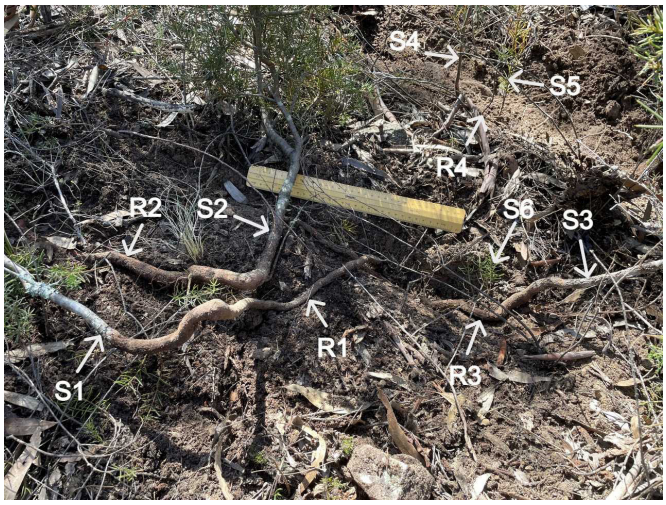



**Figure 9.** *Hakea decurrens* subsp. *decurrens* - Three single-stem shrub ramets (S1–S3) appearing as extensions of their respective lateral roots (R1–R3), all with right-angled bends where they have originally grown upwards as suckers before toppling over due to lack of anchoring roots. Small young suckers (S4 & S5) from small separate lateral root (R4) and small sucker (S6) from underside of R3 shown. Wambool NR August 14th 2025 (30 cm scale ruler).




**Figure 10.** *Hakea decurrens* subsp. *decurrens* - Patch of previously unburnt ~2m high, single stem shrub ramets (1) with lateral root connections (see detail, Figure 7), and (2) expanding or reoccupying network of progressively smaller shrub ramets, on progressively finer lateral roots (see Figure 6). Wambool NR August 14th 2025.

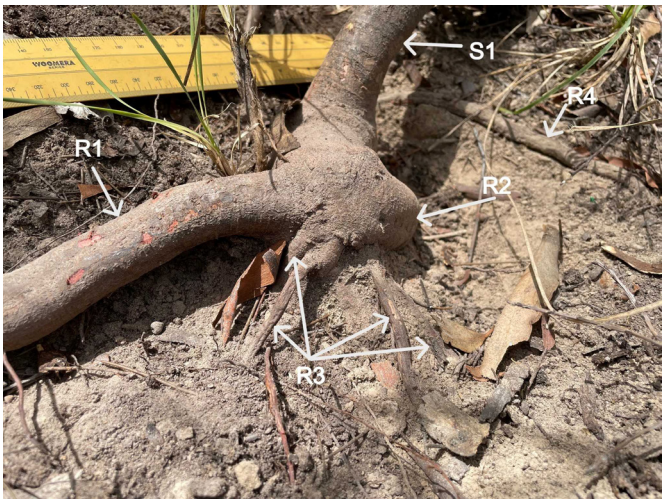



**Figure 11.** *Hakea decurrens* subsp. *decurrens* - Single stem shrub sucker (S1) at the end of lateral root (R1), with two large (one hidden) descending roots (R2) and four smaller descending feeder (anchor) roots (R3), and a separate shallow lateral root (R4) behind. Wambool NR August 14th 2025.

### *Fire effects*

We observed the survival of lateral root networks following a low intensity fire in Clandulla State Forest in mid-2025, but the connected clonal shrubs were typically killed by such fire, except for those in localised fire refugia (Figure 12). There was no vegetative regrowth, including new suckers, evident at the time of survey several months later. There was evidence of some lateral roots or sections thereof, particularly shallower or exposed roots, also being killed by fire. These observations at Clandulla were consistent with our observations at Wambool. We saw no evidence of serial resprouting from the base of fire-killed stems leading to the formation of any structure that could be referred to as a lignotuber.




**Figure 12.** *Hakea decurrens* subsp. *decurrens* - Fire-killed (1) and surviving (2) single stem ramets following a patchy low intensity fire in Clandulla State Forest. September 4th 2025.

## Discussion

### Hakea decurrens *subsp.* decurrens

For *Grevillea renwickiana* James & McDougall (2014) postulated triploidy-related floral sterility as a driver for a shift to vigorous and eventually obligate suckering that is allowing its current survival as a very small population. *Hakea decurrens* subsp. *decurrens* in populations from the Pilliga Scrub to Canberra, has a much more widespread occurrence but root-suckering is similarly likely to allow fire persistence in the current landscape. Recently burnt (probably May-June 2025) populations observed in Clandulla State Forest in September 2025, had above ground growth mostly killed and woody fruits open releasing seed; no vegetative regrowth was evident at the time. Nor is the species sterile. In contrast to the lack of seedlings observed at our study sites, wild collected seed appears to germinate well, and after planting, seedlings can be established successfully in cultivation (M. Brownhill, pers. comm. 21/04/26). A 7-year-old, seed-grown, fruiting plant (2m high) in a Katoomba garden, with friable soil and thick leaf litter, had no taproot but several spreading primary roots and smaller feeder roots.

The shallowness of the lateral roots is surprising however, and there was some evidence of larger exposed lateral roots, or parts thereof, having been burnt; fire might only be of benefit when subject to low intensity fire. The fire at Clandulla, in dry sclerophyll open forest with little or low understorey and limited ground cover, suggests a history of low intensity burning. A similar history was evident at the sites in Wambool Nature Reserve. The relatively open and low fuel understorey of the forest where the species grows is unlikely to be able to sustain a much higher intensity ground-layer fire which could potentially otherwise result in greater lateral root mortality and threaten persistence of the populations.

The spreading shallow roots, however, may also be important for drought survival, being able to pick up surface water from occasional showers across its relatively low rainfall range (600–1000 mm p.a.), with longevity allowing drought persistence. In current climatic conditions the small, localised clusters of plants are essentially persisting, except for some very localised patch expansion or recolonization of former area. Its genomic makeup is unknown although individual patches may include one or more networks of clonal plants (genets). Death of lateral root sections results in fragmentation of these networks of connected shrubs, so over time, patches will also include multiple groups of clonal networks functioning independently but consisting of the same clone.

### *Fire ecology in* Hakea: *Current success v. long-term survival*

*Hakea* species have large woody fruits with two seeds released on dehiscence after death or fire. Many are serotinous, retaining most seeds until canopy death, in fire, drought, or when individual branches are broken or die. Seeders are killed by fire and respond with post-fire seedling recruitment. These species are often short-lived and colonisers of disturbed sites (e.g., *Hakea sericea*, *Hakea teretifolia*). Resprouters may be long-lived. Some have relatively small lignotubers, e.g., *Hakea bakeriana* and *Hakea microcarpa* (Benson and McDougall 2000); others have large lignotubers; *Hakea laevipes*, with very long-lived individuals in stable sites may develop lignotubers 0.5-1 m in diameter presumably in response to a long history of periodic fires. Of the 13 mostly Sydney Basin *Hakea* taxa eight are seeders and four resprouters (Table 2).

### *But is one group more successful than another?*

The 13 Sydney area *Hakea* species can be arranged in five groups (clades) following Cardillo et al.'s (2017) *Hakea* phylogenies (Table 2). Seeders make up the majority in each group and in current fire-impacted environments, generally appear to be more successful ecologically than resprouters. For example, in Victoria, Enright and Goldblum (1999) found the seeder *Hakea decurrens* subsp. *physocarpa* showed faster height growth, higher seed production and higher seed viability than the resprouter, *Hakea rostrata* (only distantly related). The success of seeder *Hakea decurrens* subsp. *physocarpa* is also demonstrated by its extensive spread and success as an invader when introduced to overseas habitats (Gerber et al. 2024). An additional advantage might be allelopathy (Nogales et al. 2025). Other seeder species show similar success. *Hakea gibbosa* and *Hakea sericea* are invasive weeds in New Zealand and Europe (Jacobson et al. 2023, Van Valkenburg et al. 2024). *Hakea salicifolia* subsp. *salicifolia* is now a common environmental weed in Victoria and New Zealand, and is naturalised in South Australia and various countries.

The resprouters (resprouting, lignotuber or root-suckering) tend to have more restricted occurrences. The four species with persistence traits each fall within separate Sydney groups, suggesting resprouter traits may have arisen independently in each group. *Hakea decurrens* subsp. *decurrens* was not included in Cardillo et al. (2017) but its other two subspecies, *physocarpa* and *platytaenia,* cluster with *Hakea sericea* and *Hakea gibbosa,* both successful seeders. If subsp. *decurrens* is also in this clade, it would be the only resprouter in a group of seeders, and similar to other resprouters in being relatively restricted in occurrence; it is not sympatric with its other subspecies.

An interesting comparison of closely related species with contrasting fire response traits is between *Hakea dactyloides* (killed followed by seedling recruitment -Bradstock et al. 1994) and *Hakea laevipes* (resprouting from lignotuber with little seeding recruitment reported -Benson and McDougall 2000). These are genomically sister species in Cardillo et al. (2017) and equally common with similar overall Sydney Basin sandstone and Tablelands distributions (Figure 13), and soil/climate requirements. *Hakea dactyloides* tend to occur in woodland and heath and *Hakea laevipes* mainly in heath.

**Table 2. Sydney Basin *Hakea* taxa showing distribution, habitat and survival/fire response. *Hakea decurrens* subspecies included. Resprouters in bold (Species groups based on Cardillo et al. 2017).**

| *Hakea* taxa | Distribution | Botanical Subregion | Habitat | Elevation m | Fire response |
|---|---|---|---|---|---|
| **Group 1** | | | | | |
| *H. sericea* | Widespread | CC CT NC ST Q | Woodland, sandstone, clay | 0–1000 | killed |
| *H. gibbosa* | Coast/plateaus | CC SC | Scrub on coastal cliffs | 0–300 | killed |
| *H. decurrens* subsp. *physocarpa* | Victoria, Tasmania | SC V T | Woodland | 0-300 | killed |
| H. *decurrens* subsp. *platytaenia* | South coast Vic, Tasmania | SC V T | Heath | 0-300 | killed? |
| ***H. decurrens* subsp. *decurrens*** | **Central NSW** | **CT ST NWS CWS SWS NWP** | **Woodland** | **300-900** | **root-suckers** |
| **Group 2** | | | | | |
| *H. constablei* | Upper Blue Mtns | CC CT | Rocky outcrops, cliffs | 500–1100 | killed |
| *H. pachyphylla* | Upper Blue Mtns | CT ST | Mallee heath | 1000–1100 | killed |
| *H. propinqua* | Widespread | CC CT | Rocky ridges, plateaus | 0–1100 | killed |
| ***H. bakeriana*** | **Hornsby plateau** | **NC CC** | **Ridges, hillsides** | **0–300** | **resprouts, lignotuber** |
| **Group 3** | | | | | |
| *H. salicifolia* subsp. *angustifolia* | Coast Hornsby-Helensburgh | CC | Riparian scrub, creeks | 0–100 | killed? |
| *H. salicifolia* subsp. *salicifolia* | Widespread | CC CT NC NT SC | Gullies, ridges, moist open forest | 0–1200 | killed |
| ***H. microcarpa*** | **Tablelands** | **SC NT CT ST Q V T** | **Wet places near creeks** | **600–1200** | **lignotuber** |
| **Group 4** | | | | | |
| *H. dohertyi* | South Blue Mtns restricted | CT | Dry rocky ridgetops | 100–1100 | killed |
| *H. dactyloides* | Coast, Tablelands | CC SC CT ST CWS V | Slopes, ridges, watercourses | 0–1200 | killed |
| ***H. laevipes*** | **Coast/ranges** | **NC CC SC CT ST** | **Slopes, ridges** | **0–1000** | **lignotuber** |
| **Group 5** | | | | | |
| *H. teretifolia* subsp. *teretifolia* | Blue Mtns to Braidwood | NC CC ?CT ST | Sandstone heath | 0–1000 | killed |
| *H. teretifolia* subsp. *hirsuta* | Coastal Sydney to Tasmania | CC SC CT ?ST | Coastal heath | ? | ? |

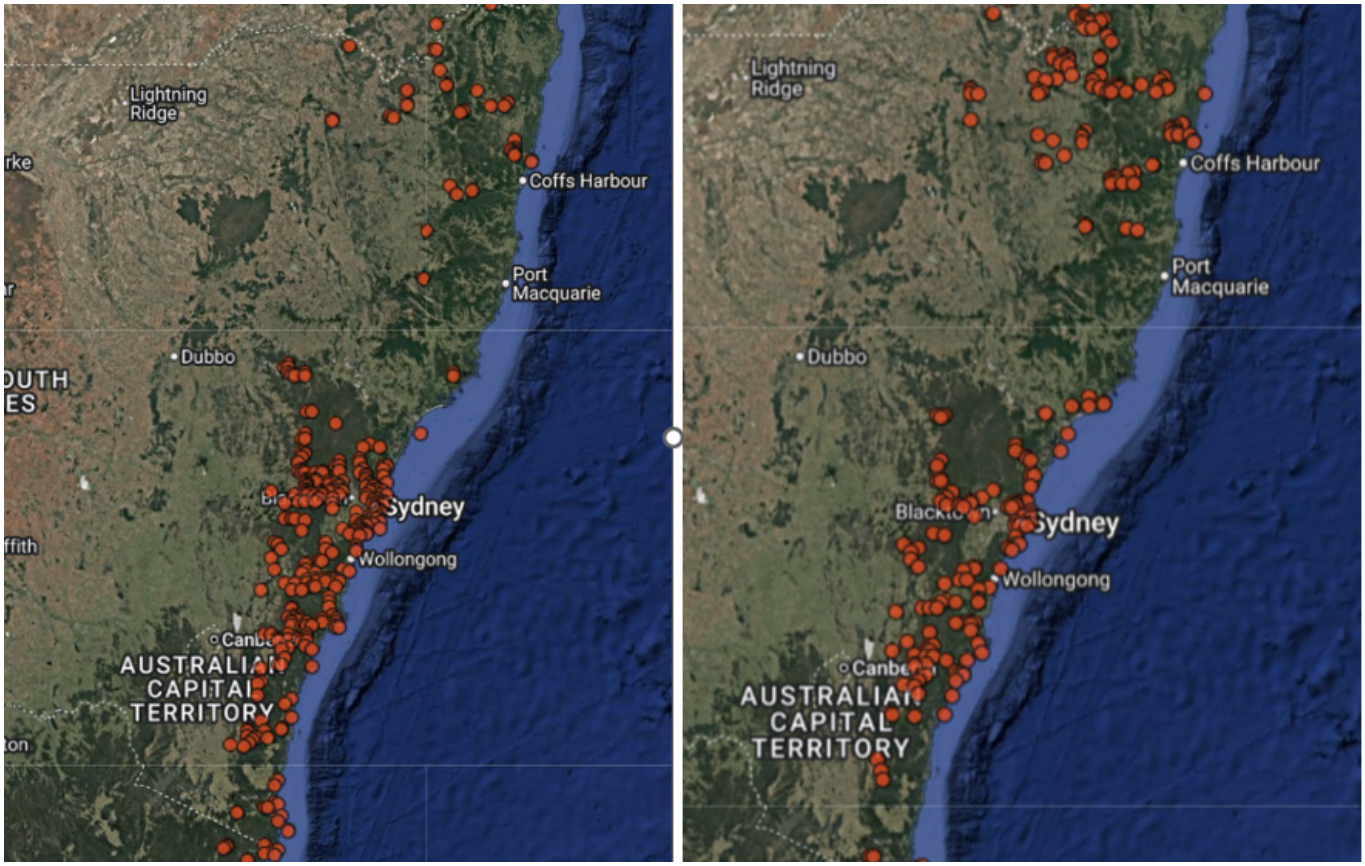



**Figure 13.** Distribution map of *Hakea dactyloides* (LEFT) and *Hakea laevipes* (RIGHT). Much of the northern occurrence of *Hakea laevipes* is subsp. *graniticola* (AVH 2026).

### *Ecological and historical success*

Evolutionary survival, even in the short term, has to cope with historic periods of climatic change. In *Hakea* an evolutionary history over 15 million years has involved geographic expansion and speciation into adjacent habitats in southwestern Australia, with shifts into the Arid zone since the early Pleistocene or in association with contraction of coastal wet forest habitats to coastal margins of eastern Australia (Lamont et al. 2016, Cardillo et al. 2017).

Climate changes in the last 100 000 years suggest that the ecological success of species with either persistence or competitor traits is likely to have alternated. During the dry and cold conditions of the Last Glacial Maximum, 20 000 years ago, species with persistence traits such as resprouting, longevity and slow growth are likely to have coped best, particularly at higher elevations (Benson 2024). This would have applied to the resprouter species of *Hakea*. The warmer and wetter conditions leading to the Holocene Climatic Optimum, however, are likely to have promoted quick growth and vigorous seedling recruitment traits, benefiting the spread of seeders, including *Hakea* species, particularly with their seedlings needing good growing conditions for establishment. In the last 6 000 years with the ENSO influence the increasing incidence of fire is likely to have further favoured seeder species in more mesic sites while limiting the spread of resprouter species to persistence in open stable sites, such as sclerophyll heath.

Over time, therefore, the relative abundance of species with these alternative survival traits appears to have changed and is likely to continue to change in response to warming climatic trends. A possible historical scenario for *Hakea dactyloides* and *Hakea laevipes* is that during alternating glacial/interglacial cycles, the two species have co-occurred, but with alternating abundance and geographical extent. Stress tolerator *Hakea laevipes* could have coped and been widespread during the harsh, cold, short growing season conditions of the LGM, while seeder *Hakea dactyloides* was perhaps confined at that time to coastal refugia. In the ENSO warming conditions and with increased fire *Hakea dactyloides* was able to spread. At the same time, despite its persistence and longevity, *Hakea laevipes* was gradually confined to harsher sites, generally without tree competition. Despite different strategies, both species can occupy the landscape at the same time, with success fluctuating with long-term climate trends.

Similarly, the seeder *Hakea decurrens* subsp. *physocarpa* is widespread and currently successful in invading new habitats. In contrast, subsp. *decurrens*, though geographically widespread (Pilliga Scrub to Canberra), now occurs in small, localised populations where its root-suckering traits may have allowed persistence during perhaps millennia of increasingly unfavourable conditions, which are probably ongoing. Though its suckering networks indicate some degree of clonality, some patches of plants may include more than one unique clonal network (genet), as plants flower, fruit and evidently produce viable seed. This suggests there is likely to be some genetic diversity at least within studied populations. While *Hakea*

*decurrens* subsp. *decurrens* benefits from root-suckering and seeding capability, its local populations appear geographically relatively confined and isolated from others. However, compared with *Hakea asperma* which has lost seed production functionality, only persisting vegetatively by ramet production, and with very limited geographical occurrence and genetic diversity, the future persistence of *Hakea decurrens* subsp. *decurrens* is perhaps better assured in terms of reproduction-related selection pressures, though its populations may be vulnerable to increased temperatures and drying conditions associated with ongoing climate change.

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## References

Baird, I.R.C. and Benson, D. (2022) Root-suckering and clonality in a Blue Mountains *Banksia* taxon (Proteaceae). *Proceedings of the Linnean Society of New South Wales* 144: 109-127.

Barker, R.M., Barker, W.R. and Haegi, L. (1996) *Hakea*. In: Walsh, N.G.; Entwisle, T.J.,†*Flora of Victoria Vol. 3, Dicotyledons: Winteraceae to Myrtaceae*†, pp. 870–882. Inkata Press, Melbourne.

Benson, D. (2024) Vegetation Patterns across the Sydney Basin during the Last Glacial Maximum based on plant biogeography, ecology, geomorphology and climate. *Proceedings of the Linnean Society of New South Wales* 146: 1-47.

Benson D. and McDougall, L. (2000) Ecology of Sydney plant species: Part 7b Dicotyledon families Proteaceae to Rubiaceae. *Cunninghamia* 6(4): 1016–1202.

Bradstock, R.A., Gill, A.M., Hastings, S.M. and Moore, P.H.R. (1994) Survival of serotinous seedbanks during bushfires: comparative studies of *Hakea* species from southeastern Australia. *Australian Journal of Ecology* 19: 276-282. DOI

Cardillo, M., Weston, P.H., Reynolds, Z.K., Olde, P.M., Mast, A.R., Lemmon, E.M., Lemmon, A.R. and Bromham, L. (2017) The phylogeny and biogeography of *Hakea* (Proteaceae) reveals the role of biome shifts in a continental plant radiation. *Evolution* 71(8): 1928-1943. DOI

Enright, N.J. and Goldblum, D. (1999) Demography of a non-sprouting and resprouting *Hakea* species (Proteaceae) in fire-prone *Eucalyptus* woodlands of southeastern Australia in relation to stand age, drought and disease. *Plant Ecology* 144: 71-82. DOI

Gerber, D., Azevedo, J.C., Nereu, M., de Oliveira, A.S., Marchante, E., Jacobson, T.K.B. and Silva, J.S. (2024) *Hakea decurrens* invasion increases fire hazard at the landscape scale. *Biological Invasions* 26(11): 3779-3793. DOI

Gill, A.M., Groves, R.H. and Noble, I.R. (1981) *Fire and the Australian Biota*. Australian Academy of Science, Canberra.

Grierson, P.F. and Attiwill, P.M. (1989) Chemical characteristics of the Proteoid root mat of *Banksia integrifolia* L. *Australian Journal of Botany* 37: 137-143. DOI

Gross, C.L., Nelson, P.A., Haddadchi, A. and Fatemi, M. (2012) Somatic mutations contribute to genotypic diversity in sterile and fertile populations of the threatened shrub, *Grevillea rhizomatosa* (Proteaceae). *Annals of Botany* 109(2): 331-342. DOI

He, T., Lamont, B.B. and Downes, K.S. (2011) *Banksia* born to burn. *New Phytologist* 191: 184-196. DOI

He, T., Lamont, B.B. and Pausas, J.G. (2019) Fire as a key driver of Earth's biodiversity. *Biological Reviews*, 94: 1983-2010. DOI

Hunter, J.T. (2002) Vegetation and floristics of Mount Canobolas State Recreation Area, Orange, New South Wales. *Cunninghamia* **7**: 501-526.

Jacobson, T.K.B., Gerber, D. and Azevedo, J.C. (2023) Invasiveness, monitoring and control of *Hakea sericea*: a systematic review. *Plants* 12(4): 751. DOI

James, E.A. and McDougall, K.L. (2014) Spatial genetic structure reflects extensive clonality, low genotypic diversity and habitat fragmentation in *Grevillea renwickiana* (Proteaceae), a rare, sterile shrub from south-eastern Australia. *Annals of Botany* 114: 413-423.

Lamont, B.B. (1988) Sexual versus vegetative reproduction in *Banksia elegans*. *Botanical Gazette* 149: 370-375.

Lamont, B.B., He, T. and Lim, S.L. (2016) *Hakea*, the world's most sclerophyllous genus, arose in southwestern Australian heathland and diversified throughout Australia over the past 12 million years. *Australian Journal of Botany* 64(1): 77-88. DOI

Makinson, R.O. (2000) *Grevillea*, *Flora of Australia* 17A, ABRS/CSIRO: Australia.

Molyneux, W.M. and Forrester, S.G. (2009) A new *Hakea* species (Proteaceae: Grevilleoideae) from East Gippsland, Victoria. *Muelleria* 27(2): 224-226.

Nogales, L., Alías, J.C., Blanco-Salas, J., Montero-Fernández, I. and Chaves, N. (2025) Allelopathy and identification of allelochemicals in the leaves of *Hakea decurrens* subsp. *physocarpa* WR Barker. *Plants* 14(11): 1646. DOI

PlantNet NSW. 2026. FloraOnline. URL

Specht, R.L. and Rayson, P. (1957) Dark Island heath (Ninety-mile Plain, South Australia). III. The root systems. *Australian Journal of Botany* 5: 103-114. DOI

Stacy, H. (2015) The Flowering of *Hakea bakeriana*: Enjoyment for half a lifetime. *Hakea study group newsletter* no. 57, Australian Native Plant Society, Australia.

Van Valkenburg, J.L.C.H., Beyer, J., Champion, P., Coetzee, J., Diadema, K., Kritzinger-Klopper, S., Marchante, E., Piet, L., Richardson, D.M. and Schönberger, I. (2024) Naturalised *Hakea*. What species are we actually talking about in Europe? *Botany Letters*, 171(3): 357-370. DOI

Witkowski, E.T.F. and Lamont, B.B. (1997) Does the rare *Banksia goodii* have inferior vegetative, reproductive or ecological attributes compared with its widespread co-occurring relative *B. gardneri*? *Journal of Biogeography* 24: 469-482. DOI