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Fig. 2.4: Fire dependence. (*upper*) *Nuytsia floribunda* (Loranthaceae), 3 m tall, in the first flowering season after a wildfire (November-January) (*upper left*) compared with the flowering season 3 years later (*upper right*). This species survives fire and produces new growth from protected buds hidden within the stem. Flower production occurs 10 months after a fire, followed by the formation of new foliage (called protanthy) (Lamont & Downes, 2011). It is an example of facultative fire-stimulated flowering. (*lower left*) After a summer-autumn fire *Stirlingia latifolia* (Proteaceae) produces numerous new shoots arising from an underground lignotuber, followed by a profuse production of panicles during the spring (seranthy). (*lower right*) *Pyrorchis nigricans* (Orchidaceae) is entirely dependent on fire for flowering (obligate), producing foliage before flowering (seranthy) (photo taken by S. Spencer). Obligate fire-stimulated flowering occurs in many SouthWest orchid species (Lamont & Downes, 2011). —— 42

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Fig. 3.3: Stomatal responses and leaf morphology are important drivers of a species summer water-use response in temperate SouthWest woodlands. Species response occurs along a water-use spectrum, varying from drought dormant (extremely drought tolerant) to water-expensive. Summer drought responses in the SouthWest flora are a function of position in the landscape, underlying hydrology, species rooting depth and xylem cavitation resistance. (*lower left*) Salmon gum (*Eucalyptus salmonophloia*), a deep-rooted tree species that transpires large amounts of water all year round. Deep roots enable this species to access soil moisture (or groundwater) at considerable depth during dry summers. (*lower right*) *Olearia muelleri* (Asteraceae) a shallow-rooted shrub small species that tolerates drought by becoming summer

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'dormant' and displaying significant osmotic adjustment and stomatal closure. Figure adapted from Mitchell *et al.* (2008a). —— **65**

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along watercourses in the SouthWest. (*right*) *Allocasuarina fraseriana,* 5 m tall, though nodules have yet to be found on this species. —— **94**

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Fig. 6.5: Tripartite relationship between a mycophagous marsupial (*Bettongia*), ectomycorrhizal fungi and their host plant species. Adapted from Lamont *et al.*, 1985. —— **104**

Fig. 6.6: Proteoid roots of (*upper left*) 3-month-old *Hakea lissocarpha* (Proteaceae) root, displaying successive formation of root clusters — from recently formed (lower) to senescent (upper). Middle cluster is 8 cm long. (*upper middle*) *Viminaria juncea* (Fabaceae) showing two clusters, as well as root nodules and pneumatophores (roots for aeration that point up into the water when flooded). Larger cluster is 5 cm long. (*upper right*) A cluster of dauciform roots on the sedge, *Cyathochaeta avenacea* (Cyperaceae). Scale = 1 mm. (*lower left*) *Hakea prostrata*, widespread through the SouthWest, with axillary flower clusters protected from florivores by rigid 4-cm-long leaves with a sharp apex. 2-mm-wide transverse section of one of its young proteoid roots (*lower right,* stained with safranin and fast green), with the rootlets arising in seven rows from the stele and often in pairs, explaining how it may have up to 1,000 rootlets per cm length of parent root. —— **105**

Fig. 6.7: The root system of *Kingia australis*. (*upper left*) Two plants 1.8 and 2.3 m tall with crowns of flower spikes. Undulations on the persistent leaf bases correspond to annual growth increments (Lamont & Downes, 1979). (*upper right*) Leaf bases removed to reveal rings of aerial roots running down the stem from near the apex. In young plants they are produced annually but in older plants their production is stimulated by fire (Lamont, 1981a). Section is 10 cm wide. (*lower left*) Transverse section of caudex 20 cm above ground to show ring of root primordia on the 6-cm-wide stem surrounded by hundreds of aerial roots pushing through the leaf bases. *(lower right*) lateral roots proliferate in the spaces between leaf bases and may sometimes be seen protruding beyond them. Squares are 1 cm. —— **107**

Fig. 7.1: (*upper*) *Diplopeltis huegelii* (Sapindaceae), a monoecious species (i.e both female and male flowers on the same plant). *(left*) Female flower, with vestigial stamens that fail to mature, with ovary. *(right*) Male flower with no style or ovary but prominent stamens. To the left is a fruit with three carpels that developed from the female. Flowers 1 cm wide. (*lower*) female inflorescences of dioecious *Allocasuarina* (Casuarinaceae) (*left*) *A. humilis* with 5 mm wide inflorescences. (*right*) *A. campestris* with 4-cm long cone with woody bracts protecting the fruits to the left of the female inflorescence. *Allocasuarina* female flowers have long protruding styles that enhance their ability to collect wind-dispersed pollen produced by male flowers on separate plants. —— **110**

Fig. 7.2: Overview of angiosperm breeding mechanisms. —— **111**

Fig. 7.3: Protandry in the genus *Eucalyptus*. Photograph is of a recently opened flower of *E. caseia*, 3 cm wide, with inner stamens erect. —— **112**

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Fig. 7.4: Protandry in the genus *Pimelea*. Photograph is of *Pimelea aeruginosa*, capitulum 3 cm wide. —— **112**

Fig. 7.5: Protandry in the family Goodeniaceae, showing the function of the indusium. Photographs are of *Lechenaultia macrantha* (wreath lechenaultia). (*left*) flower with reddish indusium visible enveloping the hidden stigma, (*centre*) close up of pollen-laden indusium, (*right*) entire plant in full flower. Flowers are 2.5 cm diameter, plant 40 cm diameter. —— **113**

Fig. 7.6: Protandry in the genus *Banksia* involves a pollen presenter, a swollen spindle-shaped tip on their elongated styles. Photographs are of *B. menziesii* (*left*) with open florets a predominantly yellow colour due to the yellow pollen presenters. Unopen florets are predominantly red due to the colour of the style and perianth. (*right*) close up of florets at the transition zone (between open and unopened florets) with the yellow pollen presenter (pollen already removed by birds) prominent on the open florets. —— **114**

Fig. 7.7: Pollen presenters in (*left*) *Petrophile linearis* and (*right*) *Isopogon dubius*. A change in colour, from yellow to orange-red, occurs after the removal of the deposited pollen, and as the stigma becomes receptive. Note pollen grain adhering to tip of pollen presenter in red condition of *I. dubius*. Pollen presenters 5 mm in length. —— **114**

Fig. 7.8: Protandry in the genus *Grevillea*. Diagram depicts the positioning of the pollen presenter in close proximity to the anthers in the closed flower. Immediately before the flower opens, pollen is deposited onto the pollen presenter. The stigma then springs aloft carrying the pollen to a position where it will be scraped off the presenter by a pollinator feeding from the nectary. From Lamont (1982) for *G. leucopteris* that is mainly pollinated by night-flying beetles (*Pachytricha* spp.) that spring open the flowers as they move over the panicle and deposit pollen on flowers in the pistillate condition. Photograph shows various stages of flowering in *G. wilsonii*, fully open flower 4 cm long. —— **115**

Fig. 7.9: Protandry in the genus *Persoonia*. Flowers, 15 mm long, are of *Persoonia saundersiana*. —— **116**

Fig. 7.10: (*upper)* A Bombyliid fly (*Aleucosia tridentata*) feeding on the nectar of *Stylidium scandens* with the androgynoecious column hidden below the 7 mm long petals (*left*). When triggered by touch the column bends in less than 30 milliseconds, hitting the fly with considerable force. In the left image pollen is visible on the fly's dorsal abdomen confirming it has previously visited another *Stylidium* recently, although the positioning of the triggered column (*right*) on the fly suggests it may have been a different species. Images provided by Lochman Transparencies. (*lower*) Recurved column of *Stylidium bulbiferum* (arrows) before and after it has been triggered by touch. Flower 15 mm across. —— **117**

Fig. 7.11: Bird-pollinated *Eremophila maculata* (latin for spotted in reference to the markings on the inside of the corolla) flower, 4 cm long, in male condition, with ripe anthers brushing against the bird when it probes for copious nectar in the 'gullet' (*left*) followed after a day by the flower in the female condition with the stigma now protruding beyond the spent anthers so this is met first when the bird visits (*right*).—— **118**

Fig. 7.12: Flowers of facultative autogamous species. (*left*) *Thysanotus multiflorus*. Flower is 1.5 cm long. (*middle*) Various permutations of autogamy prevail in *Thelymitra*. Pictured *is T. villosa*. Flower is 3 cm long. (*right*) *Calochilus uliginosus* is a terrestrial orchid possessing a labellum covered in dense, long red or blue hairs. All *Calochilus* species are Scollid wasp-pollinated, but will self-pollinate if wasp-mediated pollination does not occur within the day. Flower is 1.5 cm long. *Thelymitra* and *Calochilus* provided by Allen Lowrie. —— **119**

Fig. 7.13: Large floral bracts aid pollination. (*left* to *right*) Red-coloured bracts attract birds as in *Pimelea physodes* (Thymelaeaceae) (flower head 5 cm long), *Diplolaena grandiflora (Rutaceae)* (flower head 4 cm wide), and *Darwinia meeboldii* (Myrtaceae) (flower head 5 cm long) are both bird-pollinated. *Banksia* (*Dryandra*) *proteoides* (*far right*) produces orange-brown floral bracts

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surrounding a head of florets (capitulum is 10 cm long) that is pollinated by small mammals (marsupials and rodents). —— **120**

Fig. 7.14: (*upper left***)** *Conostylis setosa* (Haemodoraceae). Head is 4 cm wide. (*upper right*) *Melaleuca radula* (Myrtaceae). Flowers are pink ageing to white. Spike is 5 cm long. (*lower left*) *Verticordia huegelii* (Myrtaceae). Flowers are creamish-white ageing to a dark maroon. Note the flowers form an overall attractive surface (corymb) of colour. Individual flowers are 12 mm wide. (*lower right*) *Hakea aculeata* (Proteaceae) flowers are white aging to yellow. Axillary cluster is 5 cm wide. —— **121**

Fig. 7.15: *Banksia ilicifolia* (Proteaceae), one of the few species that exhibits flower colour change at the inflorescence rather than individual flower level and, in addition, is predominantly visited by birds. (*left*) young flower head, 5 cm wide, and (*right*) 5-day older flower head. That it is the only one of five co-occurring banksias that shows colour change has been attributed to the facts that it has by far the smallest flower heads and its distribution is much patchier than the others (restricted to winter-damp depressions). By directing birds to the most rewarding heads, colour change appears to enhance foraging and pollination efficiency without reducing the tree's overall attractiveness since yellow and red heads are equally visible, so increasing its relative fitness. —— **122**

Fig. 7.16: Extrafloral nectaries (EFNs) are universal on the leaves and phyllodes of SouthWest acacias. They can be grouped into three types: (*left*) sessile (e.g. 2-mm-long in *Acacia iteaphylla*), (*middle*) sunken (e.g. 1.5-mm-wide in *A. aneura* which also possesses T-shaped and glandular hairs in lines along its terete phyllode) and (*right*) stalked (e.g. 2.5-mm-long in *A. pulchella* also showing thorn in axil). Ants feeding from EFNs: (*left*) *Iridomyrmex bicknelli* on *Adenanthos cygnorum* – note how the 2-mm-wide EFNs surround the new foliage in the centre, and (*right*) *Iridomyrmex* aff. *conifer* on *A. cuneata* – note flower at lower left surrounded by young 30-mm-long, red leaves perhaps serving as a supplementary attractant to bird pollinators? Nectar produced by ant-attracting EFNs is not accessible to birds as the amount is so small. —— **124**

Fig. 8.1: Examples of the taxonomic, stuctural and colour diversity within insect-pollinated flowers in the SouthWest flora. —— **129**

Fig. 8.2: *Grevillea leucopteris* has all the characteristics of a species pollinated by night-active insects. (*upper left*) two plants with naked scapes holding thousands of white flowers during spring up to 4 m above the scrub-heath in the northern sandplains. (*upper right*) Flowers in terminal panicles of racemes, 8-12 cm long, open towards the apex suggestive of an adaptation to flying pollinators. (*lower*) Giant scarab beetles, *Pachytricha* spp., 4 cm long, are the main pollinators. —— **130**

Fig. 8.3 *Verticordia* (Myrtaceae) is an advanced genus with highly modified flowers in a family that stretches back 65 million years. All but two of the known 104 species are endemic to the SouthWest (George & Pieroni, 2002; George & Barrett, 2010). (*lower left*) *V. nitens* is a slender shrub that appears top heavy because of the broad surfaces of brilliant orange flowers (corymbs) it produces in early summer atop a thin main stem, 0.5–1.75 m tall. This species is locally abundant in the understorey of banksia low woodland of the Swan Coastal Plain. The corymbs act like a single large flower (pseudanthium) as a device for enhancing attractiveness to pollinators, serving as a landing platform and facilitating movement from one flower to the next. Unlike many other oligolectic verticordias that present their pollen to visitors (Lamont, 1985a), *V. nitens* has a specialist pollinator (monolectic), a tiny solitary bee, *Euryglossa morrisoni* (Colletidae), that is entirely reliant on this verticordia for its nutrition (Houston *et al.*, 1993). (*upper left*) a female bee squeezing the hood of an anther with its mandibles and lapping up the pollen–essential oil mix from the terminal spout through which it is released. Note globs of pollen on its head and thorax. Flowers, 8 mm wide, with their highly reflective petals and hypanthium make the specific name, *nitens* (latin for shining) most appropriate. (*upper right*)

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a male bee lapping up nectar from the floor of the hypanthium and receiving oily pollen or brushing pollen onto the central stigma. (*lower right*) Scanning electron micrograph showing individual flower of *V. nitens* with its 10 fertile stamens: h = helmet cover over anther, s = spout through which oily pollen is passed to the bee. The dearth of nectar and the inaccessibility of both nectar and pollen appear to explain the lack of visits by larger pollinators and nectar robbers. In the absence of *E. morrisoni*, seed set is negligible. —— **132**

Fig. 8.4: *Praecoxanthus aphyllus* (*upper left*) emits a fragrant floral scent that predominantly attracts bees and prominent yellow calli on a purple and green labellum that superficially resemble pollen-bearing stamens. Flower is 4 cm wide. *Lyperanthus serratus* (*upper right*) is characterised by dense white calli that also superficially represent stamens. Flower is 5 cm wide. (*lower left*) *Ericksonella saccharata,* once classified as a *Caladenia*. Little is known about the pollination of this monotypic species. Flower is 2 cm wide. (*lower right*) *Eriochilus scabr*a is probably food deceptive and attracts native bees. Flower 3 cm wide. *Ericksonella* image provided by *Esperence Wildflowers.* All other images provided by Mark Brundrett. —— **136**

Fig. 8.5: (*left*) *Cyrtostylis robusta* produces nectar in a small reservoir at the base of the long, pointed labellum that runs down a narrow central groove and entices microdiptera (Hoffman & Brown, 2011). Flower length 15 mm. (*right*) *Prasophyllum regium* flowers are upside down (labellum faces upwards) and up to 25 mm long (Hoffman & Brown, 2011) and in this image a flower is being visited by a wasp. *Prasophyllum* image provided by Mark Brundrett. *Cyrtostylis* image courtesy of *Esperence Wildflowers*. —— **137**

Fig. 8.6:(two *upper rows*) Flowers of *Caladenia flava* and *C. latifolia* offer food rewards to potential insect pollinators, in contrast to the sexually-deceptive flowers of *C. roei, C. discoidea*, *C. attingens* ssp. *attingens* and *C. arenicola*. All sexually-deceptive *Caladenia* species are pollinated by thynnine wasps (Phillips *et al.*, 2009). Left image shows male *Phymatothynnus* wasps visiting flowers after being lured by sexually-deceptive volatile semiochemicals (as interpreted by Phillips *et al.*, 2009). (*third row*) *Prasophyllum* attracts insect pollinators with a sweet odour. Pictured is *Prasophyllum gracile*, the smallest member of the genus. Flowers are 5 mm in length. *Diuris longifolia* flowers (*middle*) utilise mimicry of co-occurring legume flowers (e.g. *Daviesia triflora; right*) to attract pollinators. (*last row*) The non-rewarding blue flowers of *Thelymitra crinita* appear to mimic native lilies (e.g. *Dianella*) or native irises (e.g. *Patersonia*). In contrast, the cream-flowered *T. antennifera* attracts pollinators of *Hibbertia* and *Goodenia* (Dafni & Calder, 1987; Bernhardt, 1995) – all reradiate strongly in the UV range. *T. apiculata* (*right*) closely resembles the flowers of *Calectasia* (Dasypogonaceae). Flower is 3 cm wide. Images of *C. discoidea* and *T. apiculata* provided by Mark Brundrett. Image of *C. attingens* provided by Allen Lowrie. —— **139**

Fig. 8.7: Fungal gnat pollinated orchids. *Rhizanthella gardneri* (*upper)* is obligately subterranean. Images of *C. discoidea* show that the tips of the enlarged fleshly bracts are the only part of the inflorescence that may protrude through the soil. In this image the soil surrounding the inflorescence has been removed to expose the 8-cm wide capitulum of deep red florets (6 mm in length), shown in close up on the right. (*lower*) *Pterostylis* (Greenhoods) often flower in autumn or winter when the gnats are most active (Brundett, 2007). *P. angusta* (*lower left*; flower length 30 mm) has the longest labellum of all SouthWest greenhoods that protrudes between two upright fused sepals. (*lower right*) *P. barbata* (bird orchid), flower length 50 mm, has a characteristic translucent flower and sparsely fringed labellum. *Rhizanthella* (except close up of florets) and *P. angusta* images provided by Mark Brundrett. *P. barbata* provided by Allen Lowrie. —— **141**

Fig. 8.8: Wasp pollinated orchids**.** All species emit pheromone-mimicking chemicals and have labella apices modified to resemble female wasp bodies. From top left to lower right: *Drakaea glyptodon* (hammer orchid), *Paracaleana triens* (flying duck orchid), *Cryptostylis ovata* (slipper orchid) and *Spiculaea ciliata* (elbow orchid). Except for *Cryptostylis*, all genera are pollinated

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by male thynnine wasp species within the genera *Zaspilothynnus* (*Drakaea*; Hopper & Brown, 2007), *Eirone* or *Thynnoturneria* (*Paracaleana*; Hopper & Brown, 2006, Peakall *et al.*, 2010; Bower, 2014) or *Thynnoturneria (Spiculaea;* Alcock, 2010*). Cryptosytlis* is pollinated by the male ichneumonid wasp, *Lissopimpla excelsa* (Gaskett, 2012). Flowers vary in length from 20 to 30 mm. Images provided by Allen Lowrie. —— **143**

Fig. 8.9: A male winged *Myrmecia urens* ant positioning itself sideways along the wide labellum of the sexually deceptive *Leporella fimbriata.* Labellum is 10 mm wide. Image provided of Mark Brundrett. —— **144**

Fig. 8.10: Examples of honeyeaters that are common in, but not necessariy restricted to, the SouthWest. Brown honeyeater (*Lichmera indistincta*), singing honeyeater (*Lichenostomus virescens*) and white-cheeked honeyeater *(Phylidonyris nigra*). All genera arose 6–8 Ma (Joseph *et al.*, 2014). Birds pictured are 14–20 cm in length, the brown honeyeater being the smallest honeyeater in the SouthWest. (*lower left*) The floral tube of *Anigozanthos rufus* (Haemodoraceae) is elongated and partially fused as a means of ensuring only honeyeaters are cabable of accessing the nectar reward, whereas in *Eucalyptus forrestiana* (Myrtaceae) (*middle*) the upright yellow stamens create a tunnel-like barrier to nectar seeking insects, but allows access to visiting honeyeaters. (*right*) *Leptosema daviesioides* (Fabaceae), known as the upside-down pea bush, produces large red flowers from the base of the plant (geoflorous). All flowers 4 cm long. Honeyeater images provided by Geoffrey Groom; floral images by *Esperance Wildflowers*. —— **146**

Fig. 8.11: Selected examples of bird-pollinated (honeyeaters) flowers in the SouthWest flora showing their great structural diversity. The larger flowers/inflorescences (*B. coccinea, E. rhodantha, H. francisiana, H. laurina*) may also be pollinated by small marsupials such as the honey possum. —— **147**

Fig. 8.12: Red wattlebird (*Anthochaera carunculata*) (*left*) sourcing nectar from a pendulous *Pimelea physodes* (Thymelaeaceae) inflorescence, the only bird-pollinated *Pimelea* (Keighery, 1975). Flower head 5 cm long. Western wattlebird (*Anthochaera lunulata)* (*right*) using the inflorescence of *Banksia speciosa* as a landing platform, feeding from recently opened nectar-producing florets. Western Wattlebird image provided by Lochman Transparencies. —— **148**

Fig. 8.13: *Gastrolobium celsianum* (*upper*) is bird-pollinated, displaying large red flowers, 35 mm long. (*lower*) *G. bilobum* is insect-pollinated, flowers 8 mm long. —— **149**

Fig. 8.14: (*upper*) Honey possum (*Tarsipes rostratus*), an obligate nectarivore, feeding from *Banksia* inflorescences (*left*) about to probe *B. benthamiana* that does not present its pollen, (*right*) probing 20-cm-long flower head of the rare *B. tricuspis* that presents its pollen on hooked styles so that pollen is combed through the possum's fur. It is a highly effective pollinator of *B. tricuspis*. (*bottom*) Western pygmy possums (*Cercartetus concinnus*) feeding on pollen and nectar from flowers of *Eucalyptus preissiana*, 5 cm wide. Because of the many stamens, pollen is deposited on their snouts, heads and ears. One individual is also using its forelimb to collect pollen. Image of *B. tricuspis* by Stephen van Leeuwen. Other images provided by Lochman Transparencies. —— **151**

Fig. 9.1: Variability in leaf size, shape and texture of the shrub and tree species in the SouthWest flora. Species are (from top to bottom, left to right: Margins are sharply mucronated (pointed) on the leaves of *Hakea amplexicaulis* (Proteaceae), *Banksia grandis* (Proteaceae), *Hakea horrida, Grevillea bipinnatifida* (Proteaceae), *Melaleuca huegelii* (Myrtaceae), *Calothamnus sanguineus* (Mytaceae) and *Hakea psilorrhyncha* (Proteaceae) whereas the soft compound leaves of *Acacia pulchella* (Fabaceae) are subtended by sharp thorns (photo shows the pinnae of *A. pulchella* bipinnate leaves folded together in response to the summer drought). Leaves vary in length from 15 cm in *H. amplexicaulis* to < 5 mm in *M. huegelii* and in thickness from 0.5 mm in *A. pulchella* to 3 mm in *H. psilorrhyncha* —— **155**

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Fig. 9.2: (*left)* A heteroblastic *Acacia* (Fabaceae) seedling displaying the transition from pinnate leaves (1), to an intermediate stage (2) where compound leaves are subtended by a vertically-flattened petiole to the formation of phyllodes only (3). Seedling is 25 cm tall. (*right*) Selection of 'leaves' within the genus: (*top*) bipinnate leaves of *A. pulchella* each basal to a 12-mm-long thorn. This is a member of section *Pulchellae* that consists of species mostly in Western and Northern Australia that radiated 20–22 Ma (Miller *et al.*, 2013). (*middle*) Vertically-orientated phyllodes of *A. camptoclada* with a prominent central vascular vein (uninerved) that ends in a blunt spine. Phyllode 15 mm long. (*lower*) Phyllodes of *A. cochlearis* with prominent 3-4 raised veins (trinerved). Phyllode 35 mm long. Photos of *A. camptoclada* and *A. cochlearis* provided by *Esperance Wildflowers*. —— **158**

Fig. 9.3: The genus *Hakea*, with over 100 taxa in the SouthWest, contains the world's most sclerophyllous species (Wright *et al.*, 2004). Pictured are tranverse sections of the needle leaves of *(left*) *H. gilbertii* and (*right*) *H. subsulcata* that are widespread in the wheatbelt and mallee regions of the SouthWest (Chapter 1). The sections have been treated with fast green that stains cellulose, cytoplasm and cutin green and phloem blue, and safranin that stains liginin and tannin red and cutin pink. Conspicuous are the 'girders' of lignified fibres that strengthen the leaf and prevent collapse of the delicate chlorophyll-bearing double palisade during severe drought. The girders are topped by a tannin-bearing hypodermis that restricts light uptake and hence the heat load on the most exposed ridged parts of the leaf (Jordan *et al.*, 2005). There are also inner fibre groups wrapped around the vascular bundles that restrict water loss from the xylem. The inner parenchyma has walls thickened with lignin that increase the water-storing capacity of the leaf. Both the parenchyma and palisade have their vacuoles loaded with tannin that increases their osmotic concentration and assists in water retention through osmotic adjustment (Richards & Lamont, 1996). The cuticle is 2–3 times thicker than the epidermal cells and it rises over the sunken stomates (completely covering the opening) to form epistomatal cavities, sometimes with mucilaginous plugs in the substomatal cavities, all serving to restrict water loss further. These features help to explain why leaf-mass-area, as an index of sclerophylly, is higher among hakeas the lower the rainfall in the SouthWest independent of the N and P contents of the leaves (Lamont *et al.*, 2002). —— **160**

Fig. 9.4: (*left*) *Banksia petiolaris* showing its stoloniferous habit and erect leaves, 20–25 cm long, arising at ground level and known to survive for up to 13 years. (*right*) *B. baueri* is a 1.5 m tall shrub with 5–10 cm long leaves arranged at a slight angle to the horizontal that survive for up to 5 years apparently cut short by self-shading. Both species retain their dead florets and leaves that enhance plant flammability and ensure follicle opening and seed release, important as both species are killed by fire. —— **161**

Fig. 9.5: Selection of leaf-like structures (*from top to bottom*): vertically-oriented 2-cm-long phyllodes (true leaves have to twist vertical whereas phyllodes grow vertically) of *Acacia merrallii* (Fabaceae); pungent phyllodes of *Daviesia nudiflora* (Fabaceae) 3 cm long and *D. incrassata* 2 cm long; *D. euphorbioides* has prominent photosynthetic cladodes, 7 mm wide, with phyllodes reduced to recurved spines; yellow-flowered *Jacksonia sternbergiana* (Fabaceae) with thorny cladodes 5 cm long; the genus *Allocasuarina (*Casuarinaceae) is characterised by cladodinous branchlets with leaves reduced to scales and occurring in whorls around the nodes, pictured here is *A. humilis* with 5-cm-long branchlets; the bird-pollinated *Daviesia epiphyllum* (Fabaceae) with its 40-mm-long flowers seemingly arising from its leaves (hence the specific name) that in fact are flattened cladodes with phyllodes, or phylloclades. Cladodes are also a common feature in the root parasitic genus *Exocarpos* (Santalaceae), pictured here is *E. aphyllus*, with 5–10 long branchlets. —— **163**

Fig. 9.6: Leaf surface features. (*upper left*) Young foliage of *Adenanthos cuneatus* (Proteaceae) is red and covered in a fine indumentum of hairs that is still present on mature leaves, 3 cm long, giving them a hoary appearance. Note their vertical orientation. (*upper right*) The entire shoot

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system (apart from the oldest basal stems) of *Eucalyptus macrocarpa* (Myrtaceae) is covered by a waxy glaucous bloom that is densest on the youngest leaves. Apical bud 2 cm wide. (*middle left*). *Hemiphora elderi* (Lamiaceae), 50 cm tall, not only has a dense indumentum over its leaves giving the plant a hoary appearance but also woolly flowers covered with deep-red, stellate hairs. (*middle right*) *Verreauxia reinwardtii* (Goodeniaceae) has 2-mm-thick, white wool over the entire plant. When examined under the electron microscope, the intricate structure of its stellate hairs are revealed with the tips of opposing branches fused by 'plugs' and short glandular hairs near the epidermis. Scale = 100 µm. (*lower left*) *Acacia denticulosa* (Fabaceae) showing a vertically-oriented phyllode, 6 cm long, covered in resin exuded by tuberculate glands over both (isobilateral) surfaces and giving it a highly reflective appearance. (*lower right*) Surface of young leaves, inflorescences and stems of *Grevillea leucopteris* (Proteaceae) are covered in both T-shaped hairs (a common feature of hakeas and grevilleas) and simple glandular hairs, 50 µm tall, that secrete resin. These hairs capture a wide variety of insects but whether they have any role in deterring herbivores, such as lepidopteran larvae, is unknown. With respect to possible carnivory, the average capture of 50 insects per 100 cm of branch length would only meet 0.15% of the nitrogen requirements of the plant even if fully released (Lamont, 1982c). —— **165**

Fig. 9.7: Line drawings of glandular hairs (some bearing globs of resin) on leaves and stems with shiny or sticky surfaces due to the resin they produce flowing over the epidermis and reducing water loss and the summer heat load. A. *Helichrysum rosea* (Asteraceae), B. *Grevillea eriostachya* (Proteaceae), C. *Acacia aneura* (Fabaceae), D. *A. glutinosissima*, E. *Anthocercis littorea* (Solanaceae), F. *Scaevola crassinervia* (Goodeniaceae), G. *Scaevola glandulifera*, H. *Eremophila leucophylla* (Scrophulariaceae) (note stellate hairs may also be glandular and presence of raised surface stomates, usually a feature of mesophytes, that prevents resin flowing into pore and clogging it), I. *Pityrodia bartlingii* (Lamiaceae). Scale = 50 µm. From Dell (1977) and used with permission from the Royal Society of Western Australia. —— **166**

Fig. 9.8: Sclerophyllous and spinsecent leaves of *Gastrolobium spinosum* (Fabaceae), leaves 4 cm long. (*upper middle*) *Allocasuarina pinaster* (Casuarinaceae), pungent cladodes 5 cm long. (*upper right*) *Grevillea hookeriana* subsp. *hookeriana* (Proteaceae), pronged terete leaves 3 cm long. (*lower left*) *Banksia heliantha* (= *Dryandra quercifolia*) with serrated leaves, flower head 10 cm diameter. (*lower middle*) *Astroloma glaucescens* (Ericaceae), leaves 2 cm long. (*lower right*) *Daviesia pachyphylla* (Fabaceae), commonly known as the ouch bush, because of the relatively long and sharply-pointed mucro at the tip of the phyllode (2.5 cm long). —— **167**

Fig. 9.9: *(upper)* insect-pollinated *Hakea* species (from left to right) *H. costata* (with 15-mm-long *Stigmodera* (jewel) beetle pollinator), *H. spathulata* with 3-cm-wide axillary clusters and *H. gilbertii* with 2-cm-wide clusters. (*lower*) bird-pollinated *Hakea* species: *H. petiolaris* with 5-cm-wide clusters often produced on old stems (cauliflory), *H. cucullata* with 5-cm-wide cluster – the subtending leaves act as landing platforms and *H. francisiana* with 15-cm-long racemes. Note how the dense, spiny foliage of insect-pollinated species will deter avian florivores but bird-pollinated species have strong stems that also allow avian florivores, such as cockatoos, to land. However, these flowers contain high levels of toxic, cyanide-yielding compounds and there is a strong correlation between bright pink/red and the presence of cyanogens. —— **168**

Fig. 9.10: A selection of leaf-based strategies that minimise granivory in *Hakea*. (*upper left*) A heterophyllous branchlet of *H. trifurcata.* Arrows point to the woody fruits that remain green at maturity. Their shape and size resemble those of the surrounding broad leaves. Fruit 18 mm long. (*upper right*) Developing fruit (*centre*) of *H. denticulata* mimics the surrounding leaves in terms of coloration and marginal spines. Fruit 25 mm long. (*upper middle left*) *H. auriculata* with its 25-mm-long fruits enmeshed among extremely spinescent leaves. The unique prickles and brown markings on the fruits might have camouflage significance as well. (*upper middle right*) The mottled fruits of *H. polyanthema* embedded in an impenetrable nest of sharply-pointed, terete leaves. Fruits 25 mm

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long. (*lower middle left*) Mottled *H. erinacea* fruit partially camouflaged among its sharply-pointed, highly-divided, terete leaves. Fruit 20 mm long. (*lower middle right*) *H. stenocarpa* with four gnarled, elongated, 4-cm-long fruits that might be mistaken for branchlets or dead leaves by potential granivores. (*lower left*) Cup-shaped leaves of *H. smilacifolia* surround and conceal their small, thin-walled fruits from avian granivores. Leaf 30 mm long. (*lower right*) Woody fruits of *H. victoria* are well concealed by their subtending large, sharply-margined leaves. Leaves can be 15 cm wide. Photograph taken at an angle to the plant so that fruits are visible. —— **170**

Fig. 9.11: Using a mummified Carnaby's black cockatoo and a recreated head using a skull and blue moulding clay to demonstrate how the spinescent leaves of selected *Hakea* species may deter avian granivores from attacking the woody fruits. Species are (*upper left*) *H. polyanthema*. Note that the pointed leaves are pressing against the bird's eye and beak. (*upper right*) *H. psilorrhyncha*. Despite possessing sharply-pointed, stiff leaves, the fruits of this species are sometimes easily accessable to cockatoos but they are especially large and woody. (*lower left*) *H. prostrata*. Leaves have sharp marginal spines, plus the fruit (pictured at the tip of the beak) resembles the surrounding leaves. (*lower right*) *H. auriculata*. This species is heterophyllous with the leaves associated with flowering (protecting the inflorescences as well as the fruits) are narrower and three-pronged at the apex, compared with the leaves not associated with flowering. —— **171**

Fig. 10.1: Sequence of steps involved in the release of seeds from serotinous cones of *Banksia* (data refer to 85 banksias and 5 dryandras from He *et al.,* 2011). Pictured are: *B. lemanniana* (dead floret retention) - note that the cone hangs upside down in this species (it is wasp-pollinated) and that the first florets to open are the ones most likely to set fruits; *B. hookeriana* (dead florets conceal follicles); *B. candolleana* (dead leaf retention) a clonal shrub estimated to survive for up to 1,200 years (Merwin *et al.*, 2012), that also retains its dead florets on cauliflorous heads, ideally located for pollination by honey possums; *B. lanata* (resin melts). —— **174**

Fig. 10.2: Removal of *Banksia attenuata* seeds following cone harvesting can be achieved by flaming the woody fruits. This melts the resin that holds the two valves together, causing the follicle to rupture immediately. Dunking the cone in water and allowing it to dry, and repeating many times, enables the follicle to open progressively and the enclosed separator gradually lifts the two seeds out of the fruit (Lamont & Barker, 1988). Cone is 15 cm long. Image provided by Haylee D'Agui. —— **174**

Fig. 10.3: (*upper left*) Three-winged, single-seeded, fruit (samara) of *Nuytsia floribunda*. The surrounding woody bracts ensure that the fruits are only dispersed by strong gusts of wind. Winged fruits 2.5 cm wide. (*upper right*) Samaras of *Allocasuarina fraseriana* are protected by woody bracts. As the bracts dry the wing of the samara is exposed, in preparation for dispersal by wind. Samara 6 mm long. (*middle left*) Seeds of *Hakea platysperma* (left of image) are completely surrounded by a paper-thin wing. Each woody fruit (centre) contains two winged seeds. Seed plus wing 5 cm in diameter. (*middle right*) Open woody fruit (top) and winged seed (below) of *Xylomelum angustifolium*. Note the two empty seed cavities surrounded by the protective woody fruit walls. The seed proper (left) and wing (right) are both mottled, apparently providing camouflage from granivores in the post-fire environment. (*lower*) The awned calyx of *Calytrix* (Myrtaceae) flowers (*left*) is unusual in that it is persistent in the fruit (*right*) and aids in dispersal by wind. —— **176**

Fig. 10.4: Seed removal by ants is almost entirely due to two *Rhytidoponera* species, especially *R. violacea (left*), in the northern sandplains (Gove *et al.*, 2007). Ant is 9 mm in length. Rhytidoponeras are relatively large ants and may prefer to remove large seeds like those that occur in the Fabacaeae, such as *Acacia lasiocalyx* (*scanning electron micrograph shown right*) that bears a highly convoluted basal elaiosome. Seed 7 mm long. —— **179**

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Fig. 10.5: (*upper*) Seeds of *Hibbertia hypericoides* (Dilleniaceae) (*left*) and *Hardenbergia comptoniana* (Fabaceae) (*right*) bearing elaiosomes. Seeds are 2 mm and 5 mm in length respectively. (*lower*) Potential fate of myrmecochorous seeds. Adapted from Hughes and Westoby (1992). —— **180**

Fig. 10.6: (*upper*) *Stachystemon axillaris* (Euphorbiaceae) is a slender, monoecious shrub in the northern Swan and Eneabba sandplains (plant in centre of photo is 50 cm tall). It usually only occurs underneath clumps of *Eucalyptus todtiana* (tree in background). (*lower left*) Its 4-mm-long seeds have a pale green aril (elaiosome) that is attractive to at least six ant species. Granivorous birds, such as bronze-wing pigeons, also consume the seeds and disperse them between *E. todtiana* clumps but feeding trials have yet to be undertaken. (*lower right*) Seeds are buried by ants in seed middens in their nests. The heat of a fire stimulates them to germinate *en masse* provided that they are located within 1–3 cm of the surface. The tallest seedling here is 8 cm. Recruited plants survive for 30 years, and since interfire germination is negligible and the stored seeds gradually die, if there is no new fire within 45 years the population dies out. Periodic fire is an essential part of the life cycle of *Stachystemon*. Photos taken by Allan Tinker. —— **181**

Fig. 10.7: *(upper left*) Adult plant of *Adenanthos cygnorum* (Proteaceae), 2 m tall. (*upper right*) Solitary flower, 25 mm long, partly embedded in foliage. (*lower left*) *Iridomyrmex bicknelli* (Formicidae: Dolichoderinae) removing fruit, 7 mm long, from the leafy cup in which it is held after release. Note elaiosome beneath thorax of the ant. (*lower right*) *A. cygnorum* fruits with and lacking the hair-covered elaiosome. —— **182**

Fig. 10.8: (*upper left*) *Acacia cyclops* (Fabaceae). Seeds, 6 mm long, are surrounded by a coiled double-backed, orange-red aril that is attractive to granivorous birds. The hard-coated seeds are often retained in the pod when it splits open (making it easy for birds to locate them), whereas ant-dispersed seeds are explosively released from the pods. (*upper right*) *Pittosporum angustifolium* (Pittosporaceae). The open fruit, 15 mm long, reveals several sticky seeds that are brown or black when dry. The genus name refers to the sticky resin that surrounds the seeds. (*lower*) *Santalum acuminatum* (Santalaceae). The comparatively large (3 cm wide) fleshy and waxy skinned, red fruits are easily spotted among the surrounding foliage and are a favoured food source for the emu. —— **184**

Fig. 10.9: (*left*) Seeds, 5 cm long, drop passively to the ground from the female cone of the cycad *Macrozamia riedlei* (Zamiaceae). A wide variety of animals feeds on the seeds but only emus distribute them widely over the landscape. (*right*) Flowers of *Daviesia triflora* (Fabaceae), 10 mm wide, whose seeds are released explosively from their pods then dispersed by ants (short distances) and, sometimes, by emus (long distances). —— **185**

Fig. 10.10: (*left*) *Corymbia calophylla* (Myrtaceae) seeds, 10 mm in length. (*right*) *Xanthorrhoea preissii* seeds resting in 10-mm-long, open fruits. Note the sharp tips to the valves that will deter avian granivores from accessing the seeds. —— **187**

Fig. 10.11: *Anigozanthos* (Haemodoraceae) species in flower. (*left*) *A. rufus*, (*middle*) *A. manglesii* ssp. *manglesii* and (*right*) *A. preissii* that have no special traits for promoting dispersal other than their small size. All flowers 4–6 cm long. These are also good examples of bird-pollinated species with their terminal location, bright colours and reproductive parts facing towards the stem where the birds land. Images provided by Katherine Downes. —— **188**

Fig. 11.1: (*left*) Spring flowering of low heath at Crystal Brook Reserve, 15 km east of Perth, on the shallow soils over Cenozoic laterite with ancient PreCambrian outcropping granite (on right). Over 80% of species visible in the photo [e.g. *Grevillea* (cream), *Hemigenia* (mauve), *Oxylobium* (orange), *Acacia* (yellow), *Diplopeltis* (pink), *Burchardia* (white 'spots')] recover after fire from soil-stored seeds. The remainder [*Hakea* (cream shrub in background), *Allocasuarina* (brown (male) and red (female) flowers), *Isopogon* (pink with yellow/red style), *Banksia* (*Dryandra*) (yellow)] recover from serotinous seeds. The one exception is *Xanthorrhoea preissii* (grasstree

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in mid-background with spent spikes produced in response to the fire 7 years before) that has fire-stimulated flowering with seeds released the year after fire that must germinate then or perish (Lamont *et al.*, 2004). (*right*) 1.5-m-tall stand of the bird-pollinated, fire-killed, serotinous *Banksia hookeriana* at Yardonogo Reserve. This species arose 5 Ma (He *et al.*, 2011). While the seeds stored by this species only weigh 0.5% of the total aboveground mass, they contain 48% of its phosphorus (P), 24% of its nitrogen (N) and 4% of its potassium (K). Pot trials have shown that the deep sands in which this species occurs are P, N and K-limited and growth of wild oats is negligible unless all three nutrients are added (Lamont, 1995). —— **189**

Fig. 11.2: (*upper left*) A woody fruit, 5 cm long, of *Hakea neurophylla* (Proteaceae). Each fruit contains two winged seeds that are wind dispersed. The fruit remains closed on the plant until the above-ground stems are killed, usually by the heat of a fire, but sometimes through physical damage, disease or drought. (*upper right*) Woody cones, 4 cm long, of *Allocasuarina campestris* (Casuarinaceae). A pair of woody valves surrounds and protects each winged fruit. Valves remain closed for many years, opening as a result of desiccation, usually from branch death as a result of fire. (*middle left*) Woody cone of *Banksia lemanniana* (Proteaceae) with several prominent woody fruits (3 cm long) each protecting 2 winged seeds. *B. lemanniana* is one of the few banksias where the inflorescences hang downwards. (*middle right*) Clustered woody fruit of *Calothamnus graniticus* (Myrtaceae). Fruits are 2 cm long. (*lower left*) Cup-shaped fruits (8 mm long) of *Eucalyptus marginata* (Myrtaceae). (*lower right*) Fruit cluster of *Melaleuca thymoides* (Myrtaceae). Note the subterminal spinescent leafless branchlets (thorns) that presumably act to deter granivores. Cluster 4 cm long. —— **191**

Fig. 11.3: (*upper*) Variability in fruit (follicle) size within SouthWest *Hakea* species, from the smallest (*H. sulcata*) to the largest (*H. platysperma*). Third row are species whose follicles remain green at maturity, and use cryptic mimicry as an additional form of protection (see Chapter 9). (*lower)* Fruit dimensions are related to level of seed protection in *Hakea*, with a trade-off between storage ability and fruit morphology, resulting in strongly serotinous species investing more into thicker-walled fruits than non- and weakly serotinous species. Diagram based on Groom & Lamont (1997). —— **195**

Fig. 11.4: *(upper left*) Carnaby's black cockatoo (*Calyptorhynchus latirostris*), 35 cm tall, perched on a *Corymbia calophylla* (marri) branch. To the right of the branch is a single still-green woody fruit. When sectioned transversely (*upper right*) the thickness of the woody wall that protects the 3-4 seeds is apparent. Fruit diameter 5 cm. (*middle left*) The extraordinarily large fruits of *Hakea platysperma*, roughly two thirds the size of a Carnaby's cockatoo head (dummy head pictured – skull covered in plasticine – positioned against easily accessible fruits) provides sufficient woody protection to defend seeds against the bird's sharp bill. (*middle right*) Scratch marks on 6-cm-wide, *H. platysperma* follicle from failed attempts by a cockatoo to open the fruit. (*lower left*) In contrast, cockatoos easily extract seeds from smaller-fruited hakeas, even those with clustered fruits (e.g. *H. scoparia)*. Fruit 2 cm long. (*lower right*) *Banksia attenuata* cones, 6 cm wide, removed from their parent stems by Carnaby's cockatoo. Note that subsequent damage is restricted to individual woody follicles. The seeds are even more vulnerable once the fruits have opened in response to fire, but remain protected by a woody separator that gradually lifts seeds out of the fruit. —— **196**

Fig. 11.5: Post-fire litter microsite full of seedlings produced from seeds that were blown there after their release from woody fruits following the fire. *Banksia* (10 cm tall) and needle-leaved *Hakea* seedlings dominate this microsite. —— **197**

Fig. 11.6: Young plants of *Paraserianthes lophantha* (Fabaceae, Mimosoideae) following burning of a stockpile of plant debris in the Darling Range near Perth. Seeds of this species already lay buried in the surface soil and were stimulated to germinate by the heat of the fire. Note how the seedlings form a ring around the stockpile: heat was excessive and killed seeds in the centre, the heat pulse was insufficient to stimulate germination beyond the ring and the

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seeds remained dormant, though they could germinate at a later date with a subsequent fire ('bet-hedging'). In a similar way, depth of burial is critical to whether seeds germinate, are killed (too shallow) or remain dormant (too deep). Typical of legumes, this species is taking full advantage of the mineral nutrients released by the fire. Photo taken by B. Dell. —— **203**

Fig. 11.7: 7-week-old seedlings of three *Hakea* species endemic to the SouthWest at the same scale (25-mm rim of pot visible in background) showing the range of variation in leaf shape and cotyledon size in this genus. (*left*) *H. sulcata* has the smallest seeds of all 140 hakeas (2.7 mg) and thus the smallest cotyledons (the first pair of 'leaves' just visible) and seedlings—its broad leaves are replaced by simple needle leaves once the eighth leaf is produced (heteroblasty). This species is confined to seasonal wetlands and this may enhance its ability to establish a strong root system before the summer drought commences by which time it only produces vertically-oriented needle leaves. (*middle*) *H. lissocarpha* has intermediate-sized seeds (23.9 mg) and occurs on shallow lateritic soils. The nutrient store is sufficient to ensure development of a deep root system by summer plus its semi-terete, highly-divided, needle leaves increase its drought tolerance. (*right*) *H. platysperma* has the largest seeds of all hakeas (508.8 mg) and thus the largest seedlings. Its cotyledons expand four times in area on germination and become strongly photosynthetic. The seeds contain more P (15 mg) than is known for any other species (Groom & Lamont, 2010). Thus, the major role of its cotyledons is the provision of mineral nutrients to the shoots that enhance photosynthesis and enable rapid elongation of the tap root in the deep sands where it occurs to ensure contact continues with groundwater over summer-autumn (Fig. 10.15, Lamont & Groom, 2013). Drought avoidance is assisted from the outset by its exceptionally-long, vertically-oriented, needle leaves. —— **205**

Fig. 11.8: The Proteaceae occurs widely in Australia and South Africa and provides the opportunity to compare seed sizes and their nutrient contents between regions. As can be seen, seeds are generally larger (by an average of 9 times) and more enriched with N (by an average of 13 times) and P (by an average of 30 times) in the SouthWest than on the east side of Australia, with mediterranean South Africa in between. From Lamont & Groom (2013). —— **207**

Fig. 11.9: Stylized epigeal seedling showing uptake and transport of carbon (C), nitrogen (N), phosphorus (P) and water from soils in the SouthWest. Note that the cotyledons are short-lived as a source of C as they soon become a sink for C following photosynthesis by the leaves. Except for small seeds and fertile soils, N and P continue to be transported out of the cotyledons until their supply is exhausted. This ready source of N and P in nutrient-limited soils enhances photosynthesis and general growth. Fixed C is shunted strongly to the root system where N, P and water uptake and elongation of the tap root in particular are promoted, as an indirect effect of greater N and P seed stores. From Lamont & Groom (2013), figure prepared by Wesley Lamont. —— **207**

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