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Ecology of Fire-Tolerant Podocarps in Temperate Australian Forests

Philip G. Ladd and Neal J. Enright

ABSTRACT. *Podocarpus drouynianus* and *P. spinulosus* are two unusual conifers restricted to southwestern and eastern Australia, respectively. The species are morphologically similar and genetically closely related to each other but rather distant from other members of the subgenus *Foliolatus*. Both species have retained ancestral podocarp characteristics such as dioecy, wind pollination, and large, animal-dispersed seeds with recalcitrant germination. They also thrive on soils with generally low nutrient content. However, they have several innovations that ensure their success in an environment that would generally be considered unsuitable for podocarps. Both species have much higher leaf length to width ratios than other *Podocarpus* species: this presumably aids their survival on low- to moderate-rainfall sites. They both resprout strongly after fires, and at least for *P. drouynianus*, seed production is cued by defoliation, and sporophylls are produced most prolifically on new growth one year after fire. The species are unique in the genus as being successfully adapted to a relatively dry, fire-prone environment.

INTRODUCTION

In almost all parts of the world where the genus occurs, the archetypical *Podocarpus* is a single-stemmed rainforest or riparian tree that is fire sensitive. However, in temperate mainland Australia two fire-tolerant shrub podocarps represent radical departures from this model. In *Ecology of the Southern Conifers* (Enright and Hill, 1995), a chapter on conifers of southern Australia (Gibson et al., 1995) noted that little was known about the ecology of several of the temperate Australian conifers, particularly *P. drouynianus* from southwestern Australia, and the eastern equivalent species (*P. spinulosus*) is not even mentioned. Only *P. drouynianus* has any commercial importance and is used as a “background foliage filler” in the cut flower industry in Western Australia. Since 1995, little has changed concerning our knowledge of the ecology of these two species, although one paper has been published on seed production and recruitment of *P. drouynianus* (Chalwell and Ladd, 2005).

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The two species are classified in *Podocarpus* subgenus *Foliolatus* and in cladistic analyses are found in a clade sister to the remaining members of the subgenus (Biffin et al., this volume). Almost all other species in the subgenus are tall forest trees, although there are a few species of lower stature that grow at high altitudes in Asia. Both species grow in lowland eucalypt forest rather than rainforest and retain many of the normal attributes of *Podocarpus*, including seed, leaf, and root morphology. However, in other respects they are similar to the much more widespread sclerophyllous Australian flora with which they co-occur. This chapter describes the ecology of these fire-tolerant species and highlights the adaptations that have enabled them to survive in environments that at first impression would not be expected to support podocarps.

METHODS

Herbarium records and personal observations of plant locations for *P. drouynianus* and *P. spinulosus* were used to produce distribution maps and BIOCLIM analyses. BIOCLIM is a computer modeling system that uses bioclimatic parameters derived from mean monthly climatic estimates to predict climatic conditions at any specified location (Busby, 1986). Using a digital elevation model and parameters such as latitude, longitude, and altitude, the climatic envelope of a species can be predicted. BIOCLIM was used to examine the climatic envelope of these two podocarp species. Mean bioclimatic details for the two species were statistically compared with a *t* test (or Mann Whitney U test if the data failed to satisfy requirements for parametric testing). Population size and structure were measured in the field in plots of various sizes, depending on the density of plants and in order to obtain a sufficient number of plants to gain a representative sample. Since these species are lignotuberous multi-stemmed shrubs, size class structures were based on number of stems for plants up to 10 stems and then the circumference of the lignotuber for larger plants. This was considered the most appropriate procedure because stem number varies with time since fire and also because longest diameter often did not reliably represent the size of the lignotuber if its outline was irregular.

SEED MASS, SEED PRODUCTION, AND GERMINATION RATE

Seed mass was determined for seeds collected from populations of *P. drouynianus* at Jalbarragup and Nannup, south of Perth, and from a population of *P. spinulosus* at

Pearl Beach, near Sydney. Seed production was examined for populations of *P. drouynianus* at Jalbarragup and Sawyers Valley, east of Perth.

Seed from natural populations at Jalbarragup and collected from garden-cultivated plants of *P. spinulosus* was germinated on the surface of soil in seed trays in controlled-temperature cabinets at 5°C temperature intervals between 15°C and 35°C and, for seeds subject to cold stratification, at 4°C (20 seeds × 5 replicates). Large seed size prevented good contact with the moist surface of filter paper, and being partially impressed into the soil surface provided a better moisture contact with the seed, so that germination on soil was the preferred method for germination testing. Whereas seed germination for many species in the fire-prone sclerophyll forests of southern Australia is enhanced by the effects of heat and/or smoke associated with fire relative to rates in the absence of these cues (Enright et al., 1997), the postfire pattern of seed production in *P. drouynianus* suggested that no fire-related stimulus is required for germination, and initial germination testing assumed no such requirement.

STEM AND LEAF MEASUREMENTS

The timing and extent of lignotuber development was examined in seedlings from seed collected at Pearl Beach and Jalbarragup. Stem outgrowths in *P. spinulosus* were studied by microscopic examination of stem sections fixed in a mixture of formalin, acetic acid, and alcohol, then embedded in plastic for sectioning and stained with toluene blue.

Leaf dimensions of *P. drouynianus* and *P. spinulosus* were compared with published measurements from other species in the subgenus *Foliolatus*. Our hypothesis was that as the two Australian species grow at the arid end of the podocarp climatic spectrum, they should have narrower leaves than most of the other species, which generally occur in much wetter environments. Leaf measurements were derived from the mean value on the basis of dimensions given for species listed on the Gymnosperm Database Web site (<http://www.conifers.org/po/po/index.htm>; accessed 7 July 2009) for *P. spinulosus* plants grown in Perth and *P. drouynianus* from plants collected in the field near Nannup.

POPULATION STRUCTURE

Size structure in *P. drouynianus* is reported for two populations (Jalbarragup and Sawyers Valley; see Chalwell and Ladd, 2005, for full details of populations and sampling methods) and in *P. spinulosus* for four populations, two at Pearl Beach (Crommelin 1 and 4), plus single

TABLE 8.1. Location, details, and attributes for the sites mentioned in the text. Abbreviations: NSW, New South Wales; WA, Western Australia.

Site name	Location	Elevation (m)	Geology	Soil	Vegetation
Pearl Beach	NSW, 33°32'S, 151°18'E	20	Sedimentary sands	Sand	Eucalypt open forest
Sydney Botanic Gardens	NSW, 33°33'S, 151°13'E	20	Sandstone	Skeletal sandy soil	Cultivated garden
Yalwal	NSW, 34°11'S, 150°37'E	200	Sandstone	Skeletal sandy soil	Eucalypt open forest
Burrill Lake	NSW, 35°22'S, 150°26'E	20	Sedimentary sands	Sand	Eucalypt open forest
Sawyers Valley	WA, 31°55'S, 116°13'E	250	Lateritized granite	Red brown earth	Eucalypt open forest
Nannup	WA, 33°59'S, 115°45'E	210	Lateritized granite	Red brown earth	Eucalypt open forest
Jalbarragup	WA, 34°03'S, 115°37'E	150	Lateritized granite	Red brown earth	Eucalypt open forest

populations at Lake Burrill and Yalwal (Table 8.1). Plants were divided into classes by size: the first two categories were by number of stems (1–2 and 3–10), and plants with more than 10 stems were then divided into 20 cm (*P. spinulosus*) or 50 cm classes (*P. drouynianus*).

RESULTS

SPECIES DISTRIBUTION

Podocarpus spinulosus and *P. drouynianus* are endemic to eastern and southwestern Australia, respectively, in areas relatively close to the coast, where rainfall is generally higher and risk of frosts lower than for sites farther inland at the same latitude. *Podocarpus spinulosus* extends over a much greater latitudinal range (approximately 24°S–36°S) than *P. drouynianus* (32°S–35°S; Figure 8.1), and although the overall climate profiles of the two species are similar (e.g., no significant difference in mean annual rainfall between habitats: *P. drouynianus*, 1039 ± 26 mm; *P. spinulosus*, 1115 ± 59 mm), there are several significant differences between them in other bioclimatic details (Table 8.2). Mean annual temperature is significantly lower for *P. drouynianus* than for *P. spinulosus*, and precipitation in the warmest quarter is significantly lower for *P. drouynianus* but is the reverse for the coolest quarter, reflecting the strong Mediterranean-type climate experienced by *P. drouynianus*.

SEED PRODUCTION AND GERMINATION

Plants of both species are dioecious. The seeds are borne on a “podocarpium,” colored deep purple when

ripe. Seed mean fresh mass for *P. spinulosus* is significantly lower (0.24 ± 0.01 g, Pearl Beach population; $U = 625$, $n = 25$, $p < 0.001$) than for *P. drouynianus* (1.74 ± 0.19 g, Jalbarragup population). However, for *P. drouynianus* there was also a difference in seed mass between nearby populations (~15 km), with seeds from the Nannup population significantly heavier (2.30 ± 0.11 g; $t = 3.89$, $p < 0.001$) than seeds from Jalbarragup.

The seed is recalcitrant and germinates several months after it is shed from the plant in summer. In southwestern Australia this coincides with the onset of winter rains. In eastern Australia rainfall is more evenly distributed through the year, but lower-temperature and higher-humidity conditions toward winter are likely to be more suitable for seedling establishment than hotter conditions earlier in the year.

Incubation of seeds at higher temperatures reduces the time to germination. For both species germination is fastest at 35°C and begins later at lower temperatures, being slowest at 15°C (Figure 8.2). However, final germination success is similar at all temperatures. Seed kept at 4°C failed to germinate during the time of the trial but did germinate once it was shifted to room temperature (~20°C). There was no germination requirement for fire-related cues such as heat or smoke in either species.

In natural forest populations, *P. drouynianus* produces major crops of seeds one year after a summer fire (Chalwell and Ladd, 2005). Both male and female plants produce sporophylls on the new shoots arising from the lignotuber. Plants that are partially burnt only produce sporophylls on new shoots, with none on any surviving unburnt stems. In the second year after fire sporophyll production is less prolific and seed is rarely produced, and three years or more after fire no sporophylls occur. However, there is no

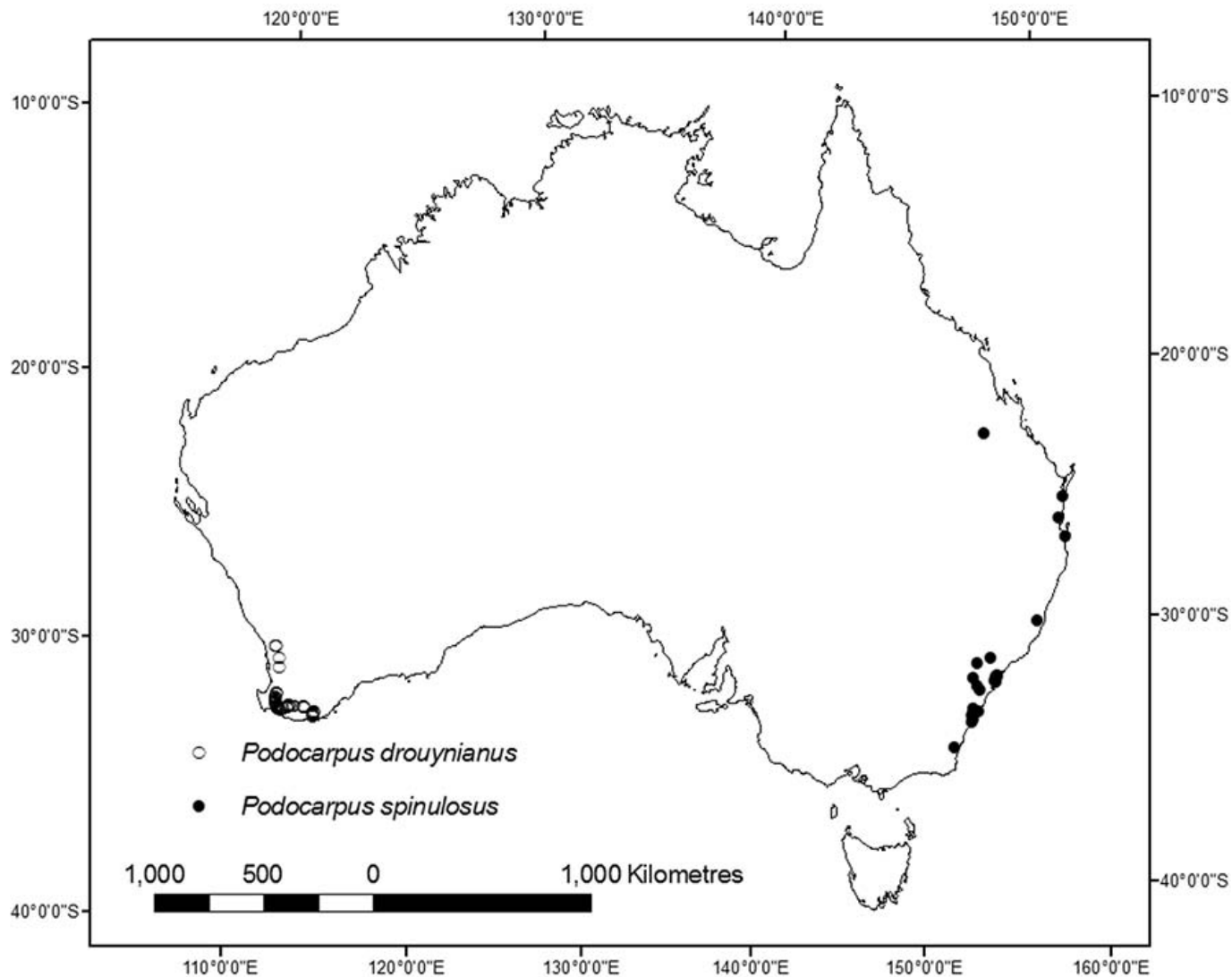


FIGURE 8.1. Map showing the location of records for *Podocarpus spinulosus* and *P. drouynianus*.

TABLE 8.2. Bioclimatic details of *Podocarpus drouynianus* and *P. spinulosus*. Abbreviations: MWU, Mann Whitney U test; NS, not significant. Values in parentheses are the standard error of the mean.

Climatic measure	<i>P. drouynianus</i> (<i>n</i> = 46)	<i>P. spinulosus</i> (<i>n</i> = 22)	Significance
Mean annual rainfall (mm)	1,039 (26)	1,115 (59)	NS
Mean annual temperature (°C)	15.6 (0.1)	17.3 (0.1)	MWU = 893, <i>p</i> < 0.001
Mean precipitation, warmest quarter (mm)	73 (3)	375 (26)	MWU = 1,012, <i>p</i> < 0.001
Mean precipitation, coolest quarter (mm)	478 (13)	231 (70)	<i>t</i> test, <i>p</i> < 0.001

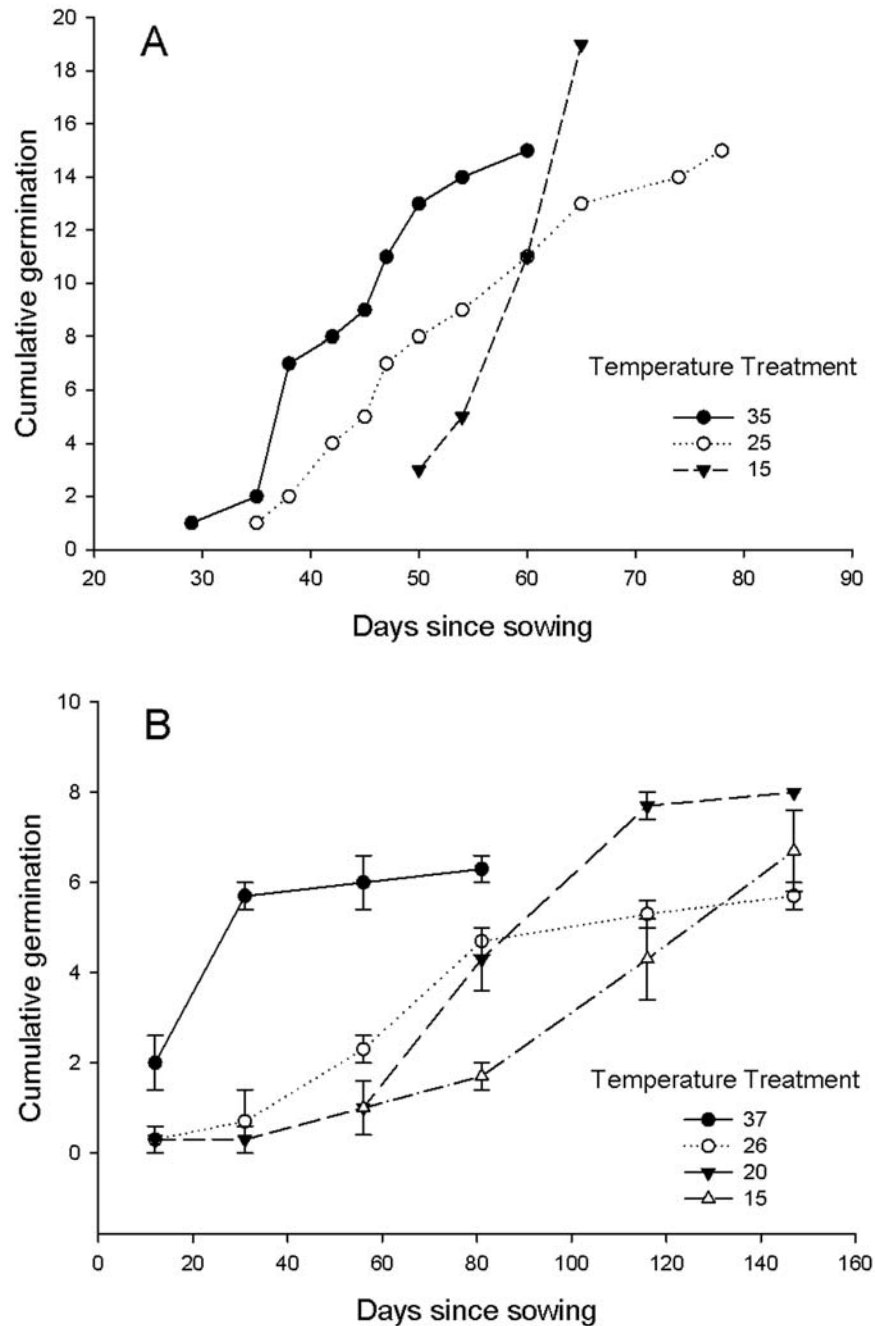


FIGURE 8.2. Seed germination at various temperatures for (A) *P. drouynianus* and (B) *P. spinulosus*. Bars are standard error of the mean ($n = 4$).

simple obligate relationship between fire, new shoots, and seed production as plants that have persisted for many years without fire in paddocks after forest clearing may produce seeds on the new growth from established stems. Thus, the reproductive response to fire appears to break down if aboveground stems grow undisturbed by fire for

long intervals. Seed production of *P. spinulosus* in natural populations has not been followed for sequential years after a fire. However, circumstantial evidence suggests that *P. spinulosus* produces sporophylls in most years. A population assessed at Pearl Beach two years after a fire was producing copious seed, and plants grown from this seed

in cultivation produced sporophylls each year once plants were 10 years old. Experimentally burnt cultivated plants did not produce sporophylls until two years after the fire. Occasional seeds were also observed on long-unburnt individuals in the Sydney Botanical Gardens. Thus, fire stimulates seed production in *P. drouynianus*, but it is not clear if this is true for *P. spinulosus*.

The transition from ovules to seeds was examined on randomly selected large plants (>30 stems >1 m tall) of *P. drouynianus* at Sawyers Valley, near Perth, in 2004 and 2005. Mean ovule production in 2004 was approximately 10 ovules per stem (3.9 seeds per stem), whereas in the following year the same stems produced only a mean of 0.8 ovules and no seed was matured (Figure 8.3).

Randomly selected plants at Jalbarragup had a mean of 0.43 seeds m^{-2} , whereas at Sawyers Valley mean seed production from three 100 m^2 quadrats was 0.58 m^{-2} in 1994 but only 0.10 m^{-2} following a patchy fuel reduction burn at the site in 2004 (Figure 8.3). At both sites the 95% confidence intervals were large, indicating high variability of seed production among plants.

At Jalbarragup only eight seedlings were produced from 6,652 seeds that were followed for six months from seed fall (Chalwell, 1994). In a 1998 census of seedlings at Sawyers Valley, establishment was patchy, with 19 seedlings growing from the 1994 seed event in one 100 m^2 plot but no seedlings in the two other plots. Seeds are eaten by emus, parrots, and mammals (including rodents and possums) but depend mainly on emus for dispersal. The passage of podocarp seeds through the gut of the emu has no effect on germinability (Chalwell, 1994). However, the concentration of seeds in emu droppings provides a focus for mammal predation on the seed, especially if feces are deposited in the open in burnt areas, where most are destroyed by secondary predation (Chalwell, 1994).

VEGETATIVE GROWTH AND REGROWTH AFTER FIRE

Seedlings of *P. spinulosus* and *P. drouynianus* begin development of a lignotuber very soon after germination. A swelling mass of stem tissue, and soon afterward buds, begins to develop in the axils of the cotyledons in both species (Figure 8.4a,b). In *P. drouynianus* cotyledonary axillary buds appear within three months of the plumule emerging from between the cotyledons. In *P. spinulosus* lignotuber development is slower, with development of a swelling at the cotyledonary node taking up to 22 months. In both species, the swelling expands and shoots are produced within five months. In *P. spinulosus* there may be asymmetrical development of the lignotuber

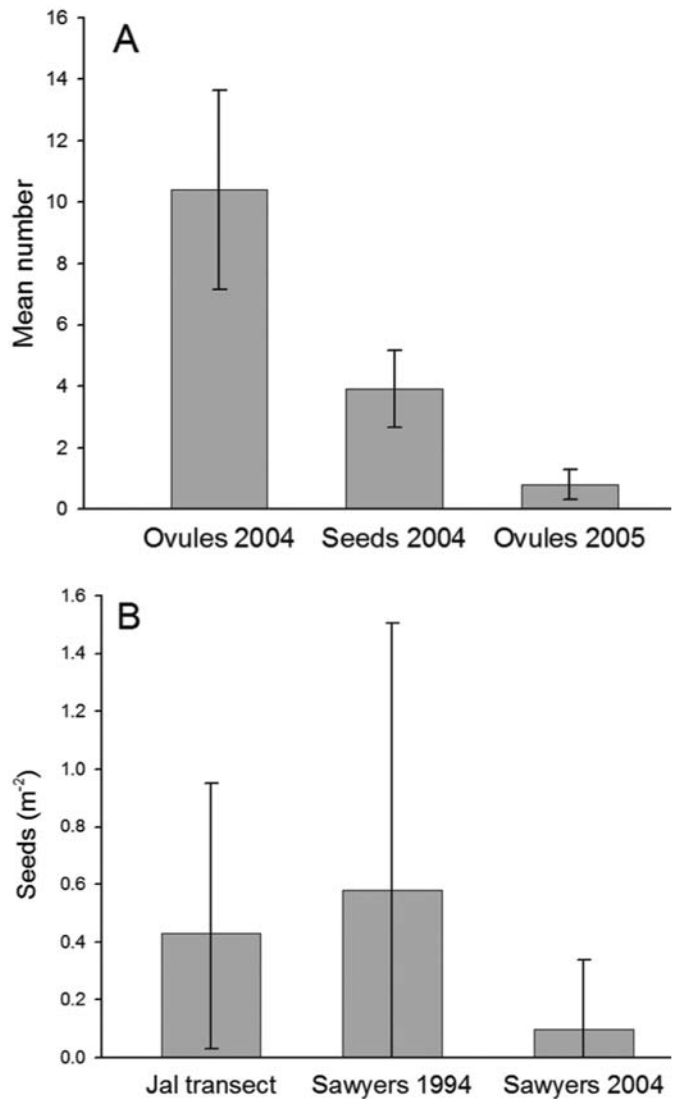


FIGURE 8.3. Reproduction in *Podocarpus drouynianus*, showing (A) ovules and seeds from marked plants over two years, produced after a fire at Sawyers Valley, east of Perth, in 2003; (B) seed production (seeds m^{-2}) from plants on a transect at Jalbarragup (Jal, south of Perth) after a fire in 1993 and from 100 m^2 quadrats at Sawyers Valley after fires in two different years (1993 and 2003). Bars are 95% confidence intervals.

with expansion on the lower side if the stem is bent, until the swelling contacts the soil. The lignotubers of these podocarps have more obvious buds than seen in lignotubers on most other Australian species. The lignotuber of *P. drouynianus* develops by extending lobes downward into the soil. With time, the underground structure may branch (Figure 8.4c), and in older plants the extent of the genet may be >1 m long (Figure 8.5f).

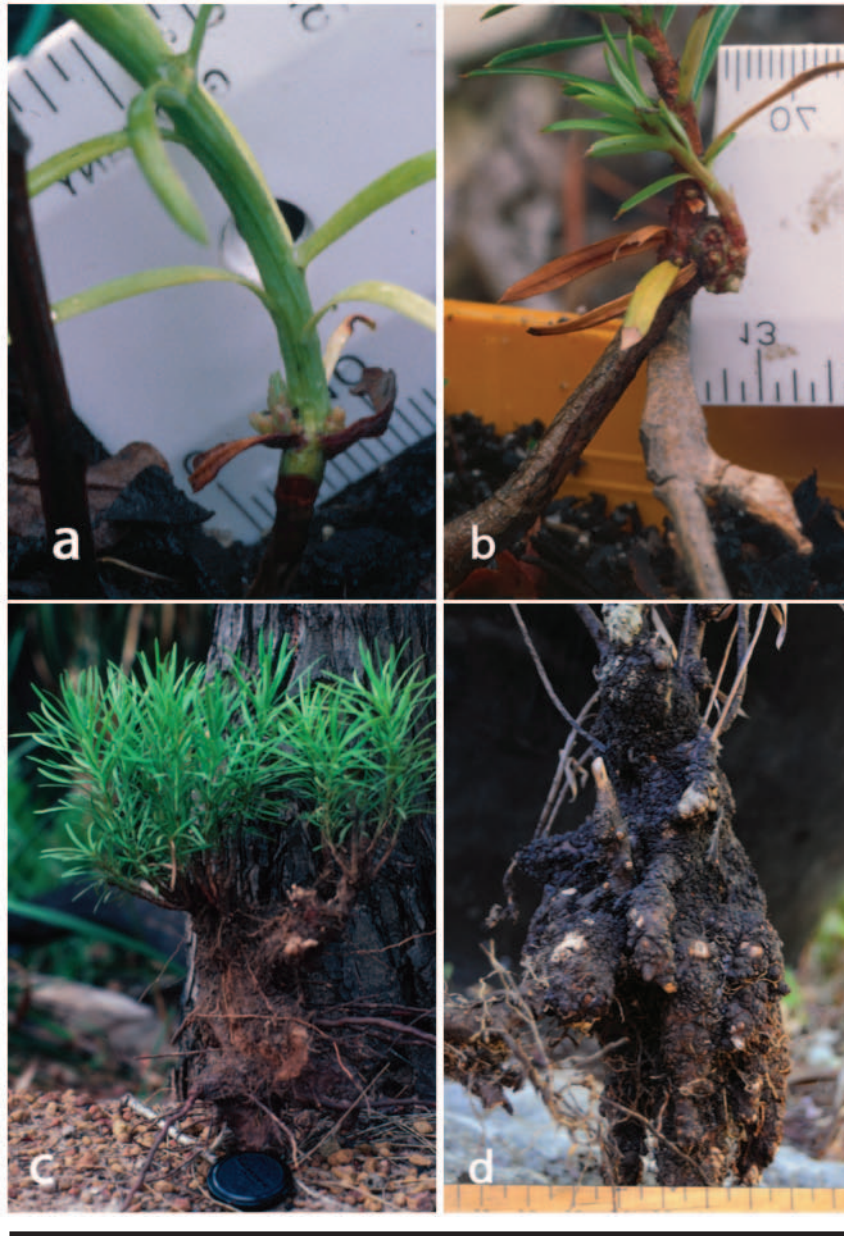


FIGURE 8.4. Lignotubers of *Podocarpus*, showing (a) very young lignotuber buds in the cotyledon axils of *P. drouynianus* (lower scale in mm); (b) new shoot on a young stem burl of *P. spinulosus* (upper scale in mm); (c) excavated adult plant of *P. drouynianus*; (d) lignotuber of *P. drouynianus* for a plant approximately seven years old (scale in cm).

Lignotubers develop quickly in both species. In cultivated *P. spinulosus*, six-year-old plants that were burnt produced new shoots from the lignotuber. Although it is not known how old the lignotuber of *P. drouynianus* needs to be before it can survive fire, its faster early development (described above) suggests that juveniles may become tolerant to fire even more quickly.

Swellings may develop in higher leaf axils of *P. spinulosus* (Lacey and Johnson, 1990) and may also occur along the stems in mature plants (Figure 8.5a), usually with a geotropic development. Although they are not in the position of a lignotuber, they are identical to the lignotuber in their morphology and bud development. There may be many outgrowths on arching stems, and if these

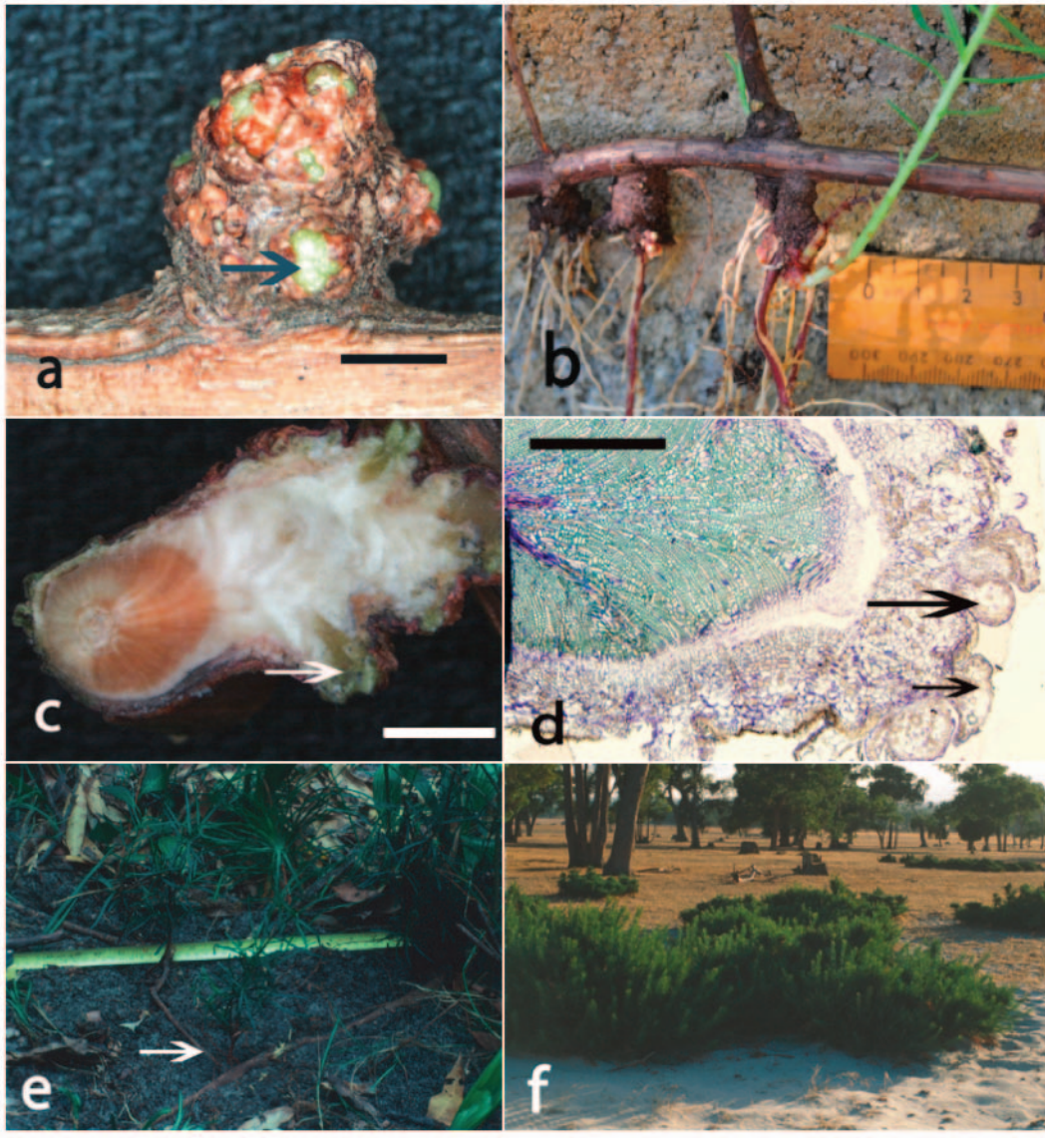


FIGURE 8.5. *Podocarpus* stem structures and growth form, showing (a) a young stem burl of *P. spinulosus*, with the arrow pointing to a bud apex covered by a bract (scale bar = 2 mm); (b) shoots and roots growing from a *P. spinulosus* stem burl that had been buried in the soil, with a large shoot originating below many of the roots (scale bar in cm); (c) transverse hand section of a stem burl of *P. spinulosus*, with the arrow pointing to a bud apex (scale bar = 10 mm); (d) light micrograph of a transverse section through a *P. spinulosus* stem burl, with the arrows pointing to bud scales (scale bar = 0.5 mm); (e) excavated prostrate stems (arrow) of *P. spinulosus*, showing shoots produced from a number of stem burls; (f) clumps of *P. drowynianus* in cleared vegetation, with each clump likely to be a genet.

touch the ground, roots develop from the base of the structure. If the stem is severed from the parent plant or burnt, shoots are produced, and an independent plant develops. The fate of the buds on the stem swelling is undetermined, and buds may develop into roots or shoots. Shoots may develop distally from roots but then grow upward (Figure

8.5b). Sections through a young stem swelling show that the xylem grows out from the main axis of the stem (Figure 8.5c), but the buds on the surface of the swelling develop in proliferated cortical tissue (Figure 8.5d) and have a vascular trace extending through the xylem of the stem toward what was the primary stem tissue as the initial

stem developed. As the stem swellings increase in size, they develop a woody core and seem to be a condensed and thickened shoot with abundant superficial buds that can develop into roots or shoots.

Adult leaves of both *P. spinulosus* (length 5.7 ± 0.1 cm, width 3.4 ± 0.1 mm, length:width ratio 16.9 ± 0.4) and *P. drouynianus* (length 8.2 ± 0.3 cm, width 3.4 ± 0.1 mm, length:width ratio 24.5 ± 1.1) are significantly narrower (Kruskal Wallis test, $p < 0.001$) and have a significantly greater length:width ratio (Kruskal Wallis test, $p < 0.001$) than the mean for other species in the subgenus *Foliolatus* (length 8.8 ± 1.1 cm, width 10.1 ± 1.1 mm, length:width ratio 9.1 ± 0.9).

POPULATION STRUCTURE

The few populations of *P. spinulosus* that have been measured contain more small plants than occur in *P. drouynianus* populations (Figure 8.6). Of the four populations measured at three sites, three had a relatively high proportion of plants in the smallest size class (Crommelin 4 is the exception, Figure 8.6B). In addition, there were few individuals with lignotubers >50 cm in circumference, whereas *P. drouynianus* populations had a much higher proportion of large individuals.

Only two population structures are shown for *P. drouynianus* (Figure 8.6C), although others are presented in Chalwell and Ladd (2005). The plants of this species generally grow much larger than those of *P. spinulosus*. Plot data from Sawyers Valley (sampled in 2003) show a high proportion of small (young) individuals, reflecting survival of recruited seedlings after a fire in 1994. In this species the population structure (ignoring seedlings recruited after the last fire) approximates a normal curve, although skewed to smaller individuals in the Jalbarragup and larger individuals in the Sawyers Valley populations (Figure 8.7), respectively.

The population structure of *P. spinulosus* is difficult to interpret in terms of recruitment of new genets to the population. Plant stems tend to be low and spreading in contrast to the upright growth of *P. drouynianus*, so that ramet proliferation by layering may be common. In the Pearl Beach Crommelin 1 population (Figure 8.6B) many apparent individuals were suckers from procumbent stems, either from stem burls or from parts of the stem without swellings (Figure 8.5e). Pearl Beach Crommelin 4 plants were generally larger. The Yalwal population seemed to consist mostly of shoots produced from stem swellings that had touched the ground and produced roots and shoots; most had only one or two shoots (Figure

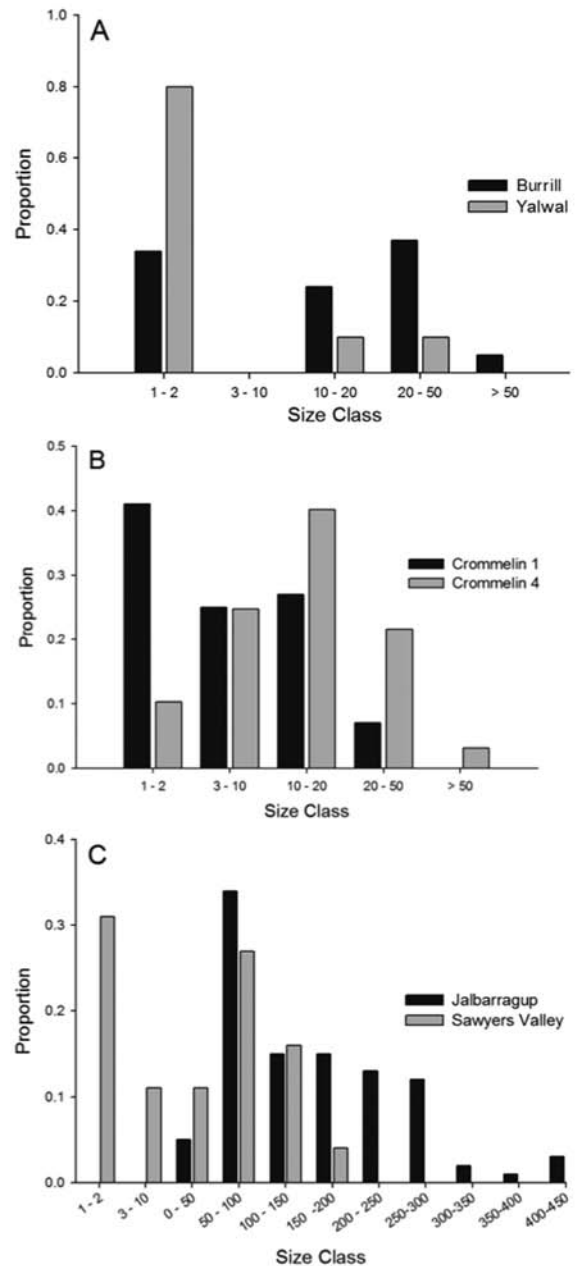


FIGURE 8.6. Size class structures for populations of *Podocarpus drouynianus* in southwestern Australia and *P. spinulosus* in eastern Australia. The first two classes are shoots per plant, and the subsequent categories are the circumference of the lignotuber. (A) *Podocarpus spinulosus* population at Burrill Lake (plot size 100 m², measured 14 July 1994) and at Yalwal (plot size 100 m², measured 15 July 1994); (B) *P. spinulosus* population at Crommelin Reserve, Pearl Beach (quadrat sizes: site 1 = 30 m², site 4 = 10 m²; measured 22 January 1994); (C) *P. drouynianus* population at Sawyers Valley (plot size 100 m², measured on 30 December 2003) and at Jalbarragup (measured January 1994, plants enumerated from 15 plots totaling 375 m²).



FIGURE 8.7. Sawyers Valley population of *P. drouynianus*, showing the size of the plants to 1.5 m in the understory of the *Eucalyptus marginata* open forest (photo by B. L. Turner).

8.6A). It was not possible to determine the original number of genets in this population.

DISCUSSION

Podocarpus spinulosus and *P. drouynianus* are both in the subgenus *Foliolatus* and are phylogenetically closely related to each other but relatively distant from the rest of the species in the genus (Conran et al., 2000; Biffin et al., this volume). Although there is abundant evidence of podocarps in the Australian fossil record, there is no evidence of podocarps in dry environments. Analyses by Brodribb and Hill (1998) concluded that modern podocarp distribution was constrained by seasonal drought, with species largely confined to moist, aseasonal or weakly seasonal climates. The occurrence of these two species on the opposite sides of the Australian continent and their adaptation to fire-prone, moderately to strongly seasonal environments that cannot have been in contact for at least 20 million years suggest early evolution of the fire-tolerant life-form in *Podocarpus* and a long history of stasis in the species. It seems more likely that these two species are a result of vicariant speciation rather than the result of long-distance dispersal.

In Australia there has been radiation of a number of angiosperm groups concomitant with the drying of the continent through the Tertiary. However, in many cases only a small number of genera within a group (such as a family) have developed the required attributes to allow persistence under conditions more arid than those under which the parental group evolved. The groups that achieved arid adaptive changes have become spectacularly successful in speciation, whereas their generic relatives in the rainforest are usually species poor (e.g., Proteaceae; Johnson and Briggs, 1981; Jordan et al., 2008). Groups that are principally represented in rainforests but have a few species in dry forests are less common. In Australia the family Meliaceae may be an example, with *Synoum* common in some eucalypt forests of the east coast but the majority of genera found in rainforests of Australia or overseas. However, *Podocarpus* fits into this category, with the two southern Australian species the only ones to make an evolutionary excursion into drier forests. To do this, they had to undergo a number of morphological changes in their typical podocarp plant form.

Both species have narrower leaves and a much greater length to width ratio than the mean dimensions for other species in the subgenus *Foliolatus*. In the podocarps (and conifers in general), water is distributed from the main leaf

vein to the photosynthetic tissue via tracheids in accessory transfusion tissue rather than from a ramified network of veins as in angiosperms. This seems to be a less-efficient water distribution system than a network of veins. Under drought stress it has been shown that the tracheids of the accessory transfusion tissue in *P. grayi*, a rainforest species with broad leaves, collapse and therefore cease to transfer water to the mesophyll cells (Brodribb and Holbrook, 2005). The narrow leaves of *P. spinulosus* and *P. drouynianus* ensure there is only a short distance to transport water to the mesophyll from the primary leaf vein, which benefits the plant in terms of drought resistance. Brodribb and Hill (1998) showed that *P. drouynianus* had the greatest water use efficiency when compared to the other 12 species studied, five of which were podocarps from areas with greater than 1,500 mm rainfall per annum.

Both fire-tolerant podocarp species have retained their ancestral reproductive characteristics of dioecy, wind pollination, vertebrate dispersal, and recalcitrant seed germination. *Podocarpus drouynianus* has retained a form of synchronized cone formation and seeding, which occurs in at least some other podocarps (Geldenhuys, 1993), but this is cued by fire rather than other environmental signals. The benefits of this equate to masting and include increased effectiveness in a wind-pollinated species (Smith et al., 1990), seed predator satiation (Donaldson, 1993), and increased propagule visibility for a species that relies on animals for seed dispersal. Pyrogenic reproduction in *P. drouynianus* makes it a member of a relatively small group of Australian woody and herbaceous plants that flower almost exclusively in the first year or first few years after fire (Burrows and Wardell-Johnson, 2003); these include *Angophora hispida* (Auld, 1986), *Doryanthes excelsa*, *Telopea speciosissima* (Denham and Auld, 2002), and the wind-pollinated *Stirlingia latifolia* (Ladd and Wooller, 1997). *Podocarpus drouynianus* has likely been constrained to this reproductive solution in a fire-prone environment by its ancestral characteristics, including the absence of a cone structure for on-plant seed storage and having a seed too large to survive in the soil seed bank. Seed maturity of *P. drouynianus* occurs in winter (following dispersal in late summer), allowing germination at a time when conditions are most likely to be reliably moist in the Mediterranean-type climate of southwestern Australia. The embryo in the seed is immature when the podocarpium is “ripe” (i.e., fully colored) and continues to grow when the seed is initially dispersed. The more rapid germination with increased incubation temperature indicates that the rate of embryo development increased with higher temperature, so the embryo matured and forced its

way out of the seed coat earlier than in seeds incubated at lower temperature.

Animal dispersal is common in podocarps, although it is not universal (Nanami et al., 1999). Geldenhuys (1993) identified birds and bats as important dispersers of South African podocarp seed, and this certainly occurs in a number of New Zealand podocarps (Ogden and Stewart, 1995). The emu is the most important disperser of *P. drouynianus*; other animals may move the seed, primarily as predators rather than dispersers. The emu is a large and wide-ranging bird. It consumes gravel that lodges in the gizzard, where it serves to grind food. However, seeds of many species pass the digestive tract unharmed and may take from 3 to 50 hours to pass through (Davies, 2002). In this time an emu may traverse several kilometers, so podocarp seeds may be deposited in feces far from the location where they were consumed. The large seed size (in the upper range of seed sizes in southwestern Australian plants) should allow seedlings to establish even in unburnt vegetation and, after a subsequent fire, to resprout in the relatively competition-free environment, so long as at least a few years are available for lignotuber development before fire (Chalwell and Ladd, 2005). Nevertheless, most recruitment probably occurs in newly burned areas relatively close to parent plants, and there seedlings have the maximum possible time to establish before fire recurs (i.e., approximately equal to the mean fire interval). The large seed size is still an advantage in an environment where most species have much smaller seeds. There are no records of dispersal of *P. spinulosus* seed, but the propagule structure is similar to *P. drouynianus*, and emus also occur along the east coast of Australia and are likely dispersers. The apparent absence of fire-stimulated fruiting in *P. spinulosus* may indicate that recruitment in this species occurs in unburned sites, but further research is needed on patterns of recruitment in this species.

Adie and Lawes (this volume) highlight podocarp regeneration failure in grassy podocarp forests in South Africa, presumably due to competition between grasses and podocarp seedlings. Western Australian eucalypt forests tend to have a relatively open ground layer, so that postfire competition with podocarp seedlings is not likely to be as severe as in the South African wet forests.

There has been some consideration in this volume of the idea that podocarps tend to occur on nutrient-poor soils. *Podocarpus drouynianus*, in particular, is found on deep sands and old lateritic soils in southwestern Australia that have been considered as among the most nutrient poor in the world and are particularly low in phosphorus (Lambers et al., 2008). *Podocarpus spinulosus* also grows

on impoverished, thin soils over Permian sandstones in eastern Australia, but it may also extend into gullies on colluvial material, where nutrient status would be better because of a relatively high organic content in the soil. However, both species, in common with many other podocarps, survive well on nutrient-poor substrates.

The most obvious innovation in the Australian podocarp species is the ability to resprout from buried stem tissue after fire. This is rare in conifers, being found in only a few species, including *Widdringtonia nodiflora* in South African fynbos (Keeley et al., 1998) and *Actinostrobus acuminatus* in southwestern Australian kwongan (personal observation by the authors), both Cupressaceae. The proliferation of buds at the cotyledonary node is similar to that described for “basal chichi” in *Ginkgo biloba* seedlings (Del Tredici, 1992) and for eucalypts. Although this is not an essential requirement for growing in a fire-prone environment, it does ensure that the plant is resilient to burning over a range of fire frequencies. A few podocarp trees have epicormic sprouts that occur after defoliation by disturbances such as fires (*P. elongatus*; Midgley et al., 1995) or hurricanes, but this is not a particularly widespread trait in conifers (Bellingham et al., 1994). The lignotuber in both species develops in the axils of the cotyledons as in *Eucalyptus* and seems most similar to the “Group C” type of Carr et al. (1984). Del Tredici (1992) described the basal chichi of *Ginkgo*, which seem morphologically similar to the lignotuber of the podocarps and the eucalypts. Basal chichi are considered anatomically identical to the aerial chichi but are considered to develop from a bud, whereas aerial chichi develop in association with wounds to the trunk (Del Tredici, 1992). The aerial stem outgrowths of *P. spinulosus* develop in association with an axillary bud and thus differ ontogenetically from the aerial chichi of *Ginkgo*. However, the aerial chichi of *Ginkgo*, like the *P. spinulosus* form, can produce both shoots and roots. Lacey and Johnson (1990) called the woody outgrowths of *P. spinulosus* as lignotubers, but clearly, ontogenetically they are not strictly equivalent, as lignotubers should originate in association with the cotyledonary node. In terms of overall attributes the term chichi for the *P. spinulosus* stem outgrowths is appropriate.

Podocarpus drouynianus is a strong resprouter after defoliation. However, unlike many other lignotuberous species with which it co-occurs, the bud bank is completely depleted after each fire (Chalwell and Ladd, 2005), so it might not be well served by its bud bank under a regime of increasingly frequent fires, as projected for southwestern Australia as climate becomes hotter and drier (Williams et al., 2009). In *P. drouynianus* the root stock/lignotuber

may produce short lateral shoots that lead to a relatively compact plant form with many stems that rarely grow >3 m tall, whereas in *P. spinulosus* the lignotuber tends to be smaller and the stems more spreading. Stems frequently become buried under leaf litter and debris, which allows rooting from the chichi and subsequent shoot development. Initial connection to the parent plant would be beneficial, allowing the ramet to develop even though it may be heavily shaded or covered with litter. However, after fire the connection to the parent may be severed, and the ramet can resprout in the more open, postfire environment. Similar asexual plant expansion is seen in other conifers and is important in their population maintenance (Hayakawa et al., 2004), although these species do not occur in fire-prone environments.

The contrasting growth forms of these two species can be considered similar to the phalanx (*P. drouynianus*) and guerilla (*P. spinulosus*) strategies of clonal growth (Begon et al., 2006). The guerilla strategy is considered to be advantageous in locating resources (light, nutrients) in a patchy environment (de Kroons and Hutchings, 1995), but it has not been considered in relation to fire and the trade-off between sexual and asexual reproduction. The guerilla strategy can access more sites more quickly than the phalanx strategy, whereas vegetative reproduction may be more secure than sexual reproduction in a fire-prone environment when seedlings have limited fire resistance in the early years of growth. Fire frequency is difficult to summarize for the Australian forests where these species occur and has varied from the Aboriginal period to the present (Abbott, 2003). Indeed, there is considerable controversy about fire frequency in Western Australian forests. It has been deduced that jarrah forest in the Mundaring area (close to Sawyers Valley) could carry a fire every three to five years and that the frequency of fires lit in jarrah forest by Aborigines in summer was two to four years (Abbott, 2003). In contrast, using fire scars on tree stems, Burrows et al. (1995) estimated an average interval between tree-scarring fires of about 80 years before European settlement and about 17 years afterward. However, they suggested that lower-intensity fires of greater frequency might not scar large trees. A fire map in Fox (1999) shows that fire return times for southwestern Australia are about 10 years, whereas for much of the area occupied by *P. spinulosus* fire return times are three to five years and thus equally or more frequent than in Western Australia.

Slower lignotuber development in *P. spinulosus* than in *P. drouynianus* seedlings may be related to the greater ability of guerilla development in the former. The guerilla strategy involves the lax branches contacting the soil and

the chichi structures developing roots to produce ramets that eventually become independent plants. In the Crommelin Reserve the plants censused in site 1 were predominantly of 1–2 shoots and were mostly produced from a network of formerly continuous procumbent stems (covered with plant litter) connecting chichi that had produced roots and a few shoots at sporadic points. A similar situation applied at Yalwal, but at that site the stems were aerial and mostly still intact. This species seems to rely heavily on asexual reproduction to maintain the population, in contrast to *P. drouynianus*, which has a much more compact growth form and can only slowly extend the area occupied by a genet. Colonization of new sites by this species will be mainly dependent on seeds, so strong postfire reproduction (masting) will be beneficial to this species in maintaining population numbers.

In frequently (and predictably) disturbed environments there has been a dichotomous selection for a seeder plant functional trait and refinement of what is often a generalized trait for resprouting. Seeder species need to develop a seed bank in preparation for the next stand-destroying fire, whereas sprouter species rely heavily on vegetative regeneration. The ancestral reproductive trait of podocarps is as a seeder rather than a sprouter. The seeds are large and not contained in fire- or desiccation-resistant cones; they are unsuitable for storage in soil because of their large size and lack of dormancy. Thus, the ancestral podocarp did not have a suitable strategy for surviving in a fire-prone environment. The development of the ability to resprout laid the foundation for the success of *P. drouynianus* and *P. spinulosus*, and the other modifications they display are incremental, not radical. By being able to resprout, *P. drouynianus* can emulate a suite of angiosperms that are cued to reproduce after fire on newly produced stems and thus distribute seeds into a relatively competition-free and nutrient-rich environment. Bellingham and Sparrow (2000) note that there are trade-offs between vegetative resprouting and seeding. The reproductive trade-off for sprouters is that they normally do not produce as many seeds as seeder species. In most podocarps, adult plants produce seeds in all years, although there may be mast years (Geldenhuys, 1993), and they may have a variable but low investment in buds for resprouting. *Podocarpus drouynianus* has an extreme form of masting, with seeds produced only after fire. In years between fires (with fire intervals ranging from 10 to 30 years) the plants can accumulate resources to fuel resprouting and reproduction after the next fire occurs. However, it is unknown whether very long intervals without fire lead to decline in the bud bank and an increased susceptibility to mortality from fire,

as has been described for some other fire-tolerant lignotuberous species (Wellington and Noble, 1985; Enright et al., 1998). Alternatively, the time since the last fire may become so long that some level of annual fruiting commences, as identified for plants in paddocks that have been isolated from fire for many decades. More work is also needed on reproduction in *P. spinulosus* to determine its pattern of seed production in relation to fire.

As predicted by Midgley (1996), the development of resprouting has meant that both *P. drouynianus* and *P. spinulosus* have to relinquish the tall monopodial form characteristic of most podocarps in wet forests. The species have become subdominants in their communities. Nevertheless, they are resilient to both stress (i.e., seasonal drought) and disturbance (i.e., fire), and if persistence at a site is any indication of evolutionary success, *P. drouynianus* has certainly achieved this (as demonstrated in Figure 8.5f), being one of the few native species to survive in the predominantly cleared area. These species clearly represent podocarps “on the edge” in terms of their adaptations to a set of environmental circumstances beyond those associated with any other members of this large, and typically conservative, plant family.

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