

A MORPHOLOGICAL INVESTIGATION OF THE UNUSUAL CRYPTOGEAL GERMINATION STRATEGY OF BUNYA PINE (*ARAUCARIA BIDWILLII*)—AN AUSTRALIAN RAIN FOREST CONIFER

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The morphology of the cryptogeal germination sequence of *Araucaria bidwillii* (bunya pine) was studied. Individual seeds were 5–6 cm in length and 2.5–3.5 cm in diameter and had an average fresh weight of ca. 16 g. In mature seeds the embryo consisted of a cotyledon tube, hypocotyl, and root cap that were 3–5 mm in diameter and 25–30, 3–4, and 5–7 mm in length, respectively. The embryo was surrounded by, but not fused into, a massive megagametophyte. Germination was rapid as a large diameter pseudo-radicle emerged from the seed 48 h after the start of imbibition. At 1 wk the cotyledon tube had elongated to 3.5 times its original length. As cotyledon growth was positively geotropic the root and shoot meristems were forced out of the seed and buried in the soil below the initial position of the seed. At week 3 the hypocotyl was 12–15 and 3–4 times its original diameter and length, respectively, and had developed into a parenchymatous tuber. It appeared that starch stored in the megagametophyte was being mobilized, translocated down the cotyledon tube, followed by resynthesis in the expanding tuber. At week 4 the tuber had developed a thin reticulate periderm and had also initiated numerous lateral roots from its lower third. At this stage a distinct abscission zone had developed at the base of the cotyledon tube and after a further 2–4 wk the cotyledon tube and megagametophyte were easily detached from the tuber at the abscission zone. In mature seed the epicotyl consisted of only a small apical dome, but at week 5 it was a small shoot that commenced its growth upward through the soil by either splitting or pushing away the cotyledon tube. Initially, the tubers possessed 4–6 pairs of strands of primary vascular tissue embedded in a parenchymatous matrix. With the commencement of secondary growth each pair of strands developed into a cylinder of secondary tissues, which are eventually incorporated into the normal secondary growth increments. While external evidence of the tuber is lost as secondary thickening of the root and stem progresses the unusual nature of the hypocotyl can be ascertained by internal examination. This germination sequence allows *A. bidwillii* to transform a large surface seed into a subterranean storage and perennation organ. Bunya pine is a rain forest emergent, and it appears that the carbohydrate reserve of the tuber allows seedlings to exist for several years under the low light levels of the forest floor, until a break in the canopy allows for rapid growth. The buried bud reserve created as the plumule grew through the soil would allow for regeneration if shoot damage occurred.

Introduction

“Cryptogeal” is the term applied to germination mechanisms that carry the plumule below the soil surface before shoot elongation, i.e., the new shoots arise from below the ground even though the seed germinated on the surface. It is relatively common in the monocotyledons and is known in a number of taxonomically unrelated families of herbaceous and woody dicotyledons (Clarkson and Clifford 1987). It is also known in the cycads, e.g., *Encephalartos* and *Stangeria*, but within the conifers only the three species in the *Bunya* and *Columbea* sections of *Araucaria* have a similar germination strategy.

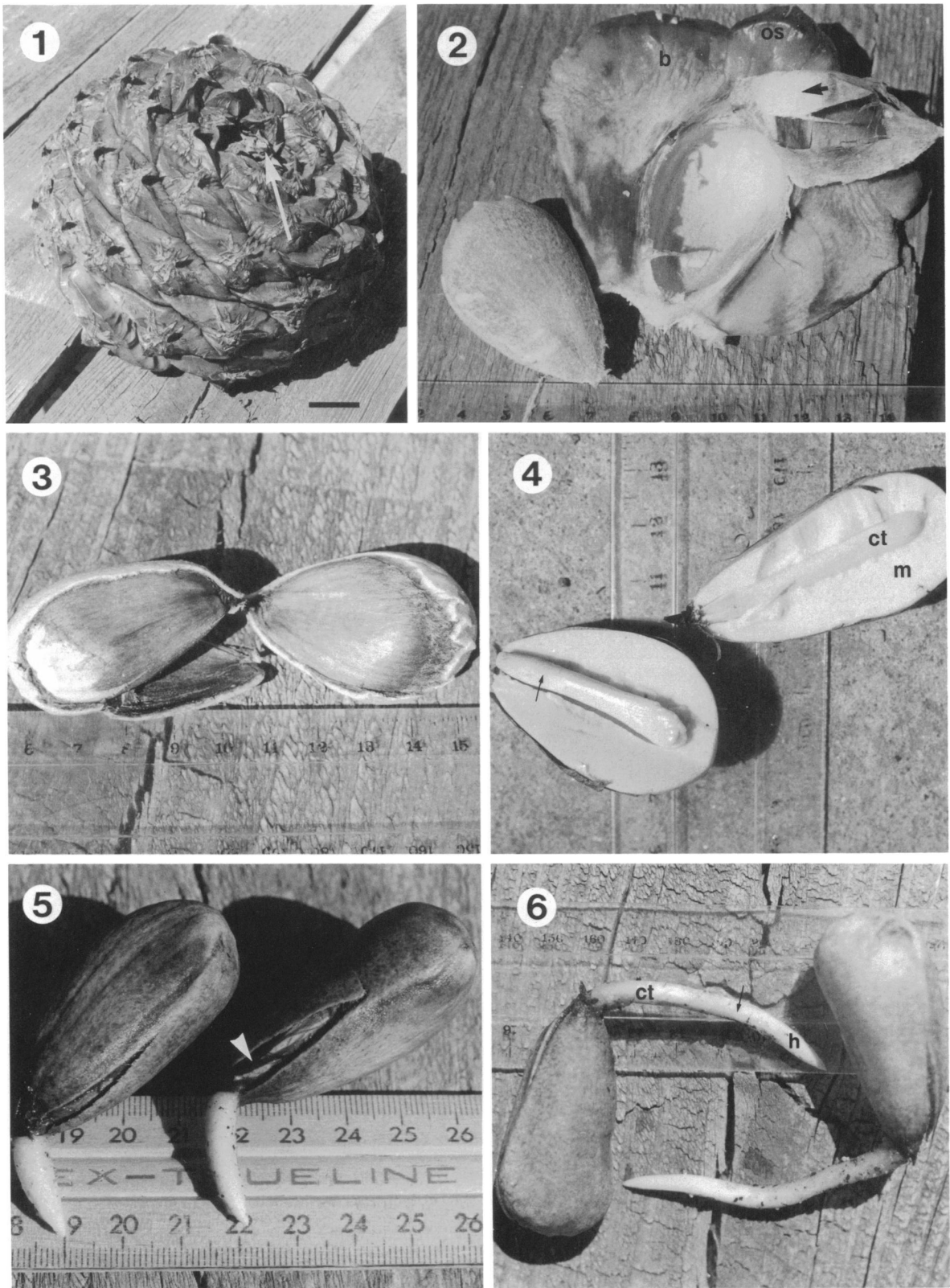
Bunya pine (*Araucaria bidwillii* Hooker) is a conifer native to Queensland, Australia, and is the only member of the section *Bunya*. It has a limited natural distribution and occurs in the Bunya Mountains–Blackall Range area in the south of the state (latitude 27°S) and the Mount Molloy/Mount Lewis area in the north (latitude 16°30'–17°40'S) (Boland et al. 1984). It is more

closely related to section *Columbea* species, *A. araucana* from Argentina and Chile and *A. angustifolia* from Brazil and Bolivia, than it is to its physically closer relatives from the sections *Intermedia* and *Eutacta* (Haines 1983a).

Bunya pine has been grown to a limited extent in plantations, 1,100 ha having been planted by the Queensland Department of Forestry. Its usefulness as a plantation species is limited by its possession of persistent, sclerophyllous, pointed leaves, although it has a greater drought and cold resistance than the widely planted (44,000 ha) hoop pine (*A. cunninghamii*) (Doley 1990). The seeds of bunya pine are considered difficult to store (Doley 1990), which creates problems in plantation establishment. The trees grow to 30–45 m in height (Boland et al. 1984) and carry cones in the upper crown that can weigh up to 10 kg (Doley 1990). Because of bunya pine's distinctive domed appearance and strict symmetry it was once widely planted in parks and larger gardens, but property damage and the risk of personal injury from falling cones has seen it decline in horticultural favor.

Cones mature in mid to late summer and fall to the ground intact, with the cone scales still green on the surface and fleshy and resinous in-

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Figs. 1-6 Various stages of seedling development in bunya pine. In figs. 4 and 6 the approximate internal position of the shoot meristems is arrowed. Scales, where present, in cm and mm. Fig. 1, Proximal half of a mature seed cone showing its large size and the arrangement of the scales. Note the small diameter of the attachment axis (arrowed). Scale, 3 cm. Fig. 2, Seed that had been separated from the cone scale unit that consisted of a large leathery winged bract (*b*) and the ovuliferous scale (*os*). The membranous layer (arrowed) holds the seed into the cone scale at maturity. Fig. 3, Seeds that have had the

ternally (Doley 1990). Their weight helps the cones to roll down slopes and hence achieve an increased dispersal. The cones rapidly disintegrate on the ground as the structure dries (Haines 1983*b*). Further drying releases the large (5 cm length, 3 cm diameter), heavy (10–17 g) seeds from the cone scales, and they are then available for dispersal by animals. Occasionally the humid conditions in the decomposing cone promote seed germination (Haines 1983*b*), and germination of seeds within sealed plastic bags is also known (Doley 1990).

The seeds were an important food source for the local Aboriginals (Cherikoff and Isaacs 1989). However, while cones are usually produced every year, they are produced in abundance only every third year (Cherikoff and Isaacs 1989). Nutritional studies indicate that over 40% of the fresh weight of fresh seed is available carbohydrate (Brand et al. 1985). Likewise, 60% of the dry weight of *A. araucana* seed is starch (Cardemil and Reinero 1982).

In the latter half of the nineteenth century the first descriptions of bunya pine's unusual germination sequence were recorded by Dürr (1864), Blanchard (1892), Heckel (1892), and Hemsley (1901–1902). Since this time there have been morphological and anatomical studies of seed and embryo formation (Wilde and Eames 1948; Haines 1983*b*) and of isolated stages of seedling development (Seward and Ford 1906; Shaw 1909; Stockey and Taylor 1978; Rouane and Woltz 1979; Stockey et al. 1990), but no sequential morphological studies of germination have been undertaken. The physiology of certain aspects of cryptogeal germination in *Araucaria* have also been investigated (Cardemil and Reinero 1982; Doley 1990). Given the continuing interest in the unusual germination sequence of bunya pine it was considered useful to undertake a thorough morphological investigation.

Material and methods

Bunya pine cones were collected on the day of fall in late summer from specimen trees growing at Wagga Wagga, N.S.W., and approximately 65 fully formed seeds were extracted. The seeds were planted in sterile potting mix in 15 cm diameter pots. Two seeds per pot were planted 1 cm below the surface, with the long axis positioned horizontally and with the radicle end of the seed

pointing toward the middle of the pot to permit unimpeded pseudo-radicle emergence and subsequent hypocotyl enlargement.

The seeds were planted below the surface to promote uniformity of germination and seedling morphology. As seed burial would be unusual under natural conditions, a further 10 seeds were planted on the surface of the potting mix and the pots were covered with 70% shade cloth to maintain a high humidity. All pots were maintained in a shade house, under prevailing conditions.

Seeds or seedlings were assessed on the day imbibition commenced, 3 and 7 d thereafter, and then weekly for a further 6 wk. The hypocotyl regions of bunya pines growing in the field at Gympie, S.E. Queensland, were also studied. These plants were 1–4 yr of age, secondary growth was well advanced, and the hypocotyl region was up to 5.0 cm diameter. The hypocotyls were cut into 6–8 mm thick discs with a radial saw, the end grain polished and photographed.

Results

WEEKS 0–8

Mature seed cones were approximately 22 cm in diameter and were comprised of numerous overlapping scales (fig. 1). Most scales were fertile, although the scales at either end were either sterile or bore small, elongated seeds. Cones were held in trees by a relatively small diameter peduncle, which indicates why the cone is shed whole, rather than the cone disintegrating while attached to the tree (fig. 1). Unlike hoop pine, where the seed is fused into the scale unit, in bunya pine the seeds were easily removed as they are held in by only a thin tissue layer (fig. 2). Seeds were ca. 5.5 cm long × 2.5 cm at their largest diameter and weighed ca. 16 g.

The embryo and megagametophyte were protected by a thick (1.0–1.5 mm), woody sclerotesta layer (fig. 3) that showed no obvious lines or points of weakness for seedling emergence. The embryos were surrounded by megagametophyte tissue, except at their radicle end, and there was no physical attachment between the embryo and the megagametophyte tissue (fig. 4). Longitudinal sections of the embryos showed that in a total embryo length of ca. 4 cm the root and shoot meristems were only 3–4 mm apart, while the bulk of the embryo was made up of the cotyledons and the "root cap." The cotyledons were fused

← middle sclerenchymatous integumentary layer partially removed, exposing the inner papery integumentary layer that covers the megagametophyte. Fig. 4, Partial removal of the megagametophyte (*m*) revealing the torpedo-shaped embryo. Note the root cap that gives the lower third of the embryo a matt appearance. *ct*, cotyledon tube. Fig. 5, Germinating seeds 2–3 d after imbibition, showing that an increase in internal volume has split the middle integumentary layer sufficiently to permit radicle extension. Note the mucilaginous sheath that covers the radicle. Note also the strands of the inner integumentary layer (arrow) in the right-hand-side embryo. Fig. 6, Germinating seeds, week 1. Note that the mucilaginous sheath covers the cotyledon tube, as shown by the trapped particles of potting mix, but the sheath does not cover the rapidly elongating hypocotyl (*h*).

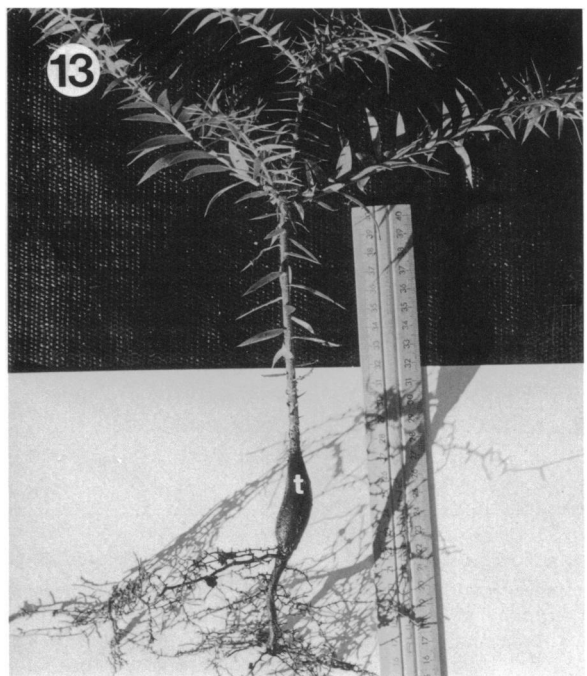
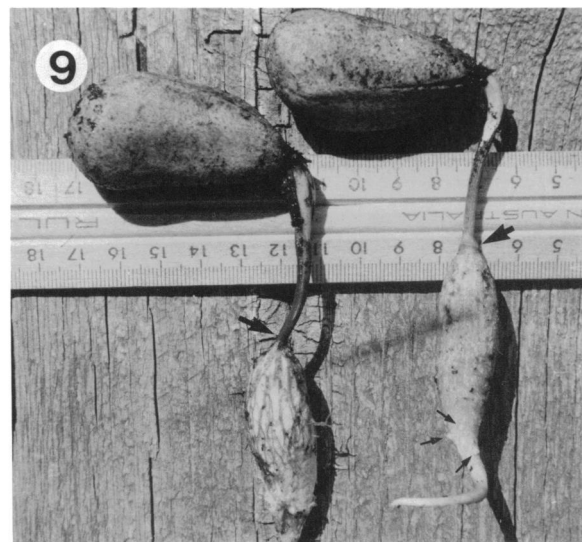
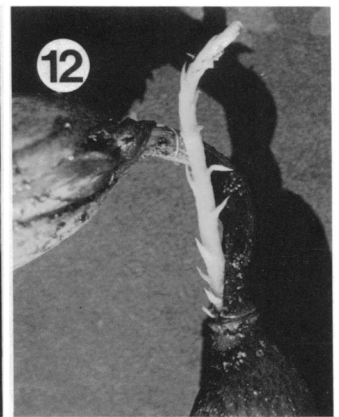
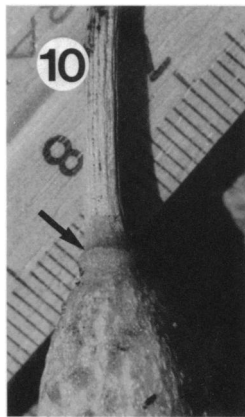
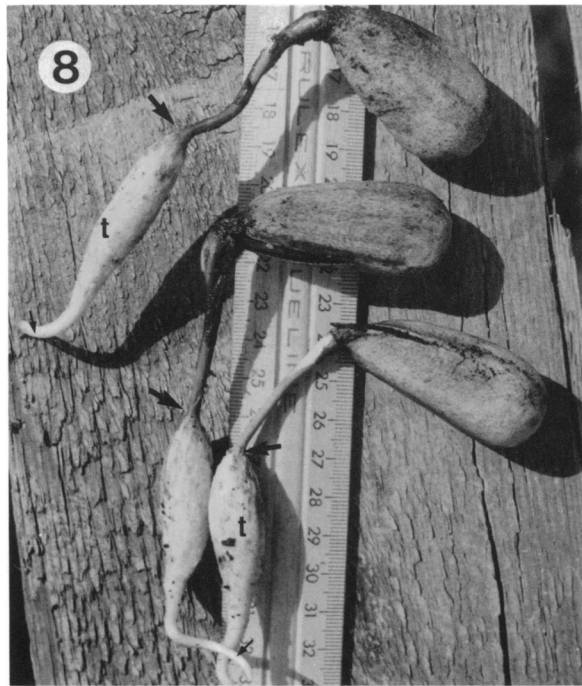
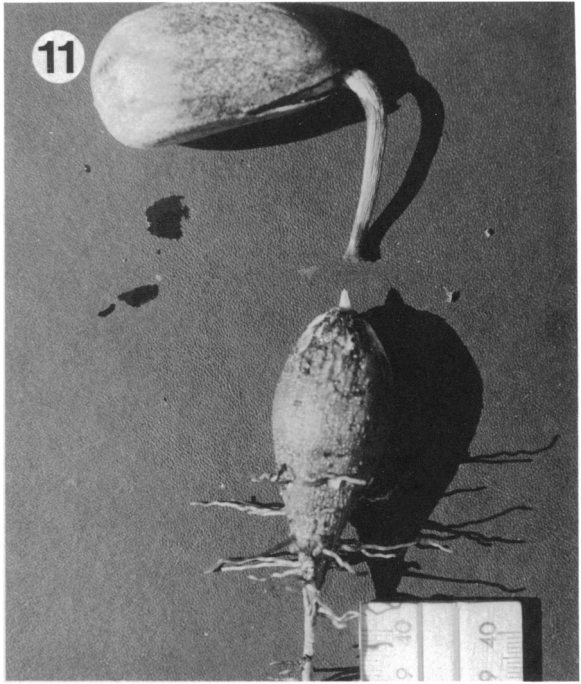
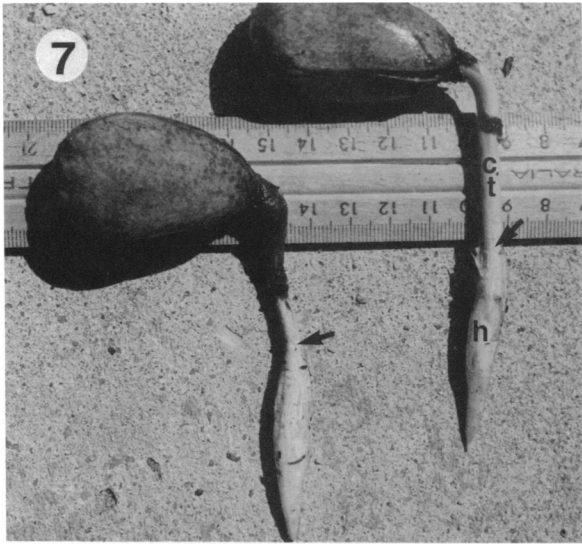


Table 1
DIMENSIONS (cm) OF VARIOUS COMPONENTS OF BUNYA PINE SEED OR
SEEDLINGS DURING THE FIRST 6 WK OF GERMINATION

Week	CT length			Hypocotyl/tuber		Root length
	Total	Outside seed	CT diameter	Length	Diameter	
0	2.5–3.0	0	.3 × .5	.3–.4	.3–.5	0
1	8.5–9.5	4.0–4.5	.3 × .5	1.5–2.0	.3–.5	0
2	8.5–9.5	4.0–5.0	.3 × .4	4.0–4.5	.5–.8	.5–1.0
3	9.0–10.0	4.0–5.0	.2 × .3	4.5–5.0	1.1–1.4	2.0–3.5
4	9.0–10.0	4.0–5.0	.2 × .25	4.5–5.0	1.5–1.7	3.5–4.0
5	9.0–10.0	4.0–5.5	.2 × .25	4.5–5.0	1.8–2.0	4.0–6.0
6	9.0–10.0	4.0–5.0	.2 × .25	4.5–5.5	1.9–2.3	7.0–9.0

Note. CT, cotyledon tube.

into a tube; however, at this stage the central hollow was only 0.1×2.0 mm in cross section (C.S.) and was not an obvious feature. The cotyledon tube was oblong in C.S. (3×5 mm) and had a smooth glossy appearance, while the lower third of the embryo was covered by relatively loose cells that gave a matt finish (fig. 4).

Seeds exhibited no dormancy and germination was rapid as pseudo-radicle emergence occurred within 48 h of imbibition. Water uptake during imbibition caused an increase in internal volume that consequently split the integument along lines of relative weakness (fig. 5). Radicle extension was always positively geotropic regardless of seed orientation. When the radicle and hypocotyl first emerged they were covered by a loose, fibrous, mucilaginous mat that could be easily removed from the underlying tissues (fig. 5).

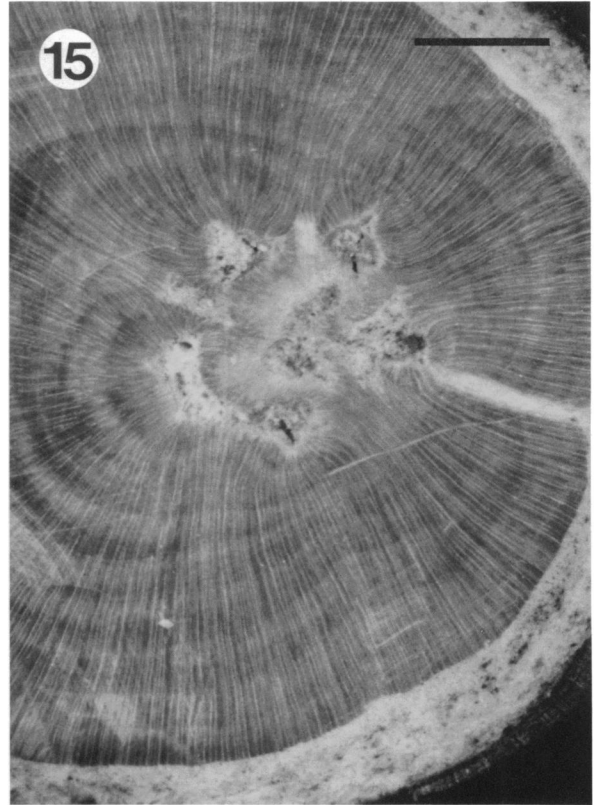
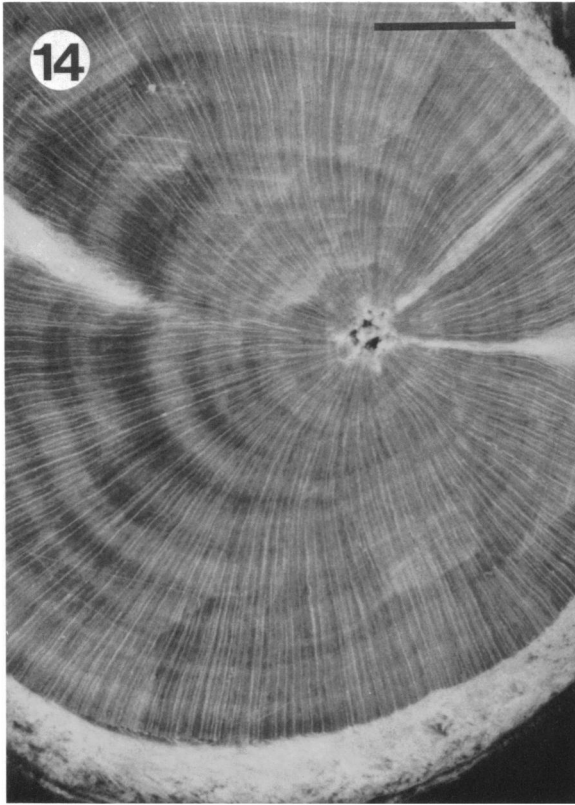
At 1 wk elongation of the cotyledon tube was largely complete, and it was three to four times its original length (table 1; fig. 6). In the same period the hypocotyl elongated by five to six times, although its diameter remained unchanged (table 1). The mucilaginous sheath now covered the length of the cotyledonary tube, but not the hypocotyl. At 1 wk there was little external evidence to indicate that each bunya pine seed had not produced a single, unbranched, rapidly growing, large diameter taproot. Dissection was needed to show otherwise.

At week 2 the hypocotyl had doubled or trebled in length during the previous 7 d and was 85%–95% of its final length (table 1). Between weeks 1 and 2 the hypocotyl began to increase in diameter, and consequently a clear external distinction between the cotyledon tube and the hypocotyl began to develop (fig. 7).

At week 3 elongation of the hypocotyl had ceased, and it was approximately 12.5 times its original length. Rapid increases in the diameter of the hypocotyl were still occurring, and consequently it could now be termed a tuber (fig. 8). The cotyledon tube began to reduce in diameter and consequently had a grooved appearance that gradually became more prominent (fig. 10). It appeared that the ridges corresponded to the position of the vascular bundles within the tube, while the furrows corresponded to the parenchymatous tissues between the bundles. The outer surface of the cotyledon tube began to darken from what appeared to be tannin or phenolic compound deposition in the surface cell layers, not from periderm formation. The tuber began to develop a thin reticulate periderm, while small white pustules formed on the lower third of the tuber. An obvious root, as distinct from the tuber, had also formed (fig. 9).

At week 4 most seedlings had developed a distinct abscission zone at the base of the cotyledon tube adjacent to the tuber (figs. 9, 10), although

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Figs. 7–13 Various stages of seedling development in bunya pine. In figs. 7–9 arrows indicate the approximate position of the shoot apical meristems. Fig. 7, Germinating seeds, week 2. Note the continued lengthening of the hypocotyl and its increased diameter. Fig. 8, Germinating seeds, week 3. Note the continued increase in hypocotyl/tuber (*t*) diameter, the reduction in cotyledon tube diameter, and the development of a root (small arrows) as distinct from the tuber. Fig. 9, Germinating seeds, week 4. Note the development of a thin reticulate periderm on the tubers and the formation of small pustules (small arrows) on the lower third of the tuber. Fig. 10, Detail of the right-hand-side seedling in fig. 9, showing periderm development on the tuber, development of a distinct abscission zone (arrowed), and reduction in cotyledon tube diameter resulting in a grooved appearance. Fig. 11, Seedling 6–8 wk of age showing separation of the megagametophyte, integumentary layer, and cotyledon tube from the hypocotyl/tuber with its root and shoot meristems. Note the numerous lateral roots that have developed from the pustules shown in fig. 9. Fig. 12, Seedling 3 mo of age showing incomplete separation of the cotyledon tube from the tuber. Note that the plumule lacks chlorophyll but is not excessively etiolated. Fig. 13, One-year-old seedling. While the hypocotyl/tuber swelling is still prominent with subsequent secondary growth in the shoot and root, it will not be externally obvious.



Figs. 14-17 Successive cross sections down through the former tuber region of a bunya pine 4 yr of age. Note the unusual patterns of xylem formation and the large pith areas. Scales, 3 mm. Fig. 14, Stem wood immediately above the previously tuberous region. Fig. 15, Section from near the "tuber" apex. Figs. 16, 17, Mid-regions of the "hypocotyl"/"tuber."

separation did not occur even with gentle force. At this stage the cotyledon tube had contracted to approximately 50% of its original diameter and had a leathery texture compared with its previous firm and turgid nature (fig. 10).

By weeks 6–8 the pustules observed at week 3 had developed into lateral roots that formed in longitudinal rows down the sides of the tuber (fig. 11). In this area of root initiation the outer tuber sloughed away to reveal another periderm covered surface beneath. The upper tuber surface remained intact. Between weeks 5 and 6 the first detachments of the tuber from the cotyledon tube occurred, although this would not have happened had the seedlings not been lifted; i.e., separation would not have occurred this early under natural conditions. Separation was usually complete at a well-formed abscission layer, although a hinge sometimes formed (fig. 12). Under natural conditions the epicotyl grows up the cotyledon tube for a short distance until it splits the tube or pushes it off (fig. 12). Dissection of fresh seeds showed that the megagametophyte had a firm solid texture, but by week 6 it had a spongy nature.

In mature embryos the shoot apex consisted of only a small apical dome, with no primordial leaves present. At week 6, well-developed shoots, 0.2–1 cm in length, with numerous leaf primordia were present. In older seedlings where the shoots had pushed through 2–3 cm of overlying soil, the leaves were small and achlorophyllous, although the internodal distances were small (fig. 12); i.e., there was no obvious etiolation when compared with shoots that had developed above ground. The tubers reached a maximum diameter of 2.0–2.3 cm at ca. 2 mo of age, but because of the collapse of the parenchyma from utilization of stored carbohydrate they shrink to be only 1.0–1.5 cm in diameter at 12 mo of age (fig. 13).

The seeds placed on the potting mix surface displayed three developmental responses: (i) 50% developed a typical large tuber, but as the cotyledon tube extended outside the seed coat by an average of only 2.5 cm, the shoot apex was buried to only 1–2 cm below the soil surface; (ii) another 30% also had 2.5 cm of cotyledon tube beyond the seed coat, but the radicle did not penetrate the surface and a much smaller (0.8 cm diameter \times 3.0 cm length) tuber was formed; and (iii) 20% did not germinate, as compared with 100% germination when seeds were planted below the soil surface.

WEEK 8—YEAR 4

In young, full-size tubers the primary vascular tissues were arranged in a continuous ring immediately below the epicotyl, but in the midsection of the tuber they had split into four to six pairs of long, narrow (0.2 \times 0.9 mm) strands embedded in a large volume of parenchyma. The

strands merged together again toward the base of the tuber. Serial examination of successive cut surfaces indicated that the strands were independent of each other for most of their length through the tuber; i.e., there were no anastomoses.

Secondary growth proceeded in a typical manner in the stem and root tissues above (fig. 14) and below the tuber/hypocotyl. In the mid-region of the tuber the vascular strands gradually commenced normal secondary growth, but after several months each pair of strands joined together, forming a small diameter ring. It appeared the vascular cambia were joined by short arcs of interfascicular cambium that differentiated across the intervening parenchyma. This occurred first across the smaller gap to the outside and later across the larger inner gap, and thus four to six cylinders of secondary vascular tissue developed within the tuber. The tracheids of the secondary xylem were formed in rows, but very few of these rows had a radial orientation (figs. 15–17), as in a normal growth increment (fig. 14). As secondary growth proceeded, the parenchyma core within each ring was crushed, as was the pith area between the rings (figs. 16, 17).

With further secondary growth it appeared that as the cambial rings increased in diameter they eventually fused or grafted into each other and thus formed a single large convoluted circle. The inner segments of cambium gradually ceased to function, while the outer arcs joined together to function as a typical vascular cambium producing normal increments of secondary xylem with the tracheids in radial rows (figs. 16–17). While the external distinction between the tuber and the remainder of the axis is lost with continued secondary growth, the unusual nature of the hypocotyl region can always be ascertained by internal examination.

Discussion

COMPARISON WITH OTHER CRYPTOGEAL SPECIES

Clarkson and Clifford (1987) noted two main characters associated with cryptogeal germination: (1) some fusion of the cotyledons is present, and usually the greater the fusion, the greater is the depth at which the short apex is buried; and (2) large-seededness. Bunya pine, a species not considered by Clarkson and Clifford, adds further support to these generalizations.

In cryptogeal species, varying levels of cotyledon fusion have been recorded. Fusion may be (i) limited, consisting only of the margins of the cotyledon petioles, as in *Marah oreganus* (Schlising 1969) and *Elephantorrhiza elephantina* (van der Schijff and Snyman 1970); (ii) complete, except for a tube extending from above the plumule to the cotyledon tips as in *Butyrospermum paradoxum* (Jackson 1968); or (iii) complete so that

the cotyledons are solid except for an air space above the plumule, as in *Jedda multicaulis* (Clarkson and Clifford 1987). Bunya pine is similar to *B. paradoxum* in the degree of cotyledon fusion.

In *J. multicaulis*, *E. elephantina*, *M. oreganus*, and several of the species described by Jackson (1974) the developing shoot must burst through the base of the fused cotyledons. From published information, bunya pine appears to be unique among cryptogeal species in the formation of a distinct abscission zone that allows for the programmed detachment of the depleted megagametophyte from the tuber. As a consequence, the epicotyl is not impeded by the cotyledon tube in its upward growth, although in other species the tube may provide the epicotyl with some protection from abrasive soil particles. While *Araucaria bidwillii* is closely related to *A. angustifolia* and *A. araucana*, the seeds of the two South American species possess two separate cotyledons rather than a cotyledon tube (Haines 1983a). In *A. araucana* (Cardemil and Reinero 1982, fig. 10) and *A. angustifolia* (Hill and de Fraine 1909, pl. 15, fig. 5; Stockey and Taylor 1978, fig. 9; Rouane and Woltz 1979, fig. 20) the epicotyl is able to grow upward between the cotyledons, and thus no advantage exists in the formation of abscission zones at the base of each cotyledon.

A comparison of cryptogeal species shows that the shoot apical meristem is buried to the following degrees: *J. multicaulis*: 2–8 cm, *E. elephantina*: up to 4 cm, *M. oreganus*: 5–25 cm, *Combretum binderanum* (Jackson 1974): 4–6 cm. Bunya pine, with 2–5 cm of cotyledon tube extension, is in the normal range displayed by cryptogeal species. Seedlings of *A. angustifolia* and *A. araucana*, as illustrated by Hill and de Fraine (1909), Stockey and Taylor (1978), Rouane and Woltz (1979), and Cardemil and Reinero (1982) would appear to have a more limited (< 1 cm) burying of the shoot apex.

In *J. multicaulis* the seedling remains attached to the seed/fruit for an extended period and the fruit can also remain attached to the parent plant, while in *E. elephantina* attachment between seedling and seed occurs for sufficient time that the vascular bundles in the cotyledon tube are secondarily thickened. This would indicate that nutrient transfer from the seed to the tuber can continue over an extended period. In contrast, the formation of an abscission zone by bunya pine means that nutrient transfer must be relatively rapid and efficient. In *J. multicaulis* and *M. oreganus* the seeds lack endosperm and the entire volume of each seed is embryo, with the bulk of the nutrients being stored in the large cotyledons. In bunya pine most nutrient and carbohydrate storage is in the megagametophyte and thus transport from this tissue to the cotyledon tube must

be apoplastic, in contrast to the entirely symplastic transport pathway that would be possible in *Jedda* and *Marah*.

The mucilaginous mat observed at days 2–7 may be a hydrated form of the outer layers of the massive “root cap,” i.e., the cells that gave the lower third of the embryo a matt finish. It could allow low-friction penetration of the soil by the pseudo-radicle. In *M. oreganus* epidermal root hair-like cells were found on the cotyledon tube but were not present in bunya pine.

LARGE-SEEDEDNESS

Seed sizes and weights for some of the better described cryptogeal species are as follows: *J. multicaulis*—fruit with one seed: 4–6 × 6–7 cm/75–100 g (Clarkson and Clifford 1987); *M. oreganus*—one seed: 0.8–1.0 × 1.5–2.5 cm/1.1 g (Schlising 1969); and *E. elephantina*—one seed: 2 × 2.5 cm/(no weight given) (van der Schijff and Snyman 1970).

These measurements and those of bunya pine (one seed: 2–3 × 5–6 cm/16 g) support the generalization (Clarkson and Clifford 1987) that large-seededness is associated with cryptogeal germination.

ECOLOGY

Cryptogeal germination is generally interpreted as an adaptation to fire (Jackson 1974; Clarkson and Clifford 1987), to heavy grazing or trampling (Clarkson and Clifford 1987), or as a drought-evasion mechanism (Schlising 1969).

Bunya pine is a tropical and subtropical rain forest emergent. Seedlings may spend several years achieving little or no growth in the low light levels of the forest floor before a break in the canopy allows for rapid upward growth. Thus, the carbohydrate stored in the tuber permits bunya pine to survive under light levels that may be too low for appreciable carbon gain through photosynthesis.

The timing of cone fall and the sequence of seedling development correlate well with the climatic patterns of S.E. Queensland. Cone fall coincides with the wettest period of the year, which allows for imbibition of the seeds, and the radicle would encounter the least resistance as it penetrated the moist leaf litter and soil of the forest floor. The seedlings would be able to establish a well-developed root and tuber system before late autumn/early winter. The tubers of bunya pine are known to be resistant to desiccation (Hemsley 1901–1902), and although bunya pine occurs in areas with an annual rainfall of 900–2,000 mm (Boland et al. 1984), winter and early spring in S.E. Queensland can be relatively dry (189 mm average rainfall in Kingaroy May–September). Thus the tubers may also have a drought-evasion function.

In growing through the overlying soil the bunya pine epicotyl buries many leaves. It is highly probable that in the axil of each of these leaves there is an axillary meristem (Burrows 1986, 1987) capable of developing into a new shoot (Burrows 1989). These relatively undifferentiated meristems are exogenous in origin but are covered by specialized periderms and are thus shielded from the soil environment. Thus the bunya pine seedling develops a bud reserve, protected by the soil. In Queensland rain forests fire is rare, and there are few herbivores that would attack bunya pine's pungent, sclerophyllous leaves. In either situation, the bud reserve should permit the reestablishment of an above-ground shoot system.

In *M. oreganus* the hypocotyl eventually develops into an immense, perennial underground tuber that initiates annual vines after the wet season, to replace those that died in the preceding dry season (Schlising 1969). *Jedda multicaulis* has a multistemmed habit with a complex crown of stem tissue (Clarkson and Clifford 1987), while in *E. elephantina* the above-ground stems die back each winter (van der Schijff and Snyman 1970). Thus in these species the tuber is a perennating organ for the life of the plant. In bunya pine the initial difference in diameter between the tuber and the stem is reduced as (i) the stem and root increase in diameter through secondary thickening and (ii) the tuber decreases in diameter through the utilization of the stored carbohydrate. After approximately 4–5 yr growth no difference in diameter exists between the hypocotyl/tuber region and the adjoining shoot and root, and anatomical study is needed to reveal the unusual nature of this region (figs. 14–17). Thus, in bunya pine the tuber is a perennating organ while the plant is small, but not subsequently.

PALEOBOTANICAL CONSIDERATIONS

Wieland (1935), Gothan (1950), Calder (1953), Stockey and Taylor (1978), Nishida (1981), and Stockey et al. (1990) have interpreted various fossilized plant remains, ranging from corm to top or turbinate in shape, as possible araucarian seedling structures.

When cut in C.S. the turbinate forms are principally composed of tracheids in radial files and a small central pith of uncompressed parenchyma cells (Gothan 1950, pl. 1, fig. 5; Calder 1953, figs. 20, 22–25; Stockey and Taylor 1978, fig. 33;

Nishida 1981, figs. 2–4, 6). These structures show no resemblance to normal bunya pine tubers at any sectioning level or at any developmental stage. Stockey et al. (1990, figs. 40, 42) illustrate a bunya pine seedling that developed a corm-type swelling after the root tip had been damaged. They suggested that in past periods many seedlings would have grown in volcanic soil subject to frequent ash fall, and thus root apex damage and the subsequent formation of turbinate swellings may have been a common occurrence.

The top-shaped structures shown by Stockey and Taylor (1978, figs. 1, 4, 5) have a greater external resemblance to bunya pine tubers, but it appears that they may not be araucarian, or at least not closely associated with bunya pine, for the following reasons:

i) There do not appear to be any vascular bundles from the cotyledon tube in the cortex (Stockey and Taylor 1978, fig. 3), as could be expected from their figure 13; however, tissue preservation of these specimens is poor; and

ii) Stockey (1975, 1978) indicates that for the extinct species *A. mirabilis* (placed in the section *Bunya*) the mature cones were a maximum of 10 × 10 cm and individual seeds were 0.2–0.6 cm wide × 0.8–1.3 cm in length, and this appears to be too small to produce, via cryptogeal germination, a largely parenchymatous structure of 2.3 cm diameter × 3.5 cm length.

As per the present study, the papers of Shaw (1909), Stockey and Taylor (1978, fig. 14), and Stockey et al. (1990, fig. 41) show some initial stages of secondary growth in bunya pine and the unusual arrangement of the tracheids. This study indicates that, for a fossil structure to be positively identified as a seedling of bunya pine, or a close relative, it should possess four to six arcs or cylinders of secondary xylem.

The studies of Seward and Ford (1906, fig. 16), Hill and de Fraine (1909), Stockey and Taylor (1978, fig. 17), and Ferreira (1981, fig. 5) indicate that the tubers of *A. araucana* and *A. angustifolia* would also produce some tracheids that are not in radial files, even if their early stages of secondary growth are not as unusual as in bunya pine. If suspected fossil seedlings were more closely related to the South American species, there should still be some evidence of tracheids in nonradial rows.

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