Natural Regeneration of Ginkgo biloba from Downward Growing Cotyledonary Buds (Basal Chichi)

Peter Del Tredici

American Journal of Botany is currently published by Botanical Society of America.

NATURAL REGENERATION OF GINKGO BILOBA FROM DOWNWARD GROWING COTYLEDONARY BUDS (BASAL CHICHI)[1]

PETER DEL TREDICI

The Arnold Arboretum of Harvard University, 125 Arborway,
Jamaica Plain, Massachusetts 02130

This study describes the origin and early development of a distinct organ of clonal regeneration in *Ginkgo biloba,* the basal chichi. These aggregates of suppressed shoot buds originate from superficial meristems located in the cotyledonary axils of all *Ginkgo* seedlings as part of their normal ontogeny. Within 6 wk of germination these buds become embedded in the cortex of the stem, and their subsequent growth and development occurs below the surface of the bark. When stimulated by some traumatic event that damages the seedling axis, one of these embedded cotyledonary buds usually grows down from the trunk to form a woody, rhizomelike basal chichi which, under appropriate conditions, is capable of generating both aerial shoots and adventitious roots. Vegetative regeneration by means of basal chichi has not only contributed to the long-term persistence of *G. biloba* in the forests of China, but may also have played a role in the remarkable survival of the genus since the Cretaceous.

The genus *Ginkgo,* represented today by the widely cultivated Chinese species *G. biloba* L., has an evolutionary lineage that dates back to the lower Jurassic, about 190 million years ago. Over this length of time, the genus has undergone much change; yet fossil leaf and wood material from the Cretaceous species *G. adiantoides* is considered indistinguishable from that of *G. biloba,* leading many authors to refer to the *Ginkgo* as a "living fossil" (Tralau, 1968; Stewart, 1983). As the only extant taxon in the division Ginkgophyta, *Ginkgo* is distinctive in several aspects of its biology, most notably the production of multiflagellated sperm cells by the highly branched male gametophyte (Hirase, 1896; Friedman, 1987; Li, Wang, and Knox, 1989). Recently the species has become commercially important as a source of the C_{20} trilactone ginkgolide compounds, which have been found to antagonize platelet activating factor (PAF) in vertebrate blood systems (Boralle, Braquet, and Gottlieb, 1988; Del Tredici, 1991). Investigations into the seedling development of *Ginkgo* reported here reveal a unique mechanism of clonal

regeneration that accounts for the species' remarkable powers of survival both in nature and under cultivation.

While the *Ginkgo* has been the subject of numerous research papers concerning its evolution, biochemistry, anatomy, and morphology, virtually nothing has been written about its ecology, because the tree, if not extinct in the wild, is very close to it. Indeed, since the late 1800s botanists have been debating, without resolution, the question of whether or not *Ginkgo* still exists in the wild. Most of the discussion has centered around a single population of "semi-wild" trees growing on the west peak of Tian Mu Mountain in western Zhejiang Province, China (119°25'E, 30°20'N; elevation 1,506 m) (Li, 1956; Wang, Xiang, and Chen, 1986; Chen, 1989). In an attempt to learn more about the natural history of *Ginkgo,* the author visited the 1,000-ha Tian Mu Shan (TMS) Reserve from 6 to 15 October 1989 (Del Tredici, Ling, and Yang, in press). Most of the *Ginkgos* that occur there were growing along eroded, rocky stream banks and steep slopes between 400 and 1,200 m. As part of the field work, the stem numbers and stem diameters of 167 spontaneously growing *Ginkgos,* approximately 68% of the total population, were counted and measured. Two important observations were made: 1) seedling establishment by *Ginkgos* was very limited or nonexistent in the closed canopy forest on TMS; and 2) 40% of the TMS *Ginkgos* could be classified as multitrunked, with at least two stems greater than 10 cm diameter at breast height (DBH). Of these trees, 73% ($N = 49$) had their primary trunk intact, suggesting that logging was not the cause of the multitrunked condition.

In most cases, the secondary trunks of the TMS *Ginkgos* were attached to woody, calluslike growths that originated from the trunk at ground level, particularly where the base

→

Figs. 1–4. Transverse sections of the cotyledonary buds of 2- to 6-wk-old *Ginkgo* seedlings. **1.** A 2-wk-old seedling showing the relationship of the superficial cotyledonary buds (arrows) to the cotyledons (c). Note the limited vascular connection to the central cylinder. Bar = 0.1 mm. **2.** Detail of the superficial bud in the axil of the cotyledon (c) from the plant shown in Fig. 1. Note the prominent foliar primordia. Bar = 0.1 mm. **3.** A 6-wk-old seedling showing the two cotyledonary buds (arrows) embedded in the stem cortex. Note the intercotyledonary swelling (s). c, cotyledons. Bar = 1 mm. **4.** Detail of a single cotyledonary bud complex from a 6-wk-old seedling tipped at a 45° angle since germination. Note the primary bud and the accessory bud with developing foliar primordia (arrows). Bar = 0.1 mm. All sections 10 μm thick.
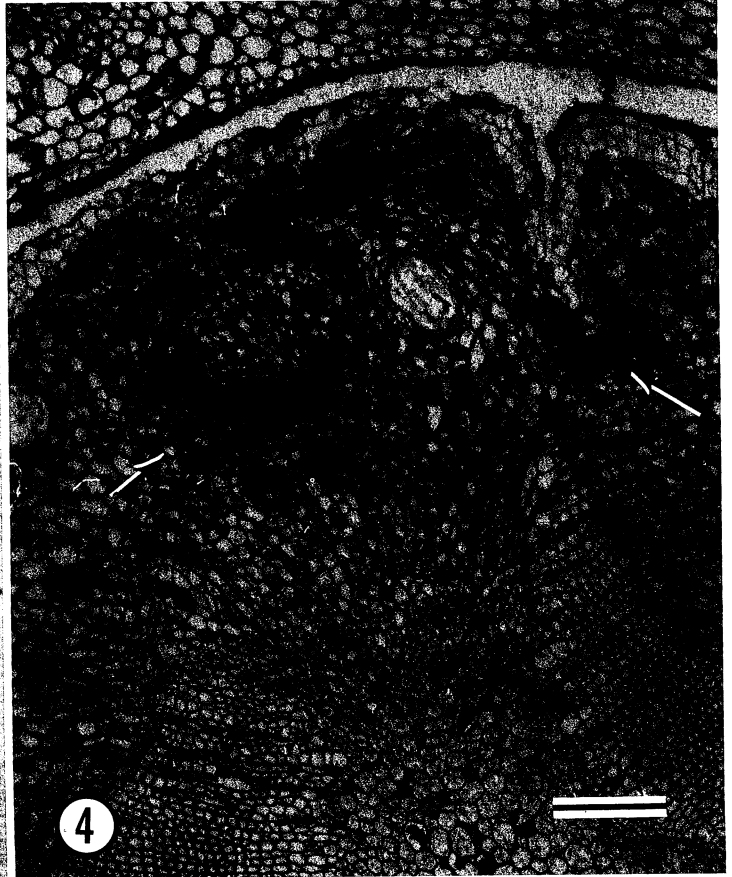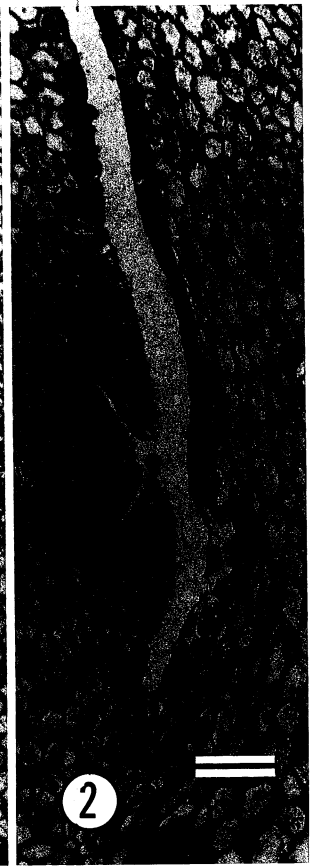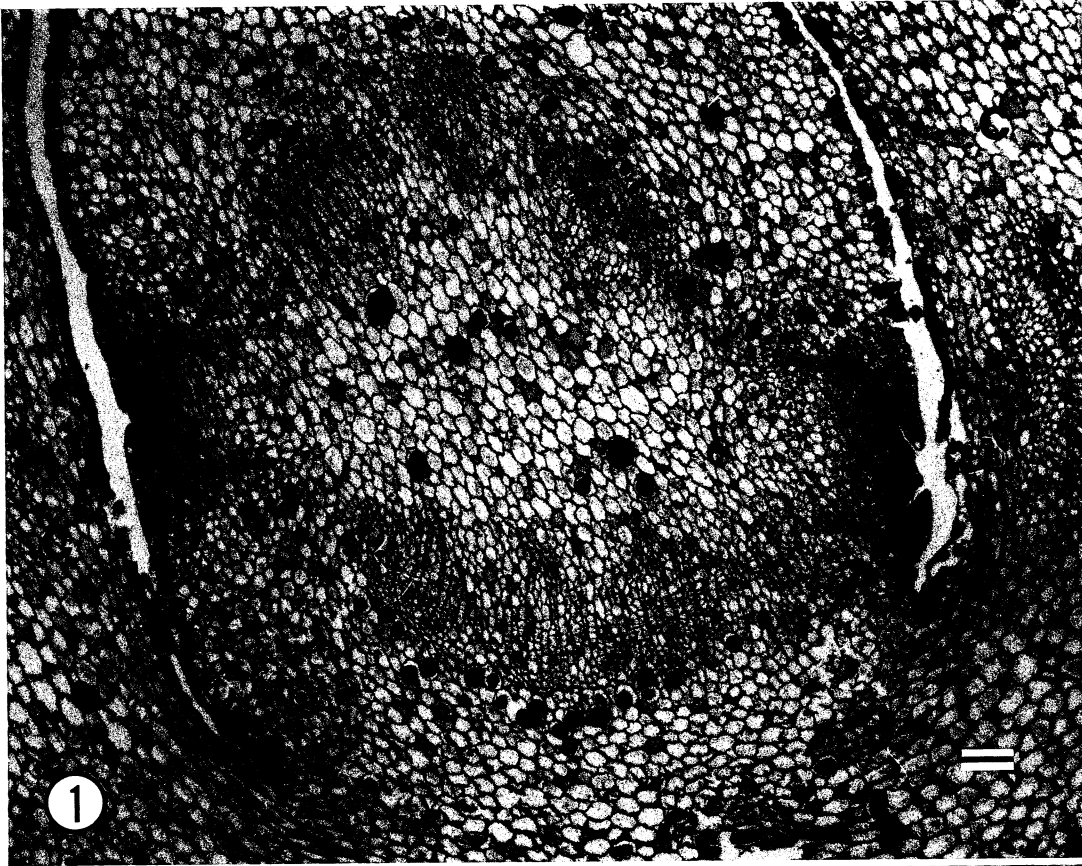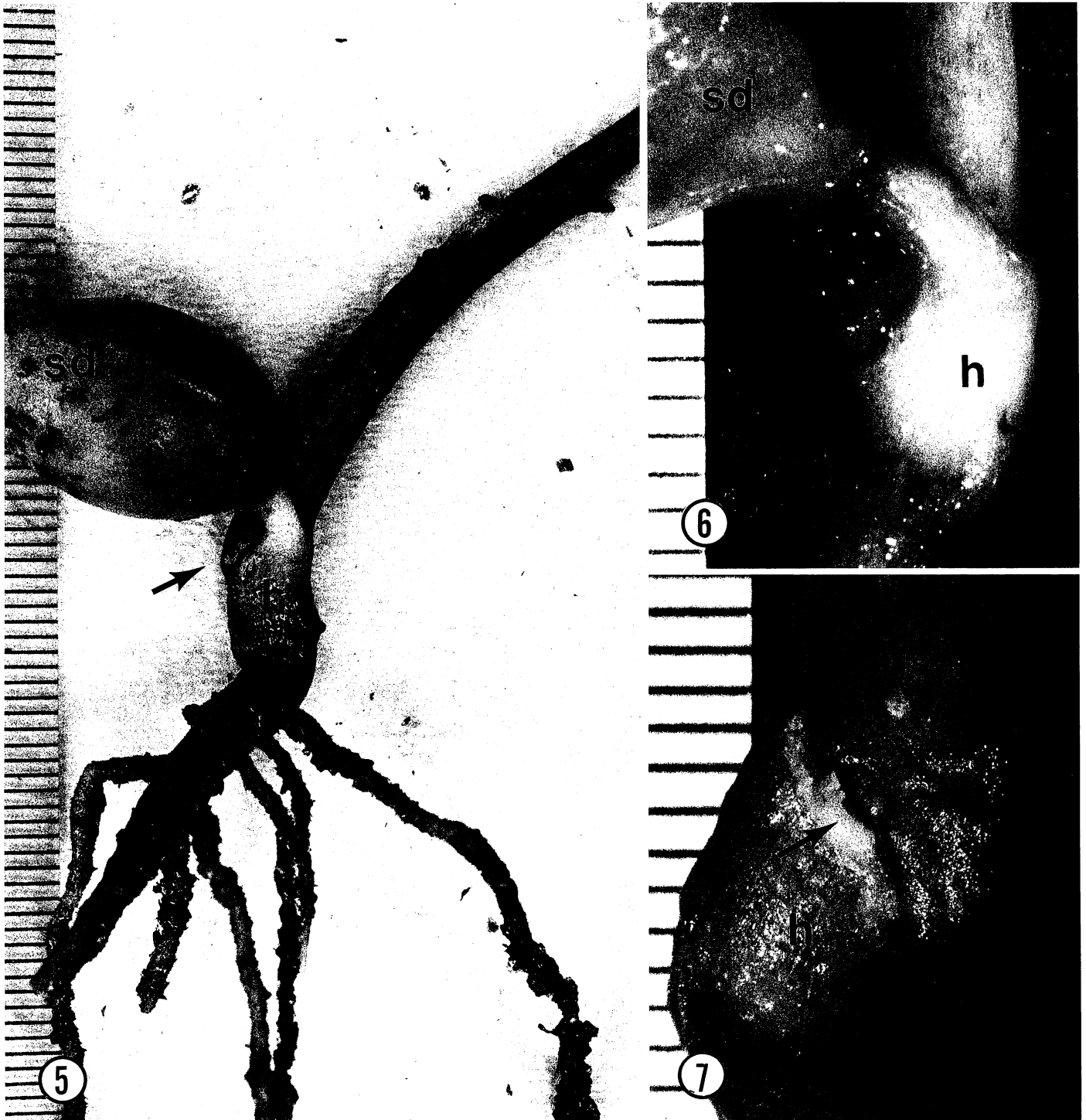
Figs. 5–7. The development of the intercotyledonary swelling in *Ginkgo* seedlings. **5.** An 8-wk-old seedling that was growing at a 45° angle. Note the intercotyledonary swelling (arrow), the hypocotyl (h), and the attached seed (sd). **6.** The intercotyledonary swelling on a 6-wk-old seedling tipped at a 45° angle since germination. sd, seed; h, hypocotyl. **7.** The intercotyledonary swelling on a 12-wk-old seedling. Note that the cotyledonary bud (arrow) in this individual did not become embedded in the periderm. h, hypocotyl. All scales in mm.

of the tree had been exposed by the effects of soil erosion. While these unusual structures displayed rootlike behavior in their downward orientation of growth and their strong clasping tendencies when in contact with rocks, they were decidedly unrootlike in their ability to produce

vegetative shoots up to 2 m from the parent trunk. Superficially these basal structures resembled the so-called air roots that are often reported to form along the underside of the large lateral branches of old cultivated *Ginkgos*, called *chichi* (nipple or breast) in Japan and *zhong*

ru (stalactite) in China. The morphology of these *aerial chichi*, which are capable of producing vegetative shoots once they reach the ground, was first described by Fujii (1895) who considered them a "pathological formation" that developed in association with an embedded shoot bud. In the only other scientific study of aerial chichi, Li and Lin (1991) examined their wood anatomy and described an anomalous branch structure in which the tracheids showed a whirled arrangement and the rays were highly distorted. Based on these observations, the authors concluded that aerial chichi were the product of abnormal growth processes that occur only in old trees.

In contrast to such aerial chichi, the *basal chichi* observed on TMS were produced by trees that were quite young, and appeared to play an important ecological role in the persistence of the species in disturbed habitats (Del Tredici, Ling, and Yang, in press).

MATERIALS AND METHODS

Shortly after returning from China, the author set up a series of experiments designed to investigate the developmental morphology of basal chichi in seedlings cultivated under greenhouse conditions. Seeds were collected from mature *Ginkgos* growing at the Arnold Arboretum and at the nearby Forest Hills Cemetery in Boston, Massachusetts, in November 1989. They were washed clean of the fleshy sarcotesta and sown in a greenhouse heated to a minimum temperature of 18 C. Seed germination commenced within 60 d and continued for about 30 d. In one set of experiments designed to test the effects of gravity on chichi development, 50 seedlings were tipped at a 45° angle upon germination while 50 others, oriented vertically, served as controls. A total of 16 seedlings from both groups was sampled at intervals of 2, 6, and 12 wk, and 1-cm-long segments of seedling axis, including tissue above and below the point of attachment of the cotyledons, were removed. These segments of cotyledonary node were dehydrated in a *t*-butyl alcohol series and embedded in paraplast. Serial sections of the cotyledonary node region were then cut on a rotary microtome 10 μm thick, and stained with Heidenhain's hematoxylin, safranin, and fast green. In order to study the earliest stages of cotyledonary node development, fully mature embryos from ungerminated seeds were similarly sampled, embedded, and sectioned.

In a second experiment, set up in March of 1990, 1-yr-old, untransplanted seedlings from Arnold Arboretum (AA) seedlot #1055-88 were subjected to treatments designed to accelerate the production of basal chichi, including being tipped at a 45° angle and decapitation of the primary aerial shoot. Two types of decapitation were employed: low, which involved cutting off the stem 1 cm above the cotyledonary node; and high, which involved cutting off the stem approximately 6 cm above the cotyledons, leaving two to three leaf nodes remaining on the stem. To test the effects of age on cotyledonary bud development, 2-yr-old seedlings from AA seedlot #431-89, which had been transplanted into individual pots, were divided into two groups: controls and tipped at a 45° angle. After one season of growth in the greenhouse, the seedlings from these experiments were allowed to go dormant, washed clean of soil, and measured for height and for girth at the cotyledonary node. Following this, the seedlings were stripped of cortical tissue in the area of the cotyledonary node, thereby exposing the xylem traces of the cotyledonary buds. This decortication made it possible to measure the length, to the nearest mm, of the two prominent cotyledonary bud traces.

The later stages of basal chichi development were studied using plants that had been cultivated outdoors in sandy soils at Sumter, South Carolina, for the purpose of ginkgolide production (Del Tredici, 1991). Following their removal from the ground, plants were washed clean of soil and scored for the presence or absence of downward growing basal chichi, aerial shoots, and adventitious roots. The 3-yr-old plants used in this study were grown in crowded, outdoor seed beds and were transplanted once. The 5- to 7-yr-old plants examined were field-grown 40 cm apart in rows 1 m apart. The plants were irrigated and heavily fertilized, and had been severely and annually cut back to 1 m or less in height for a minimum of 4 consecutive years, following the harvesting of leaves for ginkgolide extraction in late summer.

RESULTS

Early chichi development: 0–1 yr—Observations on the greenhouse-grown plants indicate that the earliest stage of basal chichi formation involves the development of buds from superficial meristems that are located in the axils of the cotyledons of all observed *Ginkgo* seedlings regardless of experimental treatment. While these cotyledonary meristems were readily visible in all paraplast-embedded 2-wk-old seedlings ($N = 6$), the author was unable to locate evidence of their presence in any of the mature embryos extracted from ungerminated seeds ($N = 6$). Cotyledonary buds have never been reported in the literature covering the anatomy of the *Ginkgo* seedling or its mature embryo (Lyon, 1904; Hill and de Fraine, 1909; Li, 1934; Ball, 1956; Wang and Chen, 1983).

On all 2- and 6-wk-old seedlings examined, the cotyledonary buds are 0.2–0.4 mm in diameter with well-developed foliar primordia and display only a limited connection to the vascular cylinder (Figs. 1, 2). Serial sections reveal that the developing vascular trace of the cotyledonary bud links up with the cotyledonary trace at the point where the cotyledon is attached to the stem.

Within 6 to 12 wk of germination, the connection of the cotyledonary bud to the central cylinder becomes well established and the cotyledonary bud becomes embedded in the periderm of the rapidly expanding seedling axis (Fig. 3). Despite being engulfed by the periderm, the cotyledonary bud continues to develop, giving rise to a relatively large primary bud with one or more accessory buds in lateral positions (Fig. 4).

Concurrently with the development of the cotyledonary buds, a dome-shaped structure often arises on the seedling axis between the attachment points of the cotyledons (Figs. 5–7). In a random sample of 65 7- to 8-wk-old seedlings, 33 individuals had produced an intercotyledonary swelling that extended more than 0.5 mm out from the seedling axis. In 19 of these cases, the swelling was on the side of the stem adjacent to the attached seed, while in the other 14 cases it was on the side of the stem opposite from the seed. In longitudinal section, the calluslike, intercotyle-
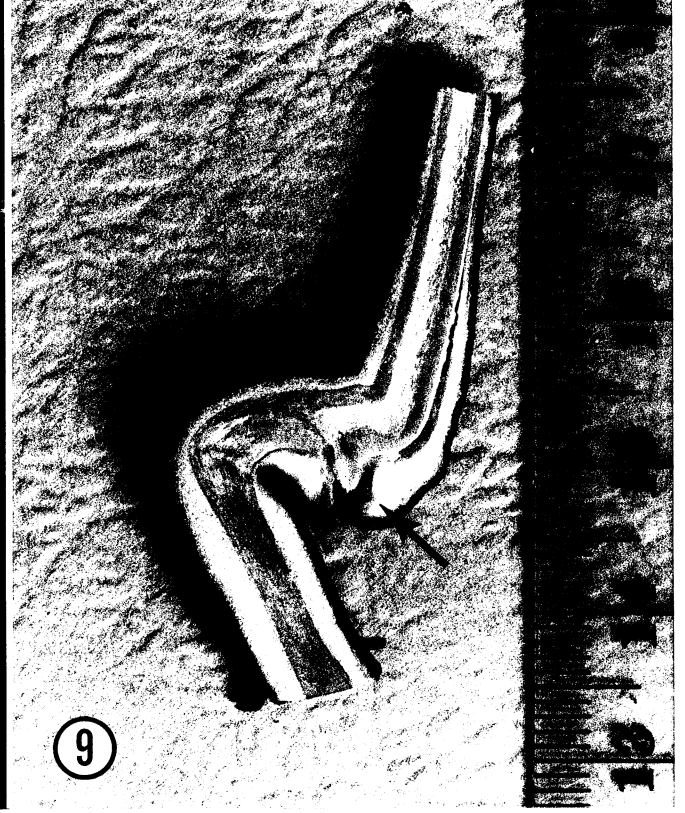
TABLE 1. *Data on the length, to the nearest mm, of the longer of the two cotyledonary bud traces in plants tipped at a 45° angle and untipped controls. Measurements were made following decortication of the cotyledonary node. Percentages in parentheses*

Longer cotyledonary bud trace length (mm)	Control plants			Tipped plants		
	1-yr (N = 24)	2-yr (N = 35)	Total (N = 59)	1-yr (N = 59)	2-yr (N = 15)	Total (N = 74)
≤1	6	4	10 (17)	18	2	20 (27)
>1 ≤ 2	6	5	11 (19)	28	5	33 (44)
>2 ≤ 3	5	6	11 (19)	9	4	13 (18)
>3 ≤ 4	3	11	14 (24)	3	3	6 (8)
>4 ≤ 5	4	5	9 (15)	0	0	0 (0)
>5 ≤ 6	0	2	2 (3)	1	1	2 (3)
>6	0	2	2 (3)	0	0	0 (0)
Mean length longer cotyledonary bud trace ± SD (mm)	2.7 ± 1.4	3.9 ± 2.4	3.4 ± 2.1	2.0 ± 1.0	2.8 ± 1.3	2.2 ± 1.0

donary swelling can be seen to originate from a proliferation of parenchyma cells in the cortex of the stem, just above the hypocotyl (see Fig. 4). In those seedlings in which it occurs, the intercotyledonary swelling generally stops expanding within 12 to 16 wk of germination, having formed a downward growing structure that is 1–3 mm long.

In the examination of 16 serial-sectioned seedlings, all between the ages of 2 and 12 wk, no clear differences in cotyledonary bud development were detected between the control and the tipped plants, suggesting that the early stages of chichi development are part of the normal ontogeny of all *Ginkgo* seedlings, and include: 1) the establishment of a vascular connection between the bud and the stele; 2) the development of the intercotyledonary swelling; and 3) the formation of an embedded bud-complex, consisting of a primary bud and one to several accessory buds.

Later chichi development: 1–3 yr—Contrary to the author's expectations, the cotyledonary bud traces of the 1-yr-old, untransplanted controls were significantly longer than those of seedlings tipped at a 45° angle. Results with the 2-yr-old seedlings displayed the same pattern as the 1-yr-old plants, with the untipped controls showing more extensive cotyledonary bud development than the tipped plants (Table 1). On both the controls and the tipped plants, however, development of the cotyledonary buds was always unequal (Figs. 8, 9).

A log linear analysis of the categorical data in Table 1 (Sokal and Rohlf, 1981) shows that all of the two-way interactions between age (1-yr or 2-yr seedlings), size of the larger cotyledonary bud trace (≤1, >1 ≤ 2, >2 ≤ 3, and >3), and experimental treatment (tipping vs. control) were highly significant because both the conditional and marginal tests of independence for all two-way interactions were significant ($P < 0.05$) (Table 2). This analysis,

when taken in conjunction with the fact that for both the tipped and control plants, the larger of the two cotyledonary bud traces was significantly longer on 2-yr-old plants than it was on 1-yr-old plants (Table 1), clearly indicates a pattern of progressive development over time. The results of these tipping experiments need to be interpreted with caution given that they were based on only one season's growth. Over a longer time period, chichi development in tipped plants could well equal or surpass that of untipped controls.

Among the 1-yr-old untransplanted seedlings that had been experimentally decapitated, the high and low treatments produced distinctly different results after 1 yr growth. The most interesting observation being that among all of the plants decapitated low on the stem axis ($N = 11$), in which only the cotyledonary node was left on the stem, one of the cotyledonary buds always grew out to form an aerial shoot, while the other bud remained poorly developed, with a xylem trace always less than 1 mm in length. In contrast, among the plants decapitated high on the stem axis ($N = 15$), in which two or three nodes were left on the stem, none of the cotyledonary buds formed aerial shoots, and 47% of the plants developed at least one cotyledonary bud trace longer than 1 mm. These results clearly indicate that while the cotyledonary buds of young seedlings have the potential to form aerial shoots,

TABLE 2. *Partial results of a log linear analysis of the data in Table 1. For all two-way interactions between the age of plant, the size of the longer cotyledonary bud trace per plant, and the experimental treatment the results were significant (P < 0.05)*

Factors	df	Conditional test		Marginal test	
		G	P	G	P
Size × age	3	10.88	0.012	22.73	0.000
Age × experiment	1	12.41	0.006	21.76	0.000
Size × experiment	3	9.90	0.001	24.27	0.000

←

Figs. 8–11. Chichi development in 2- to 3-yr-old plants. **8.** A partially decorticated, untipped 2-yr-old seedling showing the unequal development of the cotyledonary buds. The bud on the right might well have developed into a basal chichi, while the one on the left would probably have formed a suppressed bud-complex. Scale in cm. **9.** Longitudinal section of a partially decorticated 2-yr-old seedling with a strongly kinked stem often associated with the development of the cotyledonary buds. Arrow indicates the developing basal chichi. Scale in cm. **10.** A 3-yr-old field-grown seedling in which one of the cotyledonary buds had developed into a prominent basal chichi (4 cm long) while the other has not (arrow). Bar = 1 cm. **11.** A decorticated 3-yr-old field-grown seedling showing the xylem traces of the numerous dormant shoot buds on a well-developed basal chichi. Scale in cm.
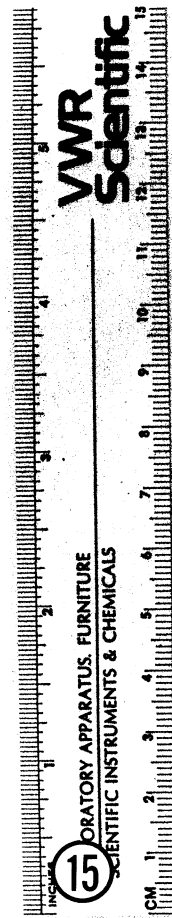
they generally will not do so except under conditions in which all other shoot buds have been removed.

Chichi development in the field—In observations made on 3-yr-old, once-transplanted seedlings that had been raised in crowded seed beds in South Carolina, 11% of 1,000 randomly selected plants had produced a single basal chichi longer than 1 cm, with the longest being 7 cm long. The incidence of chichi formation was highest near the edges of the beds where damage to or displacement of the seedling axis out of its vertical orientation was most likely to occur, primarily as a result of mechanical cultivation. In all of the plants observed only one of the cotyledonary buds ever formed a basal chichi, while the other remained comparatively undeveloped (Figs. 10, 11). While none of the observed chichi at this stage of development were producing aerial shoots, many of them had produced large adventitious roots.

Among 5- to 7-yr-old field-grown plants that had been cut back annually for 2 to 4 yr following leaf harvest, a good number of them showed massive chichi development that included not only the production of large adventitious roots, but also numerous aerial shoots (Figs. 12–15). Shoot production by basal chichi was highest among those plants that had been pushed over and partially uprooted by the harvesting equipment, suggesting that damage to the root system may be a more important factor in stimulating the development of basal chichi than damage to the shoot system. This idea is supported by data from the greenhouse experiments, in which decapitation of several nodes distal to the cotyledons was observed to actually retard cotyledonary bud development in comparison to the control plants.

The later states of basal chichi development from cotyledonary buds can be summarized as follows: in most *Ginkgo* seedlings the embedded cotyledonary bud-complexes grow just enough to keep up with the secondary thickening of the xylem without forming a downward growing basal chichi. The growth of these buds is often unequal, with one of them being more vigorous in its development than the other. When some traumatic event damages the base of the tree or its root system, however, the larger of these buds is stimulated to produce a single downward growing basal chichi that generally becomes visible to the naked eye within 3 yr. If the period of stress is both severe and prolonged, as is the case when plants are cultivated for ginkgolide production, the basal chichi can give rise to aerial shoots within 5 yr. The roots produced by basal chichi are adventitious in origin and, under conditions of stress, develop much sooner than shoots, generally within 2 yr.

DISCUSSION

From these observations it is clear that the cotyledonary buds of *Ginkgo biloba* are developmentally uncommitted and that, depending on exogenous factors, they can follow one of three morphogenetic pathways. 1) They can form clusters of dormant buds embedded in the periderm—this happens on the vast majority of plants, both injured and uninjured. 2) They can form an aerial shoot, which is actively elongating and developing leaves—this happens when all other shoot buds are removed. 3) They can form a downward growing basal chichi in which growth is limited to the proliferation of physiologically suppressed shoot buds—this happens following particularly severe injury to either the root system or the lower part of the shoot system.

The superficial origin of the cotyledonary buds in *Ginkgo* is reminiscent of certain aspects of the development of detached meristems that have been shown to exist in the "empty" needle axils of a wide range of conifers (Fink, 1984). These develop from small groups of unvascularized cells and can be induced to produce axillary buds or aerial shoots following damage to the branch on which they are located.

Basal chichi are identical to aerial chichi in their anomalous anatomy and in the fact that they always develop from a preexisting shoot bud. They are different in that basal chichi form predictably in the cotyledonary axils of all *Ginkgo* seedlings, as part of their normal ontogeny, while aerial chichi tend to develop unpredictably along the underside of large lateral branches of older cultivated trees in response to severe trunk or crown damage or in association with the callus formation that accompanies wound healing (Fujii, 1895; personal observations). It is also worth noting that both aerial and basal chichi possess the ability to produce vegetative shoots and adventitious roots when cut off from the parent trunk and planted upside down in soil (Hu, 1987; Li and Lin, 1991). This horticultural technique, which has long been used in the traditional Chinese art of *penjing,* might possibly explain some of the reports in the ancient Chinese literature of propagating *Ginkgo* by sticking cut branches directly in the ground (Li, 1956).

The process of basal chichi development from embedded cotyledonary buds is similar to the process of lignotuber formation seen in some species of the genus *Eucalyptus* (Myrtaceae). These fire-adapted, woody rejuvenation structures form at the base of seedlings in association with the proliferation of accessory buds lateral to the primary cotyledonary buds (Carr, Jahnke, and Carr, 1984). Among the gymnosperms, the nearest parallel to

---

←

Figs. 12–15.   The seedling axis and basal chichi of two 7-yr-old *Ginkgos* that had been severely cut back for the purposes of ginkgolide production. **12.** A plant freshly dug from the field. Note the relationship of the seedling axis (a) to the shoot-producing basal chichi. Bar = 2 cm. **13.** Longitudinal section of the plant in Fig. 12, showing the attachment of the chichi to the seedling axis. Note the aerial shoot growing out from one of the chichi lobes on the right. Bar = 2 cm. **14.** Longitudinal section of the base of a plant with a large basal chichi showing the attachment of the chichi to the seedling axis and the continuity between the growth rings of the chichi and those of the stem. Note that in this plant one of the cotyledonary buds had given rise to a large basal chichi with a shoot, while the other cotyledonary bud (arrow) shows comparatively limited development. Bar = 1 cm. **15.** The other half of the plant shown in Fig. 14, with the cortex peeled away to expose the vascular traces of numerous dormant shoot buds of the basal chichi. The less developed cotyledonary bud visible in Fig. 14 can be seen to have produced an aerial shoot (arrow). Note the adventitious roots (r). Scale in cm.

basal chichi seems to be with the *burls* that develop near the base of seedlings of *Sequoia sempervirens* (Taxodiaceae), the California redwood. These woody excrescences, which originate from clusters of accessory buds in the needle axils of seedlings (Stone and Vasey, 1968; Groff and Kaplan, 1988), display the ability to produce new shoots following damage to the primary trunk. On old trees, burls can become quite large and, when cut off their parent trunk and placed in a dish of water, can produce numerous vegetative shoots (Fritz, 1928).

The phenomenon of clonal regeneration from basal chichi has not only contributed to the long-term persistence of *Ginkgo biloba* in the forests of China, but may also have played a role in the survival and morphological stability of the genus since the Cretaceous. In the future, basal chichi may prove to be important in the biotechnological propagation of the species for commercial purposes.

LITERATURE CITED

BALL, E. 1956. Growth of the embryo of *Ginkgo biloba* under experimental conditions. I. Origin of the first root of the seedling in vitro. *American Journal of Botany* 43: 488–495.

BORALLE, N., P. BRAQUET, AND O. R. GOTTLIEB. 1988. *Ginkgo biloba*: a review of its chemical composition. *In* P. Braquet [ed.], Ginkgolides—chemistry, biology, pharmacology and clinical perspectives, vol. 1, 9–25. J. R. Prous, Barcelona.

CARR, D. J., R. JAHNKE, AND S. G. M. CARR. 1984. Initiation, development and anatomy of lignotubers in some species of *Eucalyptus*. *Australian Journal of Botany* 32: 415–437.

CHEN, S. C. 1989. Status of the conservation of rare and endangered plants in China. *Cathaya* 1: 161–178.

DEL TREDICI, P. 1991. *Ginkgos* and people: a thousand years of interaction. *Arnoldia* 51(2): 2–15.

————, H. LING, AND G. YANG. In press. The *Ginkgos* of Tian Mu Shan. *Conservation Biology*.

FINK, S. 1984. Some cases of delayed or induced development in axillary buds from persisting detached meristems in conifers. *American Journal of Botany* 7: 44–51.

FRIEDMAN, W. E. 1987. Growth and development of the male gametophyte of *Ginkgo biloba* within the ovule (in vitro). *American Journal of Botany* 74: 1797–1815.

FRITZ, E. 1928. Redwood burls. *American Forests* 34: 10–11.

FUJII, K. 1895. On the nature and origin of so-called "chichi" (nipple) of *Ginkgo biloba* L. *Botanical Magazine* (Tokyo) 9: 444–450.

GROFF, P. A., AND D. R. KAPLAN. 1988. The relation of root systems to shoot systems in vascular plants. *Botanical Review* 54: 387–422.

HILL, T. G., AND E. DE FRAINE. 1909. On the seedling structure of gymnosperms. III. Ginkgoaceae and Cycadaceae. *Annals of Botany* 23: 433–458.

HIRASE, S. 1896. On the spermatozoid of *Ginkgo biloba*. *Botanical Magazine* (Tokyo) 10: 325–328.

HU, Y. H. 1987. Chinese Penjing. Timber Press, Portland, OR.

LI, H. L. 1956. A horticultural and botanical history of *Ginkgo*. *Bulletin of the Morris Arboretum* 7: 3–12.

LI, T. T. 1934. The development of embryo of *Ginkgo biloba*. *Science Report of the National Tsing Hua University* (Series B) 2(1): 29–35.

LI, Y., F. H. WANG, AND R. B. KNOX. 1989. Ultrastructural analysis of the flagellar apparatus in sperm cells of *Ginkgo biloba*. *Protoplasma* 149: 57–63.

LI, Z., AND J. LIN. 1991. Wood anatomy of the stalactite-like branches of *Ginkgo*. *International Association of Wood Anatomists Bulletin* 12: 251–255 (New series).

LYON, H. L. 1904. The embryology of *Ginkgo*. *Minnesota Botanical Studies* 3: 275–290.

SOKAL, R. R., AND J. E. ROHLF. 1981. Biometry, 2d ed. W. H. Freeman, San Francisco, CA.

STEWART, W. N. 1983. Paleobotany and the evolution of plants. Cambridge University Press, Cambridge.

STONE, E. C., AND R. B. VASEY. 1968. Preservation of coast redwood on alluvial flats. *Science* 159: 157–161.

TRALAU, H. 1968. Evolutionary trends in the genus *Ginkgo*. *Lethaia* 1: 63–101.

WANG, F. H., AND Z. K. CHEN. 1983. A contribution to the embryology of *Ginkgo* with a discussion on the affinity of the Ginkgoales. *Acta Botanica Sinica* 25: 199–211 (in Chinese).

WANG, Y. W., S. D. XIANG, AND Q. C. CHEN. 1986. Studies of vegetation on the southern slope of West Tian Mu Shan. *Journal of Hangzhou University* 13: 26–42 (Natural Science Edition, supplement; in Chinese).