The *Ginkgos* of Tian Mu Shan

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Abstract: *The question of whether or not* Ginkgo biloba *still exists in the wild has been debated by botanists, without resolution, for almost a hundred years. Most of the controversy has focused on a single population of trees located on Tian Mu Shan (Tian Mu Mountain) in Zhejiang Province, China, a site of human activities for approximately 1500 years. Regardless of its origin, the Tian Mu Shan* Ginkgo *population is biologically significant by virtue of its long survival in a semi-natural state under conditions of intense interspecific competition. A total of 167* Ginkgos *were counted and measured in the 1018 ha Tian Mu Shan Reserve. Many of the trees were growing on disturbance-generated microsites, such as stream banks, steep rocky slopes, and the edges of exposed cliffs. Forty percent of the censused individuals were multitrunked, consisting of at least two trunks greater than 10 cm in diameter at breast height. Most of these secondary trunks originated from root-like "basal chichi," that are produced at the base of trees that have experienced damage from soil erosion or other factors. No* Ginkgos *less than 5 cm in basal diameter were found in the mature forests of Tian Mu Shan. This lack of seedling reproduction is caused by several factors: (1) the lack of sunny microsites suitable for seedling growth, (2) seed collection by people, and (3) seed predation by animals. In the absence of successful seedling establishment, secondary trunk formation from basal chichi is the single most important factor in explaining the long term persistence of* Ginkgo *on Tian Mu Shan.*

Resumen: *Durante casi cien años los botánicos han estado debatiendo, sin poder llegar a un acuerdo, si el* Ginkgo biloba *aún existe en forma silvestre. La controversia se ha centrado principalmente en una población única de árboles ubicada en Tian Mu Shan (la montaña de Tian Mu) en la provincia de Zhejiang, China; región en la cual la actividad humana ha existido por aproximadamente 1500 años. Cualquiera sea su origen, la población de* Ginkgo *de Tian Mu Shan tiene importancia biológica debido a su prolongada supervivencia en un estado seminatural bajo condiciones de intensa competencia interespecífica. Se contaron y midieron un total de 167* Ginkgos *en la reserva de Tian Mu Shan, con una superficie de 1018 ha. Muchos de los árboles estaban creciendo en micrositios generados por perturbaciones, tales como riberas de arroyos, laderas rocosas empinadas y bordes de acantilados expuestos. El 40% de los individuos censados poseían múltiples troncos, poseyendo al menos dos troncos con un área basal de más de 10 cm. Muchos de estos troncos secundarios se originaron a partir the "chichi basales" semejantes a raíces, y que son producidos en la base de los árboles que han experimentado daños debido a la erosión del suelo u otros factores. No se encontró ningún* Ginkgo *de menos de 5 cm de diámetro basal en los bosques maduros de Tian Mu Shan. Esta falta de reproducción a partir de semillas se debe a varios factores: (1) falta de micrositios asoleados aptos para el crecimiento de plántulas; (2) recolección de semillas por las personas; y (3) consumo de semillas por animales. Ante la ausencia del establecimiento exitoso de plántulas, el factor más importante para la persistencia a largo plazo del* Ginkgo *en Tian Mu Shan es la formación de troncos secundarios a partir de los chichi basales.*

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Introduction

The genus *Ginkgo,* represented in modern times by the widely cultivated Chinese species *Ginkgo biloba* L, has an evolutionary lineage that dates back to the lower Jurassic, about 190 million years ago. Over this time span the genus has undergone much change, yet fossil leaf and wood material of the Early Cretaceous *G. adiantoides* is considered to be very similar to that of the only extant species, *G. biloba,* leading many authors to refer to the extant tree as a "living fossil" (Tralau 1968; Stewart 1983). While modern cladistic research supports the notion that the order Ginkgoales is closely related to the Coniferales (Doyle & Donoghue 1986; Loconte & Stevenson 1990), anatomical work on the embryology of *Ginkgo* indicates that the genus, because of its multi-flagellated sperms, also has close affinities with the Cycadales (Wang & Chen 1983). As a result of this intermediate position, *G. biloba,* is generally classified in its own division, the Ginkgophyta (Friis et al. 1987).

Ginkgo has a long association with humans in China: ancient documents indicate that the tree has been cultivated for close to 1000 years, primarily for its edible and medicinally active "nuts" (Li 1956; Del Tredici 1991). The question of whether or not the *Ginkgo* still exists in the wild in China has been debated by botanists for many years. Based on limited field work in Asia in the late nineteenth and early twentieth centuries, Western botanists such as C. S. Sargent (1897) and E. H. Wilson (1914, 1919) stated that the *Ginkgo* was *probably* extinct in the wild and that it was preserved by Buddhist monks who cultivated it in the gardens surrounding their temples. This idea became imbedded in the literature, despite reports by one Western botanist, F. N. Meyer (quoted in Sargent 1916), and several Chinese botanists (Cheng 1933; Li 1956; Wang 1961) that *Ginkgo* was growing "spontaneously" at several locations in the mixed mesophytic forest zone that borders the Yangtze River, primarily in the area around Tian Mu Shan (Tian Mu Mountain) in Zhejiang Province. In 1956, a formal proposal was made to protect this isolated mountain, but it was not until 1960 that the Tian Mu Shan Reserve was officially established by the Chinese government.

Despite the establishment of the reserve, questions about the "wildness" of the *Ginkgos* growing there have persisted. A detailed census of the population published by the Zhejiang Forestry Bureau in 1984 concludes that the *Ginkgos* are wild, as does Ling (1965). Wang and Chen (1983) and Chen (1989), on the other hand, doubt the wildness of the trees, suggesting instead that they are the offspring of plants that were cultivated in the vicinity of the old temple by resident monks. One recent report (Wang et al. 1986) concludes, "The question of whether this area is part of the natural distribution of wild *Ginkgo* needs further study."

Materials and Methods

Site Description

At 1506 m in elevation, the main peak of Tian Mu Shan (119° 25′ E; 30° 20′ N) is one of the highest mountains in Zhejiang Province. Climatological data for the area are summarized in Table 1. The steep slopes are crisscrossed with a network of streams and ridges, which create a mosaic of sheltered valleys and exposed cliffs (Fig. 1). Subtropical evergreens, typical of south China, mingle with temperate conifers and deciduous plants on the slopes of the reserve, resulting in a rich flora consisting of some 1530 species of vascular plants (Zhejiang Forestry Bureau 1984; Zheng 1986). Three distinct vertical zones of vegetation have been described: (1) at 380–800 m, mixed subtropical forest with a canopy of conifers, broadleaf evergreens, and deciduous trees; (2) at 800–1200 m, warm-temperate forest with a canopy of conifers and deciduous trees and a subcanopy rich in broadleaf evergreens; (3) at 1200–1506 m, deciduous dwarf forest with a canopy of stunted trees and shrubs (Wang et al. 1986).

In addition to its high species diversity, Tian Mu Shan is also noted for its exceptionally large trees. According to the only published census of the reserve (Zhejiang Forestry Bureau 1984), the most common large tree species is *Cryptomeria japonica* var. *sinensis* (Taxodiaceae), of which there are 398 individuals with a diameter at breast height (DBH) greater than one meter. *Pseudolarix amabilis* (Pinaceae) also grows wild on the mountain, with some 98 individuals with a DBH greater than 50 cm and heights mainly between 40 and 50 m. Most notably, there are 244 large individuals of

Table 1. Climatological data for the west slope of Tian Mu Shan.*

Altitude	*Mean annual temperature (°C)*	*Mean temperature July (°C)*	*Mean temperature January (°C)*	*Mean annual rainfall (mm)*	*Mean annual evaporation (mm)*
1506 m	8.7	20.5	−3.2	1767	1553
350 m	14.9	21.9	+2.7	1536	1359

* *From* The Reserves of Zhejiang Province, *Zhejiang Forestry Bureau (1984). For additional information see Wang, et al. (1986).*

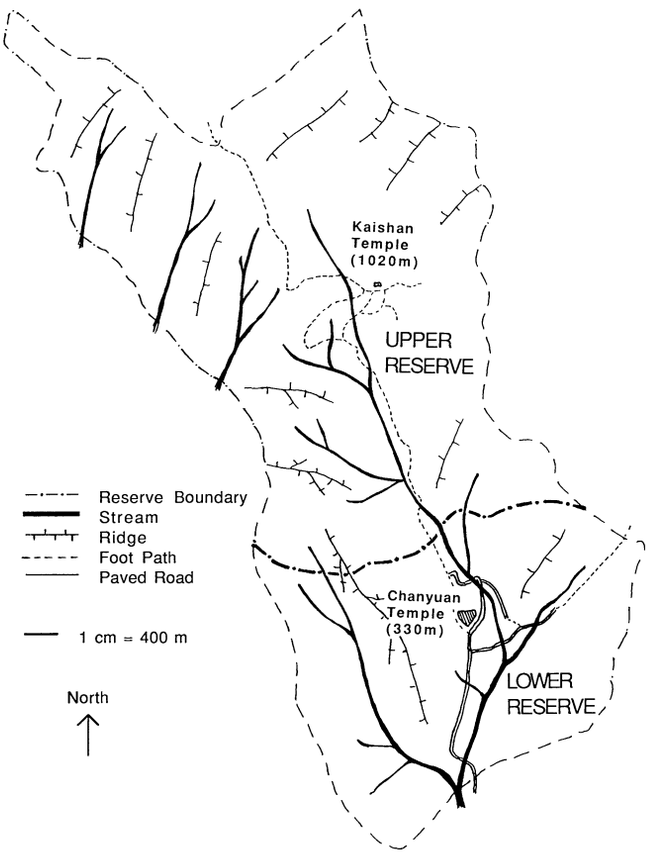

Figure 1. Map of the Tian Mu Shan Reserve. Located on the south-facing slope of the west peak of Tian Mu Shan, the total area of the upper reserve is 652 ha and the lower reserve 366 ha.

Ginkgo biloba growing throughout the reserve with a mean DBH of 45 cm and a mean height of 18.4 m. According to the Zhejiang Forestry Bureau report, about 10% of the *Ginkgo* population is estimated to be over 1000 years of age.

Along with these three gymnosperms, exceptionally large trees of *Torreya grandis, Liquidambar formosana, Nyssa sinensis, Cyclocarya paliurus, Litsea auriculata,* and *Emmenopterys henryi* are also common in the woods. Three plants are recognized as endemic to Tian Mu Shan, and a total of 29 taxa growing within the reserve are included in volume one of the *Plant Red Data Book* of rare, endangered, and threatened plants of China (Zheng 1986; He et al. 1987).

Human Activities in the Area

Because of its location, just 94 km west of the city of Hangzhou, Tian Mu Shan has been visited by monks, herbalists, poets, botanists, and tourists for close to 1500 years. The most famous structure on the mountain, at 1020 m elevation, is Kaishan temple, built by Buddhist monks between 1283 and 1287. Around 1665, a second temple, Chanyuan, was built at 330 m. Other smaller temples and shrines are located at various places on the mountain.

In 1941 the Japanese army invaded the area, bombing the mountain side and ransacking Chanyuan temple. In 1958, during the "Great Leap Forward," many of the trees in the forest were cut down to make charcoal. When the reserve was established in 1960, only the relatively undisturbed south-facing slope of the west peak was included within its boundaries. Between 1960 and 1965 considerable clean-up was done in the reserve, including the planting of more than 100 *Ginkgo* seedlings just above the main gate. Maintenance of the reserve was suspended during the 10 years of the "Cultural Revolution," from 1966 to 1976, and effective protection was not achieved until 1982 when construction of the reserve headquarters was completed.

Administratively, the reserve is divided into two sections. The lower reserve, covering 366 ha, includes the lower Chanyuan temple, numerous hotels, houses, and the reserve headquarters. With the exception of the temple, all of the other buildings were built after 1960. The upper, "special," reserve, consisting of 652 ha, has experienced relatively little disturbance in comparison (Fig. 1). The upper reserve covers both sides of a sheltered valley that extends from 420 m to the summit at 1506 m. A stone path, built about 100 years ago, follows the course of the main stream to Kaishan temple. Portions of this path are lined with large *Cryptomerias* that were probably planted at the time of its construction. Beyond the temple a narrow foot path leads to the summit, where an army weather station is located.

Census Methods

From October 6 to 15, 1989, we censused the *Ginkgos* growing in the reserve. During the course of our work, we walked all the paths and trails in the reserve and measured and mapped the locations of all the *Ginkgos* that we could locate. In early October, *Ginkgo* leaves were turning yellow, making it easy to locate the trees even at some distance. We can say, conservatively, that we located all the *Ginkgos* within 50 m of the paths.

The DBH of all trunks greater than 10 cm was measured, and the height of all the trees was estimated. The steep terrain of the site and the fact that the tops of many trees could not always be clearly seen made accurate height measurements difficult. We also recorded the presence or absence of small sucker shoots and stumps of former trunks. Under every tree a thorough search of the immediate vicinity was made for intact seeds or the remains of seeds, and for the pres-

ence of seedlings. For the purposes of data analysis, we have divided the *Ginkgos* into two groups, those in the upper reserve, which have experienced little disturbance from human activities, and those in the lower reserve, which have experienced much more human disturbance.

Results

Mature Trees

A total of 167 spontaneously growing *Ginkgos,* with a mean DBH of 52 cm, were located during the survey, a figure considerably lower than the 244 found by the Zhejiang Forestry Bureau in 1984. In the upper reserve, where 72 trees were located, the *Ginkgos* were most common on disturbance-generated microsites, including stream banks, rocky slopes, and the edges of exposed cliffs, all locations where the effects of soil erosion were readily apparent. With the exception of three large trees growing in front of Kaishan Temple, none of the *Ginkgos* in the upper reserve appeared to have been planted. In the lower reserve, where signs of human activities were much more common, many of the 95 censused trees were obviously planted. In the analysis of data, however, no attempt was made to distinguish wild from cultivated trees.

The largest *Ginkgo* in the upper reserve had a DBH of 123 cm; the largest in the lower reserve had a DBH of 121 cm. The heights of the larger trees were quite variable, with a maximum of just over 30 m. The *Ginkgos* were growing between 330 and 1200 m elevation, where the terrain has an average slope of 17%. Despite reports of *Ginkgo* seedlings in the woods (Wang et al. 1986), we were unable to locate a single plant with a basal diameter of less than 5 cm. There were only 3 trees with a basal diameter between 5 and 10 cm in the upper reserve, and only 2 trees within that range in the lower reserve. Clearly the *Ginkgo* population was not actively reproducing from seed under the shady, mature forest conditions that currently prevail on the mountain.

The most striking feature of the Tian Mu Shan *Ginkgos* was the multi-stemmed form of many of the larger trees. One individual, growing on the edge of a steep cliff at 950 m, occupied a total surface area of approximately 12 m^2 and consisted of 15 stems larger than 10 cm DBH (Fig. 2). In contrast to such multi-stemmed trees that were common in the woods, the three cultivated *Ginkgos* growing near the Kaishan temple were all single-trunked with DBHs of 68.5, 114.0, and 73.2 cm, and estimated ages of between 300 and 500 years (Zhejiang Forestry Bureau 1984).

In the upper reserve, 50% (36) of the *Ginkgos* had at least two trunks greater than 10 cm DBH, while in the lower reserve the figure was 33.6% (31). Of these 67 multi-stemmed trees, 73% had their primary trunk intact, indicating that logging in the area is not the primary cause of secondary sprouting. Table 2 summarizes the data collected on the population.

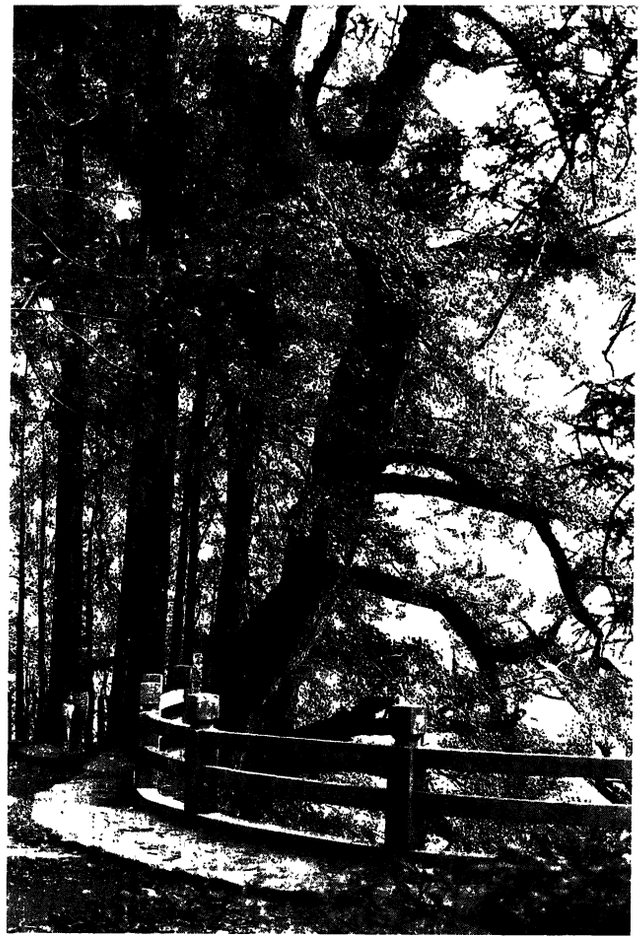

Figure 2. The "living fossil" Ginkgo on Tian Mu Shan. This ancient ovulate tree occupies an area of approximately 12 m^2 and consists of 15 stems greater than 10 cm DBH. The largest trunks have DBHs of 110 and 90 cm. The Chinese describe this tree, which is perched on the edge of a steep cliff at 950 m, as "an old dragon trying to fly." The fence protecting the tree was built in 1980.

For both the upper and lower reserves, the DBHs of the largest trunk of each individual tree were normally distributed in relation to the mean (Fig. 3A). When the basal area of all living stems greater than 10 cm was calculated, however, a somewhat bimodal distribution was apparent (Fig. 3B), suggesting the existence of two distinct age classes, an older, probably original, population with basal areas greater than 0.5 m^2 (33 trees) and a younger population with basal areas less than 0.5 m^2 (134 trees). There thus appears to be a point, around 50

Table 2. *Stem number and mean diameter at breast height (DBH) of the largest stem for 167* Ginkgos *growing in the Tian Mu Shan reserve.*

# Stems greater than 10 cm	*# Trees*	*% of Population*	*Mean DBH largest stem (cm)*	*Standard deviation DBH largest stem (cm)*	*Range largest stem (cm)*	*# Trees with cut trunk*
Upper reserve						
1	36	50	54.2	30.1	5–123	6
2	18	25	50.0	17.2	13–83	3
3	9	12.5	60.8	30.2	18–107	3
4	3	4.2	85.3	26.0	57–109	0
5	4	5.6	71.8	23.3	47–101	1
6	2	2.8	81.3	40.2	52–110	0
Totals	72	100	57.0	28.2	5–123	10
Lower reserve						
1	64	67.4	48.2	22.7	13–121	16
2	21	22.1	47.2	24.7	7–105	6
3	7	7.4	60.6	21.4	39–96	2
4	2	2.1	30.5	22.9	14–47	2
5	1	1.0	21.3	—	—	1
Totals	95	100	48.3	23.2	7–121	27
Combined	167	100	52.1	25.7	5–123	37

cm DBH of the main trunk, at which increasing biomass is achieved primarily through the production of secondary trunks rather than by the increased growth of the main trunk.

A one-way analysis of variance (Sokal & Rohlf 1981) comparing the two populations for stem number indicates that there is no significant difference ($P > 0.05$) in the mean diameter of the largest stem among three stem number classes: 1 stem, 2 stems, and 3 or more stems (ANOVA, upper reserve: $F = 2.65$, $P = 0.08$; lower reserve: $F = 0.07$, $P = 0.93$). This means that the diameter of the largest stem of each individual clone is independent of the total number of stems in that clone.

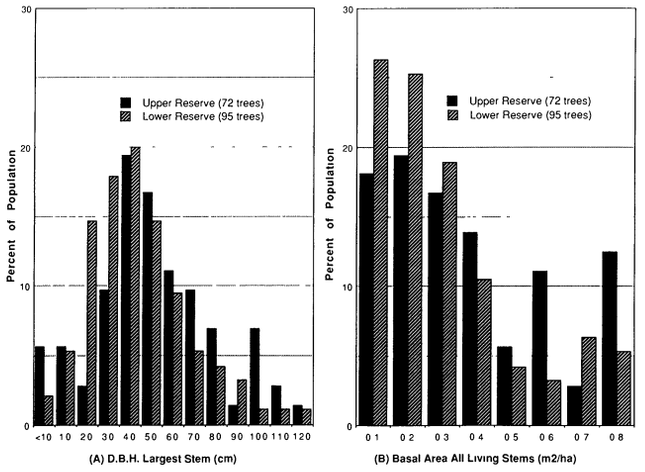

Figure 3. (A) Distribution of DBHs of the largest stem of 167 Ginkgos *on Tian Mu Shan. For the upper reserve, the mean is 57.0 cm and the standard deviation 28.2 cm; for the lower reserve, the mean is 48.3 ± 23.2 cm. (B) Distribution of the basal areas for 167* Ginkgos *on Tian Mu Shan, based on a summation of all trunks greater than 10 cm DBH.*

Vegetative Reproduction

While we could find no signs of recent seedling reproduction on Tian Mu Shan, most of the larger *Ginkgos* were reproducing vigorously from suckers arising near the base of their trunks. In some cases these basal suckers came out of the ground anywhere from 2 to 20 cm away from the trunk, and in others they were attached to large root-like structures that originated from the trunk at ground level. Wherever the base of the trunk of a large *Ginkgo* came into direct contact with a large rock or wherever its base was exposed by erosion, these structures developed. They either enveloped the rock or went around it, extending up to 2 meters from the parent trunk (Figs. 4 and 5). When these growths reached friable soil, they produced lateral roots, developed vigorous, vertically-growing shoots, and continued their downward growth.

Superficially, these structures resemble the well-known "air-roots" produced on old cultivated trees, called "chichi" (nipple or breast) in Japan and "zhong ru" (stalactite) in China. These unusual growths are positively geotropic and form along the underside of large lateral branches. The first anatomical description of chichi is by Fujii (1895), who considered them a "pathological formation" that developed in association with an imbedded shoot bud.

Figure 4. A well-developed, basal chichi growing over the face of a rock in the upper reserve. Note that the large chichi on the left has produced roots.

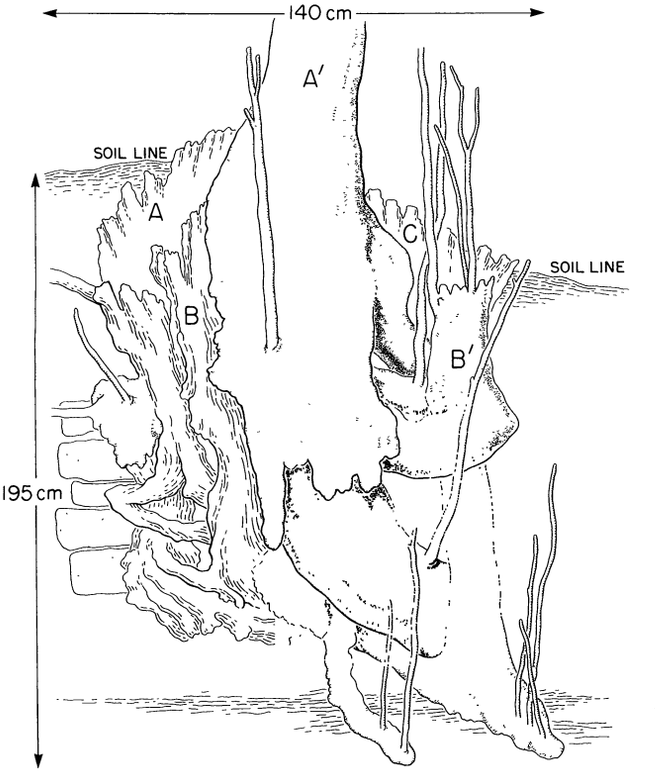

Figure 5. The chichi developed shoot system of Ginkgo *#163, probably planted, growing over the face of an old rock wall in the lower reserve. At least three generations of stems can be seen: the oldest represented by the cut trunks A, B, and C (DBHs = 55, 40, and 37 cm); the second by the living trunks A' and B' (DBHs = 26 and 20 cm); and the third by suckers arising from the zone of active chichi proliferation (stippled).*

The only chichi that we saw on the Tian Mu Shan *Ginkgos* were those that originated from the base of trees, particularly those that had experienced damage from erosion or logging. These growths should be called "basal chichi" to distinguish them from the more familiar "aerial chichi" described above. The strongly clasping nature of this unique structure makes the species well adapted to surviving on sites where disturbance to its root system is a common phenomenon. A complete description of the origin and development of basal chichi in cultivated seedlings has recently been published (Del Tredici 1992).

Seed Production and Predation

According to the reserve records, 1989 was a light year for seed production: only 60 kg of dried seeds were collected from the whole reserve. In our census we found intact seeds or the remains of seeds under 54 of the 167 trees censused. Seed drop generally occurs during the last two weeks of September on Tian Mu Shan, depending on the weather. By the time of our arrival on October 3, very few seeds were left on the trees, and we were able to collect more than 100 seeds under only 2 trees. Most of the nuts appear to have been collected by local people in late September.

Under every tree that produced seeds in 1989 we found probable signs of feeding activity by the locally abundant red-bellied squirrel (*Callosciurus flavimanus* var. *ningpoensis*) (Moore & Tate 1965). The fleshy outer coat of the seed, the sarcotesta, which is known to have vesicatory properties (Mitchell & Rook 1979), had been precisely pulled away and left uneaten while the edible kernel was consumed, leaving only fragments of the sclerified shell behind. The sarcotesta thus does not seem to delay predation by squirrels in the reserve as it does in North America (Del Tredici 1989). Since we never actually saw squirrels eating or "scatterhoarding" *Ginkgo* seeds, however, their potential role as dispersal agents of *Ginkgo* seeds is still unclear.

Long-time workers in the reserve reported to the authors that a "cat-like" animal with a long, thick tail also eats *Ginkgo* seeds in their entirety, vesicatory seed coat and all, and that some of the seeds pass through its digestive system intact. While we did not see the animal or any signs of its feeding, the workers were probably referring to *Paguma larvata,* the masked palm civet (Viveridae), which is reported to be an omnivore (Nowak & Paradiso 1983).

Discussion

The fact that *Ginkgo* is an economically important plant and that Tian Mu Shan has been the site of human activities for approximately 1500 years makes it difficult if not impossible to resolve the long-standing argument about the wildness of the *Ginkgo* population. In many ways the debate has more to do with the definition of the term "wild" rather than with the biology of the plant itself. More than any other factor, the presence of Kaishan temple has raised doubts about the origin of the *Ginkgos.* In this regard it should be kept in mind that throughout China such temple sites were selected because of their great scenic beauty and that the forests surrounding them were often preserved by the resident monks (Li 1956). The fact that some of the large *Ginkgos* and *Cryptomerias* in the reserve were planted by humans should not necessarily be interpreted to mean that all of them were. Attributing such guilt by association may be the cautious position but not necessarily the correct one.

The significance of the lack of *Ginkgo* seedlings in the reserve is also difficult to interpret. On the one hand it might be seen as evidence that *Ginkgo* is not native to the area, but on the other hand it can be viewed as evidence that *Ginkgo* does not reproduce from seed under the closed canopy of a mature forest. This latter suggestion is supported by a recent report on another "semi-wild" population of *Ginkgo* located in Hubei Province (Jiang et al. 1990). The authors concluded that *Ginkgo* is a species that requires much light and that seedling establishment occurs only in portions of the forest where the canopy is open. Interestingly, the study also records the observations of local peasants that the leopard-cat, *Felis bengalensis,* consumes *Ginkgo* seeds and that some of the nuts pass through the cat's digestive system undamaged. The existence of two independent reports of carnivores consuming intact *Ginkgo* seeds raises the possibility that they can act as dispersal agents and that the sarcotesta may attract them by mimicking the smell of rotting flesh.

While it is difficult to answer the question of whether the *Ginkgo* population on Tian Mu Shan is "truly" wild, it is clear that the phenomenon of secondary trunk formation from basal chichi is an important factor in explaining the long term persistence of the species on the mountain. It is also possible that vegetative reproduction by means of basal chichi may have contributed to the extraordinary persistence of *Ginkgo* throughout geological time.

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