Topophysis in Gymnosperms: An Architectural Approach to an Old Problem

Peter Del Tredici
Arnold Arboretum of Harvard University, 125 Arborway, Jamaica Plain, Massachusetts 02130

Topophysis is defined as the organizational status of a meristem which is determined by its position on the plant and which remains stable through vegetative propagation (Halle, et al , 1978; Molisch, 1938; Roulund, 1976) From a practical point of view, this means that if a lateral branch of a woody plant is rooted or grafted onto a seedling rootstock, the resulting propagule will continue growing in the same non-vertical orientation it maintained while it was still attached to its parent trunk. Try as one might to correct this orientation by tying the leader to a stake, the branch will continue its plagiotropic (horizontal) orientation once it reaches the top of the stake. From the propagator's perspective, the effects of topophysis are problematic because the propagules do not replicate the growth habit of the plant they were taken from.

In order to be properly understood, the phenomenon of topophysis must be examined within the conceptual framework of tree architecture, as defined by Halle, et al. (1978). In the context of the whole tree, topophysis can be considered a physiological state in that the hormonal signals emanating from an orthotropic (vertical) leader, which regulate the orientation of its subtending lateral branches, become fixed or "imprinted" on these branches—a kind of dendrological memory, if you will The persistence of these effects in subsequent vegetative propagules varies with the architecture of the species in question, the age of the plant, and location on the tree of the meristems used in propagation.

In the physiological literature topophysis is considered a manifestation of the lack of juvenility—a murky concept practically defined as a phase of growth in woody plants that is "characterized, apart from its morphological properties, by a greater readiness to form adventitious roots and an inability to form flowers" (Doorenbos, 1965). In the context of juvenility, topophysis is typically presented as an example of the irreversible changes that occur in meristems as part of the aging process (Robins, 1964). Borchert (Borchert, 1976) makes it clear, however, that this view is not altogether correct and that, over time, topophytic effects are often reversible The purpose of this paper is not to delve into the complexities of juvenility or the hormonal basis of the phenomenon of topophysis, but to look at the practical implications of topophysis as it relates to the issue of vegetative propagation.

The phenomenon of topophysis—which was first described by Vochiling in 1904 in *Araucaria heterophyllais*—is quite common among gymnosperms and numerous examples have been documented among the conifers, including species in the genera *Abies* (Busgen and Munch, 1929), *Agathis* (Molisch, 1938), *Araucaria* (Vochting, 1904), *Cephalotaxus* (personal observation), *Sequoia* (Libby and McCutchan, 1978; Bobbins, 1964), *Taxus* (Molisch, 1938; Robbins, 1964; Turner, 1958), and *Torreya* (personal observation). Many of the species within these genera

are known to produce topophytic "cultivars"—often given the name 'Prostrata'—which possess branches with a more or less plagiotropic orientation and a secondarily derived dorsiventral needle arrangement. Predictably enough many of these cultivars are unstable in their growth habit, frequently throwing up "reversions" with an orthotropic orientation and a whorled needle arrangement. No doubt such instability, in conjunction with a misunderstanding of the causes of topophysis, has contributed to the nomenclatural confusion that surrounds many dwarf conifer cultivars in the nursery trade (Welch, 1979). In the genus *Taxus*, for example, the position of the cuttings on the parent plant is often reported to determine the cultivar name they receive (Borchert, 1976; Turner, 1958).

In my own work with the genus *Ginkgo*, the effects of topophysis can be seen clearly by the inability of plants propagated by cuttings or grafts from the lateral branches of old trees to grow orthotropically (Fig. 1). This means that vegetatively propagated ginkgos seldom show the dominant central leader and whorled branch arrangement typical of seedlings. Instead, the branches grow out at erratic angles, producing low branched trees with poor form from the point of view of use as street trees.

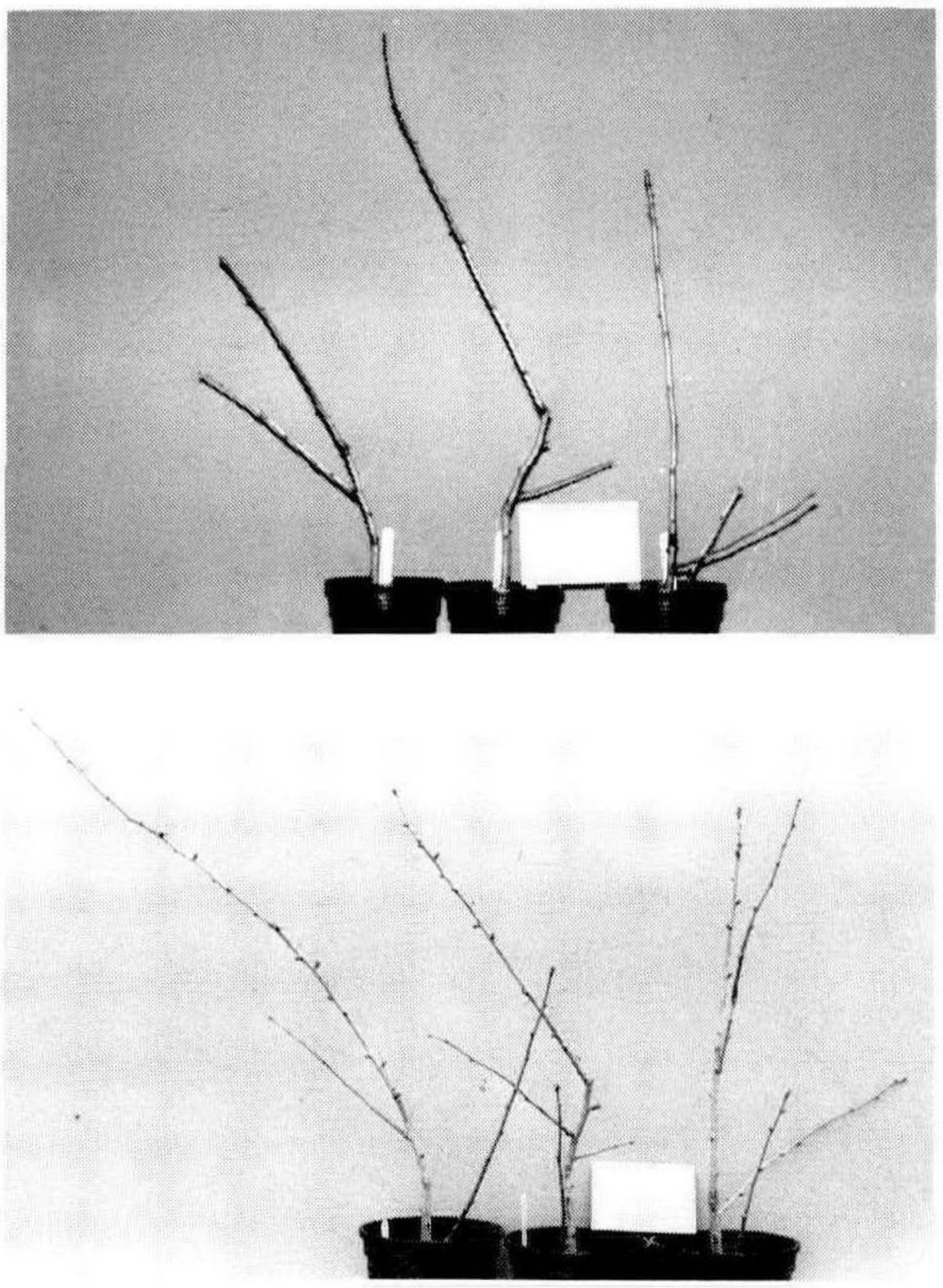

Figure 1. Topophysis in *Ginkgo biloba* "Fastigiata'. Terminal softwood cuttings were taken from a single branch in August, 1981 and rooted under intermittent mist. (A) The two cuttings on the left were taken from plagiotropic lateral shoots while the one on the right was taken from the orthotropic terminal shoot. Photographed at four years of age in December 1985. (B) The same cuttings photographed in February 1991,at ten years of age, showing that their respective orientations have remained stable over a ten year period. For scale, the index card is 7 ×13 cm.

In China, where *Ginkgo* is cultivated for its edible nuts, the effects of topophysis are put to use rather than considered a problem as it is in the United States. Female trees which produce exceptionally large seeds are propagated by grafting lateral shoots onto seedling rootstocks. Compared to seed-grown trees, with their strong leader and whorled branches, grafted trees are spreading in form, produce no central leader and are scarcely more than 5 or 10 m tall (Fig. 2). From a commercial point of view, the characteristic vase-shaped form of these grafted trees is advantageous since it makes the seeds easier to harvest (Del Tredici, 1991). The stability of the form of these propagules offers clear evidence of long-lasting topophytic effects, and provides an example of "domestication" by selective propagation. It must be kept in mind, however, that it is the size and shape of the edible nut that defines these Chinese cultivars, not their growth habit.

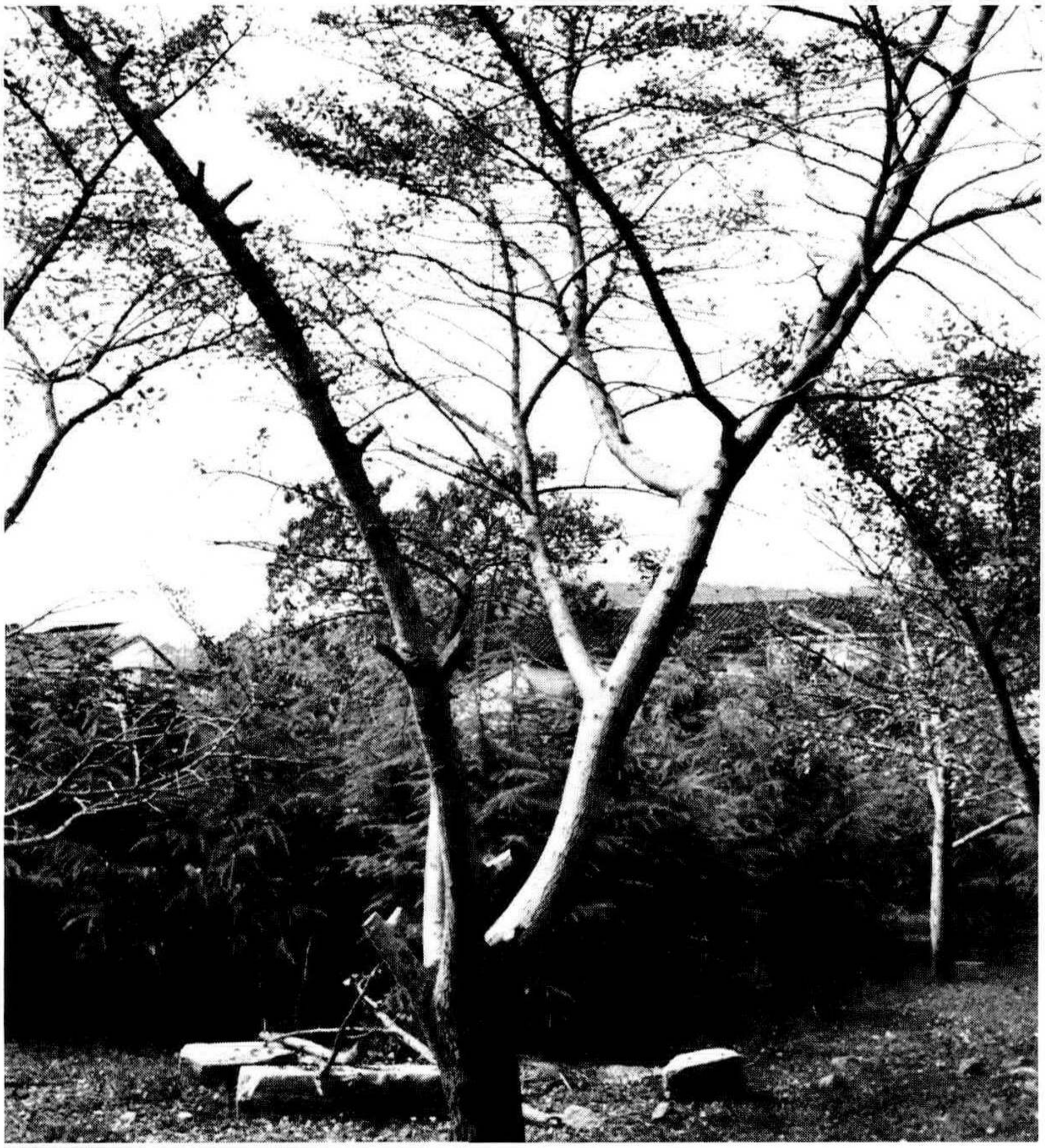

Figure 2. A grafted specimen of the commercially important *Ginkgo* cultivar 'King of Dongting Mountain' selected for its production of larger than normal nuts. The vase-shaped, leaderless from of such grafted ginkgos contrasts markedly with that of trees raised from seed. Photographed in October 1979 in Dongting Shan, Jiangsu Province,China.

In *Ginkgo*, the most practical way to circumvent the problem of topophysis is through the age-old practice of stooling, in which young stock plants are repeatedly cut back low to the ground to stimulate the production of numerous vertical replacement shoots which originate from dormant meristems embedded in the stem. When these vigorous terminals are used as propagation material—either as cuttings or grafts—they will produce vigorous, vertically growing trees (W. Flemmer III, personal communication) No doubt stooling would also be effective in overcoming topophytic effects in those conifer genera which, like *Ginkgo*, show a strong tendency to stump sprout following logging or heavy pruning (*Cephalotaxus*, *Cunninghamia*, *Sequoia*, *Taxus*, and *Torreya*) Many of these reiterative shoots — to use the terminology of tree architecture—probably originate from so-called detached meristems (Fink, 1984).

Other techniques for overcoming topophytic effects include: serial grafting of scions from mature trees onto seedling rootstocks, which has been used to rejuvenated clones of *Pseudotsuga* and *Picea* (John, 1983); and *in vitro* tissue culture, which has been reported to restore juvenility in mature clones of *Picea* (John, 1983) and *Sequoia* (Ball, 1978).

LITERATURE CITED

Ball, E. A. 1987 Tissue culture multiplication of *Sequoia* In, Cell and Tissue Culture in Forestry Volume 3 Case Histories Gymnosperms Angiosperms and Palms Martinus Nijhoff, Dordrecht.

Borchert, R. 1976 The concept of juvenility in woody plants Acta Horticulturae 56 21-36

Busgen, M. and **E. Munch.** 1929 The Structure and Life of Forest Trees, 3rd ed translated by T. Thompson Chapman and Hall, London

Chadwick, L.C., and **R.A. Keen.** 1976 A Study of the Genus *Taxus* Ohio Agricultural Research and Development Center, Res Bull 1086

Del Tredici, P. 1991 Ginkgos and people a thousand years of interaction Arnoldia 51(2):2-15

Doorenbos, J. 1965 Juvenile and adult phases in woody plants In, Encycl Plant Physiol , 15(1) 1222-1235, W Ruhland (ed) SpringerVerlag, Berlin

Fink, S. 1984 Some cases of delayed or induced development of axillary buds from persisting detached meristems in conifers Am J Bot. 71 44-51

Haile, F., R.A.A. Oldeman, and **P.B. Tomlinson.** 1978 Tropical Trees and Forests Springer-Verlag, Berlin

John, A. 1983. Tissue culture of coniferous trees In, Tissue Culture of Trees, pp 6-21, J H Dodds (ed) Croom Helm, London and Canberra

Libby, W.J., and **McCutchan, B.G.** 1978 "Taming" the redwood Am Forests 84(8) 18-23,37-39

Molisch, H. 1938 The Longevity of Plants Translated by E H Fulling. Privately published, New York

Robbins. W.J. 1964 Topophysis, a problem in somatic inheritance Proc Amer Phil Soc 108 395-403

Roulund, H. 1976 The effect of the cyclophysis and the topophysis on the torring and behavior of Norway spruce cuttings Acta Horticulturae 56·39-50

Turner, F. 1958 Form variations in *Taxus* as related to the source of the cutting on the stock plant Proc. Intl Plant Prop Soc 8.164-166

Vochting, H. 1904 Uber die regeneration der *Araucaria excelsa* Jb Wiss Botan 40 144-155

Welch, H.J. 1979 Manual of Dwarf Conifers Theophrastus, Little Compton, R I