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Cyclophysis and Topophysis in Coast Redwood Stecklings

I. Rooting and Nursery Performance

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Summary

Two studies were conducted with vegetative propagules of *Sequoia sempervirens* to improve our understanding of the effects of branch order (topophysis) on the rooting of cuttings and growth performance of the resulting stecklings.

In the first study, cuttings of three branch orders were collected from hedged trees. Hedges were used since these could provide the different branch orders without confounding effects of cyclophysis. In the second study cuttings of the same three branch orders were collected from young seedlings and from two branch orders from the same hedges used above. The second study was expected to shed some light on the possible interaction between topophysis and cyclophysis, since hedges would be in a more advanced maturation stage than seedlings.

The results indicate that both maturation stage and branch order have significant effects on the rooting of cuttings and on the growth characteristics of the resulting stecklings. The results also support the concept of interaction between cyclophysis and topophysis.

Key words: Cyclophysis, Maturation, Plagiotropism, Propagation, Rooted Cuttings, Topophysis, Vegetative Propagation.

Zusammenfassung

Zwei Studien mit vegetativ vermehrten *Sequoia sempervirens* wurden zur Verbesserung unseres Verständnisses der Auswirkungen der Topophysis auf die Bewurzelung von Stecklingen und das Wachstum der daraus resultierenden Pflanzen durchgeführt.

In der ersten Studie wurden Stecklinge von heckenartig beschnittenen Bäumen von Ästen erster bis dritter Ordnung gesammelt. Hecken werden benutzt, da diese Äste verschiedener Ordnung liefern können, ohne daß der Cyclophysis-Effekt zerstört wird. In der zweiten Studie werden Äste gleicher Ordnung von jungen Sämlingen und Äste zweier verschiedener Ordnungen der oben erwähnten Hecke verwendet. Bei der zweiten Studie wurde erwartet, daß die mögliche Interaktion zwischen Topophysis und Cyclophysis zum Teil aufgeklärt werden könnte, da Hecken sich in einem fortgeschritteneren Reifezustand befinden als Sämlinge.

Die Ergebnisse zeigen, daß sowohl Reifestadium als auch Astordnung signifikante Auswirkungen auf die Bewurzelung von Stecklingen und die Wachstumsmerkmale der daraus resultierenden Pflanzen haben. Die Resultate stützen auch das Konzept einer Interaktion zwischen Cyclophysis und Topophysis.

Introduction

Rooting techniques for a variety of forest trees are now fairly well developed (ARMSON and BIDWELL, 1971; ARMSON *et al.*, 1980; DEUBER, 1940; DORAN, 1954, 1957; FARRAR and GRACE, 1942; GIROUARD, 1970 a, b, 1971, 1972, 1974, 1975; HILL and LIBBY, 1969; LARSEN, 1955; LEPISTÖ, 1974, 1977; RAUTER, 1971; THIMANN and DELISLE, 1942; WERNER, 1979), but some problems still remain. A common problem in vegetatively propagating conifers is topophysis, in which stecklings (established rooted cuttings) maintain a growth habit similar to that of the donor shoots. Cuttings from branches often persist in growing plagiotropically for months, or even years, after grafting or rooting (DORMLING, 1980; FORTANIER and JONKERS, 1976; OLESEN, 1973, 1978; ROULUND, 1973, 1974, 1975, 1977, 1978, 1979 a, b, 1981; SCHAFFALITZKY DE MUCKADELL, 1959).

Several studies have attempted to quantify effects of topophysis on the rooting of cuttings, and the subsequent stem form of the resulting stecklings (TUFOUR, 1973; ROULUND, 1975, 1979 b). However, cuttings have generally been selected from different heights within the tree and with no attention being given to rank order of the cutting shoot on the parent branch. As OLESEN (1978) pointed out, results from these studies are unable to prove topophytic effects, since they are confounded by gradients of maturation (cyclophysis) within the crown.

During a decade's observations with various kinds of coast redwood (*Sequoia sempervirens* D. DON (ENDL)) propagules, we have noted that recently rooted young stecklings exhibit a wide spectrum of stem angles; some vertical, but most non-vertical to varying degrees. It was clear that the persistence of plagiotropic growth of stecklings was longer for cuttings taken from older plants, or for cuttings from higher in the crown of a tree. ROULUND (1975, 1979 b), and

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Tufour (1973) reported that the longer persistence of plagiotropic growth in rooted cuttings taken from higher in the crown suggests that an interaction of cyclophytic and topophytic effects exists within the tree's crown.

The present study was designed to examine in more detail the effects of branch order on the rooting of cuttings, and on the subsequent growth performance of the resulting stecklings. Cuttings were taken from three branch orders within hedged plants. Because of the hedging, all cuttings were expected to be at approximately the same stage of maturity, so that the cyclophytic effects would be minimal. Because of known variation in rooting performance during the year, the study was first conducted in November (when rooting is generally good), and repeated in July (when rooting performance is generally lower). The study in July also included comparisons of branch order between cuttings from first-year seedlings and cuttings from more mature hedges, to provide some information on the interaction between cyclophysis and topophysis.

This paper reports results on rooting and early growth of the stecklings prior to outplanting. Subsequent papers will report on growth performance of the stecklings after planting in the field.

Materials and Methods

Seeds were collected from several coast redwood trees (some of Northern California origin near the Mad River, but most of unknown origins) growing as landscape or research trees in the Berkeley, California area. Seeds were germinated in Spring 1974, and the clones from them were periodically re-established as rooted cuttings, and kept as hedges. The hedges were grown in clay pots in a greenhouse, and maintained as stock plants for cuttings by periodically hedging to a height of 30—40 cm. Although the chronological age of these stock plants in 1980 (when cuttings for the present study were first taken) was 7 years, hedging had maintained the plants in a more juvenile developmental state (Hood and Libby, 1978; Power and Dodd, 1984).

Cuttings for the first experiment were taken from 5 hedged clones on 20 November 1980. Cuttings for the second experiment were taken from 9 clones, including the same 5 clones used in experiment 1, and from 10 first-year seedlings on 18 July 1981. The seedlings were of unknown origin.

All donors in Study 1 provided cuttings of orthotropic shoots (terminals), and cuttings from two branch orders; first-order branches (primaries), and second-order branches (secondaries) (*Fig. 1*). The terminals always had radial symmetry, while the primaries and secondaries were mostly, or fully bilaterally symmetrical. In Study 2, cuttings from terminals, primaries and secondaries were taken from seedlings, but cuttings from only primaries and secondaries were taken from hedges. Ten cuttings (about 8 cm long) were taken from each branch order in the hedged plants. Ten cuttings also were taken from primary and secondary branch orders of each seedling, but since the seedlings were monoaxial, only a single terminal cutting could be taken per seedling.

Immediately after detachment, the freshly exposed bases of the cuttings were dipped in an IBA solution (4000 ppm indole-3-butyric acid in 95% ethanol) for about 5s. The cuttings were then set in pre-formed depressions in an organic rooting medium (Hill and Libby, 1969) held in 20 cm long leach tubes. The leach tubes contained rooting medium

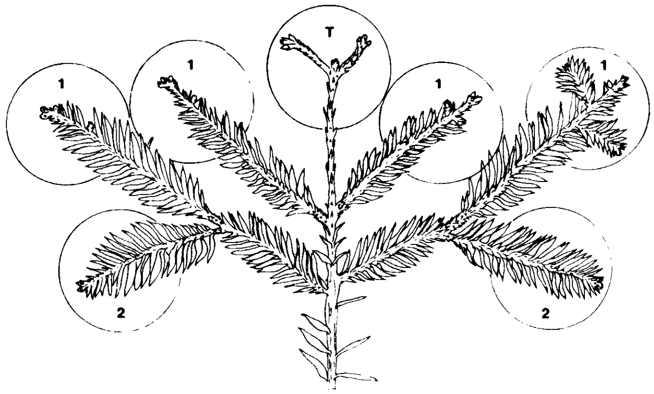

Fig. 1. — Diagram of the main stem of a hedge indicating the relative positions of terminal (T), primary (1) and secondary (2) branch orders.

in the upper third, and potting soil in the lower two thirds of the tube. The potting soil was intended to support growth once the cuttings had rooted. The cuttings in their leach tubes were maintained under intermittent mist in a greenhouse. A balanced fertiliser was applied once a week.

On the day that roots were visible at the bottom of the leach tube, each steckling was moved to a shade house, and arranged to avoid contact with other trees or surface that could modify growth form. Each steckling then remained in the shade house for exactly 8 weeks, at which time morphological measurements were made.

Rooting dates of the cuttings were recorded when root tips emerged from the bottom of the leach tubes. After 8 weeks in the shade house, stem angle, total main stem length, distance to first lateral branch, basal stem diameter and main stem taper were measured. Stem angle, which was the angle of deviation of the main stem from the vertical, was classified by matching the stem form of the steckling with a set of growth curves drawn on a card (*Fig. 2*). A stem angle class was assigned to the interval between curves. Classes were from 1 (with a midpoint of 125 degrees from the vertical) to 7 (with the midpoint strictly vertical) (*Fig. 2*). Total main stem length was the distance from soil level in the leach tube to the tip of the terminal shoot. Distance to first lateral branch was the distance from soil level in

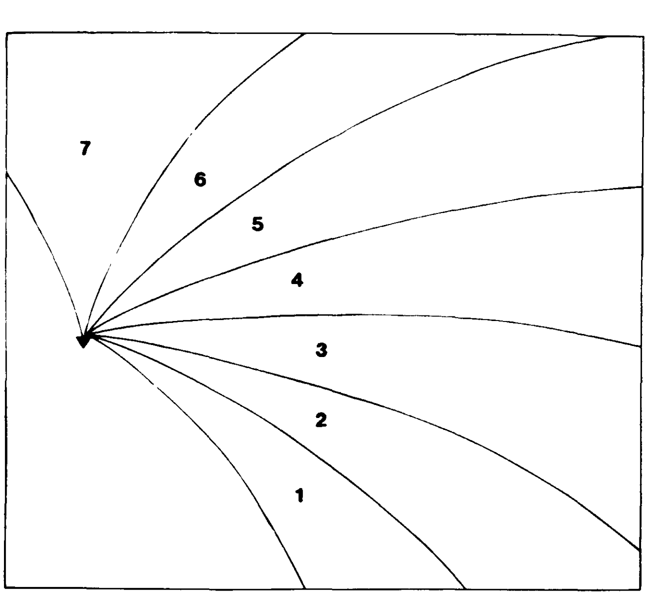

Fig. 2. — Diagram of the seven stem angle classes developed by the stecklings. ▲ indicates the base of the stem.

Table 1a and *b*. — Means of rooting, and early growth characteristic of coast redwood stecklings from different branch orders. Differences among means designated by the same letter are non-significant with alpha > .05. Note: Multiple comparisons were made only within, and not between, stecklings of seedlings or of hedge origin. Comparison between stecklings of seedlings and of hedges were not made because terminals were not included among hedges of Study 2.

Table 1a.

	Study 1		
		Hedges	
	T	1	2
2/Final rooting %	92a	88a	80a
1/Mean rooting date (days)	184a	166b	151c
1/Shoot length (cm)	22.24a	36.05b	31.85c
1/Distance to lateral (cm)	0.45a	1.79b	9.91c
1/Basal stem diameter (cm)	0.45a,c	0.45a	0.37b
1/Taper (x 1000)	0.29a	0.28a,b	0.23b
2/Stem angle class	7.00b	4.46a	3.94a

Table 1b.

	Study 2				
	Seedlings			Hedges	
	T	1	2	1	2
2/Final rooting %	100a	100a	90a	87a	87a
1/Mean rooting date (days)	91a	76a	71a	114a	115a
1/Shoot length (cm)	12.10a	14.80a,b	19.44b	14.42a	16.16a
1/Distance to laterals (cm)	0.20a	1.60a	9.11b	0.38a	3.28a
1/Basal stem diameter (cm)	0.28a	0.30a	0.27a	0.29a	0.23a
1/Taper (x 1000)	0.22a	0.31a	0.23a	0.26a	0.13a
2/Stem angle class	6.90a	6.50a	4.89b	5.75a	4.62b

1/ Comparison of means made with Tukey-Kramer procedure for unequal sample sizes (Dunnett, 1980).

2/ Comparison made with Chi-square test.

the leach tube to the point of attachment of the first lateral branch with the main stem. Basal stem diameter was measured with calipers outside of the bark, at a position just above soil level but avoiding any basal swelling.

An index of stem taper, standardizing stecklings for both height and basal diameter, was calculated by the following formula:

$$\frac{D_B - D_{H/2}}{D_B}$$

in which D_B = basal stem diameter,

$D_{H/2}$ = stem diameter at 1/2 the length of the stem.

Data were analysed using a two-way analysis of variance with fixed effects and the means compared by the Tukey-Kramer procedure for unequal sample sizes.

Results

Rooting

Rooting success was high (80% and over) for all origins of cuttings that were set (*Table 1 a*). In the second study, in which seedling and hedge-origin cuttings were compared, cuttings from seedlings had a higher final rooting percentage than cuttings from hedges. This result would be expected since the hedged plants should have been more mature than the seedlings. Cuttings from seedlings also had a much ealier mean date of rooting than cuttings from hedges (*Table 1 b*). This earlier mean date of rooting was also associated with less variation in the time taken for each of the cuttings to root. For example, fifty percent of cuttings from seedlings rooted within 11 weeks of being set, eighty percent rooted within 15 weeks, and no further rooting occurred after 20 weeks (*Fig. 3 b*). By comparison, fifty percent of cuttings from hedges rooted within 14.5 weeks from being set, eighty percent rooted within 21 weeks (*Fig. 3 a, b*).

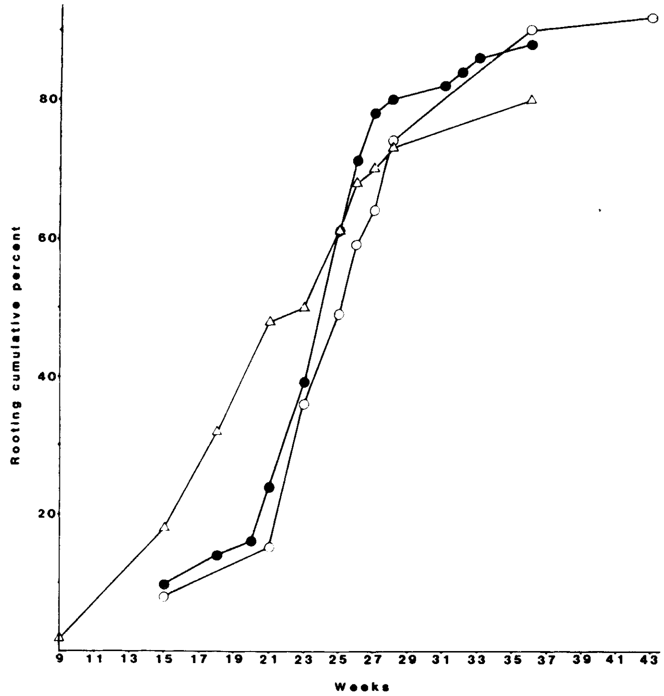

Fig. 3a. — Rooting cumulative percent of stecklings fo primary (●), secondary (△) and terminal (○) branch orders in Study 1.

Among branch orders, final rooting percentages were greatest in the cuttings from terminal shoots within each group, and lowest in cuttings from secondary branches (*Table 1 a*). Although terminal cuttings achieved the highest overall rooting percentage, their mean dates of rooting were later than cuttings of primary and secondary branch orders. Except for cuttings from hedges in study 2, cuttings of secondary branches had the earliest mean rooting date (*Table 1 b*). From *Fig. 3 a*, the times to fifty percent rooting for cuttings from hedges in study 1 were 25 weeks for terminals, 24 weeks for primaries, and 23 weeks for secondaries. In study 2, the times to fifty percent rooting for cuttings from hedges were 14 weeks for primaries, and 14.5 weeks for secondaries, and for cuttings from seedlings were 11 weeks for terminals, 9.5 weeks for primaries, and less than 9 weeks for secondaries (*Fig. 3 b*).

Stem Morphology

Stem Angle

Stecklings from the terminals and two branch orders developed marked differences in growth form by eight weeks after rooting. Stecklings from terminals generally maintained an orthotropic growth habit (class 7 for stem angle measured here) (*Fig. 2, 6*). The degree of plagiotropic growth was more marked for stecklings from secondary branch order than for stecklings from primaries (*Fig. 4 a, 4 b, 6*).

A comparison of stecklings of hedge origin with those of seedling origin suggests that the degree of plagiotropism developed by stecklings is influenced by the state of maturation of the cutting donors (*Table 1 b*). For example, stecklings of seedling origin of primary and secondary branch orders fell into higher stem angle classes, and

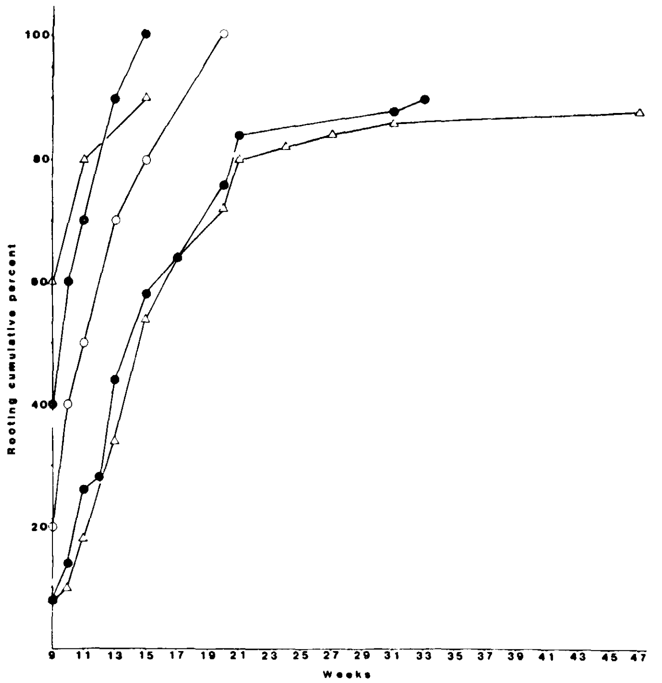

Fig. 3b. — Rooting cumulative percent of stecklings of primary (●), secondary (△) and terminal (○) branch orders in Study 2. The top three lines show stecklings of seedlings origin and the bottom two lines show the stecklings of hedge origin.

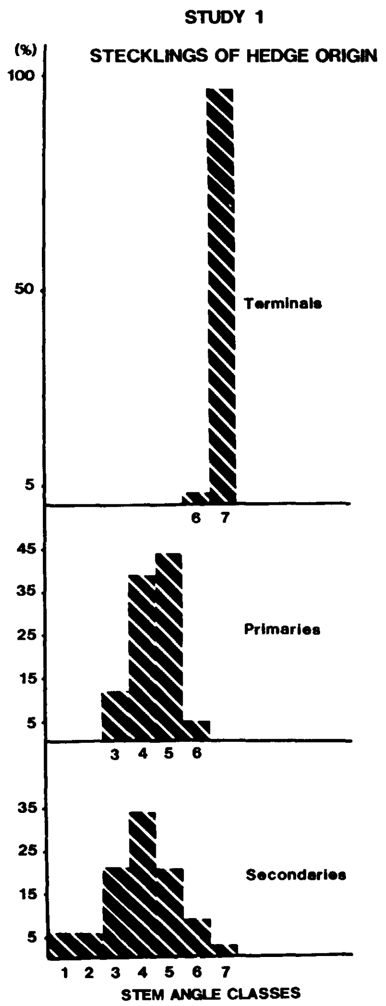

Fig. 4a. — Frequency distribution of stem angle classes among stecklings of three branch orders in Study 1.

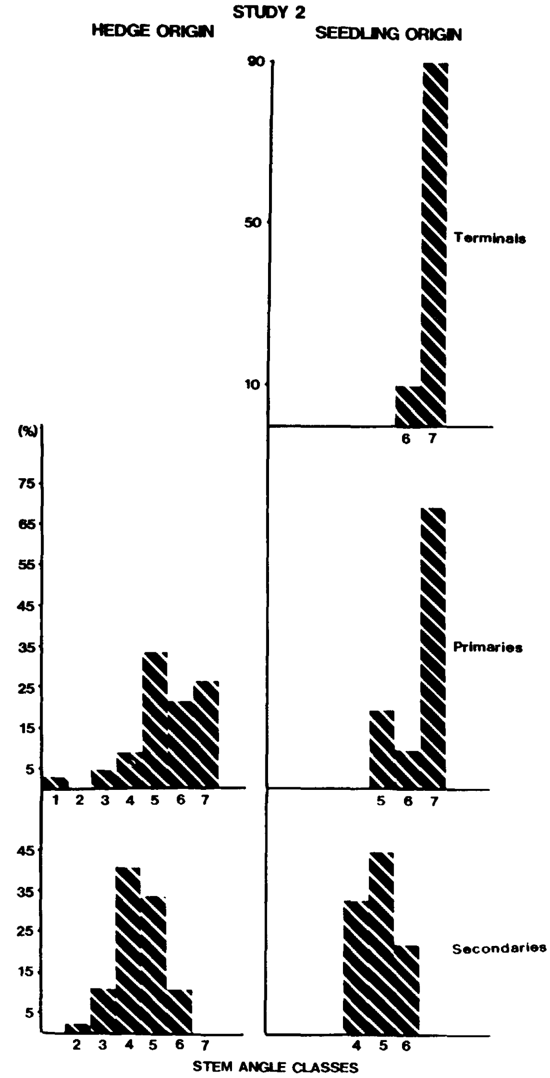

Fig. 4b. — Frequency distribution of stem angle classes among stecklings of hedge and seedling origins in Study 2.

showed less variation in stem angle than stecklings from hedge origin (*Fig. 4 b*).

Length

Stecklings from terminal cuttings were consistently shorter than stecklings from either primary or secondary cuttings at eight weeks after each was classified as rooted (*Table 1 a, b*). In Study 1, stecklings from primary cuttings were longer than those from secondaries, however the reverse was observed in study 2, both for cuttings from hedges and for cuttings from seedlings.

First Lateral Branch

Distances to the first branch along the stems varied significantly among cuttings of different origins in both stecklings from hedges and from seedlings. This was least in stecklings of terminal cuttings, intermediate in those from primaries, and greatest in those from secondaries (*Table 1a, b*). This distance was considerably greater in stecklings from secondary branches.

Basal Stem Diameter

Basal stem diameters did not vary significantly between stecklings from terminals or primaries (*Table 1a, b*). Stecklings from secondaries on hedges had significantly lower basal stem diameters than stecklings from terminals or

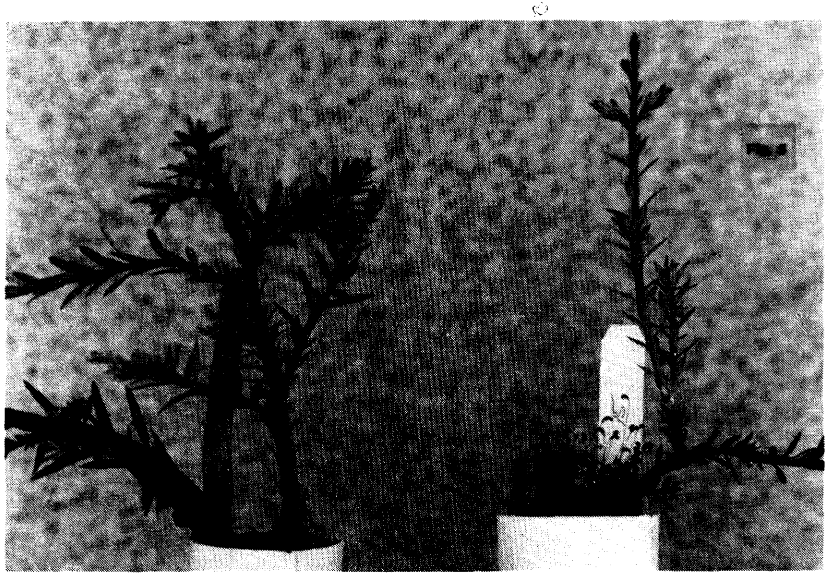

Fig. 5. — Origin or orthotropic shoots, from callus (left) and from stem (right).

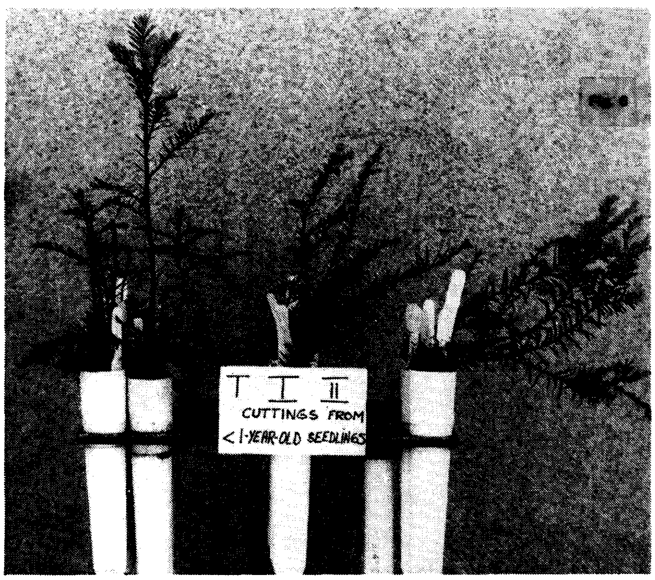

Fig. 6. — Characteristic stem angle classes of stecklings of terminal (left), primary (center) and secondary (right) branch orders.

primaries in study 1 but not in study 2. These differences were smaller and non-significant among stecklings of different origins from seedlings.

Taper

Stems of stecklings from terminal cuttings showed the greatest early taper, followed by stecklings from primaries and then by those from secondaries in study 1 (*Table 1 a*). Consistent with this, stecklings from primaries showed greater taper than those from secondaries in both cuttings from hedges and from seedlings (*Table 1 b*). Stecklings from terminal cuttings of seedlings had less taper than stecklings from both primary and secondary branch orders in study 2 (*Table 1 b*).

Recovery from Plagiotropism

Stecklings that commenced growth plagiotropically began to recover from this in three ways:

1. The apex of plagiotropic shoots gradually turned upwards. Later, the stem moved towards the vertical presumably as a result of compression wood formation.
2. Buds from the lower third of the shoot flushed and grew orthotropically (*Fig. 5*).
3. Orthotropic shoots arose de novo from the basal callus (*Fig. 5*).

There were no consistent differences between stecklings of primary and secondary branch orders as to the mode of recovery from plagiotropic growth.

Clonal Differences

Examination of variation among clones was not a primary objective of this study. However analyses of variance indicated that clones contributed significantly to the overall variation for several of the measured variables (*Table 2 a, b*). For example, variation due to clones was more highly significant than variation due to branch position for mean date of rooting in both study 1 and study 2. Variation due to clones and due to branch order were both highly significant for basal stem diameter. In contrast, variation due to clones for stem taper was non-significant while position contributed significant variation in both studies.

In study 1, clone by position interactions were also highly significant, suggesting that trends among branch order posi-

Table 2a and *b*. — Probabilities of greater F from analyses of variance of rooting and early growth characteristics of coast redwood stecklings from different branch orders.

Table 2a.

	Study 1		
	Clone	Position	C*P
Mean rooting date	.0001	.0032	.0015
Shoot length	.0001	.0001	.0001
Distance to laterals	.0001	.0001	.0001
Basal stem diameter	.0001	.0001	.0004
Taper	.0816	.0396	.0019

Table 2b.

	Study 2		
	Clone	Position	C*P
Mean rooting date	.0054	.9424	.1966
Shoot length	.0001	.0219	.0328
Distance to laterals	.0924	.0001	.0531
Basal stem diameter	.0001	.0001	.3213
Taper	.3305	.0001	.3856

tions for the different variables were not consistent for all clones.

Differences in stem angle class among branch positions were tested by chi- square methods but no tests on clonal differences were made. However, observations (not quantified here) indicated large differences in degree of plagiotropism among clones. For example, primary origin stecklings of clones T2 and T5 were predominantly assigned to stem angle class 6, whereas those of clones T1 and T0 were predominantly in classes 4 and 5.

Discussion

Earlier studies of topophysis have often confounded effects of branch order with gradients of maturation within the ortet. In this study, topophytic effects were examined relatively free of maturation effects by taking cuttings of different branch orders from hedged plants, and fom first-year seedlings. The results indicate that both branch order and maturation stage have important independent effects on rooting of cuttings and on subsequent growth and form of the stecklings. The results also support the concept that, for some characteristics, cyclophytic and topophytic effects interact in such a way that topophytic effects are more pronounced and/or last longer in more mature plant material.

As expected, rooting occurred earlier and in higher percentages among cuttings from seedlings than among cuttings from hedges. The differences in final rooting percentages and mean rooting dates were much greater between cuttings from seedlings and hedges, than they were among cuttings from different branch orders. A pattern of decreasing percentage of rooting of cuttings from terminals to primaries to secondary branch positions was clear from the data. However, in this case high rooting percentages were not associated with early commencement of rooting. Indeed cuttings from terminals commenced rooting much later than the cuttings from secondary branch order positions.

Differences in flushing patterns among the cuttings of the different origins probably accounted for the differences in stem length. At the onset of rooting of terminal cuttings, lateral buds flushed and branches grew out while the leading shoot remained inactive for several weeks. However, when or shortly after primary cuttings rooted, their leading shoots and lateral buds flushed and commenced elongation simultaneously. The leading shoots of stecklings of secondary cuttings typically did not flush until some time after rooting. Flushing of their lateral buds occurred after that of the leading shoot, and generally only few lateral branches were produced. Although flushing of leading shoots of the secondaries was delayed, a later rapid rate of stem elongation resulted in longer average stem lengths for these plants.

Presence of lateral shoots, or buds, on the cutting at the time of collection, were probably responsible for the differences in distance to the first laterals in the stecklings (*Fig. 1*). Cuttings from terminals had expanding laterals immediately below the apex of the main shoot, and these resumed growth while on the rooting bench. Cuttings from primaries had prominent lateral buds immediately below the shoot apex which also flushed early, but cuttings from secondaries had no visible buds, and meristematic tissue presumably developed close to the apex only after shoot extension had commenced.

About two months after rooting, stecklings could often be easily identified as to their branch order origin by their degree of plagiotropic growth, and by their branching habit (the change from plagiotropic to orthotropic growth was associated with a change from bilateral to radial symmetry). The topophytic effects on stem angle were more pronounced in stecklings of hedge origin than they were in stecklings of seedling origin, suggesting that the state of maturation of the ortet has an influence on the expression of these topophytic effects. The time taken for ramets to begin to turn upwards has been reported to be longer in more mature ortets by other investigators (Kleinschmit, 1977; Roulund, 1975, 1979; von Wühlisch, 1984). It would seem likely that more juvenile meristems are at a lower degree of determination, so that they are capable of more rapid adjustment than more mature meristems.

Although differences in mode of recovery from plagiotropism were observed, these did not appear to be consistently related to age or branch order of the stecklings. In contrast to stecklings of hedge origin, primary and secondary branch positions of seedling origin did not produce any orthotropic shoots from the stem but only from the callus.

Topophytic effects on several other variables (final rooting percentage, mean rooting date, basal stem diameter and stem taper) also tended to be greater among stecklings from hedges, than among stecklings from seedlings. This provided further support for the concept that topophytic effects were more pronounced or more persistent in more mature donor material.

Variation in developmental age among clones (some clones may mature more rapidly than others) might explain the significant interaction between clone and branch position in *Table 2 a, b*. Clones that mature more rapidly would pesumably show more pronounced topophytic effects than clones maturing more slowly.

From this study, it becomes clear that the concept of a clone requires careful interpretation. The development of rooted cuttings from a tree will be influenced by developmental age, and by branch order within the crown. To account for the differences among branch orders we encourage the use of the term topoclone for young stecklings exhibiting different characteristics. However, it is possible that at least some of these differences due to position will gradually disappear with time, as expression of the clone's genetic potential assumes more importance.

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Clarification of the Term Topophysis

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Summary

The term topophysis is commonly used to refer to vegetative propagules that maintain the branch-like growth habit they had as shoots on the ortet.

A definition is presented that is believed to provide a preferred use of the term. According to this definition topophysis refers to states of differentiation of meristems on the ortet that vary according to the hierarchical order of the meristem within a branched system. This definition gives topophysis a developmental meaning comparable to that of cyclophysis. Furthermore, it avoids confusion by more precisely defining the meaning of position.

Key words: topophysis, cyclophysis, ortet, ramet, plagiotropic growth, branch order.

Zusammenfassung

Der Begriff „Topophysis" wird allgemein in Bezug auf vegetativ vermehrte Pflanzen benutzt, die ihren astartigen Wuchs aufrechterhalten, den sie bereits als Trieb an „Ortet" hatten.

Der Begriff wird so definiert, daß eine bessere Anwendung ermöglicht werden soll. Die Definition bezieht sich auf den Zustand von Meristemdifferenzierungen am Mutterbaum, die in Übereinstimmung mit der hierarchischen Ordnung der Meristeme in einem Astsystem sind. Die Definition gibt dem Begriff „Topophysis" eine entwicklungsmäßige Bedeutung, vergleichbar mit dem der „Cyclophysis". Weiterhin werden Verwechslungen vermieden, wenn die Bedeutung der Position am Ortet präziser beschrieben werden soll.

The recent surge in interest on vegetative propagation of trees has brought with it the realization that considerable phenotypic variation may occur among vegetative propagules from the same ortet. Although awareness of the problem is increasing, documentation of these phenomena is not new. The so-called "retinospora" forms of some members of the Cupressaceae have been attributed to juvenile characteristics in the ortet, persisting throughout the life of the ramet (BEISSNER, 1930). In many species, basal regions of the ortet retain juvenile characteristics as the more distal regions mature. Ramets derived from the basal tissue will proceed through a life cycle from juvenile to mature, whereas ramets from the distal tissue will miss juvenile stages of their life cycle. Also, persistent plagiotropic growth of rooted lateral branches exemplified by the classical studies of VÖCHTING (1904) on *Araucaria excelsa*, illustrate the variation in phenotypic expression that may arise in rooted cuttings from different branch orders of the same ortet. Terminology has been applied to these phenomena. SEELIGER (1924) applied the term *cyclophysis* to de-

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