Journal of Research 20C, 204—211, (1942). —— Fortainer, E. J. and Jonkers, H.: Juvenility and maturity of plants as influenced by their ontogenetical and physiological ageing. Acta Horticulturae 56, 37—44, (1976). —— Girouard, R. M.: Vegetative propagation of spruce. Bi-monthly Research Notes 26 (4), 41, (1970a). —— Girouard, R. M.: Rooting plain and heel cuttings of spruce. Plant Propagator 16 (1), 7—21, (1970b). —— Girouard, R. M.: Rooting plain and heel cuttings of spruce. Commonwealth Forestry Review 50, 28—31, (1971). —— Girouard, R. M.: Variation in rooting ability of stem cuttings from clones of a superior white spruce provenance. Bi-monthly Research Notes 28 (6), 40—41, (1972). —— Girouard, R. M.: Propagation of spruce by stem cuttings. New Zealand Journal of Forestry Science 4, 140—149, (1974). —— Girouard, R. M.: Seasonal rooting response of Norway spruce stem cuttings. Plant Propagator 21 (3), 9—10, (1975). —— Hill, S. R. and Libby, W. J.: Outdoor Rooting of *Pinus radiata*. The Plant Propagator 15 (4), 13—16, (1969). —— Hood, J. V. and Libby, W. J.: Continuing Effect of Maturation State in Radiata Pine and a General Maturation Model. In: Propagation of Higher Plants Through Tissue Culture. Proc. Int. Symp. Univ. Tennessee, Knoxville, April 16—19, 1978, (1978). —— Kleinschmit, J.: Problems of vegetative reproduction. Paper, Third FAO/IUFRO World Consultation on Forest Tree Breeding, (1977). —— Larsen, C. M.: The seasonal variation in the national rooting capacity of cuttings of Norway spruce and Sitka spruce. Silvae Genetica 4, 69—80, (1955). —— Lepistö, M.: Successful propagation by cuttings of *Picea abies* in Finland. New Zealand Journal of Forestry Science 4, 367—370, (1974). —— Lepistö, M.: Vegetative propagation by cuttings of *Picea abies* in Finland. In: Vegetative propagation of forest trees-physiology and practice. pp. 87—95, Stockholm, Swedish University of Agricultural Science, (1977). —— Olesen, P. O.: On transmission of age changes in woody plants by vegetative propagation. Arsskrift, Kongelige Veterinaer-og Landbohojskole, pp. 64—70, (1973). —— Olesen, P.O.: On cyclophysis and topophysis. Silvae Genetica 27, 173—178, (1978). —— Power, A. B. and Dodd, R. S.: Early differential susceptibility of juvenile seedlings and more mature stecklings of *Pinus radiata* to *Dothistroma pini*. New Zealand Journal of Forestry Science 14 (2), 223—8 (1984). —— Rauter, R. M.: Rooting of *Picea* cuttings in plastic tubes. Canadian Journal of Forest Research 1, 125—129, (1971). —— Roulund, H.: The effect of cyclophysis and topophysis on the rooting ability of Norway spruce cuttings. Forest Tree Improvement. Arboretet Horsholm 5, 21—41, (1973). —— Roulund, H.: Comparative study of characteristics of seedlings and clonal cuttings. New Zealand Journal of Forestry Science 4, 378—386, (1974). —— Roulund, H.: The effect of the cyclophysis and the topophysis on the rooting ability and behaviour of Norway spruce cuttings. Acta Horticulturae 54, 39—50, (1975). —— Roulund, H.: Vegetative propagation of forest trees at the Arboretum in Horsholm, Denmark. In: Vegetative propagation of forest trees—physiology and pracjoint meeting of working parties on Norway spruce provenances and Norway spruce breeding. Buchaarest, Romania, pp. 174—185, tice. pp. 103—128. Stockholm, Swedish University of Agricultural Science, (1977). —— Roulund, H.: A comparison of seedlings and clonal cuttings of Sitka spruce (*Picea sitchensis* (Bong.) Carr.) Silvae Genetica 27, 104—108, (1978). —— Roulund, H.: Topophysis studies on cuttings of Norway spruce. In: Proceedings of the IUFRO (1979a). —— Roulund, H.: Stem form of cuttings related to age and position of scions (*Picea abies* L. Karst.). Forest Tree Improvement, Arboretet Horsholm 13, 1—24, (1979b). —— Roulund, H.: Problems of clonal forestry in spruce and their influence on breeding strategy. Forestry Abstracts, Oct. 1981, 42 (10), 457—471, (1981). —— Schaffalitzky de Muckadell, M.: Investigations on aging of apical meristems in woody plant and its importance in silviculture. Forstlige Forsogsvaesen i Danmark 25, 311—445, (1959). —— Thimann, K. V. and Delisle, A. L.: Notes on the rooting of some conifers from cuttings. Journal of the Arnold Arboretum 23, 103—109, (1942). —— Tufuor, K.: Comparative growth performance of seedlings and vegetative propagules of *Pinus radiata* (D. Don) and *Sequoia sempervirens* (D. Don). Ph. D. Thesis, University of California, Berkeley, (1973). —— von Wühlisch, G.: Propagation of Norway spruce cuttings free of topophysis and cyclophysis effects. Silvae Genetica 33 (6), 215—219, (1984). —— Werner, M.: Present methods of propagation in Norway spruce and future aspects. In: Proceedings of the IUFRO joint meeting of working parties on Norway spruce provenances and Norway spruce breeding. Bucharest, Romania, pp. 117—128, (1979).

Clarification of the Term Topophysis

By R. S. Dodd and A. B. Power*)

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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-

*) University of California, Berkeley, Forest Products Laboratory, 1301 South 46th Street, Richmond, California 94804, USA

scribe the effects of life cycle stage on meristematic potential. MOLISCH (1922) used the term *topophysis* to explain the differences observed by Vochting when cuttings from terminal shoots were compared with those from first and second order laterals. A third term, *periphysis*, has been used to refer to the effects of the environment in pre-conditioning tissue (HALLÉ *et al.*, 1978).

Although each of these had specific meanings to the authors, over the years use of the terms has become confused. OLESEN (1978) made a major contribution by drawing attention to the confusion that existed in the literature over the terms *cyclophysis* and *topophysis*. He proposed two definitions to clarify the distinction between these two terms: "Cyclophysis: the process of maturation of the apical meristems. Topophysis: the phenomenon that scions, buddings and cuttings for some time after grafting, budding or rooting maintain the branch-like growth habit they had as shoots on the ortet."

We fully support the definition proposed by Olesen for *cyclophysis*, but we feel that his definition of *topophysis* requires estatement for the following reasons.

1. *Topophysis* should not be confined to phenomena in detached shoots as suggested by the definition. The developmental processes that give rise to topophytic effects take place in the intact plant, but are demonstrated by their persistence in detached parts.

2. Since the term *topophysis* refers to the nature of the plant in relation to position (Gr. *topos:* place; *physis:* nature), it should not necessarily be confined to growth habit characteristics. In conformity with the definition of *cyclophysis, topophysis* should refer to any morphological, anatomical and physiological differences that result from positional influences, and that are maintained in detached shoots.

3. Position requires precise definition. Reference to branch-like growth habit is too vague, and does not adequately separate cyclophytic and topophytic effects, since branch habit may be modified during maturation of the tree (see branch angle differences between trees of different maturation levels, BOLSTAD and LIBBY (1982)). Since the study by VÖCHTING, which prompted introduction of the term *topophysis* by MOLISCH, was based upon cuttings from first and second order laterals, it would appear to be appropriate to define position as being the rank order of shoots.

To overcome these objections, we propose that the following definition of *topophysis* should be used in the future.

Topophysis: a state resulting from differentiation in developmental and physiological potential of apical meristems among branch hierarchical orders, independent of the processes of maturation of terminal meristems.

Results of a study that support the concept of topophytic differences based upon branch hierarchical position are reported elsewhere (POWER, DODD and LIBBY, 1985). From these results, and from previous unpublished observations, the authors conclude that the development of shoots (whether it is rooting, stem form, or shoot growth) after detachment from the tree, varies according to the maturation level of the shoot, and also with the branch order position from which the cutting was taken. The results further indicate that within the ortet, the processes of cyclophysis and topophysis interact, such that with increasing maturation of the ortet the degree of differentiation among branch order positions becomes more pronounced.

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References

BEISSNER, L.: Handbuch der Nadelholzkunde. 3rd Ed. Paul Parey, Berlin, 765 pp., (1930). — BOLSTAD, P. V. and LIBBY, W. J.: Comparisons of Radiata pine cuttings of hedge and tree-form origin after seven growing seasons. Silvae Genetica **31** (1), 9—13, (1982). — HALLÉ, F., OLDEMANN, R. A. A. and TOMLINSON, P. B.: Tropical trees and forests. An Architectural Analysis. Springer-Verlag, (1978). — MOLISCH, H.: Pflanzenphysiologie als Theorie der Gärtnerei. Jena, 5th Ed., (1922). — OLESEN, P.: On cyclophysis and topophysis. Silvae Genetica **27** (5), 173—178, (1978). — POWER, A. B., DODD, R. S. and LIBBY, W. J.: Cyclophysis and topophysis in coast redwood stecklings. I. Rooting and Nursery Performance. Submitted to Silvae Genetica, (1985). — SEELIGER, R.: Topophysis und Zyklophysis pflanzlicher Organe und ihre Bedeutung für die Pflanzenkultur. Angew. Bot. **6**, 191—200, (1924). — VÖCHTING, H.: Über die Regeneration der *Araucaria excelsa*. Jb. Wiss. Botan. **40**, 144—155, (1904).

C Effects and Second Generation Clone Performance in Picea sitchensis and Pinus contorta

By M. G. R. CANNELL, L. J. SHEPPARD and C. M. CAHALAN*)

Institute of Terrestrial Ecology, Bush Estate,
Penicuik, Midlothian EH26 0QB, Scotland

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Summary

Clonal variation in 5-year heights was partitioned into genetic and C effects by two-generation cloning, where the first generation was grown in two contrasting environments.

Four clones of each of 5 provenances of *Picea sitchensis* and *Pinus contorta* were propagated from 14 to 15-year-old trees and grown for 5 years at an upland and a lowland site. Second-generation clones were then grown for 5 years at the lowland site. There was no evidence for C effects on 5-year heights in the second generation attributable to the upland and lowland environments of the first generation mother trees.

The second-generation clones grew equally as well as the first generation clones, suggesting that maturation was arrested by repropagation.

*) Department of Forestry and Wood Sciences, University College of North Wales, Bangor, LL57 2UW, Wales, Great Britain