



The factors that control this process are very likely different from those that control the process of maturation in the apical meristems, and cyclophysis should, therefore, not be included in the term topophysis. There is some evidence of interaction between these two sets of factors (the more advanced the process of maturation the longer the period of plagiotropic growth), but this is not a reason for including one in the other.

There is no doubt that Molisch included what we now term cyclophysis in topophysis, as he mentions that cuttings from the flowering zone have a particularly strong tendency to the formation of flowers, but it must be remembered that the concept 'cyclophysis' had not been defined in 1915. It was not done until 1924 by SEELINGER, who considered the two concepts to be identical. His standpoint, however, was rejected by BÜSGEN and MÜNCH (1927) and by SCHAFFALITZKY (1959). However, some authors, f.ex. WAREING (1959), believe that the two processes are closely related although not identical. So, this is the key point as to whether cyclophysis is to be included in the term topophysis or not, and it will be considered briefly later.

3. *Periphysis*. This term is introduced "to cover the qualities occasioned by environment", SCHAFFALITZKY (l.c.). In contrast to this, WRIGHT (1976) defines periphysis as "A form of topophysis in which effects due to position in tree are transmitted through a cutting or graft." — This so-called position effect is quite clearly defined by SCHAFFALITZKY and other authors as topophysis, whereas periphysis is due to factors outside the tree, i.e. the environment. As an example of periphysis SCHAFFALITZKY writes on page 322: "It is a well-known fact that some years may pass before a young beech plant grown in heavy shade will recover and form sun leaves when it is suddenly moved to a locality with full light . . . this example of periphysis thus manifests itself as a certain aftereffect caused by previous conditions."

I would like to recommend the definition given by SCHAFFALITZKY.

#### Reflections on cyclophysis and topophysis

Cyclophysis plays an important part in vegetative propagation as scions, buds or cuttings are often taken from older trees, i.e. from ortets with more or less matured apical meristems. This will influence the ramets as to for instance flowering, bark type, and wood characteristics. But what causes the process of maturation, and what happens in the apical meristems? Our answers are very limited, but the changes are not a question of age — although we often talk about 'age changes' — because age as such cannot affect anything. This view is supported by an investigation by LONGMAN and WAREING (1959), who found that *Betula verrucosa* could be forced to produce catkins before the age of one year by constant growth under long-day or continuous illumination in a green house at approximately 15–25° C. This forced maturation was permanent, as scions from flowering branches of the seedlings often initiated catkins in the following season after wintering outside, whereas juvenile tissue never does. LONGMAN and WAREING concluded "that the onset of flowering depends upon the attainment of a certain size, though how this 'size-factor' is operative remains obscure."

Also SCHAFFALITZKY (1959) touches on the idea that growth rate might be a cause of the maturation of the apical meristem. He mentions the fact that low branches of *Fagus sylvatica* retain their dead leaves in the winter on the innermost parts of the branches nearest the stem even after

the time when the rest of the crown (including the outermost parts of the lowest branches) has entered the adult phase and sheds the dead leaves in winter. As the apical meristems derive from the original apical meristem of the embryo through continual mitotic divisions, it may be stated that all the apical meristems of a tree have the same age (with the exception of apical meristems derived from adventitious buds), and therefore, it could be expected that the beech after a certain age would stop retaining the dead leaves in winter on all branches. But as this is not the case, SCHAFFALITZKY interprets the phenomenon as "... a delayed transition of the interior lower branches to the leafless stage caused by their slow growth." Several more investigations (review by ZIMMERMAN, 1972) support the theory that the process of maturation is dependent on or correlated with the growth of the plant, and so do more recent papers by BORCHERT (1976), FORTANIER and JONKERS (1976), HACKETT (1976), and ROMBERGER (1976).

This theory can also explain why trees trained as hedges remain in the juvenile stage much longer than normal as reported by LIBBY, BROWN and FIELDING (1972) and LIBBY and HOOD (1976), because only the innermost of low branches are left after training trees as hedges. Also formation of adventitious buds from the lower stem, that is from tissue formed by a cambium derived from a young apical meristem, leads to the formation of juvenile shoots, cf. OLESEN (1973). Also shoots from dormant buds, which are characterized by particularly slow growth, belong to the juvenile phase. By continual clipping of pine hedges more and more shoots are formed from fascicle meristems. Thus, LIBBY, BROWN and FIELDING (l.c.) reported that all shoots on four to six-year-old *Pinus radiata* hedges clipped annually to waist height, originated from fascicle meristems. These meristems, too, represent the juvenile form, as only a moderate growth or relatively small number of cell divisions precede the formation of these fascicle meristems. Strictly speaking, if the theory is sufficient, no part of the plant can enter the adult phase within a certain distance from the base of the tree. However, the truth may not be as simple as that.

The hypothesis that the total growth is a deciding factor for the process of maturation in woody plants is supported in other ways, too. For instance, DORMLING (1976) finds that grafts taken from the lowest branches of *Picea abies* have the poorest flowering, whereas the top branches produce grafts with the best flowering. Likewise, ROULUND (1975) found that the rooting ability of *P. abies* cuttings is better the lower the cuttings are taken. Both observations indicate that the apical meristems of the shoots are less matured the lower in the crown they are placed. This fits in with the above mentioned hypothesis, as the total growth behind the apical meristems is smaller the lower in the crown they are placed. The process of maturation is supposed to be most advanced in the apical meristem of the terminal leader, as this shoot normally will have had the biggest total growth behind it. The apical meristems of the top whorl are supposed to be the second most matured ones. They are derived from the apical meristem of the terminal leader within the latest year. At the time of their formation they are supposed to have had the same degree of maturation as the apical meristem of the terminal leader. Since then the top whorl has normally growth slightly less than the terminal leader, and this would, according to the hypothesis, result in a slightly less advanced maturation of the apical meristems of the top whorl than that of the terminal leader. The apical meristems of the second

whorl from the top are supposed to be the third most matured ones, and so on down through the whorls.

The process of maturation is apparently not dependent on age, but with age something happens which affects this process, and it seems that growth (or may be number of cell divisions of the apical meristem, ROBINSON and WAREING, 1969) better than age reflects the factors\* which control the maturation process. If this is correct, the following working hypothesis may be deduced: *The process of maturation is unequally advanced in the apical meristems of a tree, and is positively correlated with the total growth behind each apical meristem* (or with the number of cell divisions of these). That the process of maturation is unequally advanced within a tree seems to be certain and has been reported by many authors.

When the above hypothesis is applied to ROULUND's (1975) results, we come to a conclusion slightly different from his. ROULUND supposes that the differences in level between the lines in figure 1 are due to cyclophysis; as to this I agree. But, that the gradients of the lines are due to topophysis is questionable. The fact that the rooting ability is better the lower the cuttings are taken is more likely due to the lower branches' slower growth and, with this, their less advanced maturation compared with that of the branches higher in the tree. This means that probably also the gradients are a result of cyclophysis. This does not disprove that topophysis may play a part in this, but I see no evidence for such an explanation.

This brings us to the discussion of topophysis, but first a few examples.

At the Arboretum at Hørsholm it is normally found that grafts of *Picea abies* continue the growth habit of branches for a few years before they change to orthotropic growth, whereas grafts of *Abies nobilis* from 1954 still grow like side-branches. They have also experienced great individual differences within species, for instance with *Pseudotsuga menziesii* of which some grafts have adjusted in only a few years' time while other genotypes retain the side-branch character for many years. Furthermore, some individuals with a side-branch character flower few years after being grafted, which is several years before seed-

lings of the same age would flower. Thus, such ramets are affected by both cyclophysis and topophysis, as the flowering according to our definition is a result of cyclophysis and the side-branch character a result of topophysis. Whether these two effects are independent of one another will be discussed in the following.

Cyclophysis is by definition changes in the apical meristems as to the process of maturation. These changes are likely to be due to changes of both gene pattern and the gene activity. (By changes of the gene pattern is understood that all genes are not functioning at the same time and that the combination of these active genes varies with age, i.e. a qualitative change. By changes of gene activity is understood that active genes may be more or less active, i.e. a quantitative change, which may well explain the gradual changes that happen with age.)

Unlike cyclophysis, topophysis is not a change of the process of maturation, but an influence that decides which position the shoot will take up in relation to other shoots of the tree, an influence that may last for many years after the shoot has been grafted or rooted. The factors that decide the position of a shoot are not known for sure, but it is supposed that auxin plays a decisive part, ZIMMERMANN and BROWN (1974, p. 151). A change in the hormone balance will influence the gene activity and perhaps the gene pattern too, but nothing indicates that it influences the genes that are involved in the process of maturation. For instance, apical control (leading to plagiotropic growth of lateral branches) is found in all conifers irrespective of their being in the juvenile or mature phase, and when a tree has reached the mature phase, the flowering is not a question of apical control. Also the apical meristem of the terminal leader matures although it has never been exposed to apical control by any other bud or shoot. Furthermore, cyclophysis is rarely a reversible process, whereas topophysis normally is. For example, grafts and cuttings from mature ortets of *Pinus sylvestris* keep the adult form as to bark (OLESEN, 1973) and grafts of mature *Fagus sylvatica* flower willingly after drought treatment (HOLMSGAARD and OLSEN, 1966). Similar observations as to the ability to flower when the ramet originates from a mature ortet have been reported by many authors, and it may well be asked whether true rejuvenation as to the process of maturation can be obtained by normal grafting, budding or cutting, DUNBERG (1977). In contrast to this, the effect of topophysis normally lasts a few years whereafter the ramet develops into a normal plant, and it is questionable whether any effect of topophysis is then left in the plant. The factors which cause the topophysis effect seem to be different from those causing the cyclophysis effect, and therefore cyclophysis and topophysis are supposed to be two different processes in the sense I have defined these terms. This does not mean that topophysis does not affect flowering; on the contrary, I believe it does, but I also believe that we have to distinguish between two sets of factors in connection with flowering. 1) One set which affects the process of maturation and, as explained above, I don't believe topophysis plays a role in this process. 2) Another set which may provoke the flowering after a certain degree of maturation is attained, and this provocation seems to take place the easier the more advanced the process of maturation. The provocation also seems to be dependent on an interplay between several factors such as nutritional state of the shoot, water stress, temperature, and, with special interest in this connection, the position of the shoot in relation to the rest of the crown.

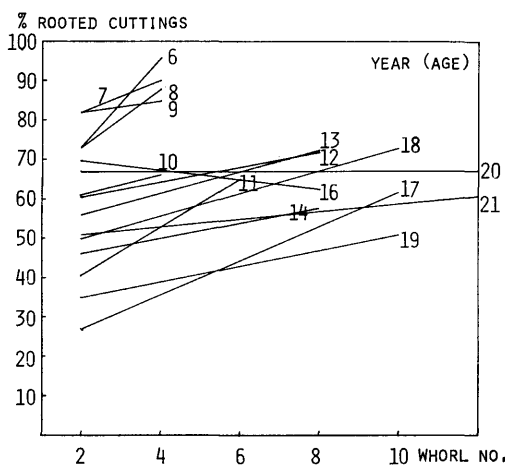


Figure 1. — The dependence of rooting percentage of cuttings on whorl number of ortet for 6–21-year-old ortets. According to ROULUND (1975) the figure shows: "The effect of topophysis (gradient) and cyclophysis (level). Mean of each age group."

\* These factors are not known, but have been the subject of much discussion. Among the more recent reviews the reader is referred to SAX (1962), DOORENBOS (1965), ZIMMERMAN (1972), HACKETT (1976), ROMBERGER (1976), and WAREING and FRYDMAN (1976).

So far, it is mainly changes of the apical meristem that have been discussed. However, changes of the lateral meristem, of which the cambium is the most important in this connection, are also of importance, as the xylem derives from this.

The cambium in the very first terminal leader is derived from a one-year-old apical meristem; the cambium in the twentieth terminal leader from a twenty-year-old apical meristem, etc. This means that the lower part of the stem is formed by a cambium originating from a juvenile apical meristem, whereas the upper part of the stem is formed by a cambium originating from a matured apical meristem. This explains why the lower part of the stem remains in the juvenile stage even after the upper stem has reached the adult phase. Apparently the process of maturation of the apical meristems is different from that of the cambium since this remains juvenile as to certain characters even for hundreds of years. The phenomenon, that the upper, younger parts of a tree are in the mature phase while the lower, chronologically older parts retain juvenile characters, is called a 'puzzling situation' by BORCHERT (1976). However, if one considers the maturation process of the apical meristems, of which the various parts of a tree are derived, the situation is straight forward, because all mature parts are derived either directly from a matured apical meristem or from a cambium derived from a matured apical meristem, and vice versa OLESEN (1973). BORCHERT also calls the attention to the increasing complexity of growing trees and believes that this can explain many of the morphological and physiological changes related to what he terms 'physiological aging\*'). I believe that the increasing complexity of growing trees strongly affects what I have termed topophysis, but I don't believe that it has much influence on what I have termed cyclophysis. For example, grafts and cuttings of aged *Pinus sylvestris* ortets are easily provoked to flower, and they all produce the adult bark type typical of the upper stem of the ortets whatever the scions or cuttings are taken from the terminal leader or from 1st., 2nd, or 3rd order shoots. Furthermore, ROBINSON and WAREING (1969) have demonstrated the following phase change: Stem tips of young seedlings of *Ribes nigrum* were rooted. After some growth the tips of these 1st. cycle cuttings were rooted again, and so on. After the 3rd, and 4th rooting cycle, the cuttings flowered. In other words, the cuttings eventually matured after a certain growth, although they never reached any large size or high degree of complexity.

An example of phase change of a derivative of the lateral meristem is the change in bark type with increasing height; this is clearly seen with *Pinus sylvestris*. It may be claimed that the change of bark type with height not is a result of cyclophysis, but for example a result of increasing water stress. However, such a theory is not valid, as vegetatively propagated *Pinus sylvestris* always develop the characteristic adult bark type also in their lower stem when propagated from aged ortets. Similar observations with *P. radiata* are recorded by FIELDING (1970). Nor is the above-mentioned difference in bark type due to changes of the lateral meristem of the scion or cutting while still a part of the ortet, as the scion is less than one year old at the time of clipping. As, however, the bark is derived from the lateral meristem, the adult phase must have been trans-

mitted to the scion or cutting in some other way; probably from the apical meristem to the cambium when the latter was derived from the former. Thus, it is supposed that age changes of certain characters which take place in the upper stem or crown only are a result of the process of maturation of the apical meristems. So, when ramets from mature ortets show the adult type of bark and wood characteristics in their lower stem, it is an effect of cyclophysis only, OLESEN (1973 and 1977).

## Discussion

The previously mentioned definitions and hypotheses I would like to discuss in connection with a paper by NICHOLLS, PAWSEY and BROWN: "Further studies on the ortet-ramet relationship in wood characteristics of *Pinus radiata*" (1976).

In an earlier publication NICHOLLS and BROWN (1971) define 'topophysis' as: when cuttings or grafts "... retain the characters of that part of the shoot (i.e. position on the tree) from which they arise." Thus it seems as if they include cyclophysis in the term topophysis.

1. *Spiral grain and average tracheid length.* NICHOLLS PAWSEY and BROWN have found that the development of wood characteristics such as spiral grain and average tracheid length with increasing ring number from the pith is similar in the upper stem of ortets and at breast height of ramets. They explain this as a result of topophysis or a result of topophysis and cyclophysis. As mentioned in the preceding section, I consider wood characteristics typical of the upper stem of ortets which reappear at the lower stem of ramets a result of cyclophysis only.

2. *Tracheid length.* One could also try to imagine theoretically how a possible effect of topophysis would influence tracheid length. Investigations by JACKSON (1959) and PANSHIN and DE ZEEUW (1970) show that the tracheid length of the first formed secondary xylem of the first incomplete annual ring is the same in branches and stem of the same internode. Thus, in scions or cuttings less than one year old one starts off with an average tracheid length like the one of the first incomplete annual ring of the ortet, and this is according to investigations by BISSET and DADSWELL (1949), HATA (1949), Queensland Forestry Department (1958), JACKSON (1959), and DINWOODIE (1963) relatively constant through the whole length of the tree. So, we can except to find, both in ortets and ramets, more or less the same tracheid length in the first annual ring round the pith. The tracheid length now increases with increasing ring number, but the increase is normally more rapid higher in the stem (up to a certain height) than in the lower bole. This phenomenon is supposed to be due essentially to cyclophysis and can have no connection with topophysis as we are talking about the variation within the stem of an ortet. An effect of topophysis as to tracheid length in ramets would be tracheid lengths similar to those found in branches, i.e. shorter tracheids in ring number two and outwards than in corresponding rings in the stem of the ortet, as the tracheid length increases more rapidly in the stem than in the branches. But this branch characteristic does not reappear in the ramets; on the contrary, NICHOLLS, PAWSEY and BROWN found longer tracheids at breast height in the ramets than in the ortets at this height. The tracheids at breast height in the ramets were as long as in the upper stem of the ortets, thus (following my hypothesis) a result of cyclophysis. If one includes cyclophysis in the term topophysis, it is of course correct to call the phenomenon an effect of topophysis, but as the phenomenon presumably entirely is a

\*) "physiological age" ... is used whenever reference is made to a particular development stage or phase as manifested by the presence of phase-specific characters." BORCHERT (1976).

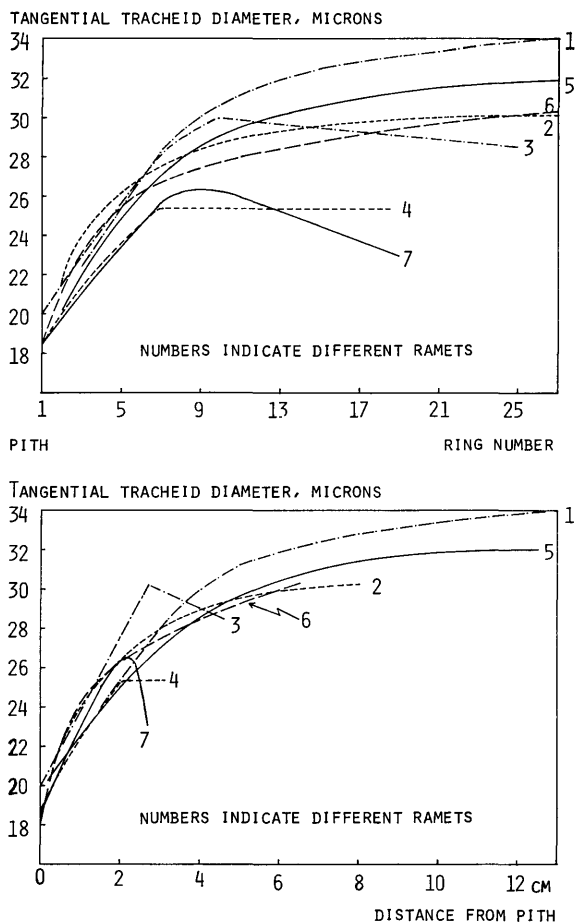


Figure 2. — The interrelation between average tangential tracheid diameter at breast height and (1) ring number, and (2) distance from pith for seven different ramets of the same clone. The average tracheid width is calculated from two (ramets No. 3 & 4), three (ramets No. 1 & 2), or four (ramets No. 5, 6 & 7) increment cores per ramet taken in different compass directions.

result of the maturation of the apical meristems, I find this terminology unfortunate.

3. *Ring number as independent variable.* To illustrate this topic NICHOLLS, PAWSEY and BROWN's discussion of the effect of cyclophysis and topophysis on minimum density will be used.

NICHOLLS, PAWSEY and BROWN do not include the variation in ring width in their discussion of minimum density although it is striking how the curves for minimum density almost show a reverse picture of the curves for ring width. Now, the density is mainly dependent on tracheid diameter and cell-wall thickness of which only the tangential tracheid diameter will be considered in the following. The existing literature unanimously shows that the tangential tracheid diameter increases with increasing ring number or distance from the pith until a relatively constant size is reached in the adult wood. On the other hand we know little of how the tracheid diameter develops in the juvenile wood at different growth rates, in other words whether the tracheid diameter is dependent on the distance from the pith, ring number, or some other factors. To throw some light on the question I have investigated the increase in tangential tracheid diameter with 1) increasing ring number and 2) increasing distance from the pith within a clone of *Picea abies*. The material originates from clone V525 at the Arboretum, Hørsholm. This clone was propagated by cuttings in 1941/42 and transplanted in 1943 in the Arbo-

retum at 1 × 1 m and 2 × 2 m respectively, in two adjoining plots. In November 1977 increment cores were taken from the thickest trees and from co-dominant and suppressed trees. The average tracheid width is calculated from 100–150 earlywood tracheids of ring Nos. 1, 2, 3, 5, 7, 10, 15, 20, 25, and 27 (the last annual ring at breast height). The result of this pilot study is shown in fig. 2. It is seen that the average tracheid width varies considerably between ramets, especially for the same ring number, but also for the same distance from the pith, even that the ramets all are of the same genotype and growing on the same site. Thus, neither the ring number nor the distance from the pith reflects satisfactorily the factors which control the average tracheid width. Therefore, none of the two measures is applicable independent variables in a comparative study of the effect of cyclophysis and topophysis on average tracheid width. And, as the minimum density most probably is markedly affected by the tracheid width, it means that nor is the ring number an applicable independent variable when comparing minimum densities, especially when the ring widths vary as much as in NP&B's material.

Neither ring number nor distance from the pith as such can influence any wood characteristic, and therefore the condition of using such factors as independent variables in comparative investigations must be that they reflect (at least partly) one or more of the factors actually affecting the dependent variable. Therefore, I would like to draw the attention to the often uncritical use of ring number as independent variable within wood technology. Ring number is an excellent abscissa in graphs showing the variation of a wood property along a stem's radius, but such a picture does not always reflect a causal interrelation. If such a causal interrelation does not exist, or if it is very weak, the ring number cannot be used as independent variable in comparative investigations.

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## Zur Stecklingsvermehrung bei *Nothofagus procera* (Poepp. et Endl.) Oerst

Von A. BECKER<sup>1)</sup> und H. DAUTZENBERG<sup>2)</sup>

(Eingegangen Mai 1978)

### Zusammenfassung

Der an sich wünschenswerte Versuchs-anbau mit *Nothofagus procera* wird durch Schwierigkeiten der Saatgutbeschaffung und eine empfindliche Jugendphase der Baumart erschwert. Ein Ausweg besteht in der vegetativen Vermehrung durch Stecklinge. Anhand der Versuchsergebnisse der Jahre 1976 und 1977 im Gewächshaus Burgholz wurde dargestellt, daß die vegetative Vermehrung von *N. procera* durch Grünstecklinge unter Sprühnebel mit wirtschaftlich diskutablen Erfolg möglich ist, wenn eine geeignete Steckperiode (etwa 1. Junihälfte) gewählt wird und geeignetes Sprühwasser zur Verfügung steht. Anschlußversuche zur Optimierung des Verfahrens durch Substratwahl, Wuchsstoffbehandlung und Terminierung nach phaenologischen Merkmalen werden empfohlen.

### Summary

The experimental cultivation of *Nothofagus procera* while desirable in itself, is impeded by difficulties in seed-supply and by sensitive juvenile stage. An alternative is to use vegetative propagation by cuttings. Results of trials in 1976 and 1977 in the greenhouse at Burgholz near Wuppertal have shown, that vegetative propagation of *N. procera* by leaf cuttings under mist is possible with economic usefulness, if a suitable planting period (around the first fortnight in June) is chosen and sufficient water for irrigation is available. Experiments aimed at optimising by choosing rooting medium, treatment with growth-regulators and phenological identification of the optimum period are recommended.

**Key words:** *Nothofagus procera*, propagation by cuttings, propagation period, vegetative propagation.

<sup>1)</sup> Landesanstalt für Ökologie, Landschaftsentwicklung und Forstplanung NW, (LÖLF), Recklinghausen.

<sup>2)</sup> Forstbetriebsbezirk Burgholz des Forstamtes Mettmann, Rhld.

### Einleitung

Die bisherigen Anbau-Erfolge mit *Nothofagus procera* in Deutschland und England (HOGREBE 1973, MITCHELL 1975) sowie der Holzwert dieser Baumart (KÖNIG *et al.* 1972, KOZDON 1958, TESDORFF 1963) lassen zumindest weitere Versuchs-anbauten wünschenswert erscheinen (KRÜSSMANN 1977). Hierbei ist der Umstand hinderlich, daß die Beschaffung generativen Vermehrungsmaterials nicht immer ohne weiteres möglich ist.

Es kommt hinzu, daß die Sämlinge der Baumart offensichtlich in der Jugend früh- und winterfrostempfindlich sind. Diese Erfahrung machte im Gegensatz zu der Annahme KRÜSSMANN'S (1938, 1977) schon REINHEIMER (1961); sie wird durch Beobachtungen an einjährigen Sämlingen der Herkunft Las Nabras Prov. Nuble (750—800 m) aus einer norddeutschen Baumschule bestätigt, welche im Winter 1976/77 zu großen Teilen stark zurückfroren und teilweise ganz erfroren. Ältere (8- bis 17jährige) Pflanzen im Anbau-revier Burgholz bei Wuppertal weisen solche Frostempfindlichkeit nicht mehr auf. Die Vermutung REINHEIMERS (1961), daß es sich um eine altersphasenbedingte vorübergehende Erscheinung handelt, scheint berechtigt. Eine mit hohem Risiko belastete Jugendphase ist jedoch, sei sie auch kurz, ein schwerwiegender Mangel einer Baumart, der zur Abhilfe herausfordert. Es lag daher nahe, eine Methode der vegetativen Vermehrung von *Nothofagus procera* zu erarbeiten, um einerseits die Schwierigkeiten der Saatgutbeschaffung zu umgehen, andererseits unter Ausnutzung der bekannten „Cyclophysis-Effekte“ (LYR *et al.* 1967) die frostempfindliche Jugendphase zu überspringen.

### Material und Methode

Seit Sommer 1976 wurden im Gewächshaus Burgholz des Forstamtes Mettmann unter Leitung der LÖLF bisher insgesamt 3230 Stecklinge von zehn 8- bis 17jährigen Mutterpflanzen abgesteckt.