INVESTIGATIONS ON AGING OF APICAL MERISTEMS IN WOODY PLANTS AND ITS IMPORTANCE IN SILVICULTURE

UNDERSØGELSER OVER ALDERSFORANDRINGER I VEDPLANTERNES APIKALE MERISTEMER OG DERES BETYDNING FOR SKOVDYRKNINGEN

BY

M. SCHAFFALITZKY DE MUCKADELL

KØBENHAVN
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Denne afhandling er af Den kgl. Veterinær- og Landbohøjskoles jordbrugsvidenskabelige fagråd antaget til offentlig at forsvares for den jordbrugsvidenskabelige doktorgrad.

København, den 17. oktober 1958.

H. C. Aslyng,
formand for
det jordbrugsvidenskabelige fagråd.

To my father
who taught me
to observe.

CONTENTS

PREFACE

The present studies were made in the period, 1953—58, at the Hørsholm Arboretum of the Royal Veterinary & Agricultural College of Copenhagen. I am extremely grateful to the Director of the Arboretum, C. Syrach Larsen, Dr. agro., for providing excellent facilities and for inspiring discussions of the problems. I am also indebted to my colleagues at the Arboretum and to the technical staff.

Further I wish to thank Professor Carl Mar:Møller, Dr. phil., who made possible and stimulated a continuation of the work during 1955—56 when I was attached to the Forestry Department.

To the Royal Veterinary & Agricultural College I am grateful for a scholarship, which since April, 1957, has allowed me to concentrate on the assessment of the experimental work and on writing the present publication.

The Scientific Foundation of the Danish State (Statens almindelige Videnskabsfond) has repeatedly supported the work by grants, for which I also wish to express my sincere thanks.

K. F. Andersen, M.F., was consulted on statistical questions and Mrs. M. Tovborg Jensen has read my English manuscript and suggested necessary linguistic improvements. I am very grateful for their help and for the support in printing the paper afforded by the Carlsen Lange and Eide legacies.

INTRODUCTION

Studies on tree breeding in *Fagus sylvatica* at the Hørsholm Arboretum encountered one main difficulty when it became clear that only occasional flowering took place in our vegetatively produced plants. Flowering is an all important matter in tree breeding for without flowers no artificial pollination can be made, and in many ways controlled crossing is the basis of breeding work.

This difficulty led to many experiments on a prospective formation of flower buds. We tried the classical methods of horticulture with ringing, girdling, manuring and root pruning, but always with negative results.

Contacts with horticultural research literature, however, called attention to the existence of development stages in woody plants.

Development stages represent separate phases in the ontogenesis from seedling to adult tree. They may be characterized by morphological or physiological features as shape and physiology of leaves, or by occurrence of certain shoot types and types of phyllotaxis. When parts of a tree have passed into a new stage they will usually not reproduce the previous one.

Nearly all research in this field is concentrated upon the juvenile stages, which comprise the specially characteristic development stages in many young woody plants. In many previous papers the above definition of development stages was actually used for juvenile stages. It is however preferable to reserve the latter term for true juvenility, of which the most general character is sterility. It seems illogical to speak of "juvenile" stages for stages commencing late in life.

It is the often striking difference between juvenile and adult characters which has called forth the term "stage". The term is, indeed, applicable to the often so evident qualitative change at the end of juvenility.

Applied to later stages, however, the term seems less suitable, because the changes, if any, are much more gradual. The natural and logical wish to fix stages of puberty, adolescence, maturity and senility seems to lead to rather speculative and poorly defined development stages. Further it should be realized that in many woody plants even the juvenile stage may be poorly established and therefore difficult to distinguish from the succeeding stage.

In order clearly to incorporate also these gradual and less obvious changes, the expression, *aging of apical meristems in woody plants,* is used in the title of the present paper.

The existence of development stages must be based upon certain changes in the apical meristems with age. After transition from one stage to the following, meristems possess specific qualities which they did not have earlier.

Hence in this paper existence of development stages and occurrence of meristematic aging will be regarded as two different modes of expression for exactly the same phenomenon.

Already at this point attention should be called to a phenomenon of fundamental importance in the present account: When the upper part of a tree has reached the adult phase, the lower part still remains in a juvenile stage. This will be termed the *juvenile zone* and is characterized either by still showing features of the juvenile type, or by the ability to reproduce these by stooling or pruning.

Many of the obvious differences in the habitus of young trees as opposed to old, are largely due to influence of environment. However, scattered throughout the literature is evidence to support the view that the meristems actually change during the ontogenesis of the plant.

Chapter I of the present paper deals with this literature; the account has the character of historical review. To give a practical survey of the material it is divided into subject sections. The division seems reasonable, also because of the often periodical discussion of the topic.

The botanical nomenclature is in accordance with Rehder (1947). A few species, not included in his work, were checked after *Jackson* (1946).

Chapter I

EARLIER INVESTIGATIONS

1. Clonal Senility.

Curiously enough, the oldest literature on ontogenetic development in woody plants takes up an aspect of our problem, which in a way is the most difficult of all — the question of senility in fruit tree varieties.

It is well-known that for instance apple and pear varieties are clones propagated vegetatively, usually by grafting. *Knight* (1795) was the first to suggest that by repeated vegetative propagation the lifetime of a fruit tree was prolonged unnaturally. He maintained that the vigour of the grafted clones will gradually decline until finally senile decay becomes more and more evident through severe attacks from diseases such as cancer. The basis of this view is that the apical meristem not only ages, but even becomes senile. *Knight* expressed this by saying that neither pear nor apple "would vegetate with vigour much, if at all, beyond the life of the parent stock, provided that died from mere old age".

The idea originated from practical gardeners, and it is interesting that *Knight* first believed it to be incorrect. His experiments were actually laid out to prove that it was "a vulgar error". From some of the old, cancered, suspected senile apple clones, he grafted scions on healthy young stocks. When the grafts were one year old he took scions from them and again grafted on other young stocks. He repeated this six times, but much of his material "inherited all the diseases of the parent trees". Although this experiment gives no proof he became convinced "that all efforts, to make grafts from old and worn out trees grow, were ineffectual". In support of the idea of senility in clones he drew attention to the fact that many earlier famous varieties of apple no longer existed; only their names remained.

Knight observed that the wood of the old clones felt "more soft and spongy under the knife, than that of the new varieties" obtained from seed. He grafted scions from two year old seedlings of apple on twenty year old bearing trees and showed that no flowers were produced for nine years. His conclusion is that "every cutting, therefore, taken from the apple (and probably from every other) tree, will be affected by the state of the parent stock". In other words *Knight* believed that a young tree is in a state which is different from that of an old tree.

Knight was aware that scions from bearing branches gave less vigorous grafts than scions from low epicormics. He grafted these two categories of scions from old, *ungrafted* pear trees on the same stocks. His results were, "the former grew without thorns, as in the cultivated varieties, and produced blossoms the second year; whilst the latter assumed the appearance of stocks just raised from seeds, were covered with thorns, and have not yet produced any blossoms".

In the first half of the 18th century the discussion on senility in fruit tree varieties went on, especially in French and German horticultural literature, but no important new view points were brought forward, and no experiments threw new light on the problems. In 1854, however, *Jessen's* prized treatise was published, and it comprised a detailed review of this discussion. He gave a complete translation of *Knight's* paper and supported his views without reservation. Especially he emphazised that many diseases of cultivated plants were conditioned by senile decay. Referring to these diseases he concludes (p. 120): "Ich trage kein Bedenken, bestimmt zu behaupten, dass die Ursache der oben angegebenen Erscheinungen das übermässige Alter oder die über das Maass durch Ableger oder abgetrennte Sprosse verlängerte Existenz der Abkömmlinge einer Samenpflanze ist".

2. *A False Genus.*

The history of the false genus *Retinispora* is an interesting chapter in the studies on development of woody species.

According to *Beissner* (1891, p. 35) the genus *Retinispora* was established by *Siebold* and *Zuccarini* to comprise the Japanese species *Chamaecyparis obtusa* and *Chamaecyparis pisifera.* Very soon dendrologists abandoned this idea and grouped the two species within the genus *Chamaecyparis.* But the *Retinispora* in most dendrological textbooks were kept within the *Cupressineae* as a genus the characteristics of which were acicular foliage, dense ramification, brown-red colour during winter and usually sterility.

Although *Carrière* (1867) still grouped *Retinispora* as a subgenus he was the first to doubt the justice of so doing. He drew attention to the fact that many *Retinispora* did not flower, which made classification difficult, and he actually regarded the subgenus as a temporary group of which the individuals were not identified with certainty. In one case he contributed directly to increased clarity when he stated that in 1850 *Chamaecyparis thyoides var. andelyensis* because of acicular foliage believed to be a *Retinispora,* had been raised from seed of *Chamaecyparis thyoides,* which bears scale-like leaves.

It was *Koch* (1873) who established connection between the *Retinispora* question and the problem of meristematic aging in woody plants. He realized that all *Cupressineae* bear acicular foliage in their first youth, also the species which have earlier been described with scale-like leaves only. "Bei allen Arten", *Koch* says (p. 109), "wo später schuppenförmige Blätter vorkommen, müssen daher 2 besondere Lebensstadien bei jedem Individuum geschieden werden".

Koch set up no *Retinispora* genus and rightly placed some of the so-called *Retinispora* as varieties under various *Cupressinea.* However, he made some errors and was still uncertain where to place a few of the forms with acicular leaves.

Whereas *Carrière* and *Koch* contributed in some degree to an understanding of the origin of certain *Retinispora,* it was *Beissner* (1879 a) who finally placed the last doubtful plants with acicular foliage in their proper genera. Using sowing experiments, he demonstrated that seed of *Chamaecyparis pisifera squarrosa* which had been regarded as a *Retinispora* gave seedlings of *Chamaecyparis pisifera.* The seedlings first developed *squarrosa* — later *plumosa* leaves. In a similar way *Thuja orientalis meldensis* seed gave plants of *Thuja orientalis,* and from seed of *Chamaecyparis thyoides var. andelyensis Beissner* raised a single plant of *Chamaecyparis thyoides,* which for a short period produced acicular leaves like those of *Chamaecyparis thyoides var. ericoides,* also believed to be a *Retinispora.*

Beissner maintained that the former *Retinispora,* now shown to be certain varieties, originated from cuttings of young plants still with acicular foliage. He speaks of the varieties as "jugendlichen durch Stecklinge künstlich fixirten Formen", but no proof of this theory is given. In another paper (1879 b) *Beissner* emphasized the importance to select for cuttings "die kleinen Zweigchen mit kreuzständigen Blättern, welche wir dicht über den Samenlappen finden". In many cases he was not able to fix the varieties, but he believed that final success lay in repeated propagation. Even when he claimed to have fixed some *Retinispora,* it is no proof, as the experiments were too short termed.

Ignorant of *Beissner's* works, *Carrière* (1880) had obtained many of the same results when he reviewed the *Retinispora* situation. It is especially interesting that he states that *Thuja occidentalis Ellwangeriana* originates from seed of *Thuja occidentalis* and not from cuttings of basal branches.

Hochstetter (1880) is completely in accordance with Beissner, and the paper simply repeats the *Beissner* classification of the former *Retinispora.* It appears too that *Beissner* and *Hochstetter* met in 1878 and discussed the question. *Hochstetter* claims to have confirmed the fixation of *Retinispora* by cuttings, but the proof is non-valid as his cuttings are not even one year old. He says that cuttings from two and three year old *Pinus canariensis* and *Pinus pinea* "wachsen leicht an und in der Primordialform verharren".

In his publications, 1879, *Beissner* did not refer to *Carrière* (1867), but he admitted later (1881 a) that already *Carrière* regarded the *Retinispora* as a temporary group only. *Beissner* compared young seedlings still with acicular foliage of *Chamaecyparis thyoides* with *Chamaecyparis thyoides var. ericoides* and found no difference.

Beissner (1881 b) recounts the experience of *Hochstetter* and others that cuttings from young conifers will root more easily than those from old trees. He regards *Cryptomeria japonica elegans* as a "jugendliche Stecklingspflanze von *Cryptomeria japonica*".

In his Handbuch der Coniferen-Benennung (1887) *Beissner* introduced the term *Jugendform* (*juvenile form*). According to *Beissner* a juvenile form within the Cupressineae is an individual of a scale-leaved genus which has kept the acicular foliage of the young seedling. Such juvenile forms must originate from repeated propagation by basal cuttings and not from seed.

It is quite evident that *Beissner* (1888) had noticed the individual variation in progenies from many *Cupressineae,* but he did not consider this variation sufficiently great to be the sole explanation of the origin of the *Retinispora.*

Beyerinck (1890) reviewed the papers by *Beissner* and *Hochstetter,* but believed the variation in duration of juvenility to be due exclusively to influence of external factors. He especially stressed that under poor nutritional conditions in pots, *Pinus Pinea, Pinus canariensis, Chamaecyparis thyoides andelyensis* and others preserved juvenile foliage. He goes so far as to say that "der Verlust der Fähigkeit zur Erzeugung der Hauptform, wie derselbe bei *Retinispora* und ähnlichen Jugendpflanzen vorliegt, muss als ein durch äussere Bedingungen erworbener Character betrachtet werden, welcher, bei vegetativer Vermehrung, erbliche Constanz besitzt".

In his Handbuch der Nadelholzkunde (1891 p. 35) *Beissner* expressed his opinions in the most concise way on the *Retinispora* question. There are, however, no important new observations although here *Beissner* also mentions longer duration of juvenility in pots. The book has many fine illustrations of juvenile versus adult branches within the *Cupressineae.*

Beissner usually published no figures to enable the reader to judge his experiments. However, exact figures were mentioned in a fine example on segregation as regards juvenile period in a small progeny from seed of a *Chamaecyparis pisifera squarrosa* (1899). When seven years old, *twelve* out of *fifteen* plants were normal *pisifera,* whereas *two* had *squarrosa* characters at their base but *plumosa* characters in their tops and the last one was still a typical *squarrosa.*

Although *Beissner* (1900) gives more examples of variation in duration of juvenile stages, it is astonishing that even in his latest important publication (1909) he does not believe that this variation might lead to the perpetual juvenile type. He sticks to the idea of fixation by basal cuttings.

There is no definite proof that *Beissner*'s claim is incorrect, but of late doubts of its probability have arisen.

Woycicki (1954) tried to repeat *Beissner*'s experiments with *Thuja occidentalis* and *Thuja orientalis,* and all his cuttings from seedling shoots with acicular leaves passed into the adult stage.

Also *Passecker* (1954) reported that he without success had tried to fix the juvenile stage of *Thuja orientalis* by propagation of basal cuttings.

3. Terminology.

Although *Beissner* concentrated on the juvenile forms within the *Cupressineae,* he was aware of their existence within other genera.

He (1888) was probably the first to explain the heterophylly of *Hedera Helix* on the theory that this species has a juvenile form with creeping or climbing, non-flowering shoots bearing leaves with three to five lobes. At a greater age upright flowering shoots are formed with entire elliptic leaves.

The latter are propagated by cuttings and called *Hedera Helix var. arborea.* Also *Ficus pumila* has a very different appearance when young because of the small leaves and in *Eucalyptus globulus* the leaf form varies greatly with age. In all these three cases juvenile leaves are intimately connected with sterility.

Goebel (1889) used the term *"Jugendform"* (*juvenile form*) for any plant which bears "Primärblätter" (primary foliage), but contrary to *Beissner* he used the term for young plants which later produced *"Folgeblätter"* (*adult foliage*), i.e. developed into the *"Folgeform"* (*adult form*). *Goebel* referred to *Beissner* and *Hochstetter* as to the method of fixing juvenile forms by basal cuttings, but it is important to notice that *he distinguished between juvenile forms and fixed juvenile forms. Goebel* emphazised the anatomic differences between juvenile and adult foliage, the latter being less adapted to shaded and humid environment.

In his book "Beiträge zur Lehre von der Fortpflanzung der Gewächse" (1897) *Möbius* thoroughly investigated the literature on senility in clones. *Knight*'s and *Jessen's* (l. c.) statements in support of the existence of the phenomenon were sharply criticized, and a number of papers from the last decades of the 19th century were cited, all of which disagreed with *Knight* and *Jessen. Möbius* draws attention to the existence of cultivated plants which have been grown for ages without any signs of senile decay. Note should be made that two of his examples, the cultivated banana and the date palm, are both propagated by cuttings from suckers; the same is largely true of the cultivated figs and olives. The often diseased and stag-headed appearance of the fastigiate Lombardy poplar has often been considered a case of senile decay, but *Möbius* rightly states that it has never been proved. This is also true of weeping willows and cultivated grapes. Also among the apples and pears there seem to be many very old varieties which should have disappeared if the hypothesis of senility in clones was correct.

In the classic work, "Organographie der Pflanzen", *Goebel* (1898—1901) *was the first to give a clear description of the life stages in the ontogenesis of a plant.* Although he mainly concentrated on herbaceous plants which lie outside the scope of this paper, he mentioned some examples from woody species. He gave us many of the terms which are still in use and more or less common to all kinds of plants. Some terms already are mentioned above (*Goebel* 1889).

Goebel states that after germination a plant gradually passes through some juvenile stages (Jugendstadien) before it finally reaches the adult stage (Folgeform). It is often impossible to fix sharp limits between the various juvenile stages, and in many cases the juvenile and adult forms are so much alike that it may even be difficult to distinguish between them. Even when a plant can be characterized as adult, a certain development may still be noted.

When the juvenile and adult stage are very similar and transition from one to the other very gradual, *Goebel* speaks of *homoblastic development.* When each stage is very characteristic and transition sudden, it is a case of *heteroblastic development.* He again stressed that the duration of juvenility was greatly influenced by environmental conditions, which might even cause a recurrence to juvenile form, a *rejuvenation.* Propagation by seed is generally regarded as the condition on which complete rejuvenation must be based, but *Goebel* mentioned that even *Hedera Helix var. arborea* might produce juvenile shoots. He had observed, however, that "Rückschlagssprosse" usually appeared at the base of woody plants.

Although it is difficult to place historically the observations of *Michurin* because his "Selected Works" was published in 1949, after his death, yet it is clear that much of his work was done late in the 19th century. Though he cites no results from actual experimental research, it is evident that he had observed the existence of juvenile stages in fruit trees. He even tried to grow cuttings from different shoot generations in order to study the duration of the stages. *Michurin* further reported that he had been able to provoke early flowering in almond seedlings by treating the shoots with an aqueous solution of potassium permanganate.

Vöchting (1904) made cuttings from first and second order side branches of *Araucaria excelsa.* When planted, cuttings of first order developed horizontally and resembled an ordinary side branch; cuttings of second order developed as single thread-like horizontal shoots, with no side branches at all. Only with scions from the terminal shoot was production of normal plants possible. These now classic experiments have a bearing on ontogenetic development studies, but will be discussed in greater detail below.

Probably the largest number of examples of woody plants with heteroblastic development was mentioned by *Diels* (1906). Most of his material are trees in Australia and New Zealand, especially numerous *Eucalyptus* and *Acacia* species. *Diels* stresses the influence of external factors on the duration of the juvenile stages.

For a modification which is constant by vegetative propagation, *Baur* (1914 p. 60) introduced the term *"fest induzierte Modifikation"*. In other words this term stands for *a modification that can never or only with great effort be forced away from its course of development.* The term actually covers *Goebel*'s Folgeform, and it is a definite case of heteroblastic development, i.e. a sudden change with age of the apical meristem.

Baur's example of a "fest induzierte Modifikation" is the already mentioned, *Hedera Helix,* and this example is found again in many later textbooks of genetics and plant physiology because the juvenile and adult forms in this species differ so strikingly. *Baur* believes that the nutritional state of the terminal twigs determines whether transition is to take place or not. He warns against concluding from the terms, juvenile and adult forms, that transition is strictly connected to a certain age of the plant.

In his classical "Pflanzenphysiologie als Theorie der Gärtnerei" *Molisch* (1915) gave an instructive review of development studies in woody plants. He especially called attention to *Vöchting*'s experiments with *Araucaria* which had made him pay more attention to shoot individuality as related to relative position than as to age.

Molisch said (p. 237) "Die Laubsprosse sind demnach an vielen Pflanzen, je nach dem *Orte,* an welchen sie stehen, nicht alle untereinander gleich, sondern mehr oder minder individualisiert und behalten diese ihre Verschiedenheiten, ihre *Natur,* als Steckling oder Impfling gezogen, dauernd bei". He proposed to use the term, *"topophysis"* (Ortsnatur) for this phenomenon.

In order to describe the shoot individuality as dependent on life stage or meristematic age in one single word *Seeliger* (1924) introduced the useful term *"cyclophysis"* (Kreisnatur). *Hence we speak of cyclophysis in a woody plant shoot referring to properties conditioned exclusively by the development stage of that shoot.*

The term, meristematic age, suggests the well-known expression, physiological age. The two terms may be used as synonyms but the former is more accurate in relation to development stages, as the latter is generally used when only external factors are under discussion.

Generally speaking the annual shoot is rightly considered the youngest part of a tree. It is important to notice that in studies of ontogenetic development, the situation is quite the contrary. The annual shoot should be looked upon as the latest developed or even the "oldest" part of the plant. In other words, it is the shoot produced in the furthest developed meristem.

The object of our development studies is to discover whether any annual shoot character is dependent on its meristematic age. According to the above definition we may just as correctly say dependent on cyclophysis.

However, *Seeliger* (l. c.) regarded the two terms, topophysis and cyclophysis, as completely identical. He expressed this view by saying "Wenn wir also dem Begriff der örtlichen Natur der Organe den Begriff der zeitlichen Natur (Zyklophysis) hinzufügen wollen, so ist damit kein Gegensatz konstruiert, sondern nur der Standpunkt gewechselt".

In accordance with *Büsgen* and *Münch* (1927 p. 52) the author rejects *Seeliger*'s view and prefers to use the term cyclophysis in the sense defined above. The term, topophysis, should be reserved for shoot individuality in relation to different shoot order only. *Hence cuttings or grafts are said to show topophysis when they preserve the individual characters of that very part of the shoot from which they originate.*

It is evident that grafting and cutting experiments on juvenile versus adult stages may be complicated in species such as *Araucaria,* which display marked topophysis. It is very important therefore to keep these phenomena in mind.

The third edition of the classical work "Bau und Leben unserer Waldbäume" (*Büsgen* and *Münch* l. c. p. 50—52) was enlarged by *Münch* after the death of *Büsgen.* The very clear and exact review of literature on the subject, supplemented with further information from the Tharandter Forstgarten and elsewhere is of special interest in the present study. The terms cyclophysis and topophysis were used in the sense given above and a third term "*periphysis*" (Umweltnatur) was introduced to cover the qualities occasioned by environment.

Also these qualities may to some extent and for some time be maintained in a plant after change of environment and will often represent the most potent factor for blurring observations and experiments on cyclophysical characters. Fortunately, however, the qualities of periphysical origin will generally not persist to the same degree as those caused by cyclophysis or topophysis. 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. *Münch* mentions this example of periphysis which thus manifests itself as a certain aftereffect caused by previous conditions. If insufficient heed is paid to periphysical phenomena there is danger of confusing them with both cyclophysical and topophysical matters.

As these three terms will often be used in this paper, and as they may seem somewhat obscure at first, the author will illustrate their meaning by a few examples from *Büsgen* and *Münch* (l. c. p. 52).

The adult form of *Hedera* is conditioned by cyclophysis and periphysis, but not by topophysis, because it arises only in old age and in full light, but everywhere on the old tree where it is exposed to full light.

The form of the cotyledons of a seedling is exclusively caused by cyclophysis because they arise at the first stage of the life cycle on the whole of the shoot and in any environment.

The threadlike form of the *Araucaria* cuttings from second order side branches may be caused by topophysis alone, because it is not associated with a particular age nor with special environmental conditions.

In the present paper the definitions and terms proposed by *Münch* are adopted in pleno. There is every reason to quote his views which are summarized in the following way: "Die Topo-, Zyklo- und Periphysis der Pflanzenteile sind natürlich für jede Pflanzenart, ja für jedes Individum verschieden. Innere Erbanlagen schreiben schon in der befruchteten Eizelle der entstehenden Pflanze für alle ihre Teile, für jedes Alter und für alle mögliche Aussenumstände eindeutig die Eigenschaften vor. Wir haben diese mit dem Keimplasma überkommenen inneren Kräfte unter dem Begriff Genotypus kennen gelernt. Genotypus, Umwelt, Alter und Baumteil bestimmen im Zusammenwirken zwingend die Beschaffenheit aller Pflanzenglieder, also den gesamten Phänotypus".

Whereas some workers had observed — as mentioned above — that rejuvenation most often took place in shoots near *the base of woody plants* it was *Büsgen* and *Münch* who first claimed that *this type of rejuvenation was due to the origin from dormant buds of such shoots, the meristems of which had not undergone the same development as those of the normal branches.* In other words any kind of epicormics which originate from dormant buds laid down by a young tree seems to retain the juvenile characters even if the rest of the tree passes into the adult stage. Thus it is not a case of true rejuvenation but rather of delayed development.

Molisch (1929) reviewed much of the literature but presented no observations or view points which had not been mentioned in his previous review (1915).

It has been mentioned that *Büsgen* and *Münch* (l. c.) realized that both cyclophysis and periphysis played a part in explaining heterophylly in *Hedera.* Some papers of less importance however attempt to present the phenomenon so as to exclude either influence of age or of environment. For instance *Kranz* (1931) insisted on cyclophysis as the exclusive explanation. Presumably ignorant of *Büsgen* and *Münch*'s opinion of delay of development in dormant buds, he formed the same idea and was convinced that all examples of rejuvenation in *Hedera* could be referred to low epicormics from dormant buds.

About 1930 the Russian biologist *Lyssenko* advanced his theories on the existence of development stages in plants. He mainly concentrated on development in herbaceous plants, in which he recognized the existence of a vernalisation and a light stage. In the former stage the future development of a plant especially the duration of the growing season, could be changed by thermal influences, whereas in the light stage photoperiodic conditions governed certain aspects of development.

The only principal difference between development stages in *Lyssenko*'s sense of the term and others' seems to be that *Lyssenko* warns against believing "dass das Auftreten neuer morphologischer Kennzeichen stets das Resultat des Übergangs der Pflanzen in ein neues Stadium darstellt" (*Maximov* 1951 p. 550).

Lyssenko only touched upon woody plant development, but he was repeatedly cited by Russian investigators who were studying development stages and their importance in silviculture. *Lyssenko* was regarded as the follower of *Michurin* and with him as the father of most basic knowledge on ontogenetic development in plants. Because of this exceptional position, there is reason to refer to *Lyssenko* in this paper. Translations of *Lyssenko*'s works are available in Denmark, but the most clear account of his theories is found in *Maximow* (l. c.).

Only second hand information has been available on *Krenke*'s theory of "the cyclic aging and rejuvenation in the ontogenesis of a plant". The work on the principles of his theory dates from about 1930 to 1940, when the most important paper was published.

Mainly based upon the accounts in *Plant Breeding Abstracts* (1945) and by *Maximow* (l. c. p. 569—73) the distinguishing point in *Krenke*'s theory from the general theory of life stages in the ontogenesis of a plant, is that he describes the gradual aging processes in the meristem as "a struggle between senescence and rejuvenation, until the inevitable death of the organism supervenes, senescence having won the struggle". *Krenke* considers the formation of new shoots and leaves a periodical recurrence of juvenility. However "with each recurrence the character of the rejuvenation is seen to have changed; the leaves and shoots formed by the plant when it is young differ biochemically, physiologically and morphologically from those formed when it is old. Each leaf or shoot is therefore said to have two kinds of age: its own age, and that of the plant on which it is formed" (*Plant. Breed. Abstr.* l. c.).

Krenke based his theory on observations of the regular changes in such morphological characters as the leaf form and the length of petiole. He paid no heed to influence of external factors.

It has a special bearing on woody plants that *Krenke* emphasized that dormant meristematic cells, for instance in the apical meristems of dormant buds, aged very slowly. Therefore shoots developing from dormant buds of the stump of a felled tree show juvenile characters.

Stoutemyer (1937) observed the existence of a very short juvenile stage with entire leaves in *Malus Sargenti* which later bear deeply lobed leaves. In experiments he was able to show that juvenile apple shoots struck roots much more readily than mature shoots. He also observed that anthocyan production was abundant in juvenile shoots.

Stoutemyer further was able to produce juvenile shoots from adventitious buds on roots of older ungrafted trees, thus showing that it is not only basal shoots from dormant buds which are juvenile, but *the whole root system and the lower portion of the plant seem to remain in the juvenile condition* after other parts have passed into a mature type of growth.

Stoutemyer made anatomical studies which showed that watersprouts or epicormics in apple generally origin from dormant buds. By severe pruning of some trees the formation of so-called sphaeroblasts were however forced. They are small round woody bodies in the bark on which adventitious buds may be formed.

Shoots from these buds seemed to be of juvenile type, but the experiments were stopped too early to be conclusive.

Stoutemyer believed the development from juvenile to adult stage to be dependent upon certain biochemical factors, the character of which was not yet clearly understood.

Keeping in mind the history of the false genus *Retinispora* (p. 314) it is interesting to note that similar mistakes of regarding juvenile forms as separate woody species have been committed in New Caledonia. *Guillaumin* (1952) has clarified the relationships within some of the species as *Beissner* did in the *Retinispora.*

A striking demonstration of the frequency of heteroblastic development in many Australian species has lately been published (*Anonymous* 1957).

Finally it may be mentioned that *Passecker* (1954) called attention to the fact that also *Parthenocissus tricuspidata* has an upright juvenile stage with trifoliolate leaves and a creeping adult stage with simple leaves.

In the same paper *Passecker suggested that the cambium aged at a slower rate than the apical meristem. In this way it was possible to explain that not only the dormant buds but the whole lower portion of trunks remained juvenile.*

4. Leaf Anatomy.

A number of workers have studied the ontogenetic development of some woody plants through investigations of leaf anatomy. As anatomical leaf characters are greatly influenced by environment it is very important that observations are not blurred by periphysis. Also a few studies on anatomy of other organs than leaves will be included in this section.

In a number of our important forest trees *Schramm* (1912) compared the primary leaves of seedlings in full light with shade and sun leaves of grown-up trees. Although *Schramm* selected the leaves by a very uniform and reliable method, his material was extremely scanty and his figures however striking, were not statistically treated. He observed an anatomical difference between primary sun leaves and normal sun leaves, and he regarded the former as the hereditarily fixed juvenile forms of normal leaves. There was usually a definite resemblance between primary sun leaves and shade leaves from old trees. It is stressed that there is a gradual development from primary leaf anatomy to typical sun leaf anatomy, which takes about 20 years in

Fagus sylvatica. According to *Goebel* it is a case of homoblastic development. *Schramm* also noticed that primary sun leaves of *Ulmus carpinifolia* were extremely small and not oblique.

Nordhausen (1912) made investigations very similar to those of *Schramm,* and reached the same conclusions. His seedlings in full light however were able to produce sun leaf types, and he therefore considered *Schramm* to underestimate the "Reaktionsvermögen der Sonnenprimärblätter".

Nordhausen observed that even in full light the first leaves on any shoot will be more or less of the shade leaf type. Towards the shoot tip a gradual development into sun leaves takes place.

These findings agree with *Krenke*'s theory of cyclic aging and rejuvenation (cf. p. 324) and they illustrate the difficulty of correct selection of leaves for investigations on meristematic aging.

The most convincing and most often cited paper on aging of the meristematic tissue in woody plants was published by *Benedict* (1915). Using a large leaf material, selected under the most uniform external conditions, he was able to demonstrate definite correlations between size of meshes between the veins, hence called vein islets, and age in *Vitis vulpina.*

Benedict selected for his studies about twenty pairs of plants which grew under identical conditions but were of different age. He picked 10 leaves of each plant at the same height above ground. The results from each leaf are given in his tables and seem to be the most striking evidence of meristematic aging. From vines of different age, cuttings were also taken and grown under identical conditions with similar results. He found the same tendency in some other woody species, but his material was rather scanty. Contrary to other workers *Benedict* definitely maintains that leaves on suckers and low epicormics show a venation corresponding to the age of the stump.

Ensign (1919) assumed *Benedict*'s observations on connection between size of vein islets and age to be a general phenomenon. He went so far as to use it to prove that rejuvenation in citrus is brought about equally well through apogamous and through gametic reproduction. Vein islets in seedlings of apogamous and gametic origin were shown to be of the same size.

Although *Ensign*'s generalization of *Benedict*'s results may be questioned there is no doubt that apogamy or parthenogenesis will usually cause rejuvenation. Therefore *Ensign* is correct in the conclusion that "sexuality is not necessary to rejuvenation", the latter being already effected by the reduction or *"undifferentiation"* which precedes fertilization. Thus he does not deny that "undifferentiation" and sexuality often occur at approximately the same period in the life cycle of the organism, but calls attention to the fact that they are not necessarily connected with each other.

Tellefsen (1922) made cuttings from individual trees of *Salix nigra*. She graded the cuttings according to the diameter of the parent tree and found that big diameter, i. e. great age, meant smaller vein islets and smaller epidermal and cortical root cells. On the contrary xylem and meristematic root cells became larger in cuttings from older trees. The variation of *Tellefsen*'s figures seems rather great and a suitable statistical treatment is lacking.

Finardi (1925) was able to confirm *Benedict*'s and *Tellefsen*'s findings of correlation between age and smaller vein islets in *Juglans regia, Fagus sylvatica, Gleditsia triacanthos, Aesculus Hippocastanum* and others. She generally compared a very young seedling with its mother tree and took care to collect normal and fully developed leaves, if possible under same environmental conditions.

Finardi has perhaps misunderstood the question of aging in the meristem, as she seems rather surprised to find that leaves in cuttings from an old *Raphiolepis umbellata ovata* show more or less adult characters. Actually the leaves from the cuttings are of intermediate type, indicating that periphysis plays a greater part in this question than admitted by *Benedict, Ensign, Tellefsen* and *Finardi.*

Johnson (1926) compared the anatomy of juvenile and adult leaves of *Eucalyptus globulus* and found that the former had stomata only underneath, the latter on both sides. The stomata were largest in adult leaves which also possessed other sun leaf characters.

Among the papers inspired by *Benedict* are *Bergamaschi*'s investigations (1927). She too found correlation between age and small leaf vein islets. Although a suitable statistical treatment is wanting, the size of vein islets seems very different in old and young plants of *Vitis vinifera, Rosa Eglanteria, Cercis*

Siliquastrum, Camellia Thea and *Platanus occidentalis.* Contrary to *Finardi* she did not select young plants which were closely related to the old ones. Thus there is greater danger of purely genetical variation in *Bergamaschi*'s material.

Within *Salix babylonica, Nerium Oleander* and the species mentioned above, *Bergamaschi* made measurements of root cells of cuttings from old versus young trees by *Tellefsen*'s method (l. c.). She was able to confirm some of *Tellefsen's* results but not all of them. Neither *Tellefsen* nor *Bergamaschi* treated their material statistically and none of the results seems quite convincing. However the selection of the material was in both cases very carefully made.

5. *On Thorns.*

Under the previous heading, leaf anatomy, it was stressed that anatomic leaf characters are greatly influenced by environment and therefore difficult to use in investigations on ontogenetic development.

In many woody species thorniness is a very characteristic quality of juvenile stages, as already mentioned by *Knight* (cf. p. 313). As every gardener knows, however, thorn formation is greatly diminished in shade. This is often seen in *Crataegus* species growing under tree groups in parks.

Some papers dealing with this problem were published about 1900, and are briefly reviewed in the following, as they illustrate how environmental factors may blur observations on meristematic aging.

Lothelier (1893) made experiments with stooled young plants of woody species with thorns, *Ilex, Genista, Ulex, Robinia, Berberis* and *Crataegus.* He placed his rather scanty material under dry conditions versus humid, and in full light versus shade. He found that thorn formation in all these species was enormously diminished by high humidity of the air and by shade.

Goebel (1898—1901 p. 226) mentioned that *Ulex europaeus* seedlings have a short juvenile stage without thorns. In experiments with high air humidity versus low he was able to call forth a moderate decline in thorn formation.

Molliard (1907) grew seedlings of *Ulex* on substrata with different glucose contents. Thorns were provoked earlier at rather high concentrations.

Also *Zeidler* (1911) made experiments with *Ulex;* like *Goebel* he could only suppress thorn formation to a very moderate degree by high humidity and shade. He used two year old plants, which were not stooled, and stressed that *Lothelier*'s striking results were due to his stooled material, which represented "Jugendformen bzw. Rückschlagssprosse im Sinne *Goebels*". *Zeidler* observed that the basal parts of annual shoots were often thornless even in older *Ulex*. He says, that an annual shoot repeats the ontogenesis of the whole plant to a certain degree. This is in accordance with *Nordhausen* and *Krenke* (cf. p. 327 & 324).

Lothelier (1912) was prepared to agree that he had used juvenile forms, but he rightly maintained "que si ces formes de jeunesse ne se sont produites que dans l'air humide, c'est le milieu modificateur qui en a été la cause, puisque rien de tel ne s'est produit sur la plante vivant à l'état normal".

Boodle (1914) grew more than a thousand *Ulex* seedlings on loamy versus sandy soil. The plants produced more compound leaves on loam, i. e. the thorn formation began later. He concluded in a very clear way "that the actual number of compound leaves, formed by a given seedling, may be regarded as determined by three factors viz. a. the number of compound leaves that would be produced by this individual under normal conditions b. the plasticity of this seedling c. the deviation from normal conditions".

Vischer (1915) also worked with some of the more plastic plants with heterophylly, f. inst. *Juniperus chinensis* and *Ulex europaeus*. By high air humidity he called forth the juvenile form in individuals which bore leaves of the adult type. He showed that the ash content was relatively higher in juvenile than in adult leaves. *Vischer* made probable that all methods to prolong the juvenile stage worked in the same way as they changed the metabolism of the plant towards higher ash content.

6. *Fruit Trees.*

It is only natural that the bulk of publications on meristematic aging is found within horticultural literature, because the existence of development stages becomes quite evident after vegetative propagation. So *Knight* (l. c.) and *Michurin* (l. c.) described the life stage characters in apple and pear (cf. p. 313

& 320) and the discussion of the *Retinispora* question was also based on vegetatively produced plants (cf. p. 314).

During the last 20 years observations and experiments have been so frequent on fruit trees that it seems reasonable to review this literature jointly.

Although *Stoutemyer*'s investigations (1937) mainly dealt with fruit trees they were mentioned in the section on terminology because of their great principal importance (cf. p. 325). It should however be stressed once more that *Stoutemyer* found greater rooting ability in cuttings from young apple seedlings.

This general feature was occasionally mentioned in the previous sections. The most important paper was already published in 1929 by *Gardner*. He propagated numerous fruit and forest trees by cuttings from 1, 2 and 3 year old seedlings and found much better rooting in 1 year seedlings thus showing how extremely short the "juvenile rooting stage" may be.

Also *Frischenschlager* (1939) found evident relationship between tree age and rooting capacity in apple.

In an early American paper on development stages in fruit trees *Frost* (1938) reported upon small scale grafting experiments with some citrus species which proved to have a juvenile, thorny, vigorous, non-flowering stage and an adult smooth, less vigorous, flowering stage. He discussed the aging problem in clones and emphasized that the regularly occurring "age changes are temporary but persistent modifications of the meristematic cells, which are propagated in ordinary somatic divisions but erased in seed formation".

Passecker (1940) reviewed some of the literature and reported observations on apricots in which he recognized a juvenile stage with smaller and more pubescent leaves on short petioles. On an apricot tree he noticed the gradual change from juvenile to adult stage and also observed that low epicormics carried juvenile leaves whereas high epicormics bore adult leaves. Also in peach trees differences between juvenile and adult stages were observed in leaf form and size. Further, *Passecker* drew attention to the different physiology of the stages, especially the greater rooting capacity and lesser fertility of juvenile stages.

In later publications (1941 & 44) *Passecker* gave more examples on fruit trees with juvenile and adult forms. He stressed the interesting fact that the cultivated *apple and pear sorts have lost their juvenile forms because grafting is always carried out with scions in the adult stage.*

Passecker observed both individual differences and effect of external factors on duration of the juvenile stage. Thus he emphasized the existence of what is termed "Die Erblichkeit des Phasenübergangstermines" and "Verschiebung des Phasenüberganges durch äussere Einflüsse". As to the latter he says "dass alle Massnahmen, welche die Wurzelernährung begünstigen und ein üppiges Wachstum hervorrufen, den Phasenübergang beschleunigen" (1944).

Passecker considers the juvenile forms to be usually sterile but in accordance with *Beissner* and *Diels* expects to find exceptions from this rule. He had not observed and regarded it to be an open question if fixation of the juvenile forms in fruit trees could be effected by repeated cutting propagation from basal branches as *Beissner* had maintained to be the case in some conifers. The usual horticultural method of vegetative propagation of rootstocks by cuttings after stooling and earthing up, *Passecker* considered a means of temporary fixation only.

Romberg (1944) reported on observations and small scale budding experiments which showed that the *Carya Pecan* passed through a *juvenile stage characterized by lack of flowers, pubescent leaves and reddish shoot and leaf colour. Furthermore juvenile shoots grow more erect and have a more frequent periderm formation in the bark.* Whereas the dry bark in a bearing type trunk or branch usually flakes off, it is retained in the juvenile trunks. *Romberg* mentions that "within the same tree the juvenile type of bark that occurs near the ground appears to afford greater protection against mechanical injury, fire and low winter temperatures than would the bearing type that occurs higher up". This phenomenon is clearly demonstrated in photographs.

Romberg budded juvenile and bearing type clones to a bearing tree and both retained their characteristics, a few juvenile clones changing gradually as might be expected. It was observed that "transition from juvenile to bearing characteristics is gradual, and flowers may be produced on shoots that are not of the typical bearing type". *Romberg* noticed individual variation as to duration of juvenility. He also realized that favourable external conditions would usually cause a quick change from juvenile to mature type, the time required being nearly in inverse proportion to the rate of growth.

Kemmer (1947) disagreed with *Passecker* although he admitted that fruit tree seedlings had a primary stage, but he rejected the term, "juvenile form", which should only be used, he maintained, when the primary stage could be fixed by repeated propagation by basal cuttings i. e. "Jugendform" in the sense of *Beissner*. He gave examples of important leaf modifications caused by environmental changes only and mentioned that leaves on dwarf shoots often differed considerably from those on long shoots. Further *Kemmer* called attention to the fact that some old clones were able to root very easily. His views may be summarized below: "Wir können deshalb bei den Apfelgehölzen nur von einem primären Stadium sowie von einem fertilen (Sorten-) Stadium sprechen. Beide können durch äussere Einflüsse derart modifiziert werden, dass die entwicklungsbedingten Wandlungen gegenüber den standortbedingten, also den durch Boden, Lage, Unterlage und Pflege veranlassten Besonderheiten zurücktreten".

Passecker (1949) answered the criticism of *Kemmer* by giving a brief account of his views. He emphasized that he had always paid heed to the effect of environment on duration of juvenility, and maintained that it was wrong to reserve the term, "juvenile form" to cover fixed forms in the sense of *Beissner* only. *Passecker*'s views were clearly formulated as follows: "Nach meiner Auffassung hat man unter einer Jugendform die Gesamterscheinung der äusserlich erkennbaren Ausprägung von Merkmalen zu verstehen, die für das jugendliche, noch nicht sexuell fortpflanzungsfähige Gewächs characteristisch sind".

The strongest evidence in the discussion on life stages in the ontogenesis of fruit trees was published in the thesis of *Fritsche* (1948).

Fritsche examined juvenile and adult shoots of the same seedling apple or pear trees. His material was fairly large and much care was taken to select shoots under similar environmental conditions. If possible the mean errors were calculated and proved that the results obtained were significant.

Comparative investigations showed that side branches in the juvenile stage usually stood at right or even at obtuse angles to the main axis, whereas in the adult stage the angles became perceptibly acute. The terminal buds of the juvenile shoots are usually very weak; they often dry up and fall off after which the shoot appears to be a thorn. Juvenile shoots come into leaf later than adult, and the fully developed leaves of the juvenile form average smaller than those of the adult.

Fritsche investigated the anatomical structure of the xylem and showed that juvenile wood contained fewer vessels than adult wood and they were more concentrated in the spring wood. The summer wood of juvenile branches was composed of prosenchymatic fibres mainly and appeared very compact. Parenchymatic tissue and ray tissue were more frequent in adult wood.

In accordance with the greater proportion of living tissue in adult wood, chemical investigations showed a larger content of sugar in adult branches and juvenile wood was particularly poor in monosaccharides. The quantity of starch was greatest in adult wood. Contents of mineral nutrients and nitrogen were also greater in adult wood whereas contents of cellulose, hemicellulose and lignin were smaller. Accordingly, microscopical investigations proved the proportion of cell walls to be greatest in juvenile wood.

Fritsche ringed 220 apple seedlings between 4 and 11 years old of which some had passed into the adult stage but were still showing juvenile characters at their base. He only succeeded in forcing formation of flower buds in the adult branches and in a few branches in a transition stage, thus proving "juvenile sterility". *Fritsche* explains this fact to be due to the special anatomic properties of the juvenile wood, unchangeable by artificial measures. The small number of vessels, sieve tubes and parenchymatic tissues, apparently does not suffice, he says, to make available the quantities of matter necessary for flower bud formation.

Fritsche reports that scions from tops of three year old apple seedlings were grafted on to twenty year old bearing trees. The grafts remained juvenile for three to four years, and there was no indication that the old flowering rootstocks hastened the transition. Also scions from two year old seedlings grafted on the dwarfing rootstock, East Malling type IX, did not become adult earlier than usual. *Fritsche* concluded that cyclophysis was strictly governing the development of fruit tree seedlings and expressed this by saying that the results of the two grafting experiments proved *"dass die Reiser in der Jugendform weiterwuchsen, bis die obligatorische Anzahl Jugendjahre absolviert waren".*

Fritsche was also able to demonstrate that cuttings from juvenile material rooted most easily. *He believed that the juvenile and adult forms were conditional on the influence of one or several phytohormones.*

The East Malling rootstock types are propagated by cuttings after stooling and earthing up. Like *Passecker, Fritsche* believed that in this way the juvenile stages of these clones had been maintained by temporary fixation. He supported this view by microscopical investigations of the wood of trees of E.M. type I, XVI and XIII. Although the mean errors are not given, the figures seem rather convincing.

In a number of contributions to the discussion on the existence of cyclophysis in fruit trees, *Kemmer* and his collaborators gave examples of flowering in the juvenile zone, of rooting ability in old branches and modifications of leaf characters caused by environment (*Kemmer* 1950 a & b, *Kemmer & Kirschhof* 1952, *Kemmer & Thiele* 1954). These contributions thus emphasized the importance of periphysis as opposed to *Fritsche*'s view of a solely cyclophysically governed development. One of the papers (1950 b) also gives examples to show certain deviations from the anatomic wood characters found by *Fritsche.*

All these objections to the theories of *Fritsche* and *Passecker* were usually based on few and rather scattered observations. However one important experiment was reported when *Kemmer* (1953) observed the initiation of flowering in 1029 pairs of apple seedlings of which one grew on its own roots, the other was grafted on E.M. IX. The results were that 212 pairs had not yet flowered, 40 pairs started flowering simultaneously, 740 grafts flowered from 1 to several years before their root-true "twin" seedlings and only in 37 cases did the latter flower first.

Another experiment with the same layout was published in the last paper of this group (1954). Of 368 pairs of six year old trees 61 grafted specimens flowered for the first time, whereas none of the root-true seedlings flowered.

Kemmer believes these experiments to show that the rootstock influence has hastened transition from juvenile to adult stage. But the promotion of flower buds may just as well be due to periphysis, for instance to a different nutritional state in the grafts on this extreme rootstock type versus in the root-true seedlings.

Passecker has lately contributed twice to the discussion (1952 & 1954). Both publications are mainly reviews of literature and bring little new information. Among the senile apple clones *Passecker* (1952) mentions the Rote Stettiner and the Locherapfel. The tea-rose "Maréchal Niel" is also considered to be exhausted due to aging in the meristem. He is convinced of the existence of "children's diseases" and "old age diseases" which chiefly attack the juvenile and the adult stages respectively.

Breviglieri (1947) used the term topophysis in the broad sense of *Molisch,* in which it is difficult to distinguish from periphysis and cyclophysis. An artificially produced hybrid pear, grafted six years before upon quince, produced budwood material for the following experiment laid out in 1940.

From four different types of branches budwood was collected and budded on branches of two adult pear trees. The four categories of budwood were

1. thorns of basal branches,
2. terminal slender parts of thorny branches,
3. thornlike fruit spurs,
4. slender fertile branches.

The rootstock branches were very uniform and grew under approximately the same external conditions.

The experiment was assessed in 1947, and the most important results were that from each type of budwood arose branches of the same category. For instance flowering was abundant in branches from type 4, which however produced no thorns whatever. On the contrary branches from type 1 produced many thorns and little fruit. Figures clearly showed that growth vigour was definitely least in branches from type 4. In most respects type 2 and 3 budwood showed intermediate development in comparison with type 1 and 4.

The experiment was also carried out on quince rootstocks with identical results.

Five years later *Breviglieri* (1952) again assessed the above experiments. In general the results were the same, but as expected, the thorny buddings were gradually passing into the adult stage. Further, *Breviglieri* could confirm many of *Fritsche*'s general observations; he had compared formation of flower buds in apple seedlings on their own roots and on adult rootstocks without finding any difference.

In small scale but good comparative experiments *Furr, Cooper* and *Reece* (1947) were able to force formation of flower buds in juvenile citrus seedlings by ringing. It was however much easier to cause flowering in 7 than in 3 year old seedlings. It was concluded that "the age barrier to flower formation in juvenile citrus seedlings is not insurmountable; but apparently with increasing age it becomes less difficult to effect the preparatory changes required before flower formation can take place". The time of year of ringing was very important.

Furr, Cooper & Reece also tried to call forth flowering by grafting juvenile seedling scions on to adult trees. They succeeded only in one case in which the adult rootstock branches were ringed. Thus they were not able to prove their working hypothesis that a flowering substance was transferred across the graft union from the adult to the juvenile scion.

Oldén (1952) briefly reviewed the papers by *Passecker, Kemmer* and *Fritsche* and through comparative budding experiments with buds from juvenile water-sprouts and from peripheral adult branches of the same apple seedlings, he was able to show the persistence of the stages after vegetative propagation on East Malling stock IX under identical environmental conditions.

Kolomiec (1953) carried out experiments on which however only second hand information was available. It is clear that he observed that seedlings of various fruit trees pass through certain necessary stages of development before they enter the fruiting stage. He maintained that grafting on young stocks of adult scions did not set back the stage of development which permits early fruiting. By application of fertilizers, fruiting might be hastened in seedlings after phasic readiness for fruit bearing had been achieved. *Kolomiec* thus believed that the period of juvenile sterility was usually prolonged by lack of nutrients. This idea calls to mind the words of *Passecker* (1952) not to overlook "die Tatsache dass Geschlechtsreife und Blühwilligkeit zweierlei Erscheinungen sind".

Blair & MacArthur (1956) briefly reviewed some of the classical literature on our subject. They added no new view points, but gave two examples of earlier failures due to lack of knowledge of cyclophysical phenomena.

In 1931 2400 hybrid seedlings of apple were planted for fruiting, but as they were spur pruned in the same way as normal apple varieties, a temporary fixation of the juvenile stage ensued, and no bearing commenced. Only after they were allowed to grow without pruning for a few years could apple production begin.

A specially hardy seedling Malus Robusta 5 was selected for rootstock propagation. Stool beds produced rough, thorny and twiggy shoots. When Malus Robusta 5 was allowed to grow tall the above characters were lost and lack of thorns proved to persist in buddings. The thornless material was much more agreeable to work with, and new stool beds were prepared using budwood from 18 year old bud-source. As could be expected many of the stool shoots were smooth, but the new stool bed proved rather useless because rooting was much less abundant than in the first stool bed. Knowing the phenomenon of loss of rooting ability with age the results are in accordance with the theories of cyclophysis.

Blair & MacArthur's paper is especially interesting because it admits *failures in practice due to lack of theoretical knowledge in this field.* In this connection it should be mentioned that *Dalbro* has suggested that the usually poor results in fruit tree breeding may be due to a selection among the seedlings for adult characters. The juvenile qualities have to some extent simply been considered bad or "wild" qualities (verbal communication). This method of selection probably leads to preference of specimens with short juvenile stages, which may not be advantageous.

It may also be mentioned that *Sax & Johnson* (1955) budded five buds each from a fruiting apomictic apple tree and from its young seedlings upon clonal dwarfing stocks. Budding was carried out in 1951, and in 1953 one of the five trees from "old buds" flowered and in 1953 all of them. However none of the 5 trees from "young buds" had yet flowered. The evidence is believed to suggest the presence of a flower stimulating substance in the fruiting tree which is absent in its apomictic seedlings.

In a trial including both budded and seedling progenies of four selected mother trees of tung, *Aleurites Fordii, Potter, Sitton, Merrill, Wright & Johns* (1954) proved that the budded progenies were more severely damaged by *cold injuries* and made far less satisfactory recovery than seedling trees of the same mother tree. The shoot growth of the buddings tended to be weak, and this fact was regarded as the explanation of their greater susceptibility. The layout of the experiment does not exclude the possibility of upward translocation of nutrients being impeded at the graft union.

Merrill, Lagasse, Neff & Killy (1954) reported on large scale experiments in which seedling and budded progenies of 8 selected tung trees were compared. The rootstocks used were nearly all progeny from one clone. After seven test years the buddings appeared to have had less *volume production* than corresponding seedlings, although the former had made more shoot growth during the first year in the orchard, probably because of their two-year-old roots. With reference to the preceding paper this fact does not point to any significant impeding effect of graft union on translocation of nutrients. Total *fruit production* was significantly larger in seedlings, especially under poor culture. Investigations showed that the larger fruit production was directly caused by the larger size of the seedlings.

Lately *Murawski* (1955) reported on interesting experiments with apple. He took buds from side shoots at different heights of 3 year old apple seedlings and budded them on E.M. IX, IV and XI rootstocks. The buddings from basal branches showed clearly many juvenile characters such as small leaves with large vein islets (cf. p. 327 *Benedict*) and rather few stomata. They developed vigorous horizontal branches and no flowers. The buddings from higher side branches appeared less "wild" and from the highest at about 2.5 m above ground grew plants resembling the cultivated types. It is interesting that the layout of this experiment follows the suggestions of *Michurin* (cf. p. 320).

On E.M. IX the transition to adult form was evidently hastened and this rootstock was therefore recommended in breeding work where early fruiting is of great importance.

Also *Murawski* believed that the different appearance and physiology of juvenile and adult forms were caused by phytohormones.

In another important paper (*Murawski* 1957) the buddings mentioned above were further examined. It was very clearly demonstrated that the epidermal cells of juvenile leaves were larger than those of adult leaves. Negative correlation was found between cell size and tendency to flowering.

Recently the difficult problem of senility in clones has been investigated by *Oberholzer & Hofmeyr* (1955). They discuss the serious decline of many commercial citrus varieties in South Africa where certain virus diseases seem to play an important rôle. However as these authors do not believe that meristematic senility exists they cannot claim it as predisposing to the disease. They suggest that the frequent and usually worthless somatic mutations in citrus are the direct cause of the decline. It may be mentioned that *Breider* (1956) proposes the same reason for the deterioration of many cultivated grape varieties.

Recognizing the existence of juvenile sterility in woody plants, it is important for breeders to shorten this stage artificially. If this were done the main obstacle in tree breeding, slow succession of generations, might be removed.

Early flowering was provoked in seedlings of *Prunus avium* by *Potapenko* (1939). He shortened the juvenile stage by making the seedlings pass through two annual growth cycles in one year. The experiments were based on the assumption that aging of the meristem is dependent on the number of shoot generations i. e. annual growth cycles and not upon the age in years of the seedlings.

In exactly the same way as *Potapenko, Smeets* (1956) tried to shorten the juvenile stage in seedlings of *Prunus avium*. He was able to reduce the annual cycle of the seedlings to 6 months. *Smeets* obtained results exactly opposite to those of *Potapenko,* as the control seedlings with normal annual cycles nearly all flowered, whereas only one of the treated plants flowered.

7. *Topophysis.*

As already stated, the term *topophysis* in this paper only comprises the phenomenon, cuttings or grafts preserving the individual qualities of the branch order of the scion (cf. p. 322). In this narrow sense of the word there is little information in recent literature on topophysis. However, mention may be made that *Breviglieri* (1947) repeated *Vöchting*'s experiments with *Araucaria excelsa* (cf. p. 320) and was able to confirm the existence of topophysis, although he did not seem to obtain any living material from second order branches. *Mendes* (1950) reported that vegetative propagation of orthotropic branches of two *Hydnocarpus* species gave rise to normal plants whereas abnormal plants with lateral branches only were raised from plagiotropic branch scions.

Exactly the same phenomenon was observed in *Coffea arabica* by *Carvalho, Krug & Mendes* (1950). It was added that only the plagiotropic grafts flowered.

Gerasimov (1952) reported that cuttings from leaders of *Eucommia ulmoides* showed better growth than from lateral shoots which gave rise to spindling plants, necessitating staking.

Smith, Haddock & Hancock (1954) took scions of different branch order from *Populus canadensis Eugenii* and *Populus trichocarpa* and found that cuttings from leaders grew more vigorously than from first order side branches, which were again superior to those from second order side branches.

As the latter experiments were assessed very early the different behaviour of the cuttings might be due to an environmental aftereffect i. e. to periphysis.

8. *Heredity.*

The fact was earlier touched upon that a number of workers on ontogenetic development observed individual variation in duration of the juvenile stage. A few examples should be mentioned from recent papers which show such individual variation of juvenile stages.

Johnsson (1949) crossed the 2 earliest flowering individuals among a seedling lot of *Betula pendula* and obtained a progeny of which 70 % flowered extremely early. A similar result was obtained in a progeny from a precocious *Betula pubescens.*

Michaelis (1951 a) collected seed from 17 specimens of three different provenances of *Chamaecyparis pisifera squarrosa* and from the same number of normal *Chamaecyparis pisifera* of two provenances. The seed from the latter gave rise to a progeny of which in the second year 64.7 % had passed into the adult stage with scaly leaves as against 14.0 % of the progeny from the *squarrosa* variety. In this paper and in another later paper (1951 b) *Michaelis* suggested that it might be a case of cytoplasmatic heredity.

Another case of hereditary precocious flowering was reported upon by *Nakamura* (1956), who proved that progeny from early flowering *Cryptomeria japonica* inherited the character precocity.

All three experiments prove the existence of individual variation of the "sterile juvenile stage".

9. Rejuvenation.

It was mentioned in the introduction and it appeared from many experiments and observations reviewed in this paper that young shoots from the lower portion of the trunk in a seedling tree will usually be of juvenile type. Some authors believe that only the dormant buds remain juvenile, others, that this is true of the entire basal trunk portion. By pruning or stooling this persistent juvenility is demonstrated in many woody plants through outbreak of epicormics (cf. p. 323—26).

Much greater uncertainty prevails as to the problem whether true rejuvenation takes place in adult branches. It was mentioned that *Stoutemyer* (1937) suggested that such rejuvenation might be provoked in adventitious buds from sphaeroblasts. His experiments were however not conclusive (cf. p. 325).

Dermen (1948) like *Stoutemyer,* by heavy pruning and debudding called forth adventitious buds in apple. This may be mentioned here although *Dermen* did not aim at rejuvenation but to give rise to sports from adventitious buds in special layers of periclinal chimaeras.

Also *Wellensiek* (1952) was able by debudding to force formation of sphaeroblasts in apple varieties, beech, birch and oak. Adventitious buds grew from the sphaeroblasts but the epicormics showed no juvenile characters. However the rather scanty material was inclined to root readily.

Two well rooted sphaeroblast cuttings from the apple variety, Yellow Transparent, were stooled and earthed up; new shoots formed on them, which rooted well and on their lower parts only, showed juvenile morphological characteristics such as branches with thornlike spurs, wide angle of branching and small leaves. *Wellensiek* concluded, "it looks as if the capacity of root formation has been "fixed" by applying the method of stooling".

MacDaniels (1953) carried out repeated shoot removal of apple during summer; but contrary to *Dermen* and *Stoutemyer* he was not able to call forth adventitious shoots from sphaeroblasts. He concluded that true adventitious buds could not be formed on branches of old apple clones, and he was convinced that the shoots provoked by debudding originated from dormant buds, which become widely distributed on the branches as they increase in size. He showed that true adventitious buds occurred freely on the roots of one-year-old seedlings.

Hatcher & Garner (1955) confirmed *Dermen's* and *Stoutemyer*'s findings when in debudding experiments they were able to force formation of clearly internodal sphaeroblasts with adventitious shoots. They stress the importance of complete debudding and found that the best time was towards the end of the dormant season. There seems to have been no indication of rejuvenation.

In *Baldini & Mosse's* anatomical studies (1956) it was shown that the first response to severe pruning in apple is a "transference of growth from the cambium to the preformed apical meristems of latent buds". Only if the latent buds are also removed, does sphaeroblast formation in the cortex take place. The paper has no direct bearing on rejuvenation as such.

Doorenbos (1955) grafted the juvenile form of *Hedera Helix* on to the adult form and vice versa. In many cases the adult graft partner changed towards the juvenile form by loss of capacity to flower and change of leaf form. This important experiment seems to be *the first certain case of rejuvenation.* Defoliation experiments showed that rejuvenation was stimulated by juvenile leaves and inhibited by adult leaves.

Important experiments were made by *Frank & Renner* (1956) with cuttings of *Hedera.* They found that rejuvenation took place in adult cuttings after treatment with cold and X rays. Further they grew rooted cuttings of adult and juvenile forms together in the same bottle containing a mineral nutrient solution and showed that the adult produced juvenile growth.

Both *Doorenbos'* and *Frank & Renner*'s experiments indicate the existence of a substance in the juvenile form which may cause a change in the meristem of the adult form when present in sufficient quantities.

Recently *Robbins* (1957 b) has provoked rejuvenation in adult cuttings of *Hedera canariensis variegata* by spraying the shoots with gibberellic acid. He suggests that gibberellic acid may be the very substance of juvenility.

Robbins stresses that the metabolic difference between juvenile and adult is not an all or none phenomenon, as in his experiments aerial roots might for instance develop on treated plants without change in leaf shape.

Doorenbos has kindly informed the author in a communication of January 28, 1958, that he has been able to repeat *Robbins'* experiments.

10. Recent Reviews.

Because of the increasing interest in meristematic aging of woody plants several recent reviews of literature on that subject have been published.

Felius & Doorenbos (1953) gave a review in Dutch of some papers on juvenile stages in woody plants. They preferred to speak of several overlapping juvenile stages and in this connection pointed out that the stage with great rooting capacity in apples was much shorter than the sterile stage. Thus they maintained that *Fritsche* (1948) assumed too strict correlation between juvenile stage characters (cf. p. 334). They further stressed the importance of clear definitions of the terms, cyclophysis, periphysis and topophysis, reserving the latter word exclusively for the phenomenon of side buds of different order developing differently.

A brief review of important literature in the field was given in a previous paper on experiments in ontogenetic development of *Fagus sylvatica* (*Schaffalitzky* 1954).

An extract of a thesis by *Tisseverasinghe* (1954) contains a short but excellent description and discussion of the phenomena with special importance given to Russian authors. There is however little new information except that *Kruzilin & Svedskaja*

(1950) had criticized *Krenke*'s theory (cf. p. 324), because he paid so little heed to the influence of environment on phasic development.

A Polish review of some of the literature was published by *Jentys-Szaferowa* (1955) who concentrated on the question of variation in leaf-shape. As "prominent in the foreground" was "the problem of leaf variability in connection with the physiological age of trees". It is the merit of *Jentys-Szaferowa* that she stresses how difficult it is to use leaf-shape as a character in development studies. Partly based upon own observations in a number of tree species, attention was drawn to the many other both environmental and endogenous factors influencing leaf-shape. She pointed out the relation of leaf-shape on dwarf shoots to the position of leaves and dependence of leaf-shape on the presence or absence of an inflorescence. Another factor of importance was the relation of leaf-shape to the location of leaves in the tree crown. Further she mentioned the special characters of leaves on sprouts and suckers.

Rohmeder made extensive reviews of literature on development stages in woody plants (1956 & 57). As he concentrated on the silvicultural and tree breeding aspects mainly, his observations and conclusions will be mentioned in the section on silvicultural aspects (cf. p. 349).

The problems of aging of the meristem in woody plants have usually been studied by investigators, who were interested because of the importance to one or another branch of applied botany. It was therefore a great step forward when *W. R. Robbins* took up the question from the view point of pure plant physiology in his paper on physiological aspects of aging in plants (1957 a).

Based upon an extensive knowledge of the literature and all the aspects of the problems, *Robbins*' paper represents in my opinion the most important statement since *Büsgen & Münch* (1927). It is therefore reasonable directly to quote his conclusions: "Without attempting to deal with ultimate causes or to settle the question of juvenile vs. adult meristems, I suggest as a working hypothesis that juvenility is an unstable metabolic state which exists in the meristem and which proceeds through a series of steps to a relatively stable metabolic state characteristic of the adult meristem. The change from unstable to stable may be associated with the loss in ability to synthesize physiologically important chemical substances and/or the development of the ability to synthesize others. This means that the meristem of the juvenile stage may be characterized by the presence of particular substances of physiological importance which are not present, or present to an appreciably lesser degree, in the meristem of the adult. The steady state of the adult may be upset in the direction of the unstable metabolism of the juvenile by cold, X rays, products from the juvenile, the formation of adventitious meristems and by the formation of zygotes or of asexual embryos. If these assumptions are correct, it might be possible to isolate and identify substances from the juvenile stage which, introduced into the adult, would cause it to become juvenile".

11. Silvicultural Aspects.

In the chapter on fruit trees it was stated that the interest in meristematic aging in horticulture is partly due to the extensive use of vegetative propagation (cf. p. 330).

Until recently grafts and cuttings were only exceptionally used in silviculture, and that is why the existence of development stages in trees is so little known to foresters.

Contributions on aspects of meristematic aging are scattered here and there in silvicultural literature and are of a heterogenous character.

For a Dane it is especially interesting that in his now classic book on Danish forests *Vaupell,* as early as 1863, supports the idea of a gradual change in the apical meristem with age. He says that in order to understand why a beech tree will not flower before an age of about 50 years one must rightly interpret the significance of ramification. One branch seems to be like the other; the young branch looks like the mother branch, yet it is not a case of repetition, but actual advancement takes place as the following generations of branches gradually approach the age of fertility.

Schenck (1893) had observed that one to five year old seedlings of *Larix decidua* often keep some of their leaves at the shoot tips during winter. He regards this as a juvenile character, but influenced by environment.

In a paper otherwise without general bearing on our problem, *Schreiber* (1924) drew the attention of foresters to *Schramm*'s investigations (cf. p. 326) when he emphasized that "Abweichungen im Gange der physiologischen Prozesse, wie sie aus den variablen Bauverhältnissen der Blätter gefolgert werden müssen, bedeuten für den Wirtschafter Aenderungen in den Ansprüchen der Holzart zu gedeihlichem Leben".

Büsgen & Münch (1927 p. 50) drew attention to the fact that every forester knows that shoots and needles from tops of old Norway spruce and silver fir have quite another appearance than from young five to ten feet tall trees. In old silver firs the shoots are more densely needled, the mutual position of needles is different and anatomical differences are also found. Grafts from tops of old spruces in the Tharandter Forstgarten retained many of these old age characters which were consequently caused by cyclophysis. Such grafts also flowered more profusely than even aged seedlings, and more than anything else they resembled tops of old trees cut off and stuck into the ground.

Mirov (1937) pointed out the importance of cyclophysis to forest tree breeding methods. In accordance with *Lyssenko* he distinguished between two phases only, the thermal and the light phase. He stressed that especially the topophysis phenomenon was very important in the extensive use of vegetative propagation. Forest tree breeders have usually paid astonishingly little heed to the view points presented by *Mirov* already in the childhood of tree breeding.

Janson (1938) reviewed some of the classic literature and believed *Beissner*'s fixation of juvenility through repeated propagation by basal cuttings to be a fact. In consequence he warned foresters against propagation by cuttings from young trees if they wanted to get seed production.

Following up the view points in his paper of 1937, *Mirov* (1943) reported that two cuttings from lateral branches of *Pinus radiata* had developed into straight trees thus indicating unimportance of topophysis for this species.

With special regard to silviculture *Passecker* (1947) reviewed some of the classical literature on aging of the meristem in woody plants, but he did not add much information to his earlier papers. However this review is perhaps his most complete picture of the problems. *Passecker* considered the juvenile forms to be hereditarily fixed modifications for humid and shaded conditions and the adult forms similar modifications for dry sunny environment. He stressed *the importance that in the future the juvenile forms of new sorts or clones should be kept.*

Mirov (1951) was able to cause male flowering in seedlings of a number of pine species by grafting them on to the crown of a mature ***Pinus ponderosa,*** prolific in its production of pollen and cones. After two growing seasons flowering began in the grafts, whereas control transplants did not flower. As in the experiments by *Kemmer* (cf. p. 336) the promotion of flower buds may be interpreted as an exclusively periphysical phenomenon caused by a greatly changed nutritional state in the grafts as opposed to the transplants.

It has already been mentioned several times in this review that rooting of cuttings is generally much easier with juvenile forms. During the last 20 years much evidence has been published on this special phenomenon, but only a part of the literature is included here, (*Anonymous* 1941, *Deuber* 1942, *Edgerton* 1944, *Larsen* 1946, *Toda* 1948, *Miyajima* 1951, *Borisenko* 1952, *Hough* 1953, *Heitmüller* 1954 and *Fielding* 1954).

It is in accordance with the examples from the Tharandter Forstgarten (cf. p. 322) that *Yamazaki, Iwamura & Ogasawara* (1953) in provenance experiments with ***Pinus densiflora*** found needle structure of this species to vary with age of trees. They compared needles of one, three and twenty-three year-old specimens; the mean number of stomata f. inst. increased with age.

Schröck (1956) made cuttings from epicormics at different heights of a ***Populus berolinensis.*** He was extremely careful to select uniform material, but only three cuttings were used from each different height. However he found a distinct variation of growth vigour in the different cutting categories. Maximum height growth was obtained in cuttings taken at about 4.5 m above the ground; below and above this height there was a gradual decrease in vigour. *Schröck* believes this to be of cyclophysical nature exclusively. The content of anthocyan was highest in cuttings from epicormics near the ground.

He notes that the leaves of ***Populus tremula*** are very different in young seedlings and in older trees, but Lammas shoots of the latter bear juvenile leaves. Consequently he regards this leaf character to be of periphysical origin.

It has been mentioned earlier that already the very first investigation (*Knight* 1795) connected senile decay of fruit tree varieties with greater susceptibility to cancer and other presumed old age diseases (cf. p. 313).

That a juvenile stage of a woody plant may be more susceptible to a fungal disease than the adult stage was experimentally proved for *Thuja plicata* by *Søegaard* (1956). He grew cuttings from tops of old trees together with young seedlings; in one experiment it was even possible to compare such cuttings with progeny obtained by self pollination. Whereas all the seedlings were killed or at least very badly attacked by leaf blight, the cuttings appeared highly resistant to the disease.

In a recent paper on the silvicultural aspects of meristematic aging, *Rohmeder* (1956) paid special heed to poplar growing. This is reasonable because poplars are generally propagated by cuttings; hence cyclophysical factors play an important part. He points out observations which support the idea of senility in poplar clones.

Together with *J. Barner* he compared photosynthesis and respiration of an old and a young clone. The latter had greater photosynthesis and less respiration than the former, and was thus superior from a silvicultural view point. However *Rohmeder* admits that it is not proved "ob hier genetische Ursachen für die Unterschiede im Verhalten der beiden Klone vorliegen, oder ob man das unterschiedliche Verhalten als Alterungsvorgang deuten kann".

In another paper (1957) *Rohmeder* emphasized that scion material for seed orchards should be selected in the flowering sections of tree crowns, whereas juvenile material was needed for cuttings intended for timber production.

A number of Russian and East German papers are specially interesting from the point of view of silviculture as they deal with *tending of forest stands* in relation to the teachings of *Michurin* and *Lyssenko*.

Although those two Russian workers described the life stages of plants in much the same way as *Goebel* and others (cf. p. 319), *Nikitin* (1941) stressed that they regarded as the most important character of juvenile stages the plasticity i.e. the ability to change as a result of variation in external conditions. *Lyssenko* believed in changes of the genotype itself, but there is no reason here to touch on the discussion which arose on the purely genetical aspects of this idea.

Nikitin used the aspen as example and described the separate stages of development. He spoke of an adolescent stage with an ascending trend of development during which the tree and its individual vegetative parts reach the culmination of height growth, fruit bearing commences and the basis of inheritance becomes fixed. The climax of this stage is reached after about three to five years of fruit bearing.

Heavy fruiting characterizes the next stage of full maturity, and this stage finally passes into the senile stage. The transition is accompanied by a gradual dominance of the fruitbearing branches over vegetative and a dying off, first of the small, later of the large branches, in other words, a sharply descending trend of development.

Nikitin made experiments in which cuttings from the upper part of the crown of *Betula fruticosa* flowered when one year old, whereas cuttings from one-year-old stool shoots under the same conditions did not flower but grew vigorously. Grafting experiments along the same lines were carried out with *Tilia* and *Quercus* and gave similar results.

Nikitin was probably the first who called attention of foresters to the fact that the practical consequence of the existence of such life stages in trees would be *to take cuttings from phasically old parts of a tree for establishment of plantations for seed production.* On the contrary, in raising poplars *for pulp-wood production cuttings from phasically young parts of seedlings should be used.*

Only second hand information has been available on the evidently very similar works of *Nesterov* (1952) and *Voropanov* (1950 & 1952).

Both of these Russian workers primarily distribute the trees in a forest stand into more or less classic groups of dominants, co-dominants and suppressed individuals. What is new, however, is their splitting of each class into two.

The *sub-class a* is characterized by rather slow development in youth followed by quicker growth later. On the contrary trees in *sub-class b* develop quickly when young, but their increment soon falls below that of a.

If the different growth rhythms are hereditary the two sub-classes represent nothing but the *so-called stayers and sprinters* the existence of which has been widely discussed among foresters.

Nesterov and *Voropanov* do not believe in existence of stayers and sprinters, but explain their sub-classes as results of environmental influence on development. Thus some trees grow slowly when young, exclusively because kept in a juvenile plastic stage by outer conditions.

The main practical object of classification is identification, hence removal of trees in sub-class b during thinning operations, because their increment is becoming relatively lower than in sub-class a. By removal of these furthest developed trees it may be possible to maintain a high volume production in a stand.

The utility of the classification depends on the possibility to classify the trees in practice. *Nesterov* recommends heavy fruiting as the most reliable index for sub-class b. Other characters of this class are low height increment, broad crown and horizontal branching.

Many silviculturists, also in Russia, will hardly agree that there is anything new in the views of *Nesterov* and *Voropanov,* just a use of other terms and mode of expression.

It is evident that their view points must lead to heavy crown thinning or even selection thinning. However *Liebold* (1955) stressed that it is only the trees, old in stage, which are thinned out, so the thinning system does not closely resemble *Borggreves Plenterdurchforstung* where only dominants were felled (*Dengler* 1935 p. 445).

Erteld (1955) used *Nesterov*'s classification in stands of Scots Pine and was able to show definite moves, upwards and downwards, among tree classes in accordance with *Nesterov*'s views. However *Erteld* did not use *Nesterov*'s main character of seed-bearing, because it required a fairly long period of observation. But he recommended to search for other characters.

Erteld believed that each tree had its own hereditary growth rhythm, which was however greatly influenced by environment, and concluded: "Erst bei einer Kenntnis der Zusammenhänge zwischen äusseren Eigenschaften eines Baumes und seines voraussichtlichen Wachstumsablaufs wäre es möglich, die Entwicklung eines Bestandes bewusst in Bahnen zu leiten, die dem jeweiligen Ziel wirklich dienen".

This is a very clear and reasonable conclusion on the present situation in relation to development stages and tending of forest stands.

Bormann (1954) has worked with ecological implications of juvenile stages in *Pinus Taeda.* He grew seedlings under shade and in full light and found that at the end of the first growing season 71 % of the functional leaf weight was secondary fascicled needles in the sun-grown seedlings, versus 52 % in the shade-grown. Initial measurements suggested greater shade tolerance in the primary needles. *Bormann* (1955) followed up these preliminary investigations by comparison of photosynthesis in 16 week-old and two-year-old seedlings. The experiments indicated that the former reached maximum photosynthesis at far the lowest light intensities.

In similar experiments *Bormann* (1956) compared 16 week-old seedlings with only juvenile foliage and with a mixture of primary and secondary needles. Although he found no difference in photosynthetic rates, it was evident that both sets of seedlings were more efficient under low light intensities than older pine seedlings. *Bormann* concluded that this shift in photosynthetic response with ontogeny explained why very young seedlings were able to become established under dense weed cover. Later when secondary foliage develops, it is easily understood why *Pinus Taeda* grows well in old fields but will often die out under dense forest canopies.

It may seem odd to mention development in *Hevea brasiliensis* under silvicultural aspects. However as the breeding methods are so similar in rubber and forest trees, it seems quite natural to foresters interested in genetics in silviculture.

It was early noticed in rubber breeding that buddings and seedlings showed different characters of which the most obvious was a conical stem form in seedlings versus a cylindrical in buddings (*Dijkman* 1951 p. 56). This might be explained by influence from the rootstock or from the budding operation.

In an experiment referred to by *Dijkman* (p. 214) each of 100 seedlings were compared to three of its own buddings. The result was that the buddings did not differ in their growth habit or form from their mother trees. The idea of influence only from rootstock or budding operation therefore had to be cancelled.

a. b.

Fig. 1.
Hevea brasiliensis. a. Mature type budding with cylindrical stemform. b. Juvenile type budding with conical stemform. Phot. 1956 H. Keiding.
Gummitræer. a. Okuleret alderdomsform med cylindrisk stamme. b. Okuleret ungdomsform med kegleformet stamme.

Hence the terms *JT budding (juvenile type)* and *MT budding (mature type)* arose. The explanation of the usual difference between seedlings and buddings of *Hevea* was that the latter were MT buddings from branches of mature trees, which would not reproduce the juvenile stage (fig. 1).

According to *Dijkman* (p. 57) JT buddings form a better unit and display better growth vigour than MT buddings. The bark at the stem base is thicker in JT buddings and this is the main reason for their conical stem form. Thick bark is a secondary character required in rubber breeding.

Also *Ferwerda* (1953) described JT versus MT buddings in a similar way, but certain differences between JT buddings and their seedling mother trees indicated an influence from the rootstock. It would be unreasonable to expect no rootstock effect so well known from fruit growing, and also *Dijkman* (p. 57) reported on divergences between JT buddings and their seedling mother trees, probably caused by the rootstocks.

Nowadays budding is the main procedure in rubber plantations of the Far East, and certain clones are used over thousands of acres. MT buddings are always used, which may seem astonishing in view of *Dijkman*'s stressing of the advantages of JT buddings. The difficulty of preserving the juvenile stage might be one explanation.

Recently *Tan Hong Tong* (1957) recommended more widespread use of seedlings in rubber plantations in Indonesia. He based this view upon the more vigorous growth and better resistance to wind damage and certain bark diseases of the seedlings.

12. On Leaf-Retention.

For centuries European foresters must have been aware that *young beeches will retain their withered leaves during winter whereas old beeches cast them off.*

This phenomenon was only touched upon in literature until it was thoroughly described by *Magnus* (1913) who had also observed that lower branches in old, otherwise leafless trees, might retain their leaves. The latter observation was explained by the influence of external factors of which *Magnus* was especially aware, shade versus light, but he had also observed individual variation as to degree of leaf-retention. He suggests a connection with the findings of *Schramm* and *Nordhausen* on change in leaf anatomy with age (cf. p. 326—27).

Magnus drew a parallel between the phenomenon that many tropical tree species when young retain their leaves during the dry season. For example *Simon* (1914 p. 141) observed that young trees of *Albizzia moluccana* renewed their leaves at a constant rate throughout the year, whereas leaf production in older trees was distinctly periodic. He found the same tendency in *Ficus elastica* (p. 98) and *Hevea brasiliensis* (p. 142).

In the latter species, leaf-retention or lack of "wintering" is usual also in mature type buddings in Malaya, thus showing a strong influence by external factors (*H. Keiding:* verbal communication).

It is natural to connect the phenomenon of juvenile leaf-retention with evidence in some young plants of a longer growth period or more shoot generations in a single growing season. Already *Huber* (1898) reported from Brazil that young *Hevea* *brasiliensis* might have five shoot generations in one year whereas the old trees had only one or two. And *Berthold* (1904 p. 250) called attention to the fact that young beeches, oaks and other hardwoods were more liable to produce Lammas shoots than old specimens.

Klebs (1914 p. 105) also studied this problem and considered the phenomenon to be due exclusively to a different environment which conditions a more favourable root/top ratio in young trees. He definitely rejected the idea of an influence by aging of the meristems, "als embryonale Substanzen in den ältesten Bäumen die gleichen Eigenschaften haben wie in den jüngsten Keimlingen".

Büsgen (1917 p. 224) referred to *Magnus* on leaf-retention of young beeches and had observed that a heavily cut beech hedge retained its leaves during winter.

Vegetative propagation of *Fagus sylvatica* has been in use at the *Hørsholm Arboretum* for twenty years. Both grafts and cuttings from old trees were leaf-shedding even when grafted on young seedling stocks or treated as a hedge. Cuttings or grafts from leaf-retaining scion-wood of young plants were scarce but appeared to keep the ability of not forming a separation layer. These observations were reported upon in a previous paper (*Schaffalitzky* 1954), and the subsequent experiments proved the existence of *a juvenile stage in Fagus sylvatica characterized by the ability to retain the withered leaves during winter.*

In 1952 scions were collected from basal leafy epicormics, higher leafless epicormics and top branches of the same beech tree. The three categories of scions were grafted to uniform seedling stocks, and in the winter of 1953/54 the first appeared to have produced leafy grafts only, whereas leafless grafts arose from the two latter categories.

Another experiment demonstrated that leaf-retaining scions did not shed their leaves even when grafted to leaf-shedding branches of an old beech tree. It is in accordance with this result that no evidence was ever obtained of influence as regards this character from the scion on the stock or vice versa, even if some of its own shoots were by exception kept on the stock.

The basis of this demonstration of the juvenile leaf-retaining stage in beech is that the author accepts the view that epicormics *from buds in the lower trunk portion keep the juvenile character. As basal epicormics and stump-sprouts both from dormant buds and from adventitious buds appear to be leafy, the entire lower trunk portion and the root system seem to remain juvenile. This point of view is supported by investigations in Bernstorff Park (p. 401) and should be especially noted, because it is the basis of the experimental technique in the demonstrations chapter II and therefore of the results.*

The layout of the experiment excludes any variation in genetical constitution of the scions, as they were collected from a single individual tree. As external conditions were kept uniform and as it was not a case of different behaviour in parts of shoots, everything pointed to a clear example of cyclophysis.

As no cases of simultaneous winter foliage and flower buds were known, the author stressed that in tree breeding, scions for use in seed orchards should never be collected from low epicormics but from flowering branches in old trees.

In another paper (*Schaffalitzky* 1955) it was demonstrated that old *Fagus sylvatica* possessed a development stage characterized by abundant flowering. This appeared from experiments with scions from a very old flowering beech clone grafted together with non-flowering clones on horizontal branches of a 50 year old rootstock tree. The former flowered abundantly two years after grafting, whereas the rest were sterile. It was proved that flowering was greatly influenced by environment as scions from the old clone became sterile when grafted to young vigorous plants of *Fagus orientalis* with less exposure to sunlight.

It was mentioned in the first paper (*Schaffalitzky* 1954) that shoot tips were often leafless in otherwise juvenile leaf-retaining beeches. Later experiments (*Schaffalitzky* 1956 a) showed that it was impossible by grafting to maintain in such leafless shoot tips the ability of leaf-shedding.

CHAPTER II.

INVESTIGATIONS AND EXPERIMENTS. DEMONSTRATIONS.

Once attention was called to and proof given of the existence of the juvenile leaf-retaining development stage in *Fagus sylvatica* it was but natural to look for similar phenomena in other tree species.

It soon became evident that concentration on rather few species in which preliminary observations clearly indicated existence of meristematic aging was necessary. Species with homoblastic development had to be avoided because there, a great experimental material was required. What primarily limited the extent of experimental work was the lack of sufficient suitable rootstock material growing under uniform external conditions. Furthermore vegetative propagation technique was not always sufficiently developed for certain species.

A number of hardwoods were selected even though certain conifers offered equal opportunities for studying the problem. However as beech had been the starting point, it seemed natural to continue with other hardwoods, especially those species in which the character of leaf-retention was again found.

The experimental layout of these demonstrations of development stages followed as closely as possible the original layout for beech:

Once the theory was formed that two different stages existed in a species, a suitable individual could be selected. The main criterium for selection was that scions in both presumed development stages could be obtained from that individual. Generally this criterium was fulfilled by trees with low epicormics, just as described for beech (chapter I section 12).

Table 1.

Investigations on leaf-retention and leaf-shedding in grafts of some beech clones. Repeated observations demonstrate existence of the juvenile leafy as well as the adult leafless development stage.

Clone no. *Klon no.*	Origin of scion-wood *Podemateriale fra*	Age of parent tree *Ophavstræets alder*	Graft year *Podeår*	Root-stocks *Grundstammer*
V. 440	leafless top *top uden blade*	140	1952	seedlings *frøplanter*
»	leafless epicormics *vanris uden blade*	140	1952	seedlings *frøplanter*
»	leafy epicormics *vanris med blade*	140	1952	seedlings *frøplanter*
V. 440	leafless graft from 1939 *podn. fra 1939 uden blade*	140	1952	seedlings *frøplanter*
»	leafless graft from 1939 *podn. fra 1939 uden blade*	140	1952	old tree *gl. træ*
»	leafy graft from 1939 *podn. fra 1939 med blade*	140	1952	seedlings *frøplanter*
»	leafy graft from 1939 *podn. fra 1939 med blade*	140	1952	old tree *gl. træ*
V. 440	leafless top *top uden blade*	140	1954	seedlings *frøplanter*
»	leafy epicormics *vanris med blade*	140	1954	seedlings *frøplanter*
327	leafless top *top uden blade*	120	1954	seedlings *frøplanter*
»	leafy epicormics *vanris med blade*	120	1954	seedlings *frøplanter*
1	leafless high branches *top uden blade*	20	1954	seedlings *frøplanter*
»	leafy low branches *nedre grene med blade*	20	1954	seedlings *frøplanter*
2	leafless high branches *top uden blade*	20	1954	seedlings *frøplanter*
»	leafy low branches *nedre grene med blade*	20	1954	seedlings *frøplanter*
3	leafless top *top uden blade*	220	1956	seedlings *frøplanter*
»	leafy epicormics *vanris med blade*	220	1956	seedlings *frøplanter*

Tabel 1.

Undersøgelser over nogle podede bøgekloners evne til at bevare eller kaste bladene. Gentagne iagttagelser viser forekomsten af et bladholdende ungdomsstadium og et bladkastende alderdomsstadium.

Number of leafy and leafless grafts in the winter of *Antal podninger med og uden blade i vinteren*										Remarks *Bemærkninger*
1953/54*		1954/55		1955/56		1956/57		1957/58		* published earlier (*Schaffalitzky* 1954) *offentliggjort tidligere*
leafy *med blade*	leafless *uden blade*	leafy *med blade*	leafless *uden blade*	leafy *med blade*	leafless *uden blade*	leafy *med blade*	leafless *uden blade*	leafy *med blade*	leafless *uden blade*	
0	47			1**	27	0	28	0	27	** 10 leaves *blade*
0	33			0	28	1***	27	2***	27	*** few leaves *kun få blade*
27	0			27	0	27	0	27	0	
0	30			0	20					
0	13	0	13	0	13	0	13	0	13	
58	0			40	1■	21	0	21	0	■ weak plant *svag plante*
7	0	7	0	7	0	7	0	7	0	
				0	44					replanted spring 1955 *omplantet forår 1955*
				55	9					
				0	15	0	15	0	15	
				28	1□	31	0	31	0	□ weak plant *svag plante*
				0	31	0	29			
				21	0	19	1			
				2●	32	2●	32			● one plant with few — the other with many leaves — due to error. *den ene plante med kun få — den anden med mange blade — skyldes fejltagelse.*
				25	0	24	0			
								0	14	
								32	1	

Scions from the two categories were grafted on rootstocks of identical origin, growing under similar conditions, usually in two neighbouring rows. Grafting and later treatment of the grafts were carried out simultaneously and by exactly the same methods, hence any differences caused by the treatment were excluded.

If the presumed development stage characters persisted in the two categories of grafts, the existence of the development stages were regarded as proved.

This comparative method simply represents a further development of the so-called *tree-shows,* designed by *Syrach Larsen* (1947) for comparison of clones. In the present work the technique is used within the same clone.

In a number of cases it was necessary to vary the usual layout in one way or another. These variations will be mentioned under the different species.

1. *Fagus sylvatica.*

Although conclusive evidence was presented in a previous paper (*Schaffalitzky* 1954) on the existence of the juvenile leaf-retaining development stage in *Fagus sylvatica,* it seemed reasonable to support this evidence by repeated experiments and observations.

It has been possible to follow the original grafts from 1952 of the first clone (V. 440) during several years. The results are shown in table 1 and they clearly support the original evidence.

There is reason to stress that minor deviations are ascertained and must be expected because of small environmental differences (cf. p. 397). The material was usually not assessed in winters after a replanting.

In 1954 new scion-wood was collected from the parent tree of clone V. 440. The grafts were used for special experiments, hence only assessed as to leaf-retention in 1955/56. According to table 1 they also support the original results. The material in this case had to be assessed just after replanting, which might be the cause of the 9 leafless grafts from leafy epicormics. However some of the leaf-retaining scion material might have been just at transition to the adult stage. The important feature of the demonstration is that no leaf-shedding material became leaf-retaining.

In 1954 another beech over 100 years old (table 1 no. 327) was taken in, and in successive years clearly demonstrated the existence of the two stages.

Also two beeches about 20 years old were selected for propagation. Both were showing gradual transition from juvenile to adult stage. In these cases low epicormics did not occur, but the lower interior branches retained their leaves. Both trees were thus classical examples of the usual transition picture found in young isolated beeches (fig. 20).

Table 1 shows that also these grafts were stable as to the character of leaf-retention. The author has purposely kept one graft which should have been leaf-shedding, but retains many leaves. As a single exception it rather supports the general view, but its existence must be due to a mere error at scion collection or at grafting. Such errors are human, and a statement of them takes relatively too much space, but is preferable to omittance.

Finally it is natural to include in this passage another beech tree more than 200 years old which was grafted in 1956 (table 1 no. 3). As two year old grafts, the material represents another example to show the existence of the juvenile and the adult stage in *Fagus*, characterized by winter leaf-retention.

2. *Quercus robur and Quercus petraea.*

Having observed leaf-retention phenomena in beech and the connection to meristematic aging, it soon becomes evident that similar pictures exist in our two common oak species. It is however natural to work with beech first, because so far, all beeches observed, proved to pass a leaf-retaining stage, which they all left again at a fairly early age.

Comparing beech to oak, the first great difference is pronounced individual variation. Many specimens of both *Quercus robur* and *Quercus petraea* never retain leaves, on the other hand, others remain in the leafy stage even at great age.

In leaf-retaining oaks the phenomenon manifests itself exactly as in beech. The transition picture in isolated specimens of young oak is definitely parallel to that in isolated beeches; old leafless oaks with low leafy epicormics are a common sight in Danish forests (fig. 3).

Just as *Magnus* (1913) was the first to describe thoroughly the phenomenon of leaf-retention in beech, he simultaneously pointed out that *Quercus robur* and *Quercus petraea* behaved in a similar way. *Magnus* drew attention to the great individual variation of oak, supported by personal observations in the vicinity of Potsdam. He writes: "Von Bäumen, die, soweit es zu erkennen war, unter ganz gleichen Bedingungen nebeneinander wuchsen, kann der eine das Laub im Herbst völlig verlieren, während der andere bis in das Frühjahr hinein völlig oder zum Teil mit ihm bedeckt bleibt. Dabei ist das Verhalten der einzelnen Bäume in den aufeinanderfolgenden Jahren ein recht gleichartiges".

Magnus was also aware that *Quercus petraea* was usually more inclined to leaf-retention than *Quercus robur,* hence the two popular Continental names, "winteroak" for the former and "summeroak", for the latter. Further he stressed the influence of environment on the phenomenon.

Hauch (1915) mentioned in his first report on provenance experiments in oak that because of leaf-retention, the Hald provenance plot appears as a red square among the leafless plants of the other plots.

Also *Krahl-Urban* (1957) found great differences in leaf-retention among his different oak provenances. It was extraordinary that the *robur* plots were rather more leafy than the *petraea* plots in these experiments.

In order to study the stability of leaf-retention in oak, 36 copiously leafy trees were selected in the winter of 1956/57. These trees were found in four different stands at Hørsholm and Jægersborg Forest Districts. In two of the stands 19 leafless trees were also selected.

In the following winter of 1957/58 leaf-retention was assessed in these trees. The observations showed complete consistency, thus demonstrating that ability or inability to retain leaves are stable, and probably individual, characters.

Although the ability to retain leaves in itself may be a rather indifferent tree character, there might be a possibility that the character is indicative of other, more important silvicultural or technical properties. Provisional observations in the same stands however indicated no obvious connection between leaf-retention and tree form, growth vigour or time of leafing-out.

Four young oaks were further observed during the period

a. Fig. 2. b.

Winter leaf-retention as hereditary character in oak. Progeny after controlled crossing. a. Quercus petraea no. 1 ♀ × Quercus robur no. 2 ♂. Observe the paucity of foliage. b. Quercus petraea no. 1 ♀ × Quercus robur no. 3 ♂. Observe the copious foliage. Drawn March 1958 Noll.

Evnen til at beholde løvet om vinteren er en arvelig egenskab hos eg. Afkom efter kontrolleret bestøvning. a. Quercus petraea no. 1 ♀ × Quercus robur no. 2 ♂. Bemærk den gennemgående mangel på blade. b. Quercus petraea no. 1 ♀ × Quercus robur no. 3 ♂. Bemærk de mange blade.

from 1952 to 1957. Two were constantly leafy and two were leafless. One graft from each exists at the Arboretum and behaves like the "parent". This is another example of consistency and the possibility of perpetuation by grafting is an indication of a clonal quality.

By chance other material was available in which *the hereditary character of leaf-retention ability was demonstrable.*

In 1948 *H. Barner, H. Christiansen* and *C. A. Jørgensen* artificially crossed a leafy *Quercus petraea* with four different specimens of *Quercus robur*. The progeny from these crosses were planted at the Danish State Forest Tree Breeding Station, and the three investigators kindly allowed me to assess the degree of leaf-retention (fig. 2).

The observations were made in the winters of 1956/57 and 57/58. Already at first glance it was evident that the different hybrid lots varied in degree of leaf-retention.

By the assessments each plant was classified as leaf-shedding or leaf-retaining. Originally the material was divided into five classes according to number of leaves. Because of the rather small progenies which did not permit a real segregation test, it was finally decided to use two classes only: leaf-retaining = over 50 leaves; leaf-shedding = under 50 leaves. These two classes were most suitable in 1956/57, and they were retained in 1957/58 for the sake of continuity. It is clear that with increasing tree size, a greater number of leaves are actually required for the use of the term "leaf-retaining".

Table 2.
Leaf-retention in artificial crosses between Quercus petraea no. 1 ♀ and Quercus robur no. 1—4 ♂.
Bladhold hos kunstige krydsninger mellem Quercus petraea no. 1 ♀ og Quercus robur no. 1—4 ♂.

Sow. no. *Såning no.*	Cross *Krydsning* ♀ × ♂ Quercus petraea		Quercus robur	Plants *Planter* Number *Antal*	Percent with over 50 leaves *Procent med over 50 blade* 1956/57	1957/58
1080	no. 1	×	no. 1	30	63	67
1084	—	×	— 2	31	0	19
1081	—	×	— 3	59	90	95
1082	—	×	— 4	89	66	70

The results are presented in table 2. It is evident that the two assessments give very similar results. The detailed classification is not published but shows that each plant usually behaves uniformly in the two successive years.

The important and interesting result is that *Quercus robur no. 2, as crossing partner, has produced a much more leafless progeny than the three other robur trees.* As all *Quercus robur* parent trees have now attained the leaf-shedding stage, it has not been possible to ascertain whether no. 2 has always been the most leafless of the four. However no. 3, which has produced the most leafy progeny, retains some leaves in low epicormics.

In order to obtain some answer to the question: Is *Quercus petraea* definitely more apt to retain leaves than *Quercus robur?*, *H. Vedel* and the author visited 26 natural oak scrubs in Jutland in January 1957. Based on the flora lists of *Gram, Jørgensen & Køie* (1944), we selected 13 pure *petraea* and 13 pure *robur* scrubs in approximately the same regions. Another object of the tour was to assess leaf-retention in great numbers of isolated oak trees.

We were able to confirm the assumption that the pure *petraea* scrubs contain specimens retaining the leaves more solidly and to a greater height, than the specimens of pure *robur* scrubs. Also the proportion of trees leafy right to the top was greater in the first mentioned species.

So numerous however were the exceptions, that our main result is that *winter leaf-retention can by no means be used as a fair species character.* Individual variation was once more the most striking feature.

During the five days of our tour we had opportunities to observe very many isolated oaks in all age classes and sizes which would never have been possible in the larger, more closed, Danish oak stands. We found so many examples of young trees with the gradual transition picture known from beech and of older leafless trees with low leafy epicormics, that the existence of a juvenile leaf-retaining stage in these trees seemed beyond question.

For the experimental demonstration of leaf-retention as a juvenile character, a 60 year old specimen of common oak was selected in Folehave Forest (fig. 3). It was a typical example of

Table 3.
Leaf-retention in grafts from the 60 year old oak in fig. 3.
Bladhold hos podninger fra den 60 år gamle eg i fig. 3.

Origin of scion-wood *Podemateriale fra*	Graft year *Pode-år*	Number of grafts in the winter of *Antal podninger i vinteren*					
		1955/56		1956/57		1957/58	
		leafy *med blade*	leafless *uden blade*	leafy *med blade*	leafless *uden blade*	leafy *med blade*	leafless *uden blade*
leafless top *top uden blade*	1954	0	9	0	7	0	7
leafy epicormics *vanris med blade*	1954	2	10	4	8	9	3

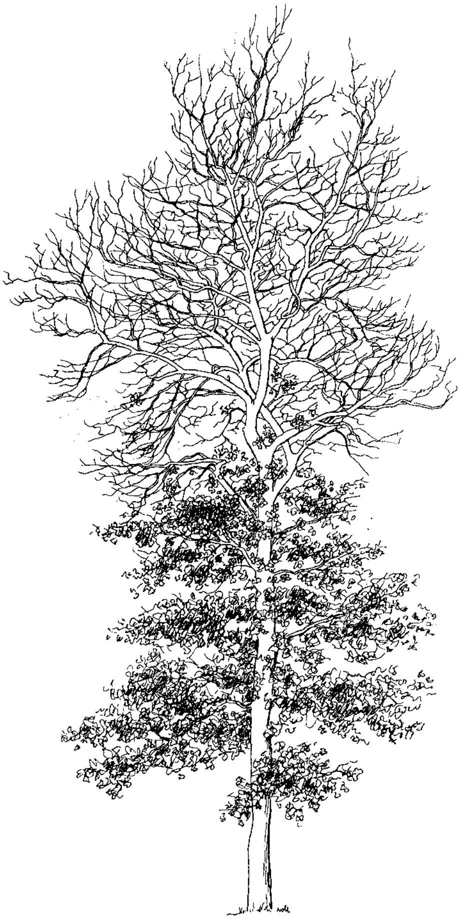

Fig. 3.
Isolated oak tree used in the demonstration experiment of table 3. Note the juvenile leafy zone and the leafless top. Typical transition picture. *Drawn, Noll, after photo from March 1954.*

Det fritstående egetræ, der blev anvendt til demonstration i tabel 3. Bemærk ungdomszonen med blade og den bladløse top. Typisk overgangsbillede.

a leaf-shedding tree with low leaf-retaining epicormics. Both in 1953 and 1954, grafting was made in the usual way with the two categories of scions.

Of the 1953 material only one graft of each kind is alive. Both of these would be termed leafy to-day, although the one from leafless scion-wood has considerably fewer leaves than the other.

The results from the second propagation are shown in table 3.

It is evident at once that the demonstration is not so striking as for beech, and it seems to take longer time before the plants are so established as to justify assessment. The grafts from leaf-retaining epicormics have only gradually become more and more leafy. Rootstock effects and other environmental factors may play a greater rôle in oak.

The conclusiveness of the latter experiment may be questioned. *However there is much evidence to support existence of a juvenile leaf-retaining stage in many oak trees.* Especially in view of the observations from the oak scrubs of Jutland, the author regards it as an undeniable fact. However it would be interesting to investigate more oak clones by the usual method.

3. *Carpinus Betulus.*

Winter leaf-retention is also common in *Carpinus Betulus,* although it was not mentioned in available literature.

According to observations in isolated individuals, the phenomenon in this species is more similar to the picture in beech than that in oak. As in beech, all seedlings of hornbeam seem leafy in full light, but the leafy period is short, and fairly old trees with leaves in their tops, as described for oak, are never found.

On the other hand, environmental influence on the phenomenon manifests itself even more clearly than in both beech and oak. Observations in the town of Hørsholm showed that this is especially evident in cut hedges, which are not overall leafy as beech hedges. However, at hedge corners, free from shade and from root competition, leaf-retention normally becomes evident, which shows that hereditary variation plays a lesser rôle than in oak.

Opportunity of making observations of transition pictures and of the behaviour of lower and higher epicormics was rather scarce in *Carpinus Betulus.* However the isolated specimens observed all behaved exactly like beeches as regards leaf-retention. Thus there was a definite indication of the existence of a juvenile leaf-retaining stage also in hornbeam (fig. 4).

Therefore in 1953/54 a typical leafless tree with low leafy epicormics was selected in Folehave Forest. Scions of the two categories were grafted after the usual system on young stocks. Later we had to take in other clones of different age (table 4).

In the present paper it seemed unreasonable to go into detail of the experiments which were unsuccessful due to poor grafting results. They are simply omitted.

Fig. 4.

Typical transition picture in young *Carpinus Betulus*. Juvenile zone with leaves and adult zone without leaves. Clone no. 3 in table 4. Drawn Jan. 1958 Noll.

Typisk overgangsbillede hos ung avnbøg. Ungdomszone med blade og alderdomszone uden blade. Klon no. 3 i tabel 4.

This is fair, but the reader may occasionally wonder why the number of grafts is so small, especially in the demonstrations within other species than beech. It was mentioned p. 357 that limited rootstock material was often available, and hornbeam is a good example of how technical grafting difficulties may also complicate the demonstrations.

Therefore in table 4 the unsuccessful attempts have likewise been listed. It appears that we never succeeded in grafting the adult flowering stage, and it is seen how alarmingly near our material may be to zero because of technical difficulties.

Table 4.

Grafting results and leaf-retention in grafts from leafless and leafy regions of Carpinus Betulus trees.

Poderesultater med og bladhold hos podninger fra grensystemer med og uden blade af forskellige avnbøge.

Clone no. *Klon no.*	Origin of scion-wood *Podemateriale fra*	Age of parent tree *Ophavstræets alder*	Graft year *Podeår*	Number of grafts *Antal podninger*					
				propagated *formeret*	living *i live*	in the winter of *i vinteren* 1956/57		1957/58	
						leafless *uden blade*	leafy *med blade*	leafless *uden blade*	leafy *med blade*
1	leaf-shedding flowering top *blomstrende top uden blade*	60	1954	18	0				
»	leaf-retaining low epicormics *lavtsiddende vanris med blade*	60	1954	18	1	0	1	0	1
1	leaf-shedding flowering top *blomstrende top uden blade*	60	1955	33	0				
»	leaf-shedding high epicormics *højtsiddende vanris uden blade*	60	1955	25	1	1	0	1	0
»	leaf-retaining low epicormics *lavtsiddende vanris med blade*	60	1955	26	2	0	2	0	2
3	leaf-shedding high branches *højtsiddende grene uden blade*	15	1955	25	7	7	0	7	0
»	leaf-retaining low branches *lavtsiddende grene med blade*	15	1955	27	5	0	5	0	5
1	leaf-shedding flowering top *blomstrende top uden blade*	60	1956	25	0				
2	leaf-shedding flowering top *blomstrende top uden blade*	60	1956	16	0				

Even if the material is scanty the reply to our question has the same character of certainty as with beech, and there are no exceptions or contradictions in it.

Thus *the existence of a juvenile leaf-retaining development stage has also been established in Carpinus Betulus.*

4. *Quercus borealis.*

In the search for tree species in which preliminary observations indicated existence of easily demonstrated development stages, the autumn colouring of *Quercus borealis* attracted attention.

While young plantations of the red oak are often a brilliant sight in October with their leaves turning red, the older stands show yellow colours.

As autumn colouring is known to be greatly influenced both by local and climatic conditions, is was not immediately certain that the two different colours represented a case of meristematic aging.

As it was impossible to find an old tree with low epicormics it was necessary to deviate from the normal demonstration procedure. Instead of comparing two graft categories from the same individual, a comparison was made between grafts from yellow-turning scions of a 150 year old tree and seedling progeny from the same tree. As these seedlings stand on their own roots one might imagine that the two plant lots were not directly comparable. However we possess grafted *Quercus borealis* in the Arboretum which turn nicely red, so grafting as such does not preclude appearance of red autumn colouring.

The red, respectively yellow, leaf colours only represent short-termed phases in the colour change from green to brown. As this change takes place at different times in various plants, and as certain climatic conditions (f. inst. in 1956) may preclude appearance of red leaf colour, it was decided to assess the colour of the midrib instead.

Colouring of the midrib appears every year and is stable throughout a fairly long period. There is no doubt that change in midrib colour is the first step in the autumn colouring of the leaf and thus indicates its normal autumn colour.

Our adult material consists of two grafts from 1954 and six from 1956. The seedling progeny comprises 18 plants from 1953. Observations were made in the autumn of 1955, 56 and 57. The midrib colour was judged separately for each plant.

All midribs of the grafts from the old tree turned yellow, whereas those of the seedlings assumed a purple colour. The best way of presenting the strikingly different colour change is a photo (fig. 5).

Fig. 5.

Autumn colouring in red oak. Upper row: Demonstration of the colour change from green over red to brown in leaves of young seedlings. Observe the purple midrib of the green leaf. Lower row: Demonstration of the colour change from green over yellow to brown in leaves of adult grafts. Phot. Oct. 1957 B. Søegaard.

Efterårsfarver hos rødeg. Øverste række: Farveforandringen fra grøn over rød til brun hos blade af unge frøplanter. Bemærk den purpurfarvede midterribbe i det grønne blad. Nederste række: Farveforandringen fra grøn over gul til brun hos blade af podninger fra toppen af et gammelt træ.

Although there is no doubt that autumn colouring in red oak is greatly influenced by environment, the above observations show that *meristematic aging hinders the change to red in older trees.*

5. *Fraxinus excelsior.*

Beforehand there was nothing obvious to indicate the existence of different development stages in ash.

However as trees with low epicormics were available near Hørsholm, and grafting known to be easy, *Fraxinus excelsior* was included in the experiments.

In 1954 scions were grafted from top branches and from very low epicormics of a circa 20 m high tree in Folehave Forest. The grafts of both categories grew vigorously in 1954, but the shoot colours were strikingly different. Whereas the 10 grafts from top branches were green, the 14 from the low epicormics were purplish in appearance. This character persisted during the following three growing seasons.

Any Danish forester will have noticed the existence of purple and green seedlings in young ash plantations. The only possible explanation of the above results therefore is that purple ash plants will gradually leave the purple stage and enter the green stage. The phenomenon primarily reminds one of leaf-retention in oak because it is a characteristic conditioned by both heredity and development.

From another ash tree with extremely low epicormics, grafts were made by the usual system in 1956 at the Arboretum by hand grafting and at the State Forest Tree Breeding Station by grafting in the nursery. Shoot colouring was only assessed in 1956. By chance we once more had a purple specimen, and at both localities the grafts from top branches, 18 and 30 plants, were all green, whereas those from epicormics, 19 and 25 plants respectively, were all purple. *Meristematic aging in purple ash seedlings thus causes decline in ability to form anthocyan.*

Another difference between juvenile and adult ash grafts was variation of leaf form. It was especially evident in the 1956 grafts that the adult grafts bore relatively narrower leaves than the young ones. In the third pair of leaflets from the tip of one normal compound leaf per plant the ratio length/width was measured. The compound leaf was selected near the top of the plant and the width measured exactly at half leaf length.

Table 5.

$\frac{\text{Length}}{\text{width}}$ ratio in leaflets of two Fraxinus excelsior clones. Comparison of grafts from low epicormics with grafts from top branches.

Forholdet mellem bladlængde og -bredde hos småblade af 2 askekloner. Sammenligning af podninger fra lavtsiddende vanris og fra topgrene.

Clone no. *Klon no.*	Age of parent tree *Ophavstræets alder*	Graft year *Podeår*	Origin of scion-wood *Podemateriale fra*	Number of leaflets measured *Antal målte småblade*		1956		1957	
				1956	1957	$\frac{\text{Length}}{\text{width}}$ ratio $\frac{\textit{Længde}}{\textit{bredde}}$	Corresponding values of t *Tilsvarende værdier af t*	$\frac{\text{Length}}{\text{width}}$ ratio $\frac{\textit{Længde}}{\textit{bredde}}$	Corresponding values of t *Tilsvarende værdier af t*
1	40	1954	top branches *topgrene*	20	20	3.4	6.7***	4.0	5.8***
»	»	»	low epicormics *lavtsiddende vanris*	28	28	2.6		2.9	
2	70	1956	top branches *topgrene*	40	44	4.5	13.5***	3.5	7.7***
»	»	»	low epicormics *lavtsiddende vanris*	36	38	2.6		2.7	

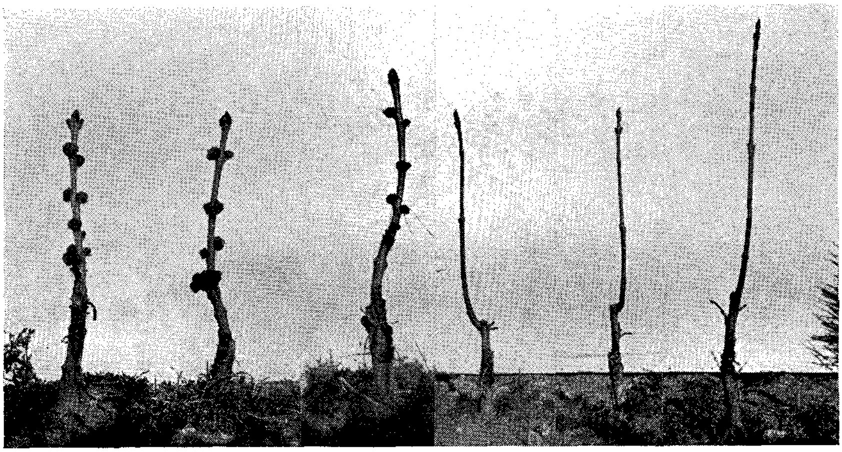

Fig. 6.
Grafts of Fraxinus excelsior clone no. 2. Left: Three typical heavily flowering specimens of top branch origin. Right: Three typical non-flowering specimens of low epicormic origin. Phot. April 1957 H. Vedel.

Podninger af askeklon no. 2. Til venstre: tre typiske kraftigt blomstrende planter fra toppen af træet. Til højre: tre typiske sterile planter fra lavtsiddende vanris.

Table 5 shows the results of the measurements in 1956 and 1957. The ratio used seems influenced by other factors, as it is not constant in the two years, but the difference between the two graft categories in this respect is highly significant for both clones in both years. *It is thus demonstrated that leaf form changes with the age of the meristem.*

The results in ash are especially interesting because two characteristics of meristematic aging were found, shoot colour and leaf form, although no working hypothesis on this matter existed beforehand. Once attention was called to these phenomena by the usual demonstration method, both characters were observed in abundance in our older ash grafts and in the forest.

The second *Fraxinus* clone has further demonstrated *a striking difference between the juvenile and adult grafts as regards flowering.* Of the lots at the Arboretum none of the juvenile grafts flowered in 1957, but 86 % of the adult grafts did so (fig. 6). The corresponding figures for the lots at the State Forest Tree Breeding Station were none and 48 %.

The *Fraxinus* material indicated existence of some physiological differences which will be described in chapter III (p. 430).

6. *Acer pseudoplatanus.*

In a number of *Acer* species a change in ramification with age is noticeable.

If mechanical damage is avoided, a young *Acer pseudoplatanus* will form a single main axis, and also the lateral axes will remain unbroken until flowering sets in from the terminal bud; flowering in sycamore actually begins in side branches. Because the inflorescence emerges from the terminal buds the two opposite buds below will take the lead und usually give rise to equally strong axes. *The typical repeatedly forking ramification in old sycamores is therefore a direct result of repeated flowering.*

Flowering from the terminal bud of the main axis usually begins later. From a silvicultural point of view the height at which the first flowering takes place is extremely important. There the main axis of the tree is broken, and the length of the bole irrevocably determined. A forked tree has been produced.

In the present investigation it is interesting to know whether flowering, hence forking, is conditioned by environment only or if meristematic aging plays a rôle.

We were faced by great technical grafting difficulties and obliged to use a herbaceous summer grafting method (*Schaffalitzky* 1956) as our first attempts were failures.

The first technically successful experiment comprises 3 grafts from low epicormics without flowers from one tree and 5 from flowering forking branches of another. The experiment may only be regarded as an indication; differences could eventually be due to clonal divergences.

Grafting was made in the summer of 1954, and all 8 grafts grew with a single main axis during 1955. However in 1956 terminal bud flowering took place in all 5 grafts from flowering material, but the 3 grafts of epicormic origin prolonged their main axis by another leading shoot.

During 1957 the 3 latter grafts behaved exactly as in the preceding year, but the 5 former produced 1, 1, 5, 12 and 16 inflorescences respectively. As was expected, flowering had provoked forking, and the 5 grafts have already lost their main axes completely (fig. 7).

In the summer of 1955 grafting was carried out with the two

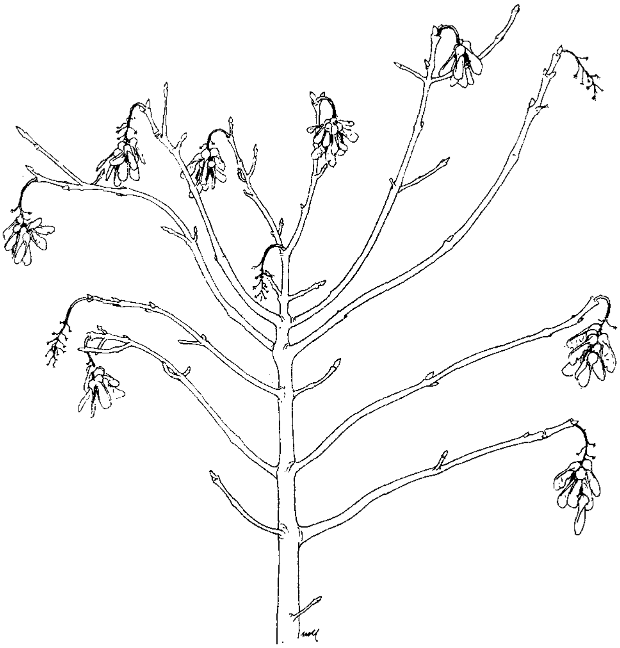

Fig. 7.

Three and a half year old graft of Acer pseudoplatanus. Scion-wood from flowering branch. Observe the precocity and hence complete destruction of tree form from a forestry point of view. Each inflorescence usually provokes a fork. Drawn Jan. 1958 Noll.

Tre et halvt år gammel podning af ær. Podemateriale fra blomstrende gren. Bemærk frugtbarheden og den heraf følgende fuldstændige ødelæggelse af formen set fra et forstligt synspunkt. Hver enkelt blomsterstand fremkalder normalt en tvege.

scion categories from one old tree. The epicormics were situated as low as the root collar.

On the lines of the preceding experiment all grafts grew vegetatively during the first season after propagation. In 1957 the 5 grafts of epicormic origin continued growth with one main axis, whereas forking through terminal bud flowering was caused in 5 of 7 grafts from the top material. Besides the terminal inflorescence these 5 grafts produced 0, 1, 2, 9 and 18 inflorescences. The two non-flowering grafts of top category were grafted to lower side branches on a stock bearing one of the flowering grafts above.

Once more though the material is limited, it is striking that it has been impossible to cause the greater part of the grafted top material to abandon its flowering habit. This is true in spite of very vigorous rootstocks, stool shoots, which evidently occasioned considerable growth vigour in the grafts.

From observations of young isolated sycamores compared to trees of almost the same age in closed stands, it was obvious how much earlier flowering, and therefore forking, took place in the former. This is no doubt the explanation of the, from a forestry view point, ugly form of isolated sycamores in gardens and along roads.

This great environmental influence by no means excludes the existence of meristematic aging in sycamore, as strongly

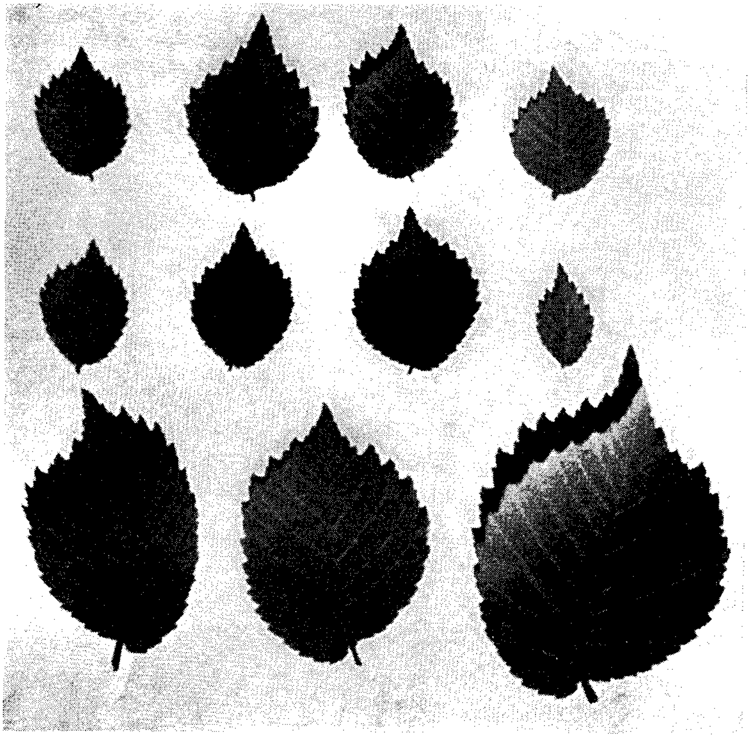

Fig. 8.

Leaf no. 6 from the tip of the leader in each graft of Ulmus carpinifolia. The two upper rows are from grafts of epicormic origin, whereas the lowest row is from grafts of top branch origin. Observe the difference in size and obliquity. Phot. Oct. 1957 B. Søegaard.

Blad no. 6 fra spidsen af topskuddet på hver enkelt podning af småbladet elm. De to øverste rækker er fra podninger af lavtsiddende vanris, medens den nederste række er fra podninger af topmateriale. Bemærk forskellen i størrelse og skævhed.

indicated by the experiments, but we are simply facing a case of external factors which change the duration of the juvenile development stage.

7. *Ulmus carpinifolia.*

Already *Schramm* (1912) mentioned that certain leaf characters in *Ulmus carpinifolia* might be explained by the existence of development stages in this species (cf. p. 327). Thus young plants bear scabrous and non-oblique leaves, whereas older trees are characterized by smooth and very oblique leaves.

A really typical *Ulmus carpinifolia* was not propagated until 1956. It was possible to obtain scions from basal epicormics and from top branches. We obtained 8 grafts of the former, 3 of the latter category.

Already at first glance the habitus of the two plant lots is strikingly different. The 8 grafts of epicormic origin bear much smaller leaves and the ramification is denser.

Also the two characters mentioned, pubescence and obliquity of leaves, proved stable when the two year old grafts were investigated in the summer of 1957. The scabrousness in the leaves of the 8 juvenile grafts was felt at first touch. The marked difference in size and obliquity is demonstrated in fig. 8.

In spite of the small scale of the experiment the *importance of meristematic aging in Ulmus carpinifolia is very obvious.*

8. *Robinia pseudoacacia.*

As already mentioned, thorniness is a juvenile character in many woody plants (p. 329).

It seemed natural therefore to search for tree species with thorns. The genus *Crataegus* seemed a suitable object for research. However preliminary observations showed a marked tendency of branches to produce vigorous thorns at considerable heights after fairly light pruning. This might indicate great influence of environment on this character and pronounced plasticity in hawthorn.

As this series of demonstration experiments with other species than beech had to depend on very limited material *Crataegus* was given up and *Robinia pseudoacacia* selected instead. Here it proved fairly easy to find specimens with low thorny epicormics.

Table 6.

According to the above system classification of the 10 most vigorous thorns in each graft of Robinia pseudoacacia. Grafted 1956, assessed winter 1956/57.

Fordeling til længdeklasser af de 10 kraftigste torne hos hver enkelt podning af falsk akacie. Podet 1956, bedømt vinteren 1956/57.

Clone no. *Klon no.*	Age of parent tree *Ophavs-træets alder*	Scion-wood from *Podemateriale fra*	Number of grafts *Antal pod-ninger*	Percent of thorns distributed to length-classes *Procent torne fordelt til længdeklasser*					Average height cm *Gennem-snitshøjde cm*
				1	2	3	4	5	
1	50	thornless 2 year old graft of top origin *tornløs 2 år gammel podning, der stammer fra topmateriale*	11	0	5	65	20	10	58 ± 2
1	50	thorny 2 year old graft of epic. origin *tornet 2 år gammel podning, der stammer fra vanris*	8	57	29	14	0	0	72 ± 7
2	100	nearly thornless top branches *næsten tornløse topgrene*	16	2	47	30	15	6	54 ± 4
2	100	thorny low epicormics *tornede lavtsiddende vanris*	9	76	13	11	0	0	82 ± 11

In March 1954, scions were collected from almost thornless top branches carrying seed and from thorny epicormics 1 m above ground in an almost 50 year old tree. Grafting was made in May, in D. T. Poulsen's Nursery on rootstocks kindly placed at my disposal.

Although the top material gave only one living graft versus eight of epicormic origin, it was striking at the first assessment in December 1954, that the former kept its rather thornless character while seven of the latter bore heavy thorns. The eighth was a thornless and very weak plant which died in the spring of 1955.

The second assessment in July 1955 gave exactly the same result, and in April 1956 one graft of each lot was transplanted in the Arboretum. Later observations of this pair of grafts in

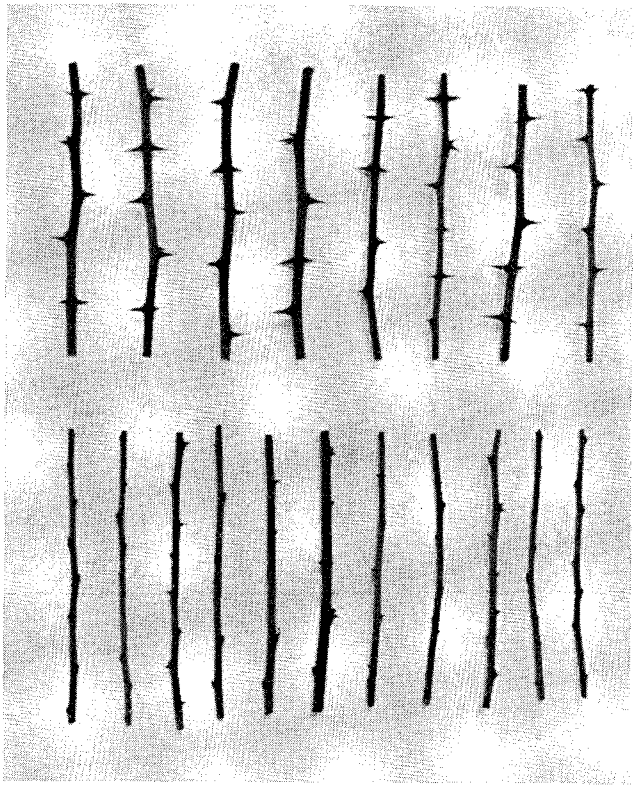

Fig. 9.
The central 20 cm long section of the leader from each graft of Robinia pseudoacacia clone no. 1. Upper row of low epicormic origin, lower row of top branch origin. Note the difference in thorniness, size and number. Phot. Jan. 1958 H. Keiding.

Det midterste 20 cm lange stykke af topskuddet hos hver enkelt podning af falsk akacie klon no. 1. Øverste række stammer oprindeligt fra lavtsiddende vanris, medens nederste række stammer fra topkviste. Bemærk forskellen i tornstørrelse og -antal.

the winters of 1956/57 and 57/58 proved the stability of the two development stages.

In order to supplement and repeat the above experiment, grafting was made in 1956 using typical and equally vigorous scions from the pair of grafts. Observations in 1956/57 and 57/58 found the results as expected.

In 1956/57 thorniness was described in the following way. In each graft the ten most vigorous thorns were classified according to length:

class	1	very vigorous,	length	10	mm	or more
„	2	vigorous	„	5—9	„	
„	3	weak	„	2—4	„	
„	4	very weak	„	2	„	or less
„	5	non-existing				

Table 6 illustrates by figures how great the differences in thorniness are. The majority of thorns on grafts of epicormic origin belong to class 1, whereas the thorns on top grafts are grouped around class 3, with none in class 1.

Both thorniness and greater height growth vigour should be regarded as juvenile characters. The difference in vigour cannot possibly be due to periphysis in this case of a secondary propagation with equally strong scions from plants grown under uniform conditions during two years.

In 1957/58 it was chosen to demonstrate thorniness, simply by the photograph fig. 9. This shows the central 20 cm long section of the leader of each graft, and no detailed classification of thorns is necessary to prove the stability of the character, thorniness.

Another 100 year old tree was propagated by the usual system in 1956. Scions were collected both from epicormics at ground level and at 3 m above ground. Assessments were made in the winters of 1956/57 and 57/58 in exactly the same two ways as for the preceding clone.

It appears from table 6 and fig. 10 that the top grafts of the second clone became somewhat thorny, but there is still a definite difference between the two scion categories.

Also a third clone taken in already 1954 by the usual system behaved much like the second one. The 18 top grafts became rather thorny, however considerably less so than the 9 grafts of epicormic origin. As it was too laborious to transplant this material of very large plants, they were only assessed in 1954 and 55, and by verbal description exclusively.

Thus all experiments show a definite drop in ability to produce thorns with age.

This main result by no means contrasts with the well known influence of environment on size and vigour of thorns (cf. p. 329), which was amply confirmed in the material. Thus within various

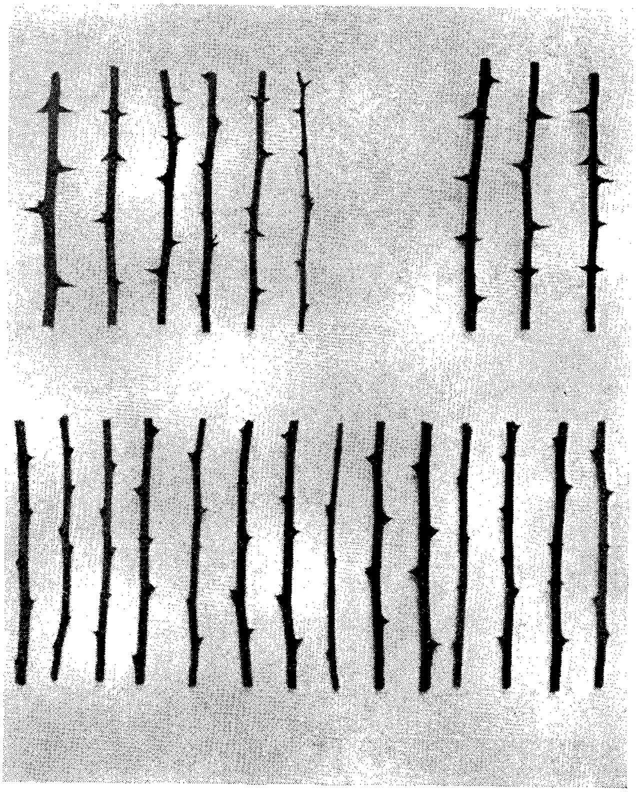

Fig. 10.
The central 20 cm long section of the leader from each graft of Robinia pseudoacacia clone no. 2. Upper row of low epicormic origin, lower row of top branch origin. Note the difference in thorniness, size and number. Phot. Jan. 1958 H. Keiding.

Det midterste 20 cm lange stykke af topskuddet hos hver enkelt podning af falsk akacie klon no. 2. Øverste række stammer fra lavtsiddende vanris, mens nederste række stammer fra topkviste. Bemærk forskellen i tornstørrelse og -antal.

graft lots a definite tendency of fewer and weaker thorns was found in small plants. This phenomenon was especially clear in specimens more or less suppressed by larger neighbours.

9. *Syringa vulgaris.*

In contrast to the preceding woody species which are all important forest trees, the common lilac only becomes a shrub, with heavy flowering at a low age. Characteristic for the lilacs is replacement of the dead terminal bud by opposite lateral buds.

However, my attention was called to the fact that one year old seedlings and root suckers from old shrubs form a terminal bud. Even if this bud is often more or less incomplete one main leading axis is developed. It should be stressed that the repeated forking in *Syringa vulgaris* is not provoked by flowering from the terminal bud as in the case of *Acer pseudoplatanus* (p. 374).

It was evident that formation of opposite pseudoterminal buds begins at a very early age in lilac thus indicating the existence

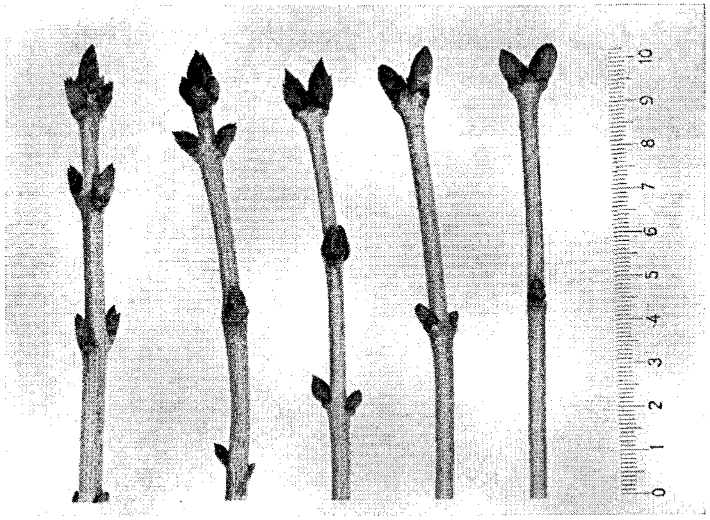

Fig. 11.

Syringa vulgaris. Different types of leaders of three year old seedlings. Some have passed into the "opposite bud stage", but others still form a single terminal bud. Note the dead apices of the two shoots on the right. Phot. Dec. 1955 Noll.

Almindelig syren. Forskellige topskudstyper hos treårige frøplanter. Nogle er trådt ind i det stadium, der karakteriseres af modsatte endeknopper, mens andre endnu danner een endeknop. Bemærk de døde skudspidser på de to skud til højre.

of a very short juvenile stage with a single main axis. Therefore it was decided to study seedlings rather than the usual two categories of grafts.

Seed of *Syringa vulgaris* was sown in the spring of 1953, and 29 seedlings were followed with close observations in the succeeding 5 years.

During the first three growing seasons all plants every fall formed terminal buds and thus possessed a monopodial axis. At the end of 1955, however, 17 seedlings formed no terminal buds but instead two pseudoterminal axillary buds whereas the remaining 12 formed single rather distinct terminal buds. The different types of bud positions are illustrated in fig. 11.

Most of the side branches had also entered what may now be termed the "opposite bud stage".

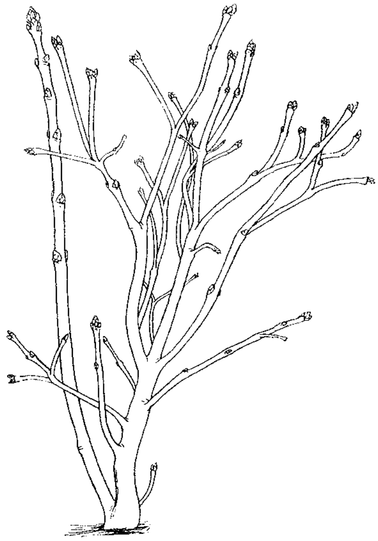

Fig. 12.

70 cm high five year old seedling of Syringa vulgaris. Note the repeated forking, which is a direct consequence of the opposite pseudoterminal buds. A vigorous epicormic with a single terminal bud, springs from the base of the plant. Drawn Jan. 1958 Noll.

70 cm høj fem år gammel frøplante af almindelig syren. Bemærk den gentagne tvegedannelse, som er en direkte følge af de modsatte endeknopper. Et kraftigt vanris med een endeknop udgår for neden på planten.

From the beginning of the fourth growing season in 1956, most of the trees consequently appeared to be what foresters term, "forks". Already those seedlings on which low epicormics were allowed to grow, had become quite shrubby.

In the winters of 1956/57 and 57/58 the terminal bud position was assessed in the 5 uppermost shoots of each seedling. These uppermost shoots did not include epicormics of which the most vigorous were higher than the top of the original plant. The epicormics nearly all formed a single, often incomplete bud.

The bud position assessment showed that in 1956/57 127 out of the 140 shoots in the remaining 28 plants had formed opposite buds, only leaving 13 with single terminal buds. In 1957/58 the corresponding figures were 123 and 17. A couple of plants flowered for the first time in 1957.

The common lilac is not used in forestry because it becomes a shrub. The above observations illustrate how the lilac loses the chance of being regarded as a forest tree as its ability of forming one main axis is lost so early in life.

It is natural to recall *Acer pseudoplatanus* in which this ability is also lost, but too late in life to prevent development into a definite forest tree.

10. Populus X canadensis serotina.

Among the poplars *Populus X canadensis serotina* was chosen for demonstration experiments, simply because it was fairly easy to find suitable trees.

The material is shown in table 7. It is evident at first sight that *the rooting capacity in the two clones used was much better in cuttings of epicormic origin.* In 1954 this could have been due to periphysis, but the difference is also clear in 1956 when clone no. 2 was propagated for the second time. The material for the second propagation was very carefully selected and consisted of quite uniform scions from the 1954-cuttings. This result is in accordance with general experience and many earlier experiments (p. 348).

It was to be expected that cuttings of epicormic origin would grow much faster than those from top material. This was true for both clones at the first propagation (table 7, fig. 13). Considering the two very different scion categories the difference in vigour might however be due to an aftereffect i. e. of periphysical origin. The vigorous growth of the three, only living top cuttings without terminal bud, pointed in this direction.

Fig. 13 is given in order to demonstrate the different heights of the two lots of clone no. 1. According to the calculated mean errors, table 7, this difference is non-significant. Fig. 13 however shows that this is due to close spacing, hence keen competition, within the juvenile lot, where a few cuttings, especially in the middle of the bed, have been suppressed.

It was not possible to find any significant difference in height

Table 7.
Propagation results with different scion categories of two specimens of Populus X canadensis serotina.

Formeringsresultater med forskellige stiklingstyper fra to individer af landevejspoppel.

Clone no. *Klon no.*	Age of parent tree *Ophavstræets alder*	Origin of cuttings *Stiklinger fra*	Cuttings *Stiklinger*: numbers *antal*: propagated *formeret 1954*	Cuttings *Stiklinger*: numbers *antal*: living *i live 1955*	Cuttings *Stiklinger*: percent living *procent i live 1955*	Average height as 2 year old, cm *Gennemsnitshøjde som 2-årige cm*
1 a	100	top branches with flower buds *topgrene med blomsterknopper*	20	0	0	—
b		top branches with flower buds, terminal bud preserved *topgrene med blomsterknopper endeknopper bevaret*	20	7	35	142 ± 6
c		epicormics 2 m above ground *vanris i 2 m's højde*	20	16	80	175 ± 12
2 a	80	top branches with flower buds *topgrene med blomsterknopper*	15	3	20	207 ± 11
b		top branches with flower buds, terminal bud preserved *topgrene med blomsterknopper endeknopper bevaret*	15	5	33	139 ± 8
c		epicormics 2 m above ground *vanris i 2 m's højde*	15	12	80	181 ± 7
			1956	*1957*	*1957*	
2	100	top cuttings. a-1954 *top-stiklinger, a-1954*	16	7	44	200 ± 12
		epic. cuttings, c-1954 *vanris-stiklinger, c-1954*	16	14	88	184 ± 9

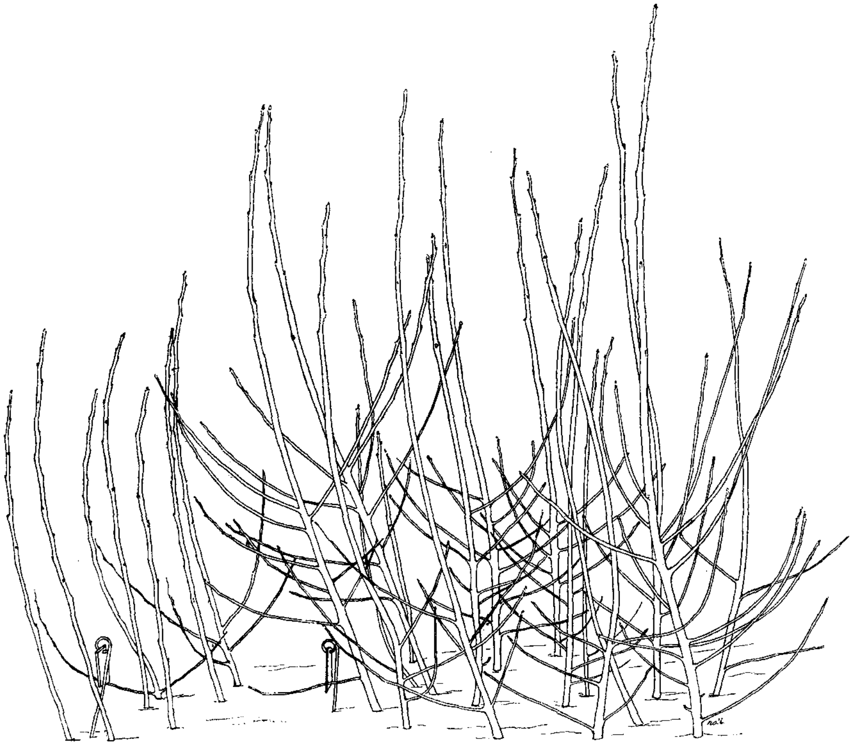

Fig. 13.
Cuttings of Populus X canadensis serotina clone no. 1. Left: 7 slow growing plants of top branch origin. Right: 16 chiefly vigorous plants of low epicormic origin. The difference in vigour is believed to be due to an environmental aftereffect and not to meristematic aging.
Drawn Noll after photo from Feb. 1956.

Stiklinger af landevejspoppel klon no. 1. Til venstre: 7 langsomt voksende planter, der stammer fra topmateriale. Til højre: 16 hovedsageligt kraftige planter, der stammer fra lavtsiddende vanris. Den forskellige vækstkraft skyldes formentlig en eftervirkning af kårene og ikke aldersfænomener i meristemet.

growth at the second propagation; the tendency is even opposed to the working hypothesis. This may be due to the limited number of cuttings, but it is primarily a demonstration of the great plasticity of *Populus X canadensis serotina. Consequently the different growth vigour at first propagation was actually of periphysical character.*

Thus the only remaining character to demonstrate existence of meristematic aging in this poplar is different rooting ability.

It should however be remembered that the two trees used no doubt originate from cuttings themselves. The unknown meristematic age of the cuttings may effect our results, and it is quite probable that these poplars by repeated vegetative propagation have lost their juvenile stage like many fruit trees.

11. Hedera Helix.

Although the existence of the juvenile and adult form of *Hedera Helix* was proved long ago, it was impossible to totally omit this classical research subject.

Scions were collected from adult and juvenile regions of two fairly old individuals. Propagation by cuttings was made in 1954. At assessment in the winter of 1957/58, the cuttings of adult origin, 25 and 15 of each clone, showed adult characteristics. All, with the exception of one weak plant, flowered. Also the two lots of juvenile origin, 25 and circa 70 respectively, kept their characteristics and produced no flowers.

Thus another pair of examples could be added to the extensive evidence on this phenomenon in *Hedera*.

In accordance with *Robbins* (1957 b) it was further observed that anthocyan formation was abundant in juvenile , but scarce in adult material (fig. 14).

12. Other Hardwoods.

Experiments with cuttings after the usual system did not indicate existence of meristematic aging in *Salix fragilis*. Two very similar plant lots arose from the two different scion categories.

Experiments along the same lines with *Salix pentandra* could not be carried through because of failure to propagate by cuttings scions from flowering top branches. This fact indicates the usual loss of rooting capacity with age.

Furthermore grafting experiments with *Castanea sativa* were inconclusive, probably because of scanty material.

Numerous hardwoods could not be included in the present demonstrations in spite of definite indication of meristematic aging. But even if conifers were left out of consideration it would lead too far to list the species with suspected development stages.

However the fact that many hardwoods seem to pass through a stage with a single main axis has a special bearing on forestry.

This is particularly evident in species such as *Acer platanoides* and *Aesculus Hippocastanum,* where the main axis is unbroken until terminal bud flowering takes place, exactly as described for *Acer pseudoplatanus.* But it is probably also due to meristematic aging when species without terminal bud flowering, like *Fraxinus excelsior, Betula pendula* and *Tilia cordata,* lose their main axis in old age. The original leader in such species seems to lose the ability to dominate the lateral axes — and the reciprocal growth correlations between main axis and side axes, so distinct in youth, become blurred.

From the comprehensive review in chapter I and from the experimental demonstrations in chapter II it appears *that aging of apical meristems is a very common and probably universal phenomenon in woody plants.* Up to date research in this field has been scanty, and also in the present work it has been necessary to concentrate on some of the more obvious objects. But the author believes that future experiments with sufficient material will demonstrate meristematic aging phenemona in all woody species.

It is only natural that research in this field primarily concentrates on species with characteristic differences between juvenile and later stages. However in the introduction of this paper it was stressed that absence of evident juvenile form in a tree species should not be identified with absence of meristematic aging. Some development stages may appear well defined, due to their easily observable characteristics, but it should be remenbered that less evident physiological qualities may be just as important.

Therefore the common idea of regarding juvenile forms as interesting but exceptional phenomena should be abandoned. Instead they should be grouped as easily demonstrable cases of meristematic aging.

This point of view is supported by the fact that the difference between juvenile and adult does not seem to be an all or none phenomenon (*Robbins* 1957 b) and also agrees with the existence (*Doorenbos & Felius* 1953) of several overlapping juvenile stages (cf. p. 344).

Fig. 14.
One clone of Hedera Helix. Above: Adult cuttings with no anthocyan formation. Below: Juvenile cuttings with abundant anthocyan formation.

En enkelt vedbend klon. Foroven: Voksne stiklinger uden anthocyandannelse. Forneden: Juvenile stiklinger med kraftig anthocyandannelse.

The present paper does not contribute to a solution of the direct causes of meristematic aging. Several investigators have lately discussed this problem, and it is reasonable to adopt their general view that *one or several particular chemical compounds are present or wanting in the juvenile meristem but respectively wanting (eventually scarce) or present in the adult (Robbins* 1957 a. Cf. p. 345).

The rejuvenation experiments of *Doorenbos* (1954) and *Frank & Renner* (1956) with *Hedera* point in this direction, and *Robbins* (1957 b) may actually in gibberellic acid have found a compound of importance to juvenility (cf. p. 344).

On the other hand the lack in beech of reciprocal influence in "double grafts" and the absence of rejuvenation in adult grafts on leafy rootstocks call for further research on rejuvenation (p. 412). But research workers should keep an open mind and not overlook the fact that the persistent juvenility in the lower trunk portion at first sight recalls a chimaeral phenomenon.

The author is not inclined to adopt the view of senility in clones, because proof is still lacking.

It was mentioned in the introduction that the starting point of the present investigations was the difficulty in provoking flower bud formation in *tree breeding.* Some of the experiments in chapter II have clearly demonstrated the importance of meristematic aging in this respect, especially the results in *Acer* and *Fraxinus.* In *Fagus* it has already been stated in a previous paper (*Schaffalitzky* 1955).

The practical conclusion for tree breeding is to *select the scions for seed orchards high in the trees and especially from flowering regions.* It should be remembered however that this technique does not represent a universal remedy, as the environmental influence on flower bud formation is very important.

On the contrary scion-wood for tree-shows designed for complete estimation of the genotype (*Syrach Larsen,* 1947) *should preferably be collected from the juvenile stage.* In many cases this is simply impossible, because low epicormics are not available. Never the less it should be stressed that juvenile material is a necessary condition in exact studies of the genotype of young trees.

Forest tree breeding is still a rather new branch of silviculture, and even if it is already too late to procure juvenile material of many clones, *we should in the future endeavour to retain as many juvenile forms as possible.* If we do not do so, we will soon be in the situation of horticulture and populiculture, where the loss of the juvenile stages of nearly all cultivated varieties is greatly regretted. But we should *not neglect studies on artificial rejuvenation,* which may one day solve the problem of the lost juvenile forms.

In the work tree breeders are doing in selection *the interplay between heredity and meristematic aging* is a problem of interest. This interplay has been demonstrated within oak and ash. Although provisional observations indicated no immediate connection between leaf-retention and certain important tree qualities, such connections may exist. It cannot immediately be ascertained whether the ability to produce anthocyan is an indifferent juvenile character in ash or not.

There is much to indicate that in breeding and seed collection *early flowering specimens should be excluded.* This character has in some cases proved to be hereditary (p. 341), and it should be avoided in forestry because it occasions a fall in volume production (*Holmsgaard* 1955 p. 75—100). In order to overcome the slow succession of generations, which is a main difficulty in tree breeding, we may be tempted to work with such early flowering individuals especially of new species, but it is a dangerous course of procedure (*Syrach Larsen* 1956 p. 180). On the contrary breeders should search for late flowering trees.

Furthermore special interest should center on *meristematic aging as regards breeding for resistance to tree diseases.*

Some of these different consequences of meristematic aging for *tree breeding* have been occasionally mentioned in earlier papers as stated in chapter I, but they are summarized here to obtain a more complete view of the entire problem.

Chapter III

FURTHER INVESTIGATIONS AND EXPERIMENTS. PHYSIOLOGICAL AND SILVICULTURAL ASPECTS

The preceding chapter dealt with experimental demonstrations of meristematic aging mostly in some hardwood species.

The present chapter mainly deals with investigations on physiological aspects connected with morphological characters found in the demonstrations and is chiefly concentrated on beech. Thus the fundamental problem may be phrased in the question; what does leaf-retention in beech indicate physiologically, hence silviculturally? In this connection it is however necessary to treat the environmental influence as in section 2, and section 3 on rejuvenation also belongs here.

1. Leafing-Out.

In the search for secondary physiological characters possibly connected with leaf-retention or leaf-shedding, attention was drawn to differences in time of leafing-out.

Before discussing the experiments it is reasonable to give some general information on leafing-out in beech.

It is an incontestable fact and probably a very old experience among foresters that leafing-out time is greatly conditioned by heredity. Usually the local forester will know the earliest flushing beeches in his woods. Stability in flushing time may however be explained by local soil conditions and water supply. The latter factors undoubtedly influence leafing-out, but any attentive observer will find numerous examples of different flushing time among beeches growing under very similar soil conditions.

It was *Raunkiær* (1918), who actually proved that flushing time was a hereditary character in beech. He collected beech nuts from 5 old trees of which some were early, others late

Fig. 15.

Leafing-out-grades of Fagus sylvatica used in leafing observations. Drawn May 1956 Noll.

Udspringsgrader for bøg anvendt i løvspringsiagttagelser.

flushers. The progenies from the former definitely flushed earlier than those from the latter.

In order to learn about important properties of our selected beech clones, flushing observations were made at the Arboretum. To standardize descriptions from year to year a system of leafing-out-grades was established (fig. 15).

These observations clearly demonstrate the hereditary character of leafing-out time. Table 8 shows results from such repeated observations in eight adult clones at one uniform locality of the Arboretum.

The leafing-out-grade of the clones was assessed at certain dates during the flushing period. An every day assessment would

Table 8.

Flushing time observations in 8 beech clones at the Arboretum. In the vertical columns are put down the date (no. I—VI), at which each clone (no. 1—8) had reached or passed leafing-out-grade 2 (fig. 15) in different years.

Udspringsiagttagelser for 8 bøgekloner i Arboretet. I de lodrette kolonner er anført den dato (no. I—VI), på hvilken hver enkelt klon havde nået eller passeret udspringsgrad 2 (fig. 15) i forskellige år.

Year *År*	Clone no. *Klon nr.*							
	1	2	3	4	5	6	7	8
1948	I	I	II	I	IV	IV	IV	V
1949	I	I	II	III	III	IV	III	IV
1950	I	I	I	II	III	III	III	III
1951	I	I	I	II	II	II	II	III
1952	I	II	III	III	IV	IV	V	VI
1956	I	I	II	I	III	III	IV	I*) IV
1957	I	I	II	II	III	III	III	IV

*) 2 heavily flowering grafts.

have been still better, but was impossible because of other work. No observations were made in the period 1953—1955.

In order to facilitate a rapid survey of the table the clones are numbered from 1 to 8 beginning with the earliest flusher.

Clones no. 3 and 4 are found to flush so simultaneously that their order interchanges in different years. There are only two other breaks in the flushing order of which one for the very latest clone, no. 8, of which two heavily flowering individuals were among the earliest flushers in 1956. The author believes this interesting occurrence to be a general feature which may explain some otherwise inexplicable variations often appearing in flushing observations. It is worth noticing that this was the sole case of significant flowering in the eight clones during the entire observation period and that in 1957 clone no. 8 was again back in its place.

Leaving the hereditary aspects of leafing-out and turning to influence of environment, *Engler*'s (1911) pioneer experiments must be mentioned.

Engler observed in Swiss beech forests that the order of flushing was as follows: "Es ergibt sich, dass der Jungwuchs unter Schirm zuerst austreibt und sich belaubt; dann folgen die Bäume des alten Bestandes, und zuletzt ergrünen die unbeschirmten Jungwüchse". He also called attention to the fact that the epicormics and lower shaded branches flushed before the crowns of a closed beech stand.

Engler's experiments with transplants of beech are not less interesting. He selected plants in shade and in full light and transferred them in well designed experiments to both shaded and sunny localities. Also control experiments with potted plants were made.

The previously shaded beeches definitely flushed first the year following transplantation. Already in the second year the difference in flushing time was considerably smaller, but seven years after transplantation it was still possible to demonstrate a now, very small difference.

As the transplants from shade and full light finally reach the same flushing time level, it is evident that it is shade which provokes early flushing. It should be noted that transplants only gradually adapt themselves to an environmental change.

Without knowing *Engler*'s experiments, *Helms* (1918) repeated some of them under Danish conditions and found an aftereffect up to five years after transplantation.

Different light conditions thus explain differences in leafing-out-time between shaded versus unshaded young beeches. More difficult is the explanation of the different behaviour of young plants and of old trees in full light.

Engler tried to explain this phenomenon by a combination of factors:

1. more shade within the old tree crown.
2. because of quicker growth a great proportion of the branches in young plants is influenced by aftereffect from last year's leader, generally in full light.
3. lower night temperatures at ground level.
4. gradual disappearance of the latest flushers which cannot compete with the early ones.

Factors 1, 2 and 4 seem to be purely speculative arguments, whereas factor 3 may be of some importance.

Engler did not realize that the most important factor was the different development stages of the young plants and the old trees.

Table 9.

Assessment of leafing-out-grade of grafted beech clones (fig. 15). Comparison of the juvenile leafy and the adult leafless development stage.

Clone no. *Klon no.*	Origin of scion-wood *Podekviste fra*	Age of parent tree *Ophavstræets alder*	Graft year *Podeår*
V. 440	leafless top *top uden blade*	140	1952
»	leafless epicormics *vanris uden blade*	»	»
»	leafy epicormics *vanris med blade*	»	»
V. 440	leafless top	140	1952
»	leafless epicormics	»	»
V. 440	leafless top	140	1952
»	leafy epicormics	»	»
V. 440	leafless top	140	1952
»	leafy epicormics	»	»
V. 440	leafless graft from 1939 *podning fra 1939 uden blade*	140	1952
»	leafy graft from 1939 *podning fra 1939 med blade*	»	»
V. 440	leafless top	140	1954
»	leafy epicormics	»	»
V. 440	leafless top	140	1954
»	leafy epicormics	»	»
327	leafless top	120	1954
»	leafy epicormics	»	»
1	leafless high branches *top uden blade*	20	1954
»	leafy low branches *nedre grene med blade*	»	»
1	leafless high branches	20	1954
»	leafy low branches	»	»
2	leafless high branches	20	1954
»	leafy low branches	»	»
2	leafless high branches	20	1954
»	leafy low branches	»	»
3	leafless top	220	1956
»	leafy epicormics	»	»

Tabel 9.

Udspringsgraden hos podede bøgekloner (fig. 15). Sammenligning af ungdomsstadiet med blade og alderdomsstadiet uden blade.

Obs. year *Obs. år*	Number of grafts *Antal podninger*	Leafing-out-grade used *Anvendt udspringsgrad*	Percent grafts at or past the leafing-out-grade used *Procent podninger med den anvendte udspringsgrad eller derover*		
			May 9	*May 13*	
1953	51	3	76	94	
»	33	3	49	91	
»	27	3	26	63	
			May 11	*May 14*	*May 18*
1955	16	2	94	100	100
»	16	2	0	13	88
			May 9	*May 12*	*May 14*
1956	15	2	13	93	100
»	16	2	0	13	69
			May 8	*May 10*	*May 13*
1957	15	3	20	47	93
»	16	3	0	0	25
			May 9	*May 13*	
1953	29	3	48	93	
»	62	3	10	45	
			May 23	*May 28*	
1955	54	3	61	100	
»	66	3	9	88	
			May 16	*May 19*	
1956	41	3	71	100	
»	61	3	16	87	
			May 13	*May 14*	
1957	15	3	13	93	
»	31	3	0	6	
			May 19	*May 21*	
1956	30	2	90	100	
»	20	2	15	60	
			May 13	*May 14*	
1957	29	2	100	100	
»	20	2	15	70	
			May 26	*May 29*	
1956	34	3	65	100	
»	24	3	0	33	
			May 16		
1957	34	2	85		
»	24	2	0		
			May 13	*May 15*	
1957	17	3	35	88	
»	35	3	3	14	

Table 9 gives a survey of a considerable number of leafing-out assessments in leafless and leafy grafts of 5 beech clones under uniform conditions at the Arboretum. It is easily seen that *juvenile material leafs later than adult material of the same clone. In other words a beech tree will flush later when young, than in old age.*

Repeated observations, especially with clone V. 440, show that it is not a case of aftereffect.

The later flushing of juvenile forms is a general character in many species, as juvenile grafts of *Fraxinus excelsior* clone no. 2 came into leaf after the adult, and *Fritsche* (1948) noted the same phenomenon for apple and pear (cf. p. 334).

2. *External Factors.*

Shade and leaf-retention.

It was mentioned in another paper (*Schaffalitzky* 1954) that young seedlings of beech shed most of their leaves when heavily shaded or impeded in other ways. This is not astonishing in view of *Engler*'s experiments, which proved the influence of shade on time of flushing and in view of the close connection between flushing time and leaf-retention, described in section 1.

The lack of leaves in juvenile beeches in heavy shade however prevents the use of our main character of juvenility. This stresses the importance of making the demonstration experiments under uniform conditions, without overhead shade.

In order to study the extent to which shade influences leaf-retention, the following experiment was made.

In a natural regeneration under a 120 year old beech stand were selected 15 leafless seedlings, greatly impeded by shade and root competition. Because of the slender stems of these 20—80 cm high plants it was possible to determine their approximate age by counting the annual shoots.

The minimum age appeared to vary from 17 to 37 years when in May, 1953, they were transplanted with wide spacing to favourable shade conditions. Informative light measurements with an electric photometer were made in bright sunshine on June 13, 1957. The light intensity averaged 0.5 % of full light under the beech stand, compared with 25 % in the new environment.

It is interesting to note that the working hypothesis in 1953 was that these beeches had left the juvenile leafy stage, and it was therefore expected that they would continue leaf-shedding.

However table 10 and fig. 16 show that instead *the experiment became a proof of the extremely great ability of shade to prolong the juvenile stage.* During the observation period 1952/53—1957/58 all surviving plants gradually became leaf-retaining.

Another small experiment showed that shade is actually the important factor in leaf-shedding, but root competition may also play a rôle.

1953/54 1955/56 1956/57 1957/58

Fig. 16.

Photographs in four winters of a circa 30 year old beech seedling, which until May 1953 grew in heavy shade. Note the gradual recovery of the plant after removal 1953 to light shade. The incipient leaf-retention shows that the plant has been kept back in the juvenile stage. *Ca. 30 årig bøgefrøplante, som indtil maj 1953 voksede i stærk skygge. Fotografier gennem en årrække viser, hvorledes den gradvis er kommet til kræfter efter at være blevet plantet i let skygge. Det begyndende bladhold viser, at planten er holdt tilbage i ungdomsstadiet.*

In each of the now leaf-retaining plants, nos. 1, 2, 3 and 4 of the preceding experiment, 8 twigs were covered with double cloth bags from June 14 to October 2, 1957.

When the bags were removed seven of the twigs were already leafless and the eighth bore few leaves as a result of the heavy shade. The twigs were not dead, in which case the leaves are not shed, but the buds were markedly etiolated.

Further experiments on influence of artificial shade on leaf-retention and leafing-out were made using grafts from 1954 of clone V. 440.

Table 10.
Leaf-retention in 20—40 year old beeches — until May 1953 impeded by heavy shade and great root competition. May 1953 transplanted with wide spacing under favourable light conditions.

Bladhold hos 20—40 år gamle bøge, som indtil maj 1953 blev holdt nede af kraftig skygge og rodkonkurrence. Udplantet på stor afstand under gunstige lysforhold i maj 1953.

Plant no. *Plante no.*	Minimum age 1953 *Minimum alder 1953*	Leaf-retention 1952/53—1957/58 *Bladhold 1952/53—1957/58* no leaves: —, few leaves: +, many leaves: ++ *ingen blade* *kun få blade* *mange blade*					
		1952/53	1953/54	1954/55	1955/56	1956/57	1957/58
2	22	—	+	++	++	++	++
1	37	—	—	+	++	++	++
3	29	—	—	+	++	++	++
4	24	—	—	+	++	++	++
13	19	—	—	+	++	++	++
14	19	—	—	+	++	++	++
10	23	—	—	—	+	++	++
15	19	—	—	—	+	+	++
6	20	—	—	—	—	+	++
12	28	—	—	—	—	+	++
8	17	—	—	—	—	—	+

During the period from July 6 to November 15, 1954, 33 of these grafts were overall shaded by a double layer of shade screens and 70 left in full light.

The degree of leaf-retention in the juvenile grafts was assessed on December 18, 1954 and is shown in table 11. The number of leaves of the shaded grafts averaged less than one half leaf per graft; the grafts in full light retained about four leaves each. Due to their small size some of the plants were still leafless. This is because shoot tips, also in juvenile beeches, usually drop their leaves (*Schaffalitzky* 1954 & 1956 a).

From June 18 to near the end of October 1956, 29 of the 58 juvenile grafts hitherto in full light were shaded from above by two layers of shade screens and from the side by one layer of sacking. The degree of shade was definitely less in 1956 than in 1954 because of the single layer of sacking. The remaining 29 grafts were kept in full light.

At leaf fall both lots appeared to retain their leaves, and at the final assessment on April 7, 1957, 90 % of the shaded and

Table 11.

Effect of artificial, rather heavy, overhead shade on leaf-retention in juvenile grafts of beech clone V. 440. Grafted spring, 1954. Shaded July 6—November 15, 1954. Number of leaves assessed on December 18, 1954.

Virkning af kunstig, ret stærk skygge på bladhold hos juvenile podninger af bøgeklonen V. 440. Podet forår 1954. Skygget 6. juli—15. november 1954. Antal blade bedømt 18. december 1954.

Leaf number class *Klasse efter bladantal*	Percent of plants per leaf number class *Procent planter pr. klasse*	
	in shade *i skygge*	in full light *i fuldt lys*
no leaves *ingen blade*	76	30
1—5 leaves	24	40
6—10 »	0	20
over 10 »	0	10
Average leaf number per plant *Gennemsnitligt antal blade pr. plante*	0,4	3,8

86 % of the control grafts bore more than 10 leaves. The lighter shade in 1956 explains why no influence on leaf-retention could be demonstrated that year.

Actual light measurements were not carried out in 1954 and 1956. However informative measurements under similar conditions in 1957 indicated a light intensity under shade of about 10 % of full day light in 1954 and about 50 % in 1956.

The expected aftereffect on leafing-out in the first spring after shading could be clearly seen in the nursery of the Arboretum and is demonstrated in table 12. The demonstration is far more striking in 1955 due to heavier shade in 1954.

Sterility and leaf-retention.

In a previous paper (*Schaffalitzky* 1954) it was stated that flowering had never been observed in beech branches and epicormics with winter foliage. This sterility of the juvenile stage was amply confirmed through later observations, including the two great mast years 1954 and 1956.

Table 12.

Effect of artificial shade — rather heavy in the summer of 1954, rather light in 1956 — on leafing-out the following spring (fig. 15). Grafts of beech clone V. 440, from 1954. The juvenile grafts, shaded in 1954, are not included in the leafing-out test of 1957.

Virkning af kunstig skygge — ret kraftig i sommeren 1954 og ret svag i 1956 — på udspringet det følgende forår. Podninger fra 1954 af bøgeklonen V. 440. De juvenile podninger, som blev skygget i 1954, indgår ikke i udspringsanalysen i 1957.

Treatment *Behandling*	Development stage *Udviklingsstadium*	Obs. year *Obs. år*	Leafing out-grade used *Anvendt udspr. grad*	Number of grafts *Antal podninger*	Percent grafts at or past the leafing-out-grade used *Procent podninger med den anvendte udspringsgrad eller derover*	
					May 23	*May 28*
Shaded 1954 *skygget*	juvenile	1955	3	26	100	100
Full light 1954 *i fuldt lys*	»	1955	3	66	9	88
					May 13	*May 14*
Shaded 1956 *skygget*	juvenile	1957	3	29	52	100
Full light 1956 *i fuldt lys*	»	1957	3	29	14	55
					May 13	
Shaded 1956 *skygget*	adult	1957	3	16	100	
Full light 1956 *i fuldt lys*	»	1957	3	26	54	

Hence flowers in root suckers (*Wind* 1877) and in low epicormics (*Petersen* 1920 p. 42) of beech were regarded as exceptional until *J. U. Wedel Heinen* during the summer of 1954 observed fruits on low shaded epicormics in some old beeches mainly in Bernstorff Park (fig. 17). These epicormics were very low and as in some cases they emerged from the root collars, or even from roots, they were presumed to be juvenile.

In the winter 1954/55 however these flowering epicormics appeared to be leaf-shedding, although neighbouring non-flowering but otherwise similar epicormics were often leafy. Closer examination of the beeches in the Park showed that the unusually

Fig. 17.
Fagus sylvatica. Old tree in Bernstorff Park with low leafless epicormics bearing cupules. Scions from these epicormics produced the two leafy grafts in fig. 18. Phot. March 1955 K. Gram.

Bøg. Gammelt træ i Bernstorffsparken med lavtsiddende vanris, hvorpå der sidder frugtskåle. De to podninger med blade i fig. 18 stammer fra disse vanris.

great number of epicormics often deriving from real epicormic cushions was due to artificial pruning.

Two explanations seemed possible. Either the environmental influences, primarily heavy shade, were strong enough to suppress leaf-retention and permit flowering, or the flowering epicormics derived from adventitious buds.

The latter explanation coincides with the view of *Büsgen & Münch* (1927) that only dormant buds retain the juvenile stage (cf. p. 323).

In order to study the phenomenon more closely scions were taken from some of the low leafless epicormics with cupules. These were grafted in 1955, but because of poor scion-wood the results were unsatisfactory.

Only 2 grafts originating from a single tree survived. These were both found to be leaf-retaining in the winters of 1956/57 and 1957/58 (fig. 18).

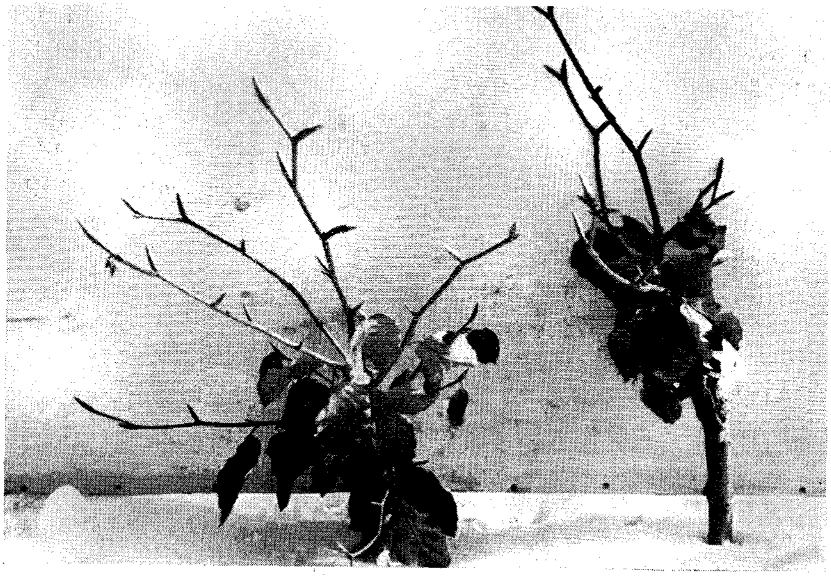

Fig. 18.

Two leafy grafts of Fagus sylvatica. Scion-wood taken from the leafless epicormics of the old tree in fig. 17. Phot. February 1958 H. Keiding.

To bøgepodninger med blade. Podekvistene blev taget fra vanris uden blade på det gamle træ i fig. 17.

Grafting was repeated in 1956. Of this material only three grafts from a second tree were alive in 1957/58. One of these is definitely leafy, but the two others bore only one leaf each in 1957/58. There is no doubt that also these two grafts will become overall leafy.

Both sets of grafts point to the fact that the flowering epicormics had not left the juvenile stage, but were forced to shed leaves and even to flower by external factors.

This explanation was further supported by observations from Bernstorff Park. South of one of the trees with flowering epicormics in 1954 another big tree was felled. The resulting better light conditions provoked leaf-retention and prevented flowering in 1956, where most other epicormics of this type flowered again.

Favourable light conditions are normally necessary for production of flower buds in beech. Thus it is an old and unquestionable fact that the border trees of a stand, especially with a southern exposure, are very fertile. The converse behaviour of these low epicormics may appear contradictory. But dense shade appears to impede use of available reserve nutrients in the trunk for vegetative growth, without at the same time preventing the use of these nutrients for flowering.

It was mentioned earlier (p. 311) that studies on meristematic aging were begun because we could not provoke flower buds in our selected beech clones. The above demonstration of the extreme power of environment to force flower bud formation may give new hope.

The investigations of the low flowering epicormics in Bernstorff Park indicate no stage difference between dormant and adventitious buds. This supports the belief that it is the entire trunk base of a tree which remains juvenile (p. 356).

The contrast between ability for leaf-retention and flower bud formation in beech is still evident. The former juvenile ability must apparently disappear before flowering can take place. On the other hand flowers may be seen immediately above the juvenile zone, as observed 1956 in three isolated beeches not more than 20 year old. As meristematic aging is probably conditioned by biochemical factors (p. 389) absence or presence of a single or several chemical compounds may have the double effect of causing leaf-retention and hindering flower bud formation.

In a previous paper (*Schaffalitzky* 1955) the connection was demonstrated between great age of the meristem and abundant flowering in a beech clone. Later observations confirm the first results, as there was fruiting under favourable conditions again in 1956 and flowering is due in 1958. In the complete off-years of 1955 and 1957 general flowering could not be expected, but it should be noted that the only female inflorescence observed in beech on the island of Zealand in 1957, was observed in these grafts.

Of the other hardwoods with juvenile leaf-retention the same

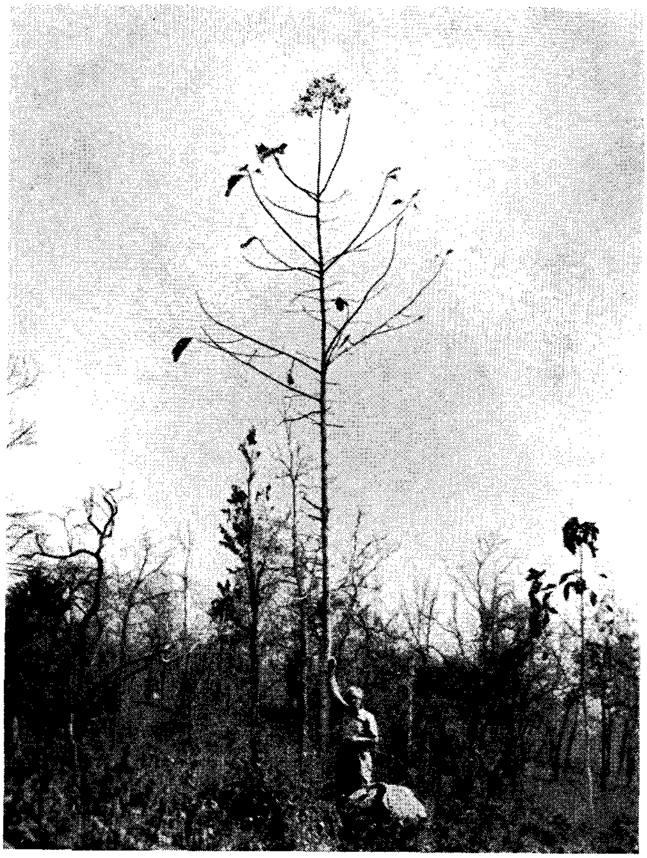

Fig. 19.

Young Tectona grandis which flowers for the first time in its life. The inflorescence appears terminal at the main axis and prevents the formation of a satisfactorily long bole. After Gram & Syrach Larsen (unpublished).

Ungt teaktræ, som blomstrer for første gang. Blomsterstanden fremkommer i hovedaksens spids og forhindrer dannelsen af en tilfredsstillende lang bul.

definite contrast between this character and flowering seems to exist in *Carpinus Betulus*. Twigs with simultaneous winter foliage and flower buds were never observed; however the number of investigated specimens of this species is small.

In oak a certain tendency in the same direction is often noticed, but cupules may be found in leafy twigs. For instance in *Quercus petraea* with winter foliage right to the top, flowering may well occur. This limited contrast between leaf-retention and flower bud formation in oaks corresponds satisfactorily with the generally great individual variation within these species (p. 361).

The more indifferent behaviour in oak recalls the conditions found within a so distant species as *Tectona grandis. Bünning* (1952) mentioned this species as an example of a tropical tree which does not start flowering until so-called "wintering" begins (p. 354). In the juvenile leaf-retaining stage, characterized by continuous renewal of leaves, flowers are not produced.

Thus *Bünning*'s observations from Java, Sumatra and Bengal tend to show a rather strict correlation between the two phenomena.

In two lectures on botanical studies in 1957 in the forests of Thailand, *K. Gram* confirmed that leaf-retention was a general juvenile character in teak, incidentally also in numerous dipterocarps. However there was great individual variation and environmental influence. Under favourable conditions old large specimens might show lack of wintering combined with heavy flowering.

While these observations are reminiscent of the oaks, the flowering in teak rather resembles that of sycamore. The injurious effect of flowering from the terminal bud of the main axis was described for sycamore on page 374. From a silvicultural point of view the flowering habits in teak are still more detrimental because the first inflorescence occurs early in life and always terminal at the main axis (*Gram & Syrach Larsen* unpublished). This means that the assumed juvenile sterile stage in teak is often too short to allow formation of a satisfactorily long bole. The beautiful straight stem of the young teak is broken too early (fig. 19). *Gram & Syrach Larsen* observed examples of delayed flowering due to deficiency of light and called attention to the possibility of prolongation of the sterile period by shade.

Topophysis and Periphysis.

It should be repeated that in this paper the term, topophysis, only covers the phenomenon of shoot individuality in relation to different shoot order (p. 322).

It is evident that topophysis is a rather unimportant factor in *Fagus sylvatica* compared to cyclophysis. In leaf-retention at any rate, bud position is unimportant, as all buds from the juvenile zone give rise to leafy branches and from the adult zone to leafless branches.

Moreover, all beech grafts very soon become fairly normal plants in appearance, and we have had no cases of horizontally growing grafts, as in *Araucaria* and other conifers.

Only one aspect of topophysis has been studied experimentally with beech. That is an investigation of the question: are the lower and lowest side branches able to become normal plants or will they, as maintained by *Beissner* for the *Retinispora,* develop into slow growing plants for ever juvenile (cf. p. 316)?

The two lowest opposite buds in beech seedlings appear in the axils of the cotyledons. Preliminary observations showed that these buds extremely seldom give rise to shoots. If the second pair of opposite buds, from the axils of the first normal opposite leaves, is allowed to produce small shoots, these will usually be completely suppressed the following year.

It is therefore impossible as a rule to study the growth habit of shoots from the lower buds.

In the autumn of 1953, 10 one-year-old seedlings were cut down to just above the opposite buds at the cotyledons. These 10 plants were lined out beside 10 untreated seedlings of the same progeny.

Already in the autumn of 1955 it was evident that the treated plants of which three had died were developing into quite normal individuals. At the latest assessment in November 1957, the 6 remaining treated plants were quite similar to the 10 controls.

Thus there was absolutely no indication of slower growth or different appearance of the shoots from the very lowest buds. Both sets of seedlings are of course still leafy, so it is an open question whether the treated plants will remain juvenile longer than the untreated.

Beissner's idea of fixation of juvenile forms by basal cuttings could not be directly tested because of a general difficulty in propagation of beech by cuttings.

In another experiment however, the behaviour of the lower side branches was again investigated. In the spring of 1955 a set of 2 year old beech seedlings was divided into 4 lots each consisting of 5—6 plants.

In each of the following years, beginning with the spring of 1955, the lots were successively cut down to just above the lowest living bud. It was not possible to test the exact original position of these buds. In some cases they may have derived from one of the two first leaf pairs, in others from one of the very first alternate leaf axils.

The primary object of this experiment was the same as the preceding. However it was also planned to see whether the plants cut down latest, would show greater tendency to slow horizontal growth and prolonged juvenility. If so, periphysis might be the cause, i. e., an aftereffect from suppressed conditions before pruning.

As the last lot is only due to be cut down in 1958, the experiment is not concluded. We can state however, that so far there is no tendency whatever to permanent aftereffects either from topophysis or from periphysis. The 10 plants cut down in the spring of 1955 and 1956 were quite normal seedlings at the latest assessment, November 1957. The four remaining plants of the lot pruned in 1957, were gradually becoming normal, but naturally still influenced at their base by the former horizontal position.

Like the "double grafts" (p. 419) the latter experiment proved another good demonstration of the strength of growth correlations between leader and side branch. Immediately after pruning the shoots from basal buds bent their tips upwards and fought for leadership.

Much evidence has already been presented in this paper to demonstrate the important influence of environment on duration of juvenility. The most striking examples are the fairly old beeches kept juvenile by shade (table 10) and the low flowering epicormics in Bernstorff Park (p. 401).

Therefore the author by no means agrees with *Fritsche* (1948) in his belief in an obligatory number of juvenile years (cf. p. 335). In that case the existence of meristematic aging would be much more pronounced, as transition from one stage to the other would be less gradual.

For instance an isolated young beech without epicormics i. e. with all shoot tips of the same meristematic age would have no conical juvenile zone (*Schaffalitzky* 1954 fig. 2). At the end of a certain growing season, all shoot tips would have passed into the adult leafless stage.

1954 Fig. 20. 1958

The same young isolated Fagus sylvatica drawn at an interval of four years. Note the fairly constant size of the conical, leafy juvenile zone. a. Drawn Noll after Schaffalitzky (1954, fig. 2). b. Drawn January 1958 Noll.

Den samme unge fritstående bøg tegnet med fire års mellemrum. Bemærk den uforandrede størrelse af den kegleformede ungdomszone med blade.

In a previous paper (*Schaffalitzky* l. c.) the transition picture in young isolated beeches was believed to point to existence of stronger topophysis in the lower branches. However the two above experiments indicate the unimportance of topophysis even in the very lowest side shoots.

Thus existence of the conical leafy zone may rather be due to a delayed transition of the interior lower side branches to the leafless stage caused by their slow growth. Therefore growth vigour, as effected by environment, may be just as important a factor to determine meristematic aging as the actual number of preceding shoot generations. Also *Romberg* (1944) suggested that quick growth usually meant quick ontogenetic development (cf. p. 332).

Such retarded development of slowly growing interior twigs is illustrated in fig. 20. This shows that the tree in fig. 2 of the previous paper (*Schaffalitzky* 1954) still, 1958, has a leafy cone of approximately the same dimensions as in 1954.

The present section brings much evidence of *the extremely important influence of external factors, especially shade, on duration of the juvenile stage in beech.* This fact underlines the necessity of making the demonstration experiments under uniform conditions. Some silvicultural consequences are mentioned in the end of chapter III.

3. *Rejuvenation.*

The present section deals only with rejuvenation of adult meristems. The ability to provoke rejuvenation by stooling or pruning a tree grown from seed is not included, as this phenomenon is a simple consequence of the persistent juvenility of the lowest trunk portion (p. 356).

In a previous paper (*Schaffalitzky* 1954) was noted that only a single case of a high leafy beech branch had been observed. Annually repeated observations 1952—1957 demonstrated constant leaf-retention in this branch (fig. 21).

In order to study whether the branch had really rejuvenated, scions were collected from it and from two neighbouring leafless branches of the same tree. Grafting experiments were made with these.

The grafts from the leafy branch carried winter foliage, whereas the grafts of leafless origin naturally shed their leaves. The former developed into odd, slow growing plants, the mean height of which in 1957/58 was only 74 cm compared to 120 and 126 cm of the latter. The leaf form seems also to be rather unusual.

These observations and the fact that fruiting took place in the high branch in spite of winter foliage strongly indicate a mere bud mutation and not a rejuvenation. The confusing point is that this sport among other characters has gained the ability of leaf-retention.

This assumed case of spontaneous rejuvenation thus appeared to be false and no more high leafy branches were ever found.

Fig. 21.
Leafy branch in the top of an old Fagus sylvatica, probably not an instance of spontaneous rejuvenation but rather a bud mutation. Phot. November 1953 K. Næss-Schmidt.

Bladholdende gren i toppen af gammel bøg. Næppe et tilfælde af virkelig „foryngelse", men snarere en knopmutation.

Hence spontaneous rejuvenation of beech must be an extremely seldom phenomenon.

Stoutemyer (1937) and *Wellensiek* (1952) both provoked sphaeroblasts by debudding (cf. p. 342). They suggested that rejuvenation might occur in adventitious shoots from such sphaeroblasts.

Until 1957 we had only succeeded in provoking internodal, hence adventitious, buds in one adult beech graft at the Arboretum. Not one of the three shoots from these buds became leafy. Thus there was no indication of rejuvenation.

By repeated debudding and severe wounding of the internodes of juvenile beech shoots we have been able to provoke sphaeroblasts with many adventitious shoots, in the summer of 1957. This technique was also applied to a few adult grafts; some sphaeroblasts but only a single shoot were produced. This shoot is still too small to be tested for leaf-retention, but the method may be the basis for future rejuvenation experiments on a larger scale.

It was mentioned (p. 343) that *Doorenbos* (1953) had been able to provoke rejuvenation in *Hedera Helix var. arborea* in graft combinations with juvenile material. When the leaves of the latter were retained rejuvenation was significantly stimulated.

At the Arboretum there is a considerable number of adult beech grafts upon rootstocks in which some juvenile leafy shoots are allowed to grow. However we have never observed any indication of rejuvenation of the adult shoots.

This lack of rejuvenating effect, which might be expected in view of *Doorenbos'* results, is also very obvious in our "double grafts". Independent of the balance between the graft partners and of the leaf number in the juvenile, each partner remains leafy, respectively leafless (fig. 24).

These observations indicate a curiously limited ability in the eventual juvenile substance(s) to move or an actual lack of stability when moved. At any rate it seems much more difficult to provoke artificial rejuvenation in *Fagus sylvatica* than in *Hedera*. In other words the adult leafless stage seems to be very firmly established.

It was attempted to repeat *Doorenbos'* experiments in 1954. Upon a typical, juvenile creeping rootstock of *Hedera* were grafted scions of adult type. In order to obtain especially marked rejuvenation the rootstock was allowed to retain its leaves but the scions were defoliated.

Only three grafts survived, but none of them showed more signs of rejuvenation than could be provoked by defoliation of the adult parent plant. Following defoliation the latter primarily formed a few leaves of a rather intermediate type, as was also the case in the grafts. Very soon, however, the parent plant and the three grafts again produced adult leaves. One of the grafts flowered in 1956 and two in 1957.

These results were discussed by letter with *Doorenbos* who suggested that the rootstocks may have been older than in his experiments. He informed me that he had repeated the experiments several times with identical results.

Because of the limited material at the Arboretum the experiment is not conclusive, but should be repeated at the first opportunity.

The problems concerning rejuvenation are not yet clarified; further investigations are especially important as their solution may explain the direct causes of meristematic aging.

4. Bark Necroses.

If an old beech stand is opened up by clear cutting from west or south west, the suddenly exposed lower trunk portion of border trees will often suffer from bark necrosis. The necroses are usually believed to be caused by sun-scorch in dry summers (*Dengler* 1935 p. 97). Opening up of a stand in this way should usually be avoided, but damage may be prevented by whitewashing the trunks.

Younger beech stands exposed in the same way will generally not suffer from bark necrosis but will produce numerous low epicormics, which seem to protect the stems.

Bark necroses towards south west are a well-known phenomenon in orchards, and here whitewashing is an old established preventive method. The injury is usually caused by the frequent temperature variations in late winter or early spring, where high temperatures by day alternate with night frosts (*Kemmer* & *Schulz* 1955).

The leafless adult beech grafts at the Arboretum and elsewhere have often suffered from bark necroses towards south west. Fig. 22 demonstrates such one-sided bark wounds of twelve year old grafts.

Fresh wounds are only observable in early spring, and it is believed that they are caused by temperature variations as described for fruit trees. On the whole it is a question whether the injuries in old beeches are also conditioned in the same way in early spring and not in hot summers.

Bark necroses were never observed in young seedlings or in juvenile grafts. The latter are however rather scarce, and no experiments have been made to compare leafy grafts with leafless as regards this character. In April 1955, however, three

Fig. 22.
Row of twelve year old adult grafts of Fagus sylvatica at the Arboretum. Arrows indicate the bark necroses which all face south west. Phot. April 1957 H. Vedel.

En række tolvårige voksne bøgepodninger i Arboretet. Pilene angiver barkslag, som alle vender mod sydvest.

beeches about 20 year old were heavily green-pruned. Although they were exposed towards south and south west no stem wounds resulted, and this in spite of considerable bark decay in adult grafts, not least the past few years. It seems to be the bark itself which is less susceptible to temperature variations in juvenile beeches because in the first few years after pruning the leafy epicormics are unable to protect the stem effectively. On the other hand the dead brown leaves no doubt moderate the temperature variations in the bark.

The phenomenon recalls the resistance of juvenile *Carya Pecan* bark to injuries and also the different bark types in JT — and MT buddings in rubber (cf. p. 332 and 353).

When ash trees are suddenly exposed towards the south west dying off of the bark may also occur (*Dengler* l. c.). Of late adult ash grafts have suffered badly at the Arboretum from similar bark necroses (fig. 23). Because of repeated transplanting before discovery of the injuries it has been impossible to demonstrate an eventual south western exposure of the wounds. Ash seedlings in the nursery of the Arboretum were not attacked.

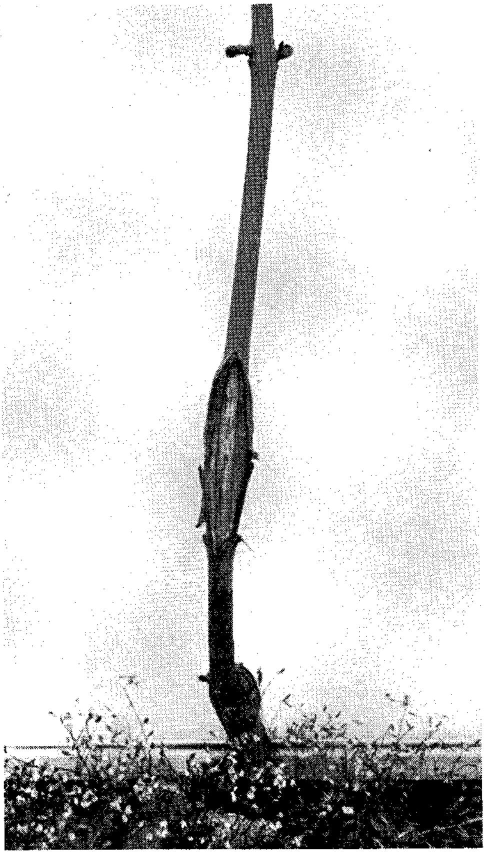

Fig. 23.
Fraxinus excelsior. Adult two year old budding with bark necrosis. Phot. April 1957 H. Vedel.
Ask. Barkslag på to år gammel okulant i alderdomsstadiet.

This lesser susceptibility of juvenile material might be due to the fact that it was growing on its own roots. The bark necroses of the adult material might be stimulated or even partly provoked by incomplete top/root connection at the graft union.

By chance however we obtained a *strong indication that the resistance was a true juvenile stage character.* Out of 10 adult grafts of *Fraxinus excelsior* clone no. 1 (table 5) 8 showed fresh bark necroses in the spring of 1956, whereas only 1, the very weakest, of the 14 juvenile grafts was affected.

5. *Growth Vigour.*

Much of the literature cited in chapter I indicates a larger growth vigour in juvenile than in adult forms. As this would naturally be of the greatest importance in silviculture a number of experiments were laid out in order to investigate the question.

Double Grafts.

A few experiments were made with "double grafting" i. e. grafting upon the same rootstock of one juvenile and one adult scion. A graft of such origin will be termed a "double graft".

The first experiment of this kind was started in 1954, when double grafts were established comprising one partner from

Table 13.

Double grafts from 1954 with one juvenile scion from a random seedling and one adult scion from a selected beech clone (fig. 24). Assessment of partner leadership in winters 1955/56 and 1957/58.

Dobbeltpodninger fra 1954. Hver plante er sammensat af een kvist med blade fra en tilfældig frøplante og een uden blade fra en udvalgt bøgeklon. Bedømmelse af førende partner om vinteren 1955/56 og 1957/58.

Clone no. *Klon no.*	Number of double grafts *Antal dobbeltpodninger*						
	Juvenile partner ahead *ungdomsformen fører*		adult partner ahead *alderdomsformen fører*		still undecided *endnu uafgjort*		total *ialt*
	1955/56	1957/58	1955/56	1957/58	1955/56	1957/58	
V. 884	3	2	1	1	0	1	4
V. 264	7	6	0	1	0	0	7
V. 439	7	7	1	1	1	1	9
V. 885	3	3	1	2	2	1	6
total	20	18	3	5	3	3	26

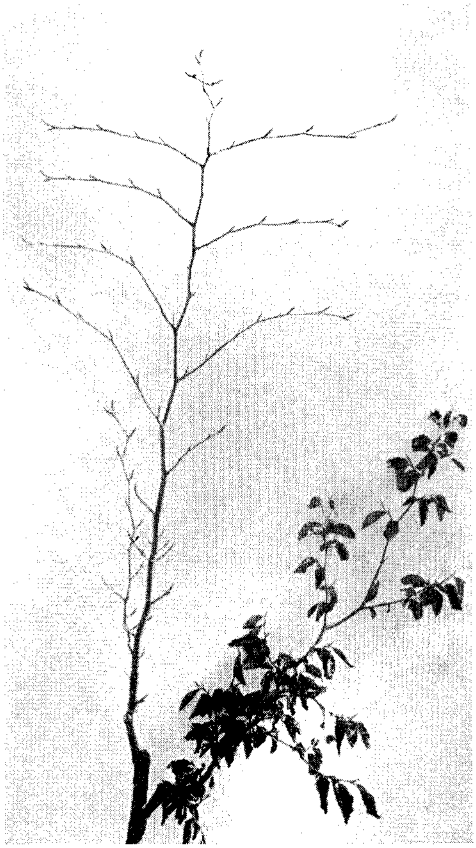

Fig. 24.
Double graft from 1954. The leafless adult partner at left has taken the lead, and the leafy juvenile form has fallen behind. Phot. April 1957 H. Vedel.
Dobbeltpodning fra 1954. Den voksne bladløse partner fører, og ungdomsformen med blade bliver holdt nede.

random selfsown seedlings in the Arboretum and one from four different selected adult clones. The scion-wood was very uniform.

The working hypothesis was that in every case the juvenile partner would outstrip the adult, which would gradually become a more or less suppressed side branch.

Table 13 shows two of the annual assessments of the grafts, namely in 1955/56 and in 1957/58. It was noted which graft partner had taken the lead, and which had fallen behind. In most cases the juvenile partner was victorious, in a few the adult (fig. 24), while three cases are still undecided.

The weak point of the experimental layout was that clonal difference could play a part, therefore another experiment was started in 1955.

From a circa 20 year old beech double grafting, using juvenile and adult scions, was made. The experiment was repeated with another beech of the same age. The scion material originated from low interior leafy branches versus higher leafless, i. e. within — respectively outside, the conical juvenile zone.

Table 14.

Double grafts from 1955 with one juvenile and one adult scion from the same 20 year old isolated beech. Made with two clones. Assessment of partner leadership in winters 1956/57 and 1957/58.

Dobbeltpodninger fra 1955. Hver plante er sammensat af een kvist med blade og een uden blade — henholdsvis fra ungdomszonen og fra topgrene af samme 20 årige fritstående bøg. Udført med to kloner. Bedømmelse af førende partner om vinteren 1956/57 og 1957/58.

Clone no. *Klon no.*	Number of double grafts *Antal dobbeltpodninger*						
	juvenile partner ahead *ungdomsformen fører*		adult partner ahead *alderdomsformen fører*		still undecided *endnu uafgjort*		total *ialt*
	1956/57	1957/58	1956/57	1957/58	1956/57	1957/58	
4	1	1	12	15	8	5	21
5	9	13	8	13	12	3	29

Table 14 shows assessments of partner leadership in the winters of 1956/57 and 1957/58. It appears that the results for clone no. 4 are directly opposed to the working hypothesis, nor does clone no. 5 indicate any superiority of the juvenile stage.

The obscure, and at first glance even contradictory result of these experiments is undoubtedly due to the research method used. *The general phenomenon of growth correlation is the reason for the "victory" of the graft partner which first becomes established,* i. e. forms the quickest and best union with the rootstock.

This explanation is based upon observations in the nursery, and is illustrated by the fact that the general result of the experiment is already evident the first or second winter after propagation. According to the working hypothesis it was expected that the juvenile graft partner which by chance had fallen behind would gradually fight its way past the adult partner. However this did not happen any more frequently than the reverse.

Every care was taken to use equally sized scion material in the double graft experiments. Nevertheless the difference as regards quicker or slower union is probably due to an environmental aftereffect.

Thus in the first experiment (table 13) the juvenile material may have been the more vigorous. In the second experiment (table 14) the adult material seemed the stronger in clone no. 4, whereas in clone no. 5 the two types of scion-wood appeared equally strong.

It was stressed at the beginning of this section that superiority *in every case* was considered necessary to prove the expected greater growth vigour of the juvenile forms. The double graft experiments instead proved that correlation phenomena render this type of competition experiment unsuitable.

Beforehand no one had suggested that growth correlations would impede fair competition between the two scions. Afterwards it seems self-evident, but *it is worth noting that the double grafts, instead of information on growth vigour, provide important knowledge on interactions between the scions* (p. 389).

It is no wonder that double grafting experiments in which the juvenile partner was placed low at already vigorous adult grafts actually demonstrated nothing but correlation. We may term this type of experiments, "handicap grafting".

A Checkerboard Plot.

Growth vigour and especially competition capacity in juvenile versus adult forms were tested in an experiment laid out in November 1953. Within a neutral isolating frame of two rows of clonal plants 16 adult and 16 juvenile grafts of beech clone V. 440 were planted in a checkerboard pattern (fig. 25). Contrary to experiments described later in the present section on growth vigour, this is the only experiment in which juvenile and adult forms were spaced so closely as to allow keen reciprocal competition. Thus superior competition capacity appears most quickly. The plant material was very uniform with practically the same average height and diameter.

Preliminary observations had indicated that one important difference between juvenile and adult beech grafts lay in their

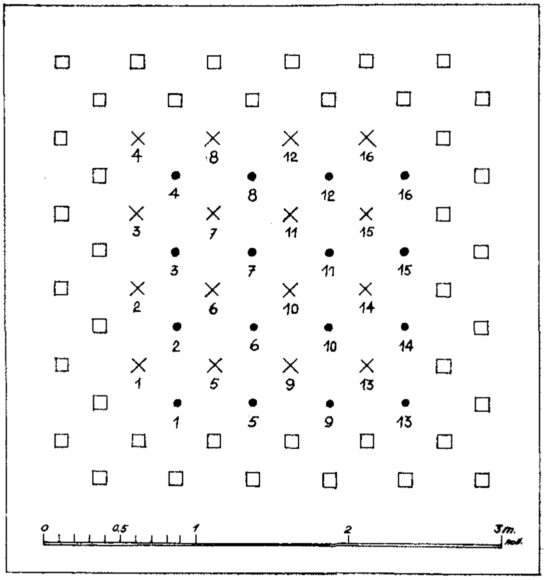

Fig. 25.

□ neutral frame of clonal plants
neutral ramme af klonplanter.

× adult grafts of clone V. 440
voksne podninger af klon V. 440.

● juvenile grafts of clone V. 440.
juvenile podninger af klon V. 440.

Plan of the checkerboard plot. Each graft numbered, cf. table 16.

Plan over skakbrætforsøget. Hver podning nummereret, se tabel 16.

Table 15.

Checkerboard plot. Plan fig. 25.
Average number of basal side shoots (shoot base under 33 cm above ground) and their basal leaves (under 14 cm from shoot base). Comparison between the 16 juvenile and the 14 adult grafts of beech clone V. 440 August 1955.

Skakbrætforsøg. Plan fig. 25.
Gennemsnitligt antal nedre sideskud (skudbasis under 33 cm over jorden) og disses nederste blade (mindre end 14 cm fra skudbasis). Sammenligning af de 16 juvenile og de 14 voksne podninger af bøgeklonen V. 440 August 1955.

	Adult grafts *podninger i alderdomsform*	Juvenile grafts *podninger i ungdomsform*
Average number of basal side shoots *Gennemsnitligt antal nedre sideskud*	4.3 ± 0.3	8.8 ± 0.5
Average number of basal leaves *Gennemsnitligt antal nedre blade*	31 ± 5	105 ± 10

ramification. The juvenile grafts showed a marked tendency to form more basal side shoots than the adult, the lower buds of which usually produced few shoots. In this way the leafless

Table 16.
Checkerboard plot. Plan fig. 25.
Comparison of height and diameter increment (Δ h and Δ d) in juvenile and adult grafts from 1952 of beech clone V. 440.

Skakbrætforsøg. Plan fig. 25.
Sammenligning af højde- og diametertilvækst (Δ h og Δ d) hos juvenile og voksne podninger af bøgeklonen V. 440.

Graft no. *Podning no.*	Development stage *Udviklingsstadium*	h cm 1954/55	Δ h cm 1955-57	h cm 1957/58	$d_{0.5}$ mm 1955/56	$\Delta d_{0.5}$ mm 1956	$\Delta d_{0.5}$ mm 1957	$d_{0.5}$ mm 1957/58
1	adult	97	84	181	10.1	1.9	3.5	15.5
2	—	88	65	153	8.5	1.2	2.6	12.3
3	—	97	35	132	11.5	0.5	0.5	12.5
4	—	118	9	127	11.3	0.5	0.6	12.4
5	—	105	69	174	9.4	2.0	2.9	14.3
6	—	106	66	172	10.2	1.2	1.2	12.6
7	—	108	27	135	10.6	0.2	0.6	11.4
8	—	99	49	148	7.6	1.9	2.1	11.6
9	—	118	72	190	11.4	1.7	2.9	16.0
10	—	96	17	113	9.7	0.6	1.0	11.3
11	—	105	104	209	10.4	2.9	2.3	15.6
13	—	93	46	139	6.6	0.6	0.8	8.0
14	—	101	58	159	9.9	1.4	1.3	12.6
16	—	118	83	201	11.1	2.7	3.0	16.8
av. *gns.*	adult	104	56	160	9.9	1.4	1.8	13.1
1	juvenile	113	72	185	10.3	3.3	5.6	20.2
2	—	100	76	176	11.1	3.0	6.0	20.1
3	—	98	49	147	7.5	1.2	1.3	10.0
4	—	99	63	162	8.1	1.6	1.8	11.5
5	—	101	45	146	7.2	1.0	2.0	10.2
6	—	111	46	157	8.9	2.0	2.2	13.1
7	—	95	99	194	9.8	2.3	3.1	15.2
8	—	106	61	167	11.4	2.0	2.8	16.2
9	—	113	87	200	11.5	2.5	3.9	17.9
10	—	119	81	200	12.3	3.1	2.3	17.7
11	—	113	76	189	12.0	2.1	3.0	17.1
12	—	93	56	149	7.5	0.9	0.6	9.0
13	—	114	41	155	9.8	1.6	3.9	15.3
14	—	135	43	178	11.6	1.1	1.5	14.2
15	—	96	48	144	10.4	1.9	2.5	14.8
16	—	116	43	159	10.2	1.5	2.5	14.2
av. *gns.*	juvenile	108	61	169	10.0	1.9	2.8	14.8

grafts became somewhat spindly as compared to the more sturdy leafy grafts.

This phenomenon is illustrated in table 15 which lists the number of basal side shoots of the two graft types in the present experiment. The important secondary effect is the greater number of basal leaves in the juvenile grafts.

These preliminary observations indicate that the difference between juvenile and adult forms of beech manifests itself primarily by greater diameter increment of the former rather than by variations in height increment. Evidently the larger number of basal shoots and leaves points towards greater ability in juvenile beeches to suppress competing ground vegetation. In other words the adult form seems to possess less regenerative power.

During four growing seasons the two graft categories have been struggling for space in the checkerboard plot. Table 16 gives detailed information on height and diameter increment, the latter measured with a slide caliper at 0.5 m above ground. The diameter measurements only comprise the two latest growing seasons as prior to the winter of 1955/56 diameters were determined with the accuracy of 1 mm only, but the slow growth demanded an accuracy of 0.1 mm.

It is obvious — and easily verified — that no significant difference exists as regards height growth. The diameter increments however are on an average 50 per cent larger in the juvenile group than in the adult. This difference is significant at the 95 per cent level when the experiment is treated as a replication experiment, the difference between years being eliminated by an analysis of variance.

In accordance with the working hypothesis *the balance within the plot has changed in favour of the juvenile grafts.* It may be added that two adult grafts have already died in the course of the experimental period.

Two Shade Plots.

The review of literature in chapter I includes several indications of a greater shade tolerance in juvenile forms. Therefore the presumably greater vigour of juvenile beeches should be expected to increase proportionally in shade. In order to investigate this question two so-called shade plots were laid out in

November 1953. The remaining 10 two-year-old leafy grafts of clone V. 440 after establishment of the checkerboard plot determined the extent of the experiment.

One shade plot was planted at Folehave Forest under a 50 year old oak stand and the other at Bjergsted Forest under a naturally regenerating old beech stand. Informative light measurements with an electric photometer were made in bright sunshine. On June 13, 1957 the light intensity in plot 1, Folehave, averaged 36 % of full light, and the corresponding figure on June 21, 1957 was 22 % in plot 2, Bjergsted. One measurement at top level of each graft was made. The intention was merely to obtain a rough idea of the light conditions.

15 grafts were planted in each plot. They are so widely spaced that so far there has been no reciprocal competition. 5 grafts are juvenile, the rest are adult, 5 of high epicormic origin and 5 of top branch origin respectively.

The working hypothesis was that the grafts of top origin would thrive very badly or even die because of inability to form ordinary shade leaves, whereas the juvenile material would quickly adapt itself to the shade and grow normally. The grafts from high leafless epicormics were supposed to resemble the top material most or perhaps to react intermediately.

It was soon evident that the shade was by no means dense enough to kill the top material as a whole. All 30 plants were surplus material after selection of the uniform stock for the checkerboard plot, therefore rather dissimilar and not suitable for such a small scale experiment, when the expected striking result failed to appear.

Table 17 gives figures for the average height and diameter growth, which were measured as in the checkerboard plot, but the table does not reveal the actual heterogeneity within the groups. When the plots are treated as a single replication experiment an analysis of variance supplies evidence that there is only an approximate 80 % probability of a true difference among the three graft categories. This applies alike to diameter and height growth. As in the checkerboard plot the former is of principal importance.

It appears, table 17, that the material has become further reduced by the death of 5 adult grafts, 3 in plot 1, and 2 in plot 2. *This fact together with the 80 % tendency convinces the author*

Table 17.

Two shade plots. Layout 1953.
Comparison of average height and diameter increment (Δ h and Δ d) in juvenile and adult grafts from 1952 of beech clone V. 440.

To skyggeforsøg. Anlagt 1953.
Sammenligning af gennemsnitlig højde- og diametertilvækst (Δ h og Δ d) hos juvenile og voksne podninger fra 1952 af bøgeklonen V. 440.

Origin of scion-wood *Podekviste fra*	number of grafts *antal podninger*	h cm	Δ h cm	h cm	$d_{0.5}$ mm	Δ $d_{0.5}$ mm		$d_{0.5}$ mm
		1953/54	1954-57	1957/58	1955/56	1956	1957	1957/58
Plot no. 1 under 50 year old oak stand *Forsøg no. 1 under 50 årig eg*								
adult top *top uden blade*	4	66	44	110	6.3	0.8	2.8	9.8
adult epicormics *vanris uden blade*	3	74	57	131	5.6	0.9	3.1	9.6
juvenile epicormics *vanris med blade*	5	76	45	121	6.2	1.1	2.9	10.2
Plot no. 2 under naturally regenerating stand of old beech *Forsøg no. 2 under gammel bøg m. opvækst*								
adult top *top uden blade*	4	73	34	107	6.8	0.4	1.9	9.0
adult epicormics *vanris uden blade*	4	116	33	149	10.1	0.2	1.4	11.7
juvenile epicormics *vanris med blade*	5	85	50	135	7.7	1.1	2.5	11.2

that an experiment on a larger scale would have proved the difference in growth vigour to be highly significant.

As the detrimental effect of shade upon adult grafts had appeared to be less than expected, a combined competition and shade experiment was established in 1956 with juvenile and adult grafts of two clones from 1954. They were planted closely and lightly shaded by a single layer of sacking in 1956 but heavily shaded by a double layer in 1957. During the latter growing season the per cent of full light on a sunny day was about 0.2 i. e. corresponding to conditions under a very dark beech stand. It was believed that the juvenile plants would be able to survive the gradual transition from lighter shade in 1956 to very heavy in 1957, but that the adult plants would be killed.

What actually happened was however a nearly complete destruction in August 1957 of the experiment which therefore had to be discarded.

It would have been better of course to work with several degrees of artificial shade, but the limited plant material and the desire for quick results led to this combined layout.

Experiments in young plantations.

To supplement information on the different growth vigour in juvenile and in adult grafts, a few experiments have been placed in normal young plantations with silvicultural conditions.

Three groups of adult grafts were placed in a normal beech plantation at Bregentved Forest District. This plantation was established with spacing 1 × 1 m under excellent conditions in 1954. Each of the 3 groups represents a single clone selected for breeding purposes and comprised originally 64 grafts. The plan is demonstrated in fig. 26.

The development of the plantation has been very satisfactory with vigorous growth and few losses. Because of this it was decided simply to compare the height increment of the clonal plants and that of seedling control frames around the groups. Even if the grafts were in advance of the seedlings at planting and to some extent still are, possible reciprocal disturbance can be disregarded because of the wide spacing.

In table 18 the gross averages of the height growth data are presented. A more detailed analysis of these data shows

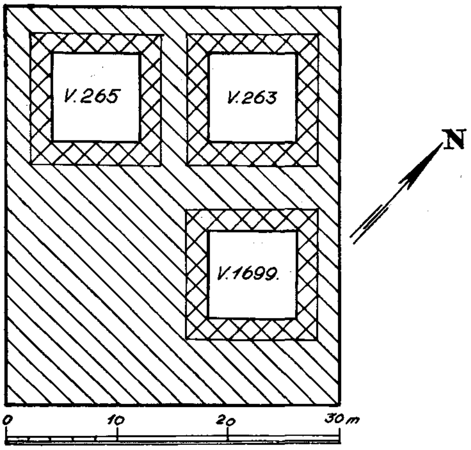

Fig. 26.

▧ casual juvenile stock
tilfældigt juvenilt materiale

▩ juvenile control frame plot
juvenil kontrol ramme

▭ clonal adult plot
voksen klongruppe

Plan of the Bregentved experiment.
Plan over Bregentvedforsøget.

1, the variation among the control frame plots is negligible to such an extent that the experimental area can be considered uniform.

2, the variance within the control plots is slightly larger than within the adult plots as was to be expected from their origin. It is safe to assume that if the difference between the means of two particular plots is greater than 3 cm it is highly significant. Hence it is easy to compare the average figures of table 18.

3, it is accordingly evident that the three adult clones differ markedly. It should be noted that clone V. 263 is one of our probably best selections and is used as standard in breeding experiments. In three other experiments, grafts of V. 263 at the nursery stage, have also displayed significantly greater height growth vigour than clone V. 265, which has therefore recently been discarded in breeding work. The difference may be of clonal character, but may also be due to an assumed greater

Table 18.

In 1957, average height growth (Δ h) of adult grafts from 3 selected beech clones compared with juvenile control stock. Young plantation from spring 1954 under excellent conditions. Bregentved Forest District, plan fig. 26.

Gennemsnitlig højdetilvækst 1957 (Δ h) hos voksne podninger af 3 udvalgte bøgekloner sammenlignet med kontrolramme af frøplanter. Plantning fra 1954 under fortrinlige forhold på Bregentved Skovdistrikt. Forsøgsplan fig. 26.

Plant stock *Plantemateriale*	Number of plants *Antal planter*	h cm 1956/57	Δ h cm 1957	h cm 1957/58	Age of parent tree *Ophavstræets alder*
adult clone no. V. 1699 *voksen klon*	62	170	30	200	circa 60
juvenile control frame plot *juvenil kontrolramme*	71	117	31	148	
adult clone no. V. 263 *voksen klon*	60	162	22	184	above 120
juvenile control frame plot *juvenil kontrolramme*	72	124	33	157	
adult clone no. V. 265 *voksen klon*	56	127	16	143	above 120
juvenile control frame plot *juvenil kontrolramme*	77	117	32	149	

meristematic age of the material of V. 265 than of V. 263. An attempt to ascertain whether the latter hypothesis could be confirmed in records from the first propagation of the trees in 1938 gave no result.

Clone V. 1699 not only grows more quickly than the slow V. 265, but more quickly even than our vigorous standard clone V. 263. This again might be due to clonal differences, but is believed to be due to a difference in development stage, as the parent tree V. 1699 is only about 60 year old as opposed to the more than 120 years of the two others.

This is supported by the fact that only the youngest clone V. 1699 is so far able to keep up with the juvenile seedlings, while the two older clones are appreciably behind. It should be stressed that it would be very depressing for us in our breeding work if random seedlings averaged better than our standard clone and equalled a still more vigorous selection. The only reasonable explanation must be that the *greater growth vigour of the seedlings is due to their juvenile stage.*

The fact that the seedling material of this experiment is not grafted but is growing on its own roots, should be noted, although it is considered unimportant in relation to the results.

In a beech plantation established in 1956 at Bjergsted Forest, one row was planted with juvenile grafts from 1954 next to another with adult material. The former row comprises to-day 71 grafts of which each represents a single seedling selected at random in a young plantation. The adult row includes 83 grafts of 12 adult clones selected for breeding purposes. The distance between the rows is about 2.4 m.

The height and diameter increments of these two artificially constructed populations were assessed by the usual method for

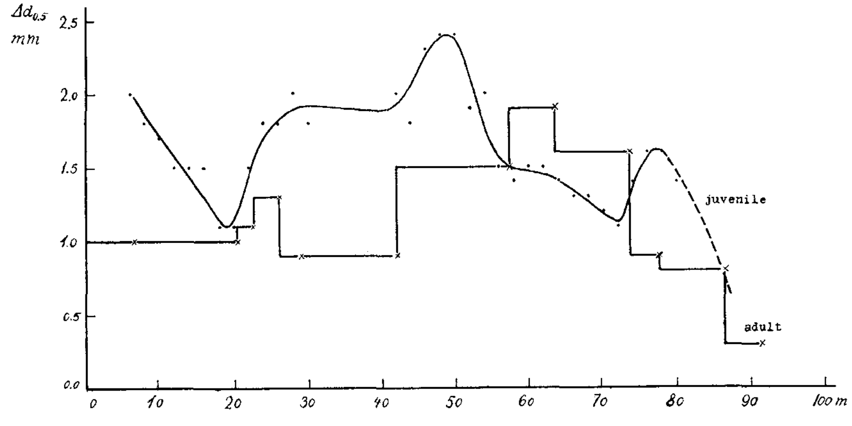

Fig. 27.

Beech experiment, Bjergsted Forest. Comparison of diameter increment (Δ d) in 1957 of juvenile grafts versus adult, cf. table 19. For the adult material are plotted average increments for each clone, for the juvenile running averages. The abrupt fall towards the eastern (right) end of the 2 rows is due to rapidly increasing frost damage.

Bøgeforsøg, Bjergsted Skov. Sammenligning af diametertilvækst (Δ d) i 1957 for juvenile og voksne podninger, se tabel 19. For det voksne materiale er afsat den enkelte klons gennemsnitstilvækst, for det juvenile løbende gennemsnit. Det pludselige fald i den østlige (højre) ende af de 2 rækker skyldes tiltagende frostskade.

Table 19.

Comparison of average height and diameter increment (Δ h and Δ d) in 1957 of juvenile grafts versus adult. One row of 71 juvenile grafts, each representing a single random seedling in a young plantation. One row of 83 adult grafts from 12 beeches selected for breeding purposes. The rows are planted at a distance of 2.4 m in a young beech plantation from 1956 at Bjergsted Forest. Grafts from 1954. Uniform treatment in the nursery.

Sammenligning af højde- og diametertilvækst (Δ h og Δ d) i 1957 for juvenile og voksne podninger. Een række med 71 juvenile podninger, som hver repræsenterer een tilfældig frøplante. Een række med 83 voksne podninger fra 12 af skovtræforædlingens udvalgte bøgekloner. 2 årige podninger indplantedes med 2.4 m's rækkeafstand i en bøgeplantning fra 1956 i Bjergsted Skov. Ensartet behandling i planteskolen.

Clone no. *Klon no.*	Age of parent tree *Ophavstræets alder*	Development stage *Udviklingsstadium*	Number of grafts *Antal podninger*	h cm 1956/57	h cm 1957/58	Δ h cm 1957	$d_{0.5}$ mm 1956/57	$d_{0.5}$ mm 1957/58	$\Delta d_{0.5}$ mm 1957
V. 263	over 120	adult	5	93	93	0	5.2	6.2	1.0
V. 265*)	»	»	13	65	69	3	4.3	5.3	1.0
V. 868	»	»	2	59	72	13	3.5	4.6	1.1
V. 1386	»	»	3	62	78	16	3.7	5.1	1.3
V. 1430	»	»	3	83	88	6	4.6	5.5	0.9
V. 1432	»	»	8	84	90	6	4.9	5.8	0.9
V. 1434	»	»	16	81	82	2	4.3	5.7	1.5
V. 2079	circa 60	»	6	101	118	17	5.6	7.5	1.9
V. 2080	»	»	10	69	81	11	4.2	5.8	1.6
V. 2081	»	»	4	123	132	10	7.8	8.7	0.9
V. 2082	»	»	8	126	130	4	7.1	7.9	0.8
V. 2083	»	»	5	86	83	—2	5.3	5.6	0.3
		adult	83	85	91	6	5.0	6.1	1.16 ± 0.08
		juvenile	71	94	98	4	5.7	7.3	1.60 ± 0.11

*) grafted 1953.

the summer of 1957. As the locality has suffered frost damage both in 1956 and 1957 no importance should be attached to the height growth, which in a few cases has even been negative. The results are shown in table 19.

Concerning the different diameter growth of the two rows a significance on the 99 per cent level may be ascertained, and *it may be safely assumed that of the two artificially constructed populations the juvenile stock on an average grows faster.* When a more detailed analysis of the individual clones is made, the results are obscured by large environmental differences and by the fact that some of the clones appear in very small numbers. The lack of uniformity may be ascertained from fig. 27 in which the diameter increments of the rows have been compared by means of running averages. It is probable that the younger stock of the adult population, approximately 60 year old, keeps up fairly well with the juvenile.

As in the Bregentved experiment it should also be stressed here that the superiority of the juvenile grafts must be due to their juvenility and not to clonal differences. If the latter possibility were true it would lead to the contradictory conclusion that random selections in a random young beech plantation were better than a selection for form and growth vigour in our best stands. In other words tree breeding efforts would immediately lead to a marked deterioration, because of a mysterious tendency of breeders to select the wrong trees.

The third experiment deals with ash and with the very grafts from 1956, already mentioned in chapter II (p. 371). It may be remembered that we had at our disposal juvenile and adult grafts of one clone and that they were grafted partly at the Arboretum and partly at the State Forest Tree Breeding Station. The former double lot of grafts was not transplanted in the spring of 1957, while the latter was placed in a young ash plantation under uniform favourable conditions at Bjergsted Forest. Reciprocal competition has so far been unimportant because of wide spacing.

Height and diameter increments during 1957 were assessed after the usual methods, and the results are given in table 20.

First, certain differences between the two lots should be explained. The smaller size in 1956/57, both as regards height and diameter, of the Arboretum lot is due to lesser rootstock vigour because of hand grafting. On the other hand the more vigorous growth of the Arboretum lot in 1957 is naturally due to non transplantation. These differences demonstrate the importance of uniform treatment in comparative experiments of this kind.

A comparison of height and diameter in 1956/57 of juvenile versus adult material *within each lot* shows so great uniformity that no important aftereffect of periphysical character disturbs the experiment.

The apparent superiority in height increment of the juvenile grafts is non-significant at Bjergsted, but approaches the conventionally adopted level of significance at the Arboretum, when the experiments are analysed separately. When the variation *between* the two localities is eliminated an analysis of variance shows a significance at the 95 per cent level.

The diameter increment is significantly larger in the juvenile material at the Arboretum, but not at Bjergsted, although there is a marked tendency in that direction.

It should be added that the Arboretum lot suffered from a heavy spring frost in May, 1957, which burnt off all the new leaves. It is believed that the considerably greater diameter

Table 20.

Comparison of average height and diameter increment (Δ h and Δ d) in 1957 of juvenile and adult grafts from the same Fraxinus excelsior, grafted 1956. One experiment in 2 neighbouring rows at the Arboretum and one in 3 rows under uniform favourable conditions in an ash plantation from 1957 at Bjergsted Forest.

Sammenligning af højde- og diametertilvækst (Δ h og Δ d) i 1957 for juvenile og voksne podninger fra samme ask, podet 1956. Et forsøg i 2 naborækker i Arboretet og et i 3 rækker under gunstige ensartede forhold i en askekultur fra 1957 i Bjergsted Skov.

Locality *Lokalitet*	Number of grafts *Antal podninger*	Development stage *Udviklings-stadium*	h cm		Δ h cm	$d_{0.5}$ mm		$\Delta d_{0.5}$ mm
			1956/57	1957/58	1957	1956/57	1957/58	1957
Arboretum	19	juvenile	37	64	27±3.5	6.0	11.0	5.0±0.3
»	22	adult	29	47	18±2.8	6.3	9.2	2.9±0.3
Bjergsted	25	juvenile	87	98	11±0.8	8.8	10.1	1.3±0.1
»	29	adult	83	93	10±1.2	8.7	9.8	1.1±0.1

growth of the juvenile grafts at this locality is especially due to their greater ability to recover, i. e. to quick formation of new shoots. This theory is in accordance with the prevalence of basal shoots and leaves in juvenile beeches (p. 420) and with the less satisfactory recovery after cold injuries of adult tung trees (p. 339).

All 6 experimental plots in *the section on growth vigour* supply evidence of a superiority in juvenile forms. Most of the results are significant, and the others point in the same direction.

The author regards greater juvenile growth vigour as a fact, but this character first appears in a greater diameter increment. The juvenile forms primarily possess an ability to become established, and their evidently greater regenerative power after frost injuries fits well into this conception. The later flushing which was clearly demonstrated in juvenile beech and indicated in juvenile ash is probably a great advantage, as spring frost damage is very common in Danish forests.

The pronounced susceptibility to bark necrosis is another undesirable property in adult beech and ash.

When adult grafts of ash and beech are used in seed orchards or in tree-shows the difficulties of their establishment may easily be overcome by careful treatment. The situation however is another when adult grafts are planted in the forest in order to cultivate the selected trees themselves. Such *clone cultivation* is a matter of course for poplars and willows, which differ from our main forest trees in their readiness to propagate by cuttings. It should further be noted that development stages could hardly be demonstrated in *Populus X canadensis serotina* and not in *Salix fragilis,* chapter II.

Some trials with clone cultivation have been laid out in various Danish forests through the Arboretum. In spite of very careful planting and treatment, establishment has generally been very difficult. These trials usually had the character of enrichment of existing young plantations and were never laid out with the object of comparing selected adult clones with random seedlings. However it was remarkable that heavy pruning of the seedlings was generally necessary if the selected clonal grafts were not to be completely outstripped and overgrown.

The author believes this general failure of clone cultivation in beech, ash and other species to be mainly due to inferior growth vigour of adult stages versus juvenile. Other causes such as poorly established graft unions, too late enrichment and topophysis (especially in conifers) may have contributed to the results, but not sufficiently to explain why our clones, often selected because of suspected growth vigour, could not hold their own against random seedlings.

Clone cultivation trials have also been laid out by a union of Danish forest estates since 1951. Some of these trials have made a remarkably good start although careful tending of the grafts and heavy pruning of neighbouring seedlings are required. This start may mainly be due to the preservation of several rootstock shoots (*Næss-Schmidt & Søegaard* unpublished). Theoretically these shoots might cause a rejuvenation in the adult scion in accordance with *Doorenbos'* (1954) experiments with *Hedera*.

The lack of leaf-retention in adult beech grafts on leafy rootstocks argues against this explanation, and the author believes the good results to be primarily due to skilful grafting directly in the plantation. The retention of rootstock shoots probably contributes to a quick establishment of the graft through the upkeep of a good root/top connection. During the period of establishment the lack of juvenile properties in the adult grafts may be compensated by the juvenility of the rootstock shoots. The retention of rootstock shoots requires "high grafting" i. e. at about 1 m above ground; this may be a technical disadvantage in relation to the immediate object of timber production.

If the main meristematic change occurs at the close of the juvenile stage, and if later changes are unimportant, quick establishment might mean complete success of adult clone cultivation. However even if the ability to become established is the most conspicuous advantage of juvenility it is probable that other advantages of juvenile forms and disadvantages of adult forms are important. *The heavy flowering and loss of main axis in adult Acer pseudoplatanus and Fraxinus excelsior grafts is a serious warning to adult clone cultivation* (p. 375 & 373).

However interesting the experiments with enrichment of plantations through grafting of selected adult material are enrichment with juvenile material if available would probably be preferable. This is another reason for preserving the juvenile forms of selected trees.

Considerations on clone cultivation lead to the conclusion that the method is in an experimental stage. At present further expansion in silvicultural practice is not recommended, and tree breeders should reckon on a continued use of seedlings.

It should be noted that *the majority of juvenile characteristics are especially useful in the normal habitat of the young plant. Passecker* (1952) discussed this question in detail and stressed the advantage of the thorny juvenile forms in many Amygdalaceae and Pomaceae, which were thus naturally protected against damage from game and cattle. He also mentioned the shade tolerance of juvenile stages among the advantageous characters.

Several examples of like nature are to be found in the review of literature in chapter I and in the present investigations on physiological and silvicultural aspects, chapter III. This applies especially to the ability of juvenile beech and ash to become established even in an unfavourable environment. This capacity seems to be made up of several qualities of which late flushing, great regenerative power and special bark type are especially important in frosty localities.

Like Passecker the author regards the phenomenon as a hereditarily fixed adaptation of juvenile stages. The appropriate juvenile qualities may be conditioned through natural selection, a survival of the fittest.

In relation to the *tending of forest stands* there is little to add to the discussion in chapter I (p. 349—52) and to the excellent conclusion by *Erteld* (1955) as the present investigations include but few experiments in this field.

However emphasis should be placed on *influence of environment on duration of ontogenetic development.* In this connection special reference is made to section 2 of chapter III. The consequences for silviculture cited below have been outlined in a previous paper (*Schaffalitzky* 1956 b).

Silviculturists should pay special attention to the fact that dense shade and difficult environmental conditions retard development in forest trees, while it is furthered by favourable conditions and light. Heavy thinnings may therefore cause quick transition into adult, slow growing and fruiting stages, and such stands may consequently be less suited for reserve stock. In other words heavy thinning is physiologically connected with low rotations. This has bearing on *the choice of thinning grade* in relation to the object of management in any particular forest.

Wiedemann (1951 p. 83) demonstrated a different increment rhythm in heavily and lightly thinned stands of Norway spruce, Scots pine and beech. He reckons that the heavily thinned stands take the lead in youth, while a study of the average increment at different rotation ages shows a superiority in the lightly thinned stands later on. This difference in increment rhythm agrees very well with the marked influence of external factors on meristematic aging.

Foresters should also note the retarded development in chronologically old natural regenerations of beech under dense canopy. By careful treatment such regenerations may be developed into good stands.

It is a well-known fact that the volume increment of our forest stands declines after a certain age. This is generally believed to be due to increased respiration and difficulty in water transport (*Boysen Jensen* 1921 and *Møller* 1945 p. 248). *Besides these explanations the author finally presents the hypothesis that meristematic aging is also responsible for this increment decline.*

SUMMARY.

The present publication deals with *observations and studies on changes which take place in apical meristems of woody plants with age.* These changes are normally irreversible and may occur rather suddenly. It is therefore justifiable to speak of development stages in trees and shrubs. *Development stages represent separate phases in the ontogenesis from seedling to adult tree.* The stages are characterized by morphological and physiological qualities.

The existence of age phenomena in the meristem and the existence of development stages are thus two expressions for one and the same thing. The former is best suited for gradual and indistinct transitions, whereas the latter is suitable for the so-called *juvenile stages.* These juvenile stages are so well defined in some tree species that the term, *juvenile forms* may be used.

The classical example is *ivy,* which passes through a juvenile stage with creeping or climbing shoots and palmately lobed leaves. When the plant comes of age the adult flowering form with upright shoots and elliptic leaves develops.

Chapter I deals with earlier investigations on such meristematic aging. In many woody plants the juvenile form differs so greatly from the adult that it has been regarded as a specific species. Such examples are well-known from Australia and New Zealand where many trees with characteristic juvenile forms are found.

Another well-known example of the same kind are the so-called *Retinispora forms,* which for many years were grouped as a single species within the cypress family. It is especially the merit of *Beissner* to have proved that the *Retinispora* belong to various species of *Chamaecyparis* and *Thuja.* They are plants which never leave the juvenile stage, so-called *fixed juvenile forms,* and their existence is probably due to hereditary variation or mutation.

The existence of the development stages becomes especially evident in vegetative propagation. Therefore the phenomenon has been noted and discussed in fruit growing during several hundred years. The most characteristic qualities of juvenile forms in many *fruit trees* are sterility and thorniness. Detailed investigations have been made especially by *Fritsche* (1948) who found many other differences, for instance in the anatomy and chemistry of the wood.

It is important to realize that due to repeated vegetative propagation *our usual fruit tree varieties have lost the juvenile stage. However a hypothesis of an actual senility in the meristem of old varieties has never been verified.*

The course of the ontogenetic development of a woody plant is not only governed by age, but to a great extent by environment as well. According to *Büsgen & Münch* (1927) those properties which are due to the age of the meristem are of cyclophysical nature, whereas the environmentally determined properties are of a periphysical nature.

A shoot may also possess qualities of a topophysical character i.e. conditioned by the shoot order itself. The classical example is *Araucaria excelsa* (*Vöchting* 1904). Cuttings from leaders of this species develop into normal plants, whereas cuttings from first order lateral branches develop horizontally and resemble ordinary side branches. Cuttings from second order lateral branches develop as single threadlike non-branching horizontal shoots.

Both *periphysis* and *topophysis* may blur properties conditioned by *cyclophysis,* while the indubitable hereditary variation in stage duration causes less disturbance.

In forestry, development stages have so far been somewhat overlooked, primarily because vegetative propagation has been little used and secondly because environmental conditions play a very important rôle in the appearance of our stands.

For example it is characteristic that the influence of light on leaf anatomy has long been a well-known fact, whereas few silviculturists have paid attention to the investigations of *Schramm* (1912), who made probable that the existence of sun and shade leaves was also conditioned by meristematic aging.

Chapter II presents the author's experiments to demonstrate meristematic aging in some tree species.

The experimental method is based upon the curious fact that low epicormics even in fully developed trees, remain in the juvenile stage. This is true both of shoots from dormant and from adventitious buds. Also root shoots show juvenile characters. The phenomenon seems to be connected with the extremely slow growth of dormant buds and to the fact that cambial meristems do not age or at least age decidedly more slowly than those of shoot tips. The basal portion of a woody plant is termed *the juvenile zone*; it is characterized either by still showing features of a juvenile type, or by ability to reproduce these by stooling or pruning.

In order to investigate whether a tree species passes through various development stages the following procedure may be used: Scion-wood from low epicormics and from top branches are propagated vegetatively and treated uniformly; disturbing effects of genotype and periphysis are thus eliminated. If the two scion categories produce mutually different plant lots we are faced with a purely cyclophysical phenomenon.

In a previous paper (*Schaffalitzky* 1954) this experimental method was used to prove that *Fagus sylvatica* passes through a juvenile stage characterized by winter leaf-retention.

This result is supported in chapter II by repeated investigations. Also in *Quercus robur* and *Quercus petraea* a juvenile stage with the same main character is demonstrated. It is however characteristic for the two oak species that the capacity to retain winter foliage is also a hereditary quality. It was likewise possible to demonstrate a leafy juvenile stage in *Carpinus Betulus.*

Experiments with *Quercus borealis* showed that the ability to assume red autumn colouring is lost with increasing meristematic age.

Similar demonstrations showed that *Fraxinus excelsior* passed through a juvenile stage with relatively wide leaflets; specimens with red shoot colour lost this character with age. In both *Fraxinus excelsior* and *Acer pseudoplatanus* there appeared to be a definitely greater ability to form flower buds in material taken from the tops of the trees than from low epicormics. In sycamore this phenomenon directly leads to repeated forking. The correlation between heavy flowering and from a silvicultural standpoint, bad form, is found again in ash and other hardwoods, although it is less conspicuous.

The juvenile form of *Ulmus carpinifolia* bears smaller, more scabrous and less oblique leaves than the adult form, while *Robinia pseudoacacia* passes through a juvenile stage, characterized by heavy thorns, and probably greater growth vigour.

Like *Acer pseudoplatanus, Syringa vulgaris* possesses a sterile juvenile form with a single main axis. This stage is however so short-termed that the common lilac cannot be used as a forest tree.

Greater rooting capacity was the sole juvenile character found for *Populus X canadensis serotina.* Besides the earlier mentioned development stage qualities in *Hedera Helix* the experiments demonstrated a decrease in ability to form anthocyan with age.

From the review of literature in chapter I and from demonstrations in chapter II the author concludes that *age changes in the apical meristem of woody plants is a common and probably universal phenomenon.* Juvenile forms should therefore not be regarded as curious exceptions, but as easily observable examples of meristematic age changes. These changes are probably due to one or several chemical compounds, specific to the different development stages.

Normally propagation by seed is a condition of complete *rejuvenation,* however recent experiments indicate that it is possible to rejuvenate adult ivy twigs by cold shock, X rays, graft combinations with juvenile material and treatment with gibberellic acid.

The age changes in the meristems of trees are of direct *importance in forest tree breeding,* as *scions for seed orchards should be collected from high flowering branches of old trees. On the contrary scion-wood for complete estimation of the genotype in tree shows and for direct timber production should be of juvenile origin.*

It is therefore important to retain the juvenile forms and prevent their disappearance by repeated vegetative propagation, as was done in fruit growing. Great attention should however be paid to research on artificial rejuvenation of adult forms. Furthermore studies on developmentally conditioned disease resistance in trees deserve special attention.

Interaction between heredity and meristematic aging is also important in tree breeding. Early flowering, i.e. short sterile juvenile stage, may thus be a hereditary character. Flowering and fruiting however, mean increment decrease, and the forest tree breeder should therefore avoid the use of precocious individuals.

Chapter III primarily treats the author's experiments on physiological, hence silviculturally important qualities in the juvenile form of beech and ash. The experiments show remarkably uniform results for the two species, as both juvenile forms, compared to the adult, have qualities of later flushing, larger growth vigour — especially more regenerative power — and greater bark resistance to temperature injuries.

Investigations on *influence of external factors* demonstrated that dense shade may condition complete leaf-shedding in juvenile beeches, thus causing the main character, withered leaves, to disappear. Shade may not only condition leaflessness in low epicormics, but even make them bear flower and fruit. Also the rather constant conical juvenile zone of isolated young beeches is connected with slow growth of the interior twigs. This again is conditioned by external factors, as observations showed topophysis to be of little importance in beech.

Some experiments on artificial *rejuvenation* of adult beech twigs gave negative results, and spontaneous rejuvenation was never observed in nature.

It is striking that many juvenile characters are specially advantageous in the normal habitat of young plants. This is for instance true for beech and ash, of which the demonstrated qualities enable a quicker establishment of the juvenile form than of the adult when planted in a forest. In the same way thorns protect many juvenile forms against game and cattle damage, and the usually greater shade tolerance in the juvenile stage is also a fortunate quality.

In accordance with Passecker (1952) these advantageous properties should be regarded as expressive of a hereditarily fixed adaptation in the juvenile forms. This adaptation is believed to be conditioned by a natural selection.

The author regards the lack of these useful juvenile qualities as the main reason for the general failure of experiments with adult clone cultivation in Danish forests. By clone cultivation is meant planting or direct grafting of selected trees in ordinary young plantations. *The method is still in the experimental stage. Further expansion in silvicultural practice is not recommended at present,* but enrichment of young plantations with selected juvenile material may be tried.

The importance of *meristematic aging in tending forest stands* has been especially discussed by Russian and East German investigators (cf. p. 349). The main school of thought subdivides each of the ordinary tree classes into two. One of these sub-classes comprises individuals believed to be forced by environment to develop slowly, the other for the same reason quickly. By gradual removal of the latter sub-class it is considered possible to maintain a high volume production of the stand. Evidently this means heavy thinnings in the upper storey or even thinnings from above.

This school of thought does not regard the different growth rhythms as hereditary, but the author considers *further investigations necessary to clarify the complicated problems of equilibrium within forest stands.*

Silviculturists should also note that dense shade retards development, whereas light and favourable conditions accelerate it. Heavy thinnings quickly bring the trees into copiously fruiting stages with lower volume production, and such stands become earlier mature and physiologically may be less suited for reserve stock. On the other hand chronologically old regenerations of beech in dense shade may, by careful tending, develop into good stands.

Finally the author presents the hypothesis that the well-known decrease in volume production of a forest stand with age is not only due to increased respiration and water transport difficulties but also to meristematic aging.

DANSK OVERSIGT.

Undersøgelser over aldersforandringer i vedplanternes apikale meristemer og deres betydning for skovdyrkningen.

Denne afhandling beskæftiger sig med de *forandringer, som finder sted i træagtige planters vækstpunkter med alderen.* Disse forandringer er normalt irreversible og kan indtræde ret pludseligt; man taler derfor om *udviklingsstadier* hos træer og buske. Derved forstås adskilte faser i ontogenesen fra frøplante til voksent træ. Stadierne kendetegnes af morfologiske og fysiologiske egenskaber.

Forekomsten af aldersfænomener i meristemet og eksistensen af udviklingsstadier er således to udtryk for det samme. Det første udtryk passer bedst til de mere gradvise og utydelige overgange, mens det andet er velegnet, når det drejer sig om de såkaldte *ungdomsstadier.* Disse er nemlig hos en række træer særdeles velafgrænsede, således at man ligefrem kan tale om *ungdomsformer.*

Det klassiske eksempel er *vedbend,* som gennemgår et ungdomsstadium med rankende eller klatrende skud og håndlappede blade. Når planten bliver ældre, udvikles den voksne blomstrende form med oprette skud og elliptiske blade.

Kapitel I handler om tidligere undersøgelser på dette område. Det beskrives, hvorledes ungdomsformen hos mange vedplanter kan være så forskellig fra den voksne form, at man har anset den for en særlig art. Eksempler herpå foreligger især fra Australien og New Zealand, hvor der findes mange træer med karakteristiske ungdomsformer.

Et andet kendt tilfælde er de såkaldte *Retinisporaformer,* som i en lang årrække var samlet i een art inden for Cypresfamilien. Det er især *Beissners* fortjeneste at have påvist, at det imidlertid drejer sig om ungdomsformer, der hører til forskellige *Chamaecyparis-* og *Thuja-arter.* Det er planter, som aldrig forlader ungdomsstadiet, og deres forekomst skyldes formentlig arvelig variation eller mutation.

Forekomsten af udviklingsstadierne er mest iøjnefaldende, når man benytter vegetativ formering. Derfor har forholdet været diskuteret inden for frugtavlen gennem flere hundrede år. De mest karakteristiske kendetegn på ungdomsformerne inden for mange *frugttræer* er sterilitet og tornethed. Nøjere undersøgelser er især foretaget af *Fritsche* (1948), som fandt mange andre forskelle for eksempel i veddets anatomi og kemi.

Det er vigtigt at gøre sig klart, at vore *almindelige frugtsorter har mistet ungdomsstadiet på grund af fortsat vegetativ formering. Egentlig senilitet i meristemet hos vore gamle sorter er dog aldrig blevet sikkert påvist.*

Forløbet af en vedplantes ontogenetiske udvikling er ikke blot aldersbestemt, men også i høj grad afhængigt af kårene. I overensstemmelse med *Büsgen & Münch* (1927) siges de egenskaber, som skyldes meristemets alder, at være af cyklofysisk natur, mens de kårbestemte egenskaber er af perifysisk art.

Endelig kan et skud have egenskaber af topofysisk natur, det vil sige betinget af selve skudordenen. Det klassiske eksempel er *Araucaria excelsa* (*Vöchting* 1904). Mens stiklinger fra topskuddet af denne art udvikler sig til normale planter, opstår der flade sideskudlignende individer af stiklinger fra sideskud af første orden og ejendommelige trådformede planter af stiklinger fra sideskud af anden orden.

Både *perifysis* (fænotypisk natur) og topofysis (stillingsnatur f. eks. sidegrensnatur) kan vanskeliggøre iagttagelsen af de af *cyklofysis* (livsløbsnatur) betingede egenskaber. Den utvivlsomme genotypiske variation med hensyn til stadiernes varighed volder derimod mindre besvær.

Inden for skovbruget har udviklingsstadierne hidtil været ret upåagtede. Dette skyldes for det første, at vegetativ formering har været en undtagelse og for det andet, at kårene spiller en meget stor rolle i vore bevoksninger.

Det er for eksempel karakteristisk, at lysforholdenes indflydelse på bladanatomien for længst er en velkendt sag, mens kun få skovbrugere har været opmærksom på *Schramms* (1912) undersøgelser, der klart tyder på, at forekomsten af lys- og skyggeblade også er afhængig af meristemets alder.

I kapitel II påvises ved forsøg forekomsten af aldersforandringer i meristemet hos en række træarter.

Forsøgsmetoden bygger på den ejendommelige omstændighed, at lavtsiddende vanris selv hos fuldt udviklede træer befinder sig i ungdomsstadiet. Dette gælder både skud fra sovende øjne og kallusknopper. Også rodskud udviser ungdomskarakterer. Forholdet synes at hænge sammen med de sovende øjnes uhyre langsomme vækst og med den omstændighed, at kambiets meristemer ikke ældes eller i hvert fald ældes betydeligt langsommere end skudspidsernes. Denne nedre del af en vedplante kaldes *ungdomszonen,* fordi den enten stadig bærer ungdomsstadiets kendetegn eller ved beskæring kan frembringe dem.

For at undersøge om en træart gennemløber forskellige udviklingsstadier, kan man derfor gå frem på følgende måde: Kvistmateriale fra lavtsiddende vanris og fra topgrene formeres vegetativt og behandles ganske ensartet. Forstyrrende virkning af genotype og perifysis er således udelukket, og dersom de 2 kvisttyper giver indbyrdes forskellige plantepartier, står man over for et fænomen af rent cyklofysisk natur.

I et tidligere arbejde af forfatteren (*Schaffalitzky* 1954) blev denne forsøgsmetode anvendt til at påvise, at *Fagus sylvatica* gennemgår et ungdomsstadium kendetegnet ved bevarelsen af de visne blade om vinteren.

I kapitel II støttes dette resultat af gentagne undersøgelser, og også for *Quercus robur* og *Quercus petraea* påvises et ungdomsstadium med samme hovedkendetegn. Karakteristisk for de to egearter er imidlertid, at evnen til at bevare bladene om vinteren også er udpræget arveligt betinget. Hos *Carpinus Betulus* kunne ligeledes demonstreres en ungdomsform, der ikke kaster løvet om efteråret.

Forsøg med *Quercus borealis* viste, at evnen til at antage de smukke røde efterårsfarver går tabt hos bladene, når meristemet ældes.

Tilsvarende demonstrationer med *Fraxinus excelsior* viste, at denne træart har et ungdomsstadium kendetegnet af relativt brede småblade, og at individer med rød skudfarve mister denne egenskab med alderen. Både hos *Fraxinus excelsior* og *Acer pseudoplatanus* demonstreredes en betydeligt større evne til dannelse af blomsterknopper hos materiale fra trætoppe. Dette forhold fører hos ær direkte til gentagen tvegedannelse; denne sammenhæng mellem stærk blomstring og forstligt set dårlig form genfindes om end mindre iøjnefaldende hos ask og andre løvtræer.

Ungdomsformen af *Ulmus carpinifolia* har små, ru og ikke skæve blade i modsætning til alderdomsformen, mens *Robinia pseudoacacia* gennemgår et stærkt tornet ungdomsstadium, formentlig med større vækstkraft.

Syringa vulgaris har ligesom *Acer pseudoplatanus* en ungdomsform kendetegnet af aksevækst og sterilitet. Dette stadium varer imidlertid så få år, at syrenen ikke kan bruges som skovtræ.

For *Populus X canadensis serotina* kunne kun påvises en større evne til rodsætning hos ungdomsformen. Foruden de tidligere nævnte kendetegn på udviklingsstadierne hos *Hedera Helix* viste forsøgene en nedsat evne til antocyandannelse hos alderdomsformen.

Ud fra litteraturgennemgangen i kapitel I og egne demonstrationsforsøg i kapitel II konkluderer forfatteren, at *aldersforandringer i meristemet hos vedplanter er et ganske almindeligt og formentlig alment fænomen.* Ungdomsformer bør derfor ikke betragtes som ejendommelige undtagelser, men som særligt iøjnefaldende eksempler på aldersforandringer i vækstpunkterne. Forfatteren slutter sig til den teori, at disse forandringer skyldes forekomsten af et eller flere kemiske stoffer, som er specifikke for de forskellige udviklingsstadier.

Mens frøformering normalt er en betingelse for fuldstændig „foryngelse“, tyder nyere forsøg på, at det er muligt at fremkalde *tilbageslag til ungdomsformen* hos voksne kviste af vedbend ved kuldechok, røntgenbestråling, podning på ungdomsformer med blade og ved behandling med gibberrellin.

Forekomsten af aldersforandringer i træernes meristemer har direkte *betydning i skovtræforædlingens praksis.* De viser nemlig, at *man bør tage podekviste til frøformering og fremavl fra højtsiddende blomstrende kviste af gamle træer. Derimod bør kvistmateriale til fuldstændig bedømmelse af genotypen i træskuer og til direkte vedproduktion tages fra ungdomsformer.*

Derfor må man forsøge at bevare ungdomsformerne, således at de ikke ved fortsat vegetativ formering helt går tabt, som det er sket i frugtavlen. I denne forbindelse må man imidlertid nøje følge forsøgene på at fremkalde tilbageslag til ungdomsformen hos voksne kviste. Særlig interesse knytter sig endvidere til studiet af udviklingsbetinget modstandsdygtighed mod sygdomme hos vore skovtræer.

Det samspil, som findes mellem arvelighed og udvikling, er også af betydning for skovtræforædlingen. Tidlig blomstring — det vil sige kort sterilt ungdomsstadium — kan således være en arvelig karakter. Blomstring og frugtsætning betyder imidlertid tilvæksttab, og skovtræforædleren bør derfor undgå at bruge de tidligt blomstrende individer.

Kapitel III behandler i første række påvisningen af fysiologisk og dermed skovdyrkningsmæssigt betydningsfulde egenskaber hos ungdomsstadiet af bøg og ask. Forsøgene giver bemærkelsesværdigt ensartede resultater for de to træarters ungdomsformer, der i forhold til alderdomsformerne har evne til senere løvspring, større vækstkraft — især bedre regenerationsevne — og mere modstandsdygtighed mod temperaturskader i barken.

Undersøgelser og iagttagelser over *kårenes indflydelse* viste, at kraftig skygge kan forårsage fuldkomment bladfald hos bøgeplanter i ungdomsstadiet, således at selve hovedkendetegnet, de visne blade, forsvinder. Skyggen kan ikke blot bevirke bladløshed hos lavtsiddende vanris, men endogså få disse til at blomstre og sætte frugt. Også den ret uforandrede kegleformede ungdomszone hos fritstående unge bøge tilskrives kvistenes langsomme vækst, som atter skyldes kårene. Iagttagelser viser nemlig, at topofysis er af uvæsentlig betydning for bøg.

En række forsøg på at fremkalde *tilbageslag til ungdomsformen* hos bøgekviste i alderdomsstadiet er ikke lykkedes, og sådanne tilbageslag er heller ikke iagttaget i naturen.

Det er påfaldende, at mange ungdomskarakterer er særlig nyttige under de kår, som den unge plante kommer ud for. Det gælder således de påviste egenskaber hos bøgens og askens ungdomsformer, som har lettere ved at klare sig ved direkte udplantning i skoven. På tilsvarende måde beskytter tornene mange ungdomsformer mod vildt- og kvægskader. Også den gennemgående større skyggetålingsevne hos ungdomsstadiet er en hensigtsmæssig egenskab.

I overensstemmelse med Passecker (1952) *må disse gode egenskaber anses som et udtryk for en arveligt fikseret tilpasning hos de forskellige ungdomsformer.* Denne tilpasning er formentlig resultatet af naturlig udvælgelse gennem tiderne.

Forfatteren er af den anskuelse, at *mangelen på ungdomsformens nyttige egenskaber er hovedgrunden til, at klondyrkningsforsøg med alderdomsformer har givet dårlige resultater i danske skove.* Ved klondyrkning forstås indplantning eller podning på stedet af udvalgte træer i almindelige kulturer.

En række klondyrkningsforsøg under Østsjællandske Skoves Træforædling har imidlertid fået en bedre start. Dette skyldes formentlig særlig omhyggelig podning direkte på stedet og bevarelsen af en del grundstammeris, der fremmer en god og hurtig forbindelse mellem top og rod. Bevarelsen af grundstammerisene betinger imidlertid såkaldt „høj podning“ ca. 1 m over jorden, hvilket til sin tid kan nedsætte kævlens værdi. Til trods for den ret gode start er en omhyggelig pleje af podningerne og kraftig beskæring af nabofrøplanter nødvendig.

Konklusionen er, at *klondyrkningen befinder sig på forsøgsstadiet. Udvidet anvendelse i skovdyrkningens praksis kan i øjeblikket ikke anbefales,* selv om det ville være interessant at prøve klondyrkning med ungdomsformer.

Udviklingsstadiernes betydning for selve bevoksningsplejen er i de senere år blevet diskuteret især i russisk og østtysk forstlig litteratur. Inden for denne „skole“ fordeler man ikke alene træerne i en bevoksning til de kendte grupper af herskende, medherskende og undertrykte træer; men man deler atter hver af disse grupper i to underklasser. Den ene rummer de individer, der har en langsom ungdomsvækst, men senere vokser stærkere, mens den anden kendetegnes ved hurtig ungdomsudvikling og derefter faldende tilvækst, som efterhånden bliver lavere end tilvæksten i den første klasse.

Hvis disse to underklassers vækstrytme er arveligt betinget, står vi over for de såkaldte „stayers“ og „sprinters“, hvis eksistens længe har været diskuteret inden for skovbruget.

Den nævnte „skole“ går imidlertid ikke ind for tanken om „stayers“ og „sprinters“, men forklarer de to underklassers opståen udelukkende som en følge af kårenes indflydelse på udviklingsstadiernes varighed. Det er klart, at disse synspunkter fører til en stærk hugst i overetagen og nærmer sig en hugst fra toppen eller endog en mere eller mindre udtalt plukhugst.

Alle disse spørgsmål er imidlertid uafklarede, og man må give *Erteld* (1955) ret, når *han konkluderer, at man først ved kendskab til sammenhængen mellem et træs ydre egenskaber og dets sandsynlige vækstforløb bliver i stand til at lede en bevoksnings udvikling på hensigtsmæssig måde.*

Skovdyrkeren bør imidlertid mærke sig, at kraftig skygge holder udviklingen tilbage, medens den fremskyndes af lys og gode forhold. Stærk hugst fører derfor hurtigere træerne over i stærkt fruktificerende stadier med nedsat tilvækst, og sådanne bevoksninger bliver tidligere fysiologisk hugstmodne og er sikkert uegnede som vedreserver. Når hugststyrken på det enkelte skovdistrikt skal tilpasses driftsformålet, må der tages hensyn til disse forhold.

Det er ligeledes af betydning for kulturplejen at gøre sig klart, at kronologisk gamle mørke selvforyngelser af bøg oftest er holdt tilbage i ungdomsstadiet og ved omhyggelig behandling kan udvikle sig til gode bevoksninger.

Det er et velkendt forhold, at massetilvæksten i vore bevoksninger begynder at falde ved en vis alder. Dette forklares som regel ved den forøgede respiration og de tiltagende vandhævningsvanskeligheder. *Sidestillet med disse forklaringer fremsætter forfatteren til slut den hypotese, at tilvækstnedgangen tillige skyldes de forandringer, som finder sted i træernes apikale meristemer med alderen.*

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