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EXPERIMENTAL INDUCTION OF FLOWERING IN BEECH

EKSPERIMENTEL FREMKALDELSE AF BLOMSTRING HOS BØG

BY

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WITH AN EPILOGUE

MED EFTERSKRIFT

BY

C. SYRACH LARSEN

INTRODUCTION

The production of mast by beech (*Fagus silvatica* L.) is very irregular. In a previous paper (*Holmsgaard* and *Olsen*, 1960) an investigation was made, using regression analyses, of the variation in beech mast in Denmark as related to the climate over a period of more than 100 years. The result of the analysis was summarised as follows: —

> "The investigation indicates that precipitation and temperature of the preceding summer influence the production of beech mast. High temperatures and low precipitation in June and July usually produce large amounts of mast the next year. However, it appears that precipitation variation has the greatest effect on the production of beech mast. This relationship between climate and beech mast is presumably due to a dependence of the extent of production of flower buds on the drying of soil and trees in June and July."

Such an inference from an analysis of empirical material naturally indicates the desirability of demonstrating in an experiment the relationship found. The results of such an investigation, if successful, could be applied to advantage in the improvement of beech by breeding. As previously suggested by *Holmsgaard* and *Olsen* (1961), it would appear to be easy to produce drought artificially, thereby inducing flowering independently of climate.

The present paper deals with experimental testing of the flower-producing effect of drought on beech.

Holst (1961) said, "The long time lapse between generations is a thorn in the flesh of most tree breeders ..." This has given rise to much work and a very comprehensive literature on attempts to induce flowering. We have deemed it reasonable to refrain from a review of literature in this paper. Reference is made, however, to *Matthews* (1961) and *Lyr* and *Hoffmann* (1964).

MATERIAL

The study was conducted in the Danish Forest Experiment Station nursery at Springforbi on beech clone V. 882-61, Frederiksgave Vesterskov, provided on April 26, 1962, by The Danish State Arboretum at Hørsholm. The plants had been grafted (spliced side grafts) in the spring of 1961 using 1—2 stocks. A description of this clone is given in Dr. *C. Syrach Larsen*'s epilogue (page 15).

Approximately 300 plants of this clone were planted immediately on receipt. Each was planted individually in a plastic bucket with a soil mixture of approximately 60 % morainic sand and 40 % nursery mull. These buckets of beech plants were then placed outdoors in five beds of 60 plants each. The spaces between the buckets were filled with morainic sand to a level nearly flush with the soil surface in the buckets.

The young beech plants were then allowed to remain outdoors in this condition for one year in order to ensure good rooting. In the summer of 1962 they were watered and sprayed against aphids and, in all cases, the wintering of the plants took place in the outdoor beds described.

DESCRIPTION OF THE STUDY

The regression analyses indicated that drought conditions during June and July produce flowering in beech stands. However, it was found desirable to establish a more definite period for the treatment of the beech clone to produce maximum flowering.

Therefore, two studies were conducted:

a) During 1963—64, a preliminary investigation was made to determine the optimum period of treatment for production of flowers.

b) In 1964—65, the main experiment was conducted. This study utilized the results of the preliminary (1963—64) study to investigate more thoroughly the increase in flowering of beech plants artificially subjected to drought as compared to plants which were optimally watered during the study period.

THE 1963—64 EXPERIMENT

The experimental treatment subjected the plants to drought conditions for periods of varying lengths and with different starting times in the summer of 1963. Drought conditions were produced by placing the potted beech plants in a greenhouse*) during the treatment period, where they were watered sparingly. The drought periods appear in Table 1, each treatment comprising two plants only. Thus, the experiment was concerned with treatment of a total of 108 plants.

Table 1. Periods in greenhouse in the 1963—64 experiment.
Tabel 1. Behandlingsperioder i drivhus i 1963—64-forsøget.

x = 1 plant.
x svarer til 1 plante.

Desiccation terminated on *Udtørring afsluttet den*	Desiccation commenced on *Udtørring påbegyndt den*							
	27/5	3/6	10/6	17/6	24/6	1/7	8/7	15/7
3/6	x x							
10/6	x x	x x						
17/6	x x	x x	x x					
24/6	x x	x x	x x	x x				
1/7	x x	x x	x x	x x	x x			
8/7	x x	x x	x x	x x	x x	x x		
15/7	x x	x x	x x	x x	x x	x x	x x	
22/7	x x	x x	x x	x x	x x	x x	x x	x x
29/7		x x	x x	x x	x x	x x	x x	x x
5/8			x x	x x	x x	x x	x x	x x
12/8				x x	x x	x x	x x	x x

Inspection and watering in the greenhouse took place each day. Individual plants were watered at the first symptoms of drought. The individual plant was supplied with an amount of water varying around 100 ml, with regard to the size of the

*) Cold house placed in open nursery, well ventilated and with whitewashed window panes.

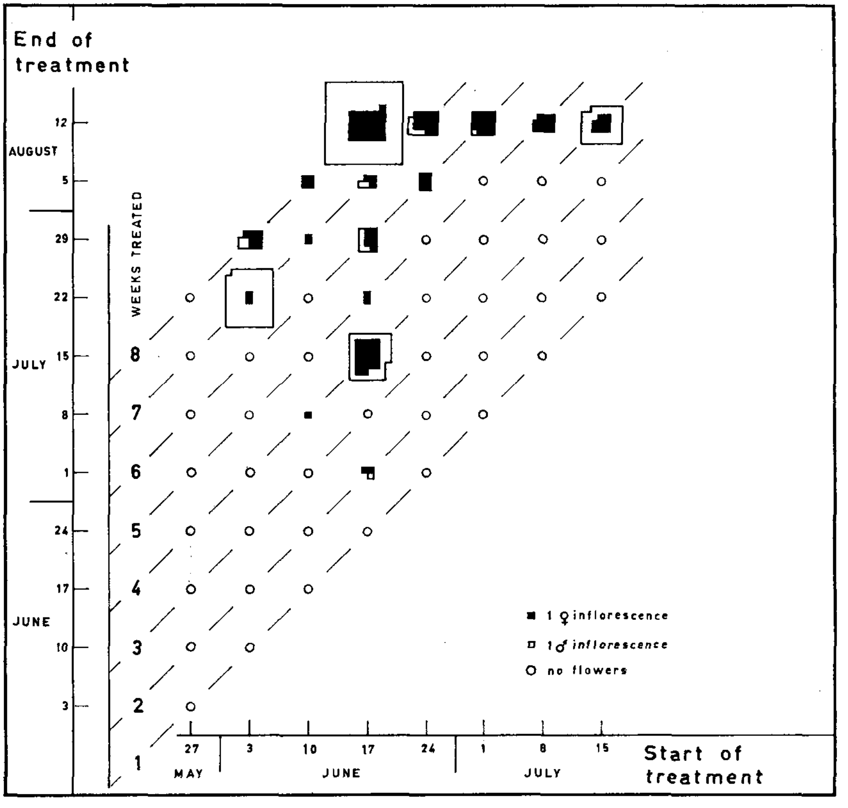

Fig. 1. Number of flowers in the 1963—64 experiment. Each indication represents the sum of inflorescences on two plants treated alike.

Figur 1. Blomsterantal i 1963—64 forsøget. Hver angivelse gælder summen af blomsterstande på to ens behandlede planter.

plant, the degree of desiccation, and the subjective estimate of the minimum amount of water the individual plant would need for the next 24 hours without its leaves beginning to wither.

In the first few days after the start of the experiment, i.e. until about mid-June, the first drought symptom was slack, drooping leaves. When the leaves begin to curl up, there is the risk of permanent injury.

Later, as the leaves became thicker and better protected, the drooping and slack leaves became a less pronounced symptom, and it was, particularly, the incipient curling-up of the top leaves of the plant which indicated the drought condition. Also the ap-

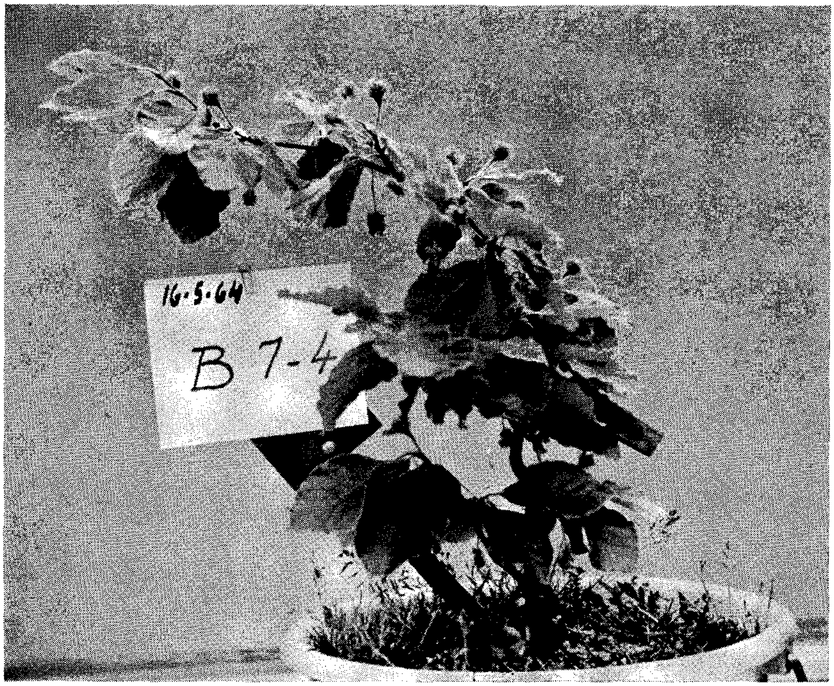

Fig. 2. Plant desiccated from June 17 to July 15, 1963, photographed on May 16, 1964. The plant had 21 ♀ and 32 ♂ inflorescenses.
Figur 2. Plante, som blev nedtørret fra 17/6—15/7 1963, fotograferet d. 16/5 1964. Planten havde 21 ♀ og 32 ♂ blomsterstande.

pearance of the weeds growing in the bucket together with the beech plant was of assistance in assessing the drought condition.

It was not possible in all cases to prevent permanent injury to the beech plants by desiccation. Several of the plants which were being treated in late July responded to a slightly excessive desiccation by the yellowing of leaves on part of the plant. Later, these yellow leaves withered completely and fell off.

Results.

The preliminary experiment was finished by counting the number of male and female flowers on May 8, 1964. As some of the flowers were not yet fully developed at that time, the census was repeated on May 20, 1964. The results of this census appears in Fig. 1. Results presented in Fig. 1 indicate that plants which were treated latest in the summer, had the best flowering. It is also evident that flowering intensity became greater the longer the desiccation continued. No doubt, the effect of the duration of the desiccation had some relation to the point of time of drying-up. This conclusion was reached from the fact that the plants subjected to treatment latest in the summer flowered after a shorter period of drought than those subjected to treatment earlier.

The number of flowers in the plants which were subjected to desiccation from June 17 was conspicuously large. Fig. 2 shows one of these plants. The fact that all the treatments which were terminated last (Aug. 12) resulted in abundant flowering seems to indicate that continuation of the treatment beyond August 12 would have given an even better result.

The best results were obtained with plants which were subjected to desiccation between June 17 and August 12.

THE 1964—65 EXPERIMENT

On the basis of the results of the 1963—64 experiment, it was decided to let the experiment comprise desiccation in the periods June 16—August 13 and June 16—August 27.

This experiment was made with 120 plants of the same clone as in the preceding experiment. At the start of the experiment (the summer of 1964) these plants had been left for 2 years in plastic buckets in the nursery. During that period the plants had been watered and sprayed against aphids, and in the month of July 1963 they had been given approximately 5 g of a mixed fertiliser (Hoechst) per bucket.

The experiment was split up into two series. In one series the treatment of the plants took place in the previously mentioned greenhouse. In the other series, the plants were left outdoors during the period of treatment.

The Greenhouse Experiment.

This experiment comprised 60 plants (one of the beds mentioned on page 4). On June 16, 1964, all 60 plants were moved into the greenhouse, with the same spacing apart as in the nursery being observed. The plants were distributed into 5 blocks of 12 plants each. Half the plants in each block, i.e. six, were given the minimum amount of water during the treatment period, in accordance with the criterion applied in the 1963—64 experiment (i.e. the plants were supplied with as little water as possible without the risk of withering of the leaves). The remaining 6 plants of each block served as controls. They were watered so abundantly that they had optimum growth conditions throughout the period of treatment.

For half the plants, the treatment was interrupted on August 13, 1964. Three of the treated plants from each block, as well as three controls, were moved back to their original sites in the nursery, after which both the desiccated plants and the controls were given the optimum amount of water. For the other half of the plants, the treatment was terminated on August 27, and they were moved back to the nursery bed, where they were watered optimally.

The Outdoor Experiment.

Also this experiment comprised one of the previously mentioned beds of 60 plants, which were likewise split up into 5 blocks of 12 plants each, six of which were treated while the other six served as controls.

As was the case in the greenhouse experiment, the treatment consisted in supplying the plants with the minimum amount of water required without the leaves withering. This was accompliced by placing the buckets and plants to be treated into plastic bags, which were in turn tightened around the lower portion of the stems of the plants, to prevent seeping-in of water. The necessary watering took place through a length of hosing inserted through the bags. No change was made in the controls (i. e. throughout the treatment period the beech plants were supplied with the optimum amount of water).

As in the greenhouse experiment, the treatment of half the plants was interrupted on August 13, 1964, when three plants of each block had their plastic bags removed, after which they were watered with the optimum amount of water. No change was made for the corresponding control plants.

For the remaining plants, the treatment was terminated on August 27, 1964.

The climatic conditions during the treatment period are illustrated by measurements taken by the Danish Meteorological Institute at Lyngby, located approximately six km from the nursery where the experiment took place:

Meteorological Data for Lyngby.
Meteorologiske data for Lyngby.

	Temperature, monthly average °C *Temperatur, månedsgennemsnit, °C*		Precipitation, monthly total, mm *Nedbør, månedssum, mm*	
	1964	Normal	1964	Normal
June *Juni*	15.0	14.5	45	52
July *Juli*	15.5	16.3	59	63
August *August*	15.1	15.4	77	82

Measurements of the minimum and maximum temperatures in July and August of 1964 showed that, on an average, the minimum temperature was 2°C higher in the greenhouse than out-of-doors, while the maximum temperature in the greenhouse was only fractions of 1°C higher than out-of-doors.

After termination of the treatment, all plants were tended carefully with watering. On September 11, all plants were given approximately 5 g of Hoechst.

Results.

Already in late July, 1964 a difference in the development of buds was noticeable in that the buds of the desiccated plants had a shorter and thicker appearance than those of the controls.

The numbers of male and female flowers of each individual plant in the experiment were counted on June 18, 1965. The results appear from Tables 2 and 3. The counting was impeded to some extent by an attack of beech leaf miner beetles (*Orchestes fagi*) at the time of bud-opening. Especially the male flowers were the object of this attack. In most cases the inflorescence proper was completely or partially gnawed away, leaving only the stalk. Also some female flowers were damaged. However, the

T a b l e 2. Main Experiment.
Number of inflorescences on 15 plants (Count on May 18, 1965).
T a b e l 2. Hovedforsøget.
Antal blomsterstande på 15 planter (optælling 18/5 1965).

Period of treatment *Behandlingsperiode*	Greenhouse *Drivhus*				Out-of-doors *Udendørs*			
	Minimum watering *Minimal vanding*		Optimum watering *Optimal vanding*		Minimum watering *Minimal vanding*		Optimum watering *Optimal vanding*	
	No. of inflorescences *Antal blomsterstande*		No. of inflorescences *Antal blomsterstande*		No. of inflorescences *Antal blomsterstande*		No. of inflorescences *Antal blomsterstande*	
	female *hun*	male *han*	female *hun*	male *han*	female *hun*	male *han*	female *hun*	male *han*
16/6—13/8	149	165	0	0	3	10	0	0
16/6—27/8	171*)	373*)	0	0	12	2	0	0
In total *I alt*	320	538	0	0	15	12	0	0

*) On 14 plants, one being broken.
**) På 14 planter, 1 plante knækket.*

T a b l e 3. Main Experiment.
Number of plants with and without flowers (count on May 18, 1965).
(+ ♀ = Female inflorescences, — ♀ = Female inflorescences absent etc).
T a b e l 3. Hovedforsøget.
Antal planter med og uden blomster (optælling 18/5 1965).

Period of treatment *Behandlingsperiode*	Greenhouse *Drivhus*										Out-of-doors *Udendørs*									
	Minimum watering *Minimal vanding*					Optimum watering *Optimal vanding*					Minimum watering *Minimal vanding*					Optimum watering *Optimal vanding*				
	+♀ −♂	−♀ +♂	+♀ +♂	−♀ −♂	In all *ialt*	+♀ −♂	−♀ +♂	+♀ +♂	−♀ −♂	In all *ialt*	+♀ −♂	−♀ +♂	+♀ +♂	−♀ −♂	In all *ialt*	+♀ −♂	−♀ +♂	+♀ +♂	−♀ −♂	In all *ialt*
16/6—13/8	5	0	8	2	15	0	0	0	15	15	1	0	1	13	15	0	0	0	15	15
16/6—27/8	2	0	10	2	14*)	0	0	0	15	15	2	0	2	11	15	0	0	0	15	15
In total *I alt*	7	0	18	4	29	0	0	0	30	30	3	0	3	24	30	0	0	0	30	30

*) One plant broken during transfer on Aug. 27, 1964.
**) 1 plante knækket under udflytning 27/8 1964.*

gnawing was not severe enough to prevent the flowers developing sufficiently to be distinctly recognisable. 83 % of the female flowers were undamaged and only 8 % of the male flowers were found to be undamaged in the count.

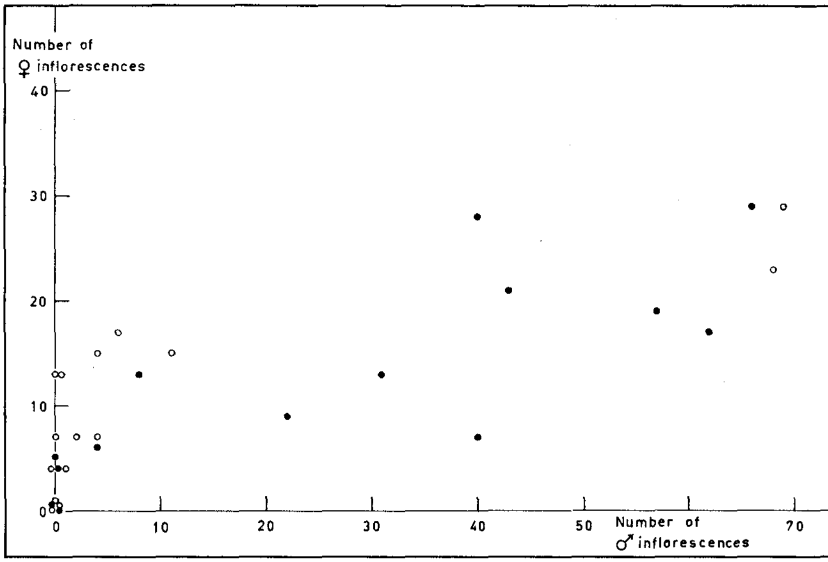

Fig. 3. Number of inflorescences on the 29 plants that were desiccated in greenhouse in the 1964—65 experiment (the missing plant was broken while being moved outdoors).

o = desiccated from June 16 to August 13, 1964.
• = desiccated from June 16 to August 27, 1964.

Figur 3. Antal blomsterstande på de 29 planter, der blev udtørret i drivhus i 1964—65-forsøget (den manglende plante knækket under udflytningen til friland).

o = nedtørret fra 16/6—13/8 1964.
• = nedtørret fra 16/6—27/8 1964.

As may be seen from Table 2, no flowers appeared at all on the plants amply watered, neither in the greenhouse nor outdoors. As far as the desiccated plants were concerned, flowers appeared on 86 % of the plants in the greenhouse experiment and on 20 % of the plants in the outdoor experiment.

The plants which were exposed to drought until August 27 had more flowers than those exposed to drought until August 13. The differences between the two periods of treatment were not significant, however, since great variation occurred within the groups (cfr. Fig. 3).

In the greenhouse experiment the increase in the number of male flowers after prolonged desiccation was conspicuous. Table 3 shows that among the plants which were desiccated until August 27 there was a slightly larger number with both male and

Fig. 4. Two plants which were kept in greenhouse from June 16 to August 13, 1964, photographed on May 22, 1965. The plant to the left was watered amply and produced no flowers. The plant to the right was watered sparingly and produced 15 ♀ and 4 ♂ inflorescenses. Only the flowers at the shoot tips are visible on the photograph.

Figur 4. To planter, som blev holdt i drivhus fra 16/6—13/8 1964, fotograferet d. 22/5 1965. Planten til venstre blev vandet rigeligt og satte ingen blomster. Planten til højre blev vandet sparsomt og havde 15 ♀ og 4 ♂ blomsterstande. Kun blomsterne i skudspidserne er synlige på billedet.

female flowers than among the plants which were only desiccated until August 13. Table 3 further indicates that in no case were male flowers found in a plant which did not have female flowers as well. This appears to indicate that female primordia are formed after desiccation for a shorter span of time than male primordia. Fig. 3 shows that the number of male flowers became ever larger in proportion to the number of female flowers the more abundant the flowering.

No relationship has been found between plant size or number of buds and the number of flowers.

Fig. 4 shows the appearance of two typical plants from the experiment.

CONCLUSION

In the outdoor experiment, as well as in the greenhouse experiment, all growth conditions, with the exception of the water supply, were equal for both the desiccated plants and the control plants. It can thus be established that the water supply is of decisive importance for the differentiation of flower buds.

The plants which were desiccated in the greenhouse have had a far more abundant flowering than the plants dried out outdoors. Temperature conditions differed somewhat for the two series of the experiment. However, although the supply of water to the buckets placed outdoors was controlled, the possibility cannot be excluded that interception by the beech leaves, as well as dew, may have influenced the supply of water to the plants. Consequently, the experiment does not lend itself to the drawing of conclusions as to temperature being a factor influencing the formation of flowers.

In the analysis of the dependence of mast years on climate, no significant effect of temperature and precipitation could be ascertained later than in the month of July of the year when the primordia were formed. We, therefore, assumed that the differentiation of flower buds has ceased by the end of July. This assumption has not been confirmed. Results of the study seem to indicate that differentiation of flower buds may also take place after mid-August.

It is a well-known fact that abundant beech mast occurs only at intervals of several years, thereby presenting difficulties, in respect to breeding work, as well as to the supply of mast in practice.

Our experiments have shown that it is relatively easy to produce flowers artificially in small beech plants in buckets. It must be emphasised, however, that it may be a prerequisite that these plants have originated from scions collected from high-flowering branches of old trees (cfr. *Schaffalitzky de Muckadell,* 1959, page 438). The procedure adopted by us, of growing the plants in buckets, can be used directly in breeding work, and it is possible by this method to eliminate the dependence of flowering on climate since in our study we produced flowers for two consecutive years.

The drought method concept might be usable on a larger scale; particularly, it might be put to advantage in seed orchards of beech. The plants might, for instance, be planted out into the seed orchard in ditches lined with plastic sheeting. In some years the plants might then be well watered, while in others their scant rooting zone was dried up by being protected against water supply by covering with plastic. Indirectly, the same drought conditions might perhaps be obtained by planting the seed orchard on very light soil, where, through fertilising and abundant watering for some years, a growth was produced which was considerably better than that which would be natural for the locality in question. In years, where watering was omitted, the production of the required drought conditions might then be expected.

EPILOGUE

by

C. Syrach Larsen.

Beech V. 882.

The designation V. 882 has its origin in the registration made by the Danish State Arboretum of trees included in vegetative propagation with a view to experiments aimed at improving forest trees. It is an exceptionally beautiful beech, about 100 years old, which is still standing among contemporary, also fine, beeches in Vesterskoven Forest at Frederiksgave.

During a visit to Wedellsborg, *Vilhelm Larsen,* the late Head Forester, directed my attention to this group of trees. Not only did he find them particularly beautiful, but he also gave the very interesting information that his experience was that they yielded an extremely good progeny. If my memory is correct, he said something like this: "It is the only progeny in which I have really seen effects taking a favourable course."

V. 882 was selected as representative of the group in 1945 and was grafted in the Arboretum. Thirteen of these grafts were later planted at the Tree Improvement Station of the Danish State Forestry near Humlebæk, where in 1960 they flowered profusely. Controlled pollination only on branches which could be reached from the ground resulted in more than 7 kg of seeds. A picture of the situation with isolating bags in the spring of 1960 is given by *Kirsten Olesen:* Forest Tree Improvement, in *Carl Mar:Møller* (1965, p. 385).

Concurrently with the V. 882 clone, a number of other clones of similar age and number, grafted from other, selected, particularly beautiful beeches had been planted at the Tree Improvement Station. V. 882 was predominantly the most richly flowering tree of them all. Besides being a beautiful tree itself, it has yielded remarkably good progeny by controlled pollination. It is thus a valuable breeding tree, which is also being utilised in other respects at the Arboretum.

It is a stroke of luck that it was possible to make just V. 882 available for the experiments dealt with in the foregoing, and we are grateful to the Danish Forest Experiment Station for the fine experiment and its result. It is a valuable contribution to future forest tree improvement.

SUMMARY

1. In a previous work the authors have found, by correlating mast years and climate in a regression analysis, that it is probable that the flowering of beech is induced by drought in June-July of the year preceding flowering.

2. To determine whether this is correct, experimental desiccation of a flowering beech clone was carried out. The small plants were planted individually in buckets.

3. In a preliminary experiment, made in 1963—64, desiccation of varying duration and commencing at different points of time, gave the results presented in Fig. 1. Plants on which the treatment was commenced after the middle of June, and the desiccation of which was of a rather long duration, gave the largest numbers of flowers. The largest numbers of flowers were found on plants desiccated between June 17 and August 12.

4. Based on the results of the preliminary experiment the main experiment was carried out in 1964—65, and gave the result represented in Tables 2 and 3. No flowers at all were produced by the plants that had been amply watered, neither in greenhouse nor outdoors. As far as the desiccated plants were concerned, flowers occurred on 86 % of the plants in the greenhouse experiment and on 20 % of the plants in the outdoor experiment.

5. For two consecutive years the authors have produced flowers on a beech clone by the same relatively simple treatment. The method applied may be assumed to be usable in the genetical improvement of beech. The results also seem to be promising for regulating the flowering in seed orchards.

RESUMÉ

1. I et tidligere arbejde har forfatterne ved undersøgelse af samvariationen mellem oldenår og klima fundet, at det er sandsynligt, at bøgens blomstring induceres af tørke i juni-juli i året før blomstringen.

2. For at afprøve om dette er rigtigt, udførtes eksperimentel udtørring af en blomstringsvillig bøgeklon. De små planter blev plantet enkeltvis i spande.

3. I et foreløbigt eksperiment udført i 1963—64 gav udtørring af forskellig varighed og indledt på forskellige tidspunkter det på fig. 1 viste resultat. Planter, hvis behandling indledtes efter midten af juni, og hvis udtørring var temmelig langvarig, gav det største antal blomster. Flest blomster gav planter, udtørret fra 17/6 til 12/8.

4. Hovedforsøget blev gennemført i 1964—65 efter de i det præliminære forsøg fundne retningslinier og gav det i tabel 2 og 3 anførte resultat. Der forekom overhovedet ingen blomster på de rigeligt

vandede planter, hverken i drivhus eller udendørs. For de udtørrede planters vedkommende forekom der blomster på 86 % af planterne i drivhusforsøget og på 20 % af planterne i udendørsforsøget.

5. Forfatterne har to år i træk frembragt blomster i en bøgeklon ved samme relativt simple behandling. Den anvendte metode må være brugbar i bøgeforædlingen. Også for regulering af blomstringen i frøplantager synes resultaterne at indebære muligheder.

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