Influence of Cone Size on the Seed Produced

(Pinus silvestris L.)

Kottviktens inflytande
på fröegenskaperna hos tall

by

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Introduction

Traits of seed produced after open pollination of two individual pine trees have been discussed in a previous work (SIMAK 1953 b) where certain relationships between cone weight, seed production and seed size were established. The results were based on the examination of one cone crop only (1952/1953). For the purpose of further studies collection of cones from both trees was continued for three more years.

The findings of this extended investigation are presented in the following chapters:

1. The relationship between cone weight and number of seeds per cone.
2. The influence of cone weight and number of seeds per cone on seed size.
3. The relationship between cone weight and frequency of empty seeds.

Material

The pine trees, described as B 1 and B 5, grow close to one another in a stand at Bogesund (Lat 59°23′ N, Long 18°11′ E). Cones were harvested in the winters of 1952/53, 1953/54, 1954/55, and 1955/56 (in the following named 52, 53, 54, and 55, respectively), each year in good time prior to the natural cone opening.

Methods

Every year all the cones accessible on each tree were collected. Only 70[1] cones per tree and annum, however, were used in the analysis. Since a wide range of cone weights was considered valuable at the statistical processing of data, the cones were selected so as to comprise a wide and uniform array of samples including the smallest as well as the largest cones. The cones were opened by hand and all the filled and empty seeds were gathered. Each cone was recorded with respect to the following characteristics.

Cone weight: The remnants of every cone examined were dried during 16 hrs at a temperature of 110° C controlled by thermostat.

Number of seeds per cone: All the empty and normally developed seeds were counted.

Frequency of empty seeds: The frequency of empty seeds was recorded for each cone by means of X-ray technique.

Seed size: The length (l) of each seed was measured in MM on contrast pictures enlarged and processed by photographic techniques (1 MM = 0.25 mm). Since the shape of seed gathered from one individual tree is constant (SIMAK 1953 a) l^3 has been used as an approximate expression of seed volume.

The data were statistically processed according to principles used in the previous work.

Results

1. The relationship between cone weight and number of seeds per cone

Since the seed production is correlated with cone weight, it is of interest to study for both trees how the number of seeds varies in relation to the cone weight. The regression analysis is based on the function $Y = a + bx$ (cf. Fig. 1). Figure 1 shows for each year and both trees that the number of seeds increases when the cone weight rises. Regarding level of the parallel regressions,

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[1] For 1952 the material previously described and examined (SIMAK 1953 b) was used. In this final analysis, however, the no. cones per tree was reduced to 70.

the difference between the years is significant for both tree B 1 ($P < 0.001$) and tree B 5 ($P < 0.001$) (cf. *a*-constants of parallel regressions for years 52—55 in table 1). The differences between years with respect to slope of regression are convincing since $P < 0.001$ for both trees (cf. *b*-coefficients for the years 52—55 in table 1).
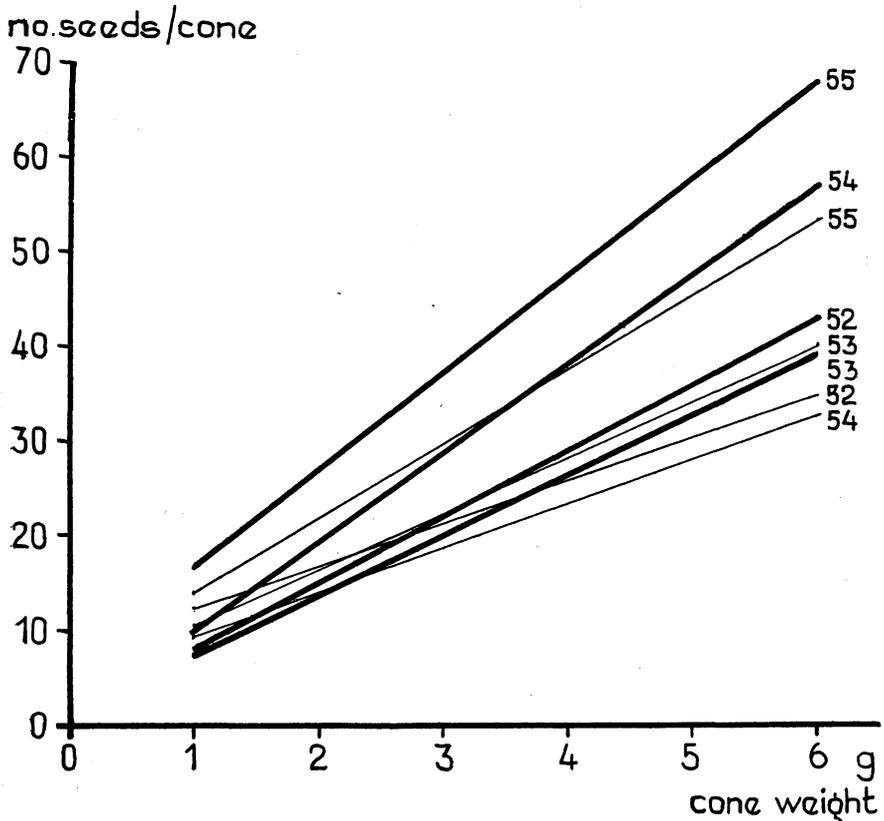
no.seeds/cone

Fig. 1. Relationships between cone weight and no. seeds/cone for the years 52—55. Thin lines: tree B 1. Heavy lines: tree B 5.

Sambandet mellan kottvikt och fröantal per kott under åren 52—55. Tunna linjer: träd B 1. Tjocka linjer: träd B 5.

A comparison between the trees with respect to the relationships of each year shows that tree B 5 has a higher average number of seeds in cones of equal weight than tree B 1 for the harvest years 52, 54, and 55. For the years 54 and 55 the difference is very significant—(cf. table 1). In tree B 5, how-
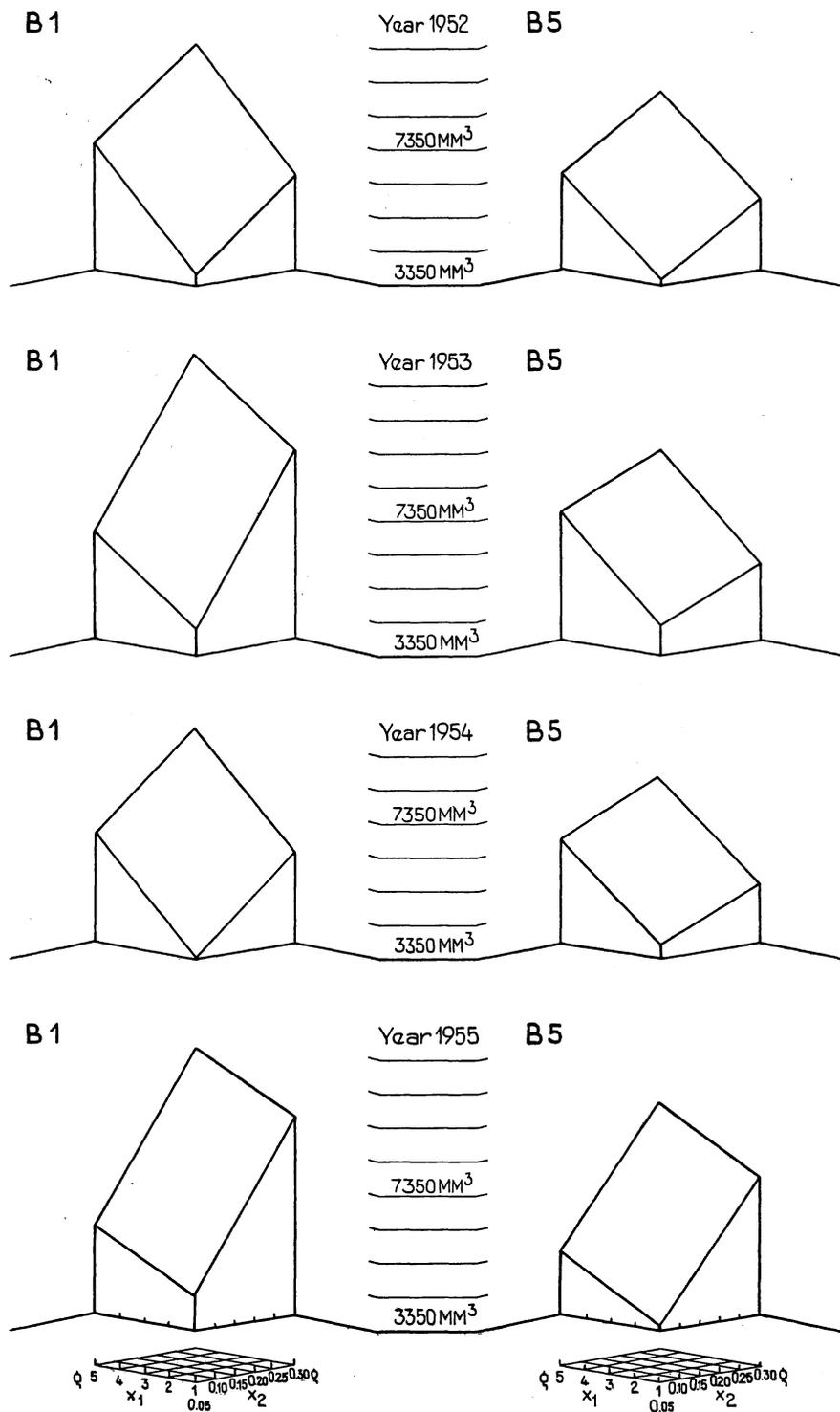
Fig. 2. The dependence of seed size (MM³) on the cone weight (x_1) and the ratio
$$\frac{\text{cone weight}}{\text{no. seeds/cone}} \ (x_2) \text{ for the years } 52\text{—}55.$$

Fröstorlekens (MM³) beroende av kottvikt (x_1) och kvoten $\frac{\text{kottvikt}}{\text{fröantal/kott}}$ (x_2) för åren 52—55.

ever, the number of seeds per cone of equal weight is s l i g h t l y l o w e r (barely significant) than that observed in tree B 1 for the year 53.

The trees differ rather clearly every year regarding the increase of number of seeds per cone at rising cone weight. The increase of tree B 5 is more rapid than that of tree B 1. This difference between the trees is statistically significant in two cases (year 52 and year 54, table 1).

2. The influence of cone weight and number of seeds per cone on seed size

Seed size is correlated with cone weight and number of seeds per cone (SIMAK 1953 b, SIMAK and GUSTAFSSON 1954). The relationship is adequately expressed by a multiple regression:

$Y = a + b_1 x_1 + b_2 x_2$ where

Y = seed size[1], x_1 = cone weight, $x_2 = \dfrac{\text{cone weight}}{\text{no. seeds}}$, a = constant, b_1 and b_2 are regression coefficients.

The results are easily recognized after a graphic presentation of the partial regressions (Fig. 2). Regarding level and slope of the regression surface, the graphs of each tree show annual differences (cf. table 3).

Analyses of covariance similar to those presented in table 3 were carried out for each year and both trees. Only the results of computation are presented in the following table.

Regarding regression level, differences between the trees could be ascertained. For each year the constant of tree B 1 exceeds that of tree B 5 (cf. diff. of a-constants in table 4) but the difference in surface level is not equal for all cone weights and number of seeds. The differences in level presented in table 4 pertain to the parallel regressions. As the individual regressions show, seed size of tree B 1 increases faster at rising cone weight and decreasing number of seeds than that of tree B 5. This difference in the slope of regression between tree B 1 and tree B 5 is statistically significant for the years 52, 53 and 54 (cf. b_1- and b_2-coefficients in table 2, fig. 2 and F-value in table 4).

3. The relationship between cone weight and frequency of empty seeds

For tree B 5 the average frequency of empty seeds calculated for all the cones is twice as high as that of tree B 1.

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[1] The computation of average seed size per cone is here based on $\dfrac{\Sigma\, l^3}{\text{no. seeds}}$ in contrast to previous work (SIMAK 1953 b) where the formula $\dfrac{(\Sigma\, l)^3}{\text{no. seeds}}$ was used.

Year of harvest	Average frequency of empty seeds, per cent		
	B 1	B 5	$\dfrac{B\,5}{B\,1}$
52	8.1	16.4	2.02
53	13.2	36.7	2.78
54	16.1	38.9	2.42
55	19.4	27.7	1.43

Since the frequency of empty seeds in small cones varies extensively due to the generally low number of seeds, the variation of the frequency of empty seeds in cones of different weights has been investigated by transforming the per cent values to $\arcsin \sqrt{\dfrac{\text{empty seeds, per cent}}{100}}$. Thus, frequency of empty seeds mentioned in the following pertains to the transformed expression of this value.

The analyses of regression show that the frequency of empty seeds is correlated with the cone weight (Fig. 3). Save for a case commented upon in the
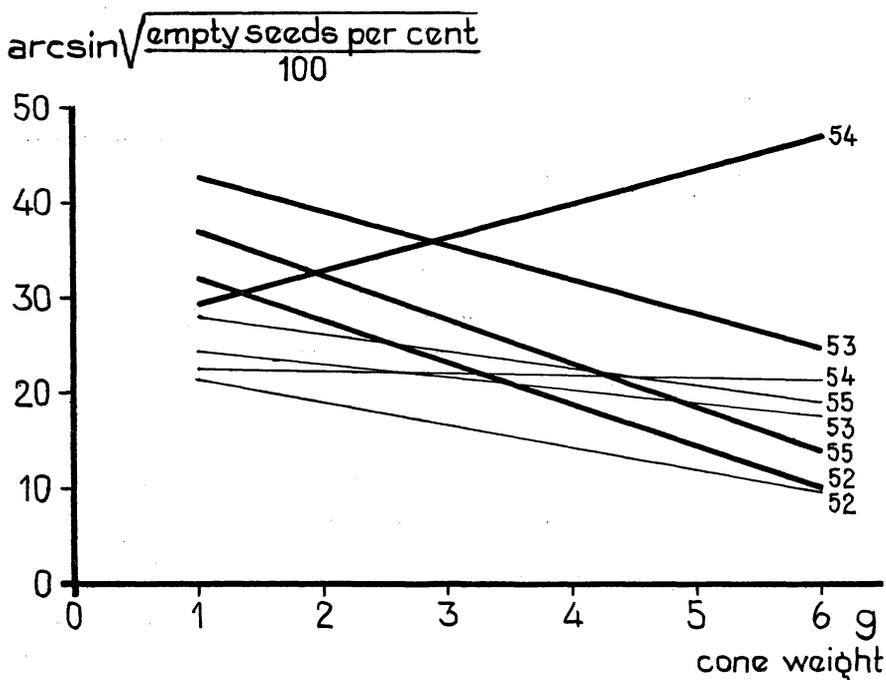
Fig. 3. Relationships between cone weight and frequency of empty seeds (transformed expression) for the years 52—55. Thin lines: tree B 1. Heavy lines: tree B 5.
Frekvensen av tomfrö i kottar av olika vikt för åren 52—55. Tunna linjer: träd B 1. Tjocka linjer: träd B 5.

following, large cones contain proportionally smaller amounts of empty seed than small cones.

The frequency of empty seeds declines for tree B 1 by 2.4 and for tree B 5 by 2.9 units per gram increase of dry cone weight. This correlation calculated for each tree and all the cones collected is not of temporary nature. The regression deviations from zero are significant for both trees ($P < 0.001$).

The slopes of the regression lines of tree B 1 are virtually equal for all the years investigated ($F = 0.82°$ for differences in slope between years). Tree B 5, too, has regression lines that are largely parallel in three cases viz. the years 52, 53, and 55. Since the relationship between cone weight and frequency of empty seeds is positive for tree B 5 for the year 54, the slope differences between the years 52—55 are significant ($F = 4.13**$). A close scrutiny of the basic data reveals that five large cones produced an unusually large number of empty seeds in relation to other cones of equal size. These cones exert a great influence on the course of regression for this relatively limited material of investigation.

Tree B 5 produced every year a higher average frequency of empty seeds than tree B 1. Regarding level of parallel regressions the difference between the trees is significant for each year (Table 5). The frequency curve of empty seeds declines at rising cone weight (exc. tree B 5 for the year 54) and much faster for tree B 5 than is the case of tree B 1. The greatest difference between the trees as regards frequency of empty seeds is found in the small cones. Differences between the trees with respect to slope of the regression lines, however, are statistically not convincing for each year (Table 5).

Discussion

The investigation ,,Beziehungen zwischen Samengrösse und Samenanzahl in verschiedenen grossen Zapfen eines Baumes'' (SIMAK 1953 b) — [Relations between seed size and seed number in differently large cones of individual trees (*Pinus silvestris* L.)] showed that the number of seeds produced by a tree depends on the cone weight and furthermore that the seed size is related with the cone weight and the number of seeds per cone. It has been confirmed in this paper that the frequency of empty seeds, too, is influenced by the cone weight.

The paper reviews an attempt to investigate whether these correlations are governed by the genotype of the trees or whether they are of temporary nature only. It has proved necessary to study the seed properties as a variable mean value. Therefore, mainly covariance analysis was applied at the biometrical computations of the material. Regressions expressing the relationships between cone weight, number of seeds, seed size and frequency of empty seeds were ascertained for each of two trees investigated.

The differences that occur between the regressions computed for each of the four years of investigation may be ascribed to the modifying influence of the environment.

Every year the regressions of the trees are related to each other. Depending on the constancy of this relationship from one year to another, it may be possible to recognize the extent to which the seed properties concerned are governed by the genotype of the tree. A judgement, however, must be made with a certain caution on account of the possibility of differences between the sites and the limited number of years investigated.

1. The number of seeds per cone is correlated with the weight of the cone

It is self-explanatory that large cones provide space for the development of a large number of seeds. The cones, however, are not equally utilized by each individual tree for development of seeds. Tree B 5, for instance, has produced a larger number of seeds per gram of cone weight than tree B1 (an average of 2.5 units more seeds). The specific potency of a tree annually to yield seed in a certain relation to cone weight may be proof that the relationship is conditioned by heredity. The influence of weather, however, is so strong as to exclude the quoting of an absolute value for the relationship between the number of seeds and the cone weight. A relative estimate is possible only. Tree B 5 has a specific capacity to produce more seed than tree B 1 per unit of cone weight.

2. The average seed size is correlated with the cone weight and the number of seeds per cone

Here also, the size and weight of the cone determine the size of the seeds. Large, heavy cones may produce large seeds that naturally have better nutritional conditions for development when the number of seeds is low, and vice versa. Seed size of tree B 1 reacts to cone weight and number of seeds much stronger than that of tree B 5. This is clearly shown by fig. 2 in addition to the statistical computations that confirm the relationships. Since the relationship between the regressions of the trees is equal for all years, heredity may be considered as the basic reason. On the other hand, the variation of the regression from one year to the other may be ascribed for both trees to the modifying effect of the environment.

It is remarkable that tree B 5 utilizes the large cone volume for high seed production whereas tree B 1 exploits this for development of better quality of seed. Thus, a certain equalization of the trees is obtained by substituting quantity for quality (cf. Figs. 1 and 2).

3. Frequency of empty seeds is influenced by cone weight

The frequency of empty seeds declines when the cone weight increases. This has been clearly established on the basis of cone data from both trees. Similar conclusions have been drawn by SIMAK and GUSTAFSSON (1954). Tree B 5 produced every year more empty seed per cone than tree B 1. The frequency of empty seeds declines more slowly for tree B 1 at increasing cone weight than that of tree B 5. An exception was the year 55 when the material investigated showed that the large cones of tree B 5 produced more empty seeds than the small ones. As explained in the text, this was probably a case where a certain disturbance of pollination hit a particular group of large cones. The incidence has manifested itself very strongly in this rather limited material of study. Possibly, it was a disturbance of climatic nature for a similar trend was noticeable to a lesser degree in tree B 1. Since the frequency of empty seeds is depending on the efficiency of fertilization, which in turn is influenced by the weather conditions during the time of pollination, it is clear that the weather is a decisive factor for the frequency of empty seeds. This is the reason why the frequency of empty seeds exhibits great variations between the years. From the fact that tree B 5 *every year* produced more empty seeds than tree B 1, it may be concluded that the frequency of empty seeds is a specific feature controlled by the genotype of the tree.

The importance of the genotype constitution of the tree for the production of empty seed is also shown in an investigation by SIMAK and GUSTAFSSON (1954) where one tree (DALFORS 6) was characterized by a rather high frequency of empty seeds (approx. 40 per cent). This trait, high frequency of empty seeds, was recorded also for the grafts originating from the same tree despite the grafts were grown and fertilized on a location different from that of the parent tree.

Each graft in a clone is a replication of the genotype of the parent tree. Data from such a material are most suitable for mathematical-statistical computations (SIMAK and GUSTAFSSON 1954, EHRENBERG et al. 1955). For this reason, scions from both trees have been used for grafting and the investigation will continue on the grafted material.

Literature cited

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Summary

The investigation is an extension of a previous work (SIMAK 1953 b) where the following relationships were established:

1. The number of seeds per cone increases approximately by a straight line relationship at rising cone weight.
2. The average size of seed increases at rising cone weight, and at equal cone weight also with decreasing number of seeds per cone.

The following supplementary statements have been made in this investigation:

3. The frequency of empty seeds decreases when cone weight increases.
4. These relationships of the properties appear to be determined by the genotype of the tree, but they are strongly modified by the environment (climate). The investigation will continue as a clone study of graft material from both trees discussed in this paper.

Sammanfattning

Kottviktens inflytande på fröegenskaperna hos tall

Denna undersökning är en fortsättning av ett tidigare publicerat arbete (SIMAK 1953 b) i vilket fastställdes följande:

1. Antalet frö per kott ökar med tilltagande kottvikt.
2. Fröstorleken ökar med tilltagande kottvikt, dock vid en bestämd kottvikt, producerar kottar med större fröantal mindre frön än kottar med litet fröantal. Den framlagda undersökningen har givit följande resultat:
3. Tomfröhalten avtar, procentuellt sett, med tilltagande kottvikt.
4. Dessa samband mellan fröegenskaper och kottvikt tycks vara bestämda av trädens genotyp, dock påverkas de mycket av miljön (klimatet). Alla samband skall vidare undersökas i en klontest med ympar från de båda försöksträden.

Zusammenfassung

Zapfengewicht und Samenertrag der Kiefer — *Pinus silvestris*

Diese Untersuchung ist die Fortsetzung einer früheren Arbeit (SIMAK 1953 b) in der folgende Zusammenhänge gefunden wurden:

1. Die Samenzahl je Zapfen steigt etwa geradlinig mit dem Zapfengewicht.
2. Mit zunehmendem Zapfengewicht steigt auch die Samengrösse, wobei Zapfen gleichen Gewichtes — durch die natürliche Streuung der Samenzahlen — bald weniger aber grössere, bald mehr dafür aber kleinere Samen produzieren. Bei der neuen Untersuchung ergaben sich folgende Resultate:
3. Mit zunehmendem Zapfengewicht sinkt der Anteil an leeren Samen.
4. Diese Beziehungen der Samenbeschaffenheit scheinen an den Genotyp des Mutterbaumes gebunden zu sein, sie werden aber stark durch die Umwelt (das Klima) beeinflusst. Die Untersuchung wird deshalb als ein Klontest mit Pfropflingen der beiden Versuchsbäume weiter geführt.

Table 1. Regression analysis for the relationship betyeen cone weight and no. seeds/cone (70 cones per tree and annum)

Regressionsanalys för sambandet mellan kottvikt och fröantal/kott (70 kott per träd och år)

Year	Tree	a-constants of parallel regressions	Diff. of level between parallel regr.[1]		b-coefficients of individual regressions[2]	Diff. between b-coefficients	
			B 5—B 1	F-value		B 5—B 1	F-value
52	B 1	+ 3,478	+ 1,107	1,374°	+ 4,562	+ 2,536	14,588***
	B 5	+ 4,585			+ 7,098		
53	B 1	+ 4,061	— 2,185	4,943*	+ 5,967	+ 0,382	0,203°
	B 5	+ 1,876			+ 6,349		
54	B 1	— 0,771	+ 7,964	115, 447***	+ 4,729	+ 4,770	30,614***
	B 5	+ 7,193			+ 9,499		
55	B 1	+ 4,073	+ 5,486	36, 166***	+ 7,930	+ 2,403	2,863°
	B 5	+ 9.559			+ 10.333		
År	Träd	a-konstanter för parallella regressioner	B 5—B 1 Skillnad i nivå mellan parallella regressioner[1]	F-värde	b-koefficienter för individuella regressioner[2]	B 5—B 1 Skillnad mellan b-koefficienter	F-värde

[1] Difference of level between the parallel regressions may be interpreted as the annual difference between tree B 1 and tree B 5 with respect to the average no. seeds in all cones.

[2] The b-coefficients express increase of average no. seeds per cone at a gain of one gram dry cone weight.

[1] Skillnaden i parallell-regressionernas nivå kan tolkas som den årliga skillnaden i det genomsnittliga fröantalet för all kott mellan träd B 1 och B 5.

[2] b-koefficienterna anger antal frö med vilket det genomsnittliga fröantalet per kott stiger om vikten på kottens torrsubstans ökar med 1 g.

Table 2. Relationships between seed size Y, cone weight (x_1) and $\dfrac{\text{cone weight}}{\text{no. seeds/cone}}$ (x_2).

Sambandet mellan fröstorlek Y, kottvikt (x_1) och $\dfrac{\text{kottvikt}}{\text{fröantal}}$ (x_2)

Tree	Year	$Y = a + b_1 x_1 + b_2 x_2$	t-test $= \dfrac{b}{\varepsilon b}$	
			b_1	b_2
B1	52	$Y = 2,340 + 851\, x_1 + 9,909\, x_2$	11.48***	3.68***
	53	$Y = 2,645 + 596\, x_1 + 19,172\, x_2$	12.25***	8.53***
	54	$Y = 1,998 + 823\, x_1 + 10,660\, x_2$	8.87***	7.48***
	55	$Y = 2,895 + 432\, x_1 + 19,574\, x_2$	2.88**	5.36***
B5	52	$Y = 2,512 + 632\, x_1 + 7,570\, x_2$	11.55***	8.86***
	53	$Y = 3,342 + 712\, x_1 + 5,149\, x_2$	7.92***	4.97***
	54	$Y = 2,865 + 665\, x_1 + 5,042\, x_2$	7.73***	4.48***
	55	$Y = 2,181 + 452\, x_1 + 15,963\, x_2$	6.10***	8.04***
Träd	År	$Y = a + b_1 x_1 + b_2 x_2$	b_1 t-test $= \dfrac{b}{\varepsilon b}$	b_2

Table 3. Analysis of covariance of Y (seed size) over x_1 (cone weight) and x_2
$\left(\dfrac{\text{cone weight}}{\text{no. seeds}}\right)$ **for tree B 1 and tree B 5. All cone data of the years 1952—55.**

Kovariansanalys av Y (fröstorlek) på x_1 (kottvikten) och x_2 $\left(\dfrac{\text{kottvikt}}{\text{fröantal}}\right)$ för träd B 1 och B 5. Hela kottmaterialet från åren 1952—1955.

a. B1 52—55: $Y = 2805 + 818\,x_1 + 8862\,x_2$

		df	SQ	DQ
A	Total regression	277	204,482,600	738,204.3
B	Parallel regression	274	158,665,600	579,071.5
C	Individual regression	268	147,402,782	550,010.4
D	A—B	3	45,817,000	15,272,333.3
E	B—C	6	11,262,818	1,877,136.3

Test of difference of level between the years 1952—1955: $F = 27.77$***
Test of difference of slope between the years 1952—1955: $F = 3.41$***
Test för skillnad i nivå mellan år 1952—1955: $F = 27,77$***
Test för skillnad i lutning mellan år 1952—1955: $F = 3,41$***

b. B5 52—55: $Y = 2561 + 670\,x_1 + 7831\,x_2$

		df	SQ	DQ
A	Total regression	277	100,457,800	362,663.5
B	Paralell regression.......	274	79,300,400	289,417.5
C	Individual regression	268	73,767,970	275.253.6
D	A—B	3	21,157,400	7,052,466.7
E	B—C	6	5,532,430	922,071.7

Test of difference of level between the years 1952—1955: $F = 25.62$***
Test of difference of slope between the years 1952—1955: $F = 3.35$***
Test för skillnad i nivå mellan år 1952—1955: $F = 25,62$***
Test för skillnad i lutning mellan år 1952—1955: $F = 3,35$***

Table 4. Analysis of covariance of Y (seed size) over x_1 (cone weight) and x_2 $\left(\dfrac{\text{cone weight}}{\text{no. seeds}}\right)$ for tree B 1 and tree B 5. Summary of the analysis for each of the years 52—55.

Kovariansanalys av Y (fröstorlek) på x_1 (kottvikten) och x_2 $\left(\dfrac{\text{kottvikt}}{\text{fröantal}}\right)$ för träd B 1 och B 5. Sammanställning av analysen för varje år (52—55).

Year	Diff. of a-constants of parallel regressions	F (level) $df = 1$	F (slope) $df = 2$
	B 1 > B 5		
52	+ 853	47.40***	3.84*
53	+ 926	66.51***	12.80***
54	+ 313	7.38**	5.21**
55	+ 975	56.54***	0.27°
År	B 1 > B 5		
	Skillnaden mellan a-konst. för parallell regression	F (nivå) $df = 1$	F (lutning) $df = 2$

Table 5. Regression analysis for the relationship between cone weight and frequency of empty seeds (transformed expression) — 70 cones per tree and annum.

Regressionsanalys för sambandet mellan kottvikt och frekvensen av tomfrö (transformerat uttryck) — 70 kott per träd och år.

Year	Tree	a-constants of parallel regressions	Diff. of level between parallel regr.		b-coeff. of individual regressions	Diff. between b-coefficients	
			B 5 > B 1	F-value		B 5 > B 1	F-value
52	B 1	21.23	+ 11.16	8.15**	— 2.40	— 1.99	1.73°
	B 5	32.39			— 4.39		
53	B 1	26.75	+ 17.84	46.10***	— 1.33	— 2.28	1.62°
	B 5	44.59			— 3.61		
54	B 1	26.39	+ 19.19	80.47***	— 0.25	+ 2.79	1.72°
	B 5	45.58			+ 2.54		
55	B 1	29.42	+ 8.40	12.65***	— 1.79	— 2.80	1.38°
	B 5	37.82			— 4.59		
År	Träd	a-konstant för parallella regressioner	B 5 > B 1	F-värde	b-koefficient för individuella regr.	B 5 > B 1	F-värde
			Skillnad i nivå mellan parallella regressioner			Skillnad mellan b-koefficienter	

The frequency of empty seeds is converted to arcsin $\sqrt{\dfrac{\text{empty seeds, per cent}}{100}}$

Värdena för tomfröprocenten är transformerade till arcsin $\sqrt{\dfrac{\text{tomfröprocent}}{100}}$