Total heights were measured in the 1961 and three 1962 plantations in the spring of 1964. The data were grouped and analyzed by five degree latitudinal classes, and subjected to analysis of variance, and DUNCAN'S Multiple Range tests. The results showed that the five degree latitudinal classes were heterogeneous, while the varieties were homogeneous with respect to total height in 1964.

Three measurements were recorded in the Cloquet 1962 and North Branch plantations in the growing season of 1965, viz. (1) total length of the current year's shoot, (2j the number of days after April 15 to the time of the maximum rate of height growth, and (3) the number of days after April 15 to the cessation of height growth.

The data were grouped and averaged by five degree latitudinal classes as well as by varieties. Analyses of variance and DUNCAN'S Multiple Range tests were conducted between zones and between varieties as well as within zones and within varieties. The varieties were found to be homogeneous with respect to the three characters.

In the 1966 growing season measurements were recorded in the six plantations on the following 11 characters:

1. The number of days after April 15 to the commencement of height growth.
2. The number of days after April 15 to the time of the maximum rate of height growth.
3. The number of days after April 15 to the cessation of height growth.
4. & 5. The periodic growth of the current year's shoot for each seed source and for each variety. The best fitting regression equation was found to be $Y = a + b \log X$ (where Y is the length of the current year's shoot after X days from April 15). The values of a and b for each seed source and each variety were calculated from these equations.

6—10. Total height in 1961 through 1966.

The data were grouped and averaged by varieties for each of these 11 characters. Analyses of variance and DUNCAN'S Multiple Range tests were performed separately for each location, both between varieties and within each variety. The following results were obtained.

Only 15 of the 19 varieties available for analysis could be analyzed. It was found that the varieties as recognized by RUBY on the basis of morphological characters are also valid on the basis of their physiological responses to the environment.

Nine of the 15 varieties analyzed appear to be uniform in growth characters and cannot be further sub-divided into sub-varieties or ecotypes. These are altaica, aquitana, borussica, carpatica, hercynica, iberica, lapponica, polonica and uralensis. One, viz., haguenensis possibly has a Belgian ecotype significantly different from the German ecotype. The eleventh, viz. septentrionalis has a large randomly distributed within variety component of variance. This variety has a high proportion of significantly different pairs of seed sources, which cannot be grouped in any distinct geographic pattern.

Four varieties, *viz.,* armena, rhodopaea, rigensis and scotica appear to be divisible into geographically distinct ecotypes as shown below:

Variety armena: — Two ecotypes, *viz.,* (1) from northeastern Turkey and Georgian S. S. R. and (2) from Rumania.

Variety rhodopaea: — Two ecotypes, viz., (1) from Czechoslovakia and southern Bulgaria and (2) from the mountains of northeastern Greece.

Variety rigensis: — Three ecotypes, occupying three different latitudinal regions, viz., 55° N., 57° N. and 58° N. latitudes.

Variety scotica: — Two ecotypes, viz., (1) from Scotland and (2) from England, designated by some authors as "East Anglia".

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The Influence of Meteorological Factors on the Cone Crop of Douglas-fir in the Netherlands

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Introduction

Douglas-fir was introduced around 1860 and has since become a successful exotic forest tree species in the Netherlands. Douglas-fir plantations now occupy more than 12,000 hectares, or almost 8 percent of the coniferous forest area of the country.

Provenance trials started in 1923 have shown that the coastal Douglas-fir seed sources from lower altitudes are best suited for the Netherlands because of their height growth, volume production, susceptibility to late frosts and resistance to needle cast disease (VEEN, 1951). Many imported provenances have nevertheless been serious failures in spite of careful attention to seed origins. The enormous extent of the seed procurement areas and the fact that large genetic differences may occur over small distances are the main reasons for these failures. Local provenances from registered seed stands are consequently in great

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demand, but unfortunately, good cone crops of Douglas-fir in the Netherlands occur on the average only once every eight years. Light to moderate crops are more frequent but seed yields are then generally very low due to attacks of the chalcid *Megastigmus spermotrophus*.

The irregularity of cone- and seed crops has serious consequences for tree breeding. Lack of flowering prevents controlled pollination work and progeny testing. Furthermore it is not unreasonable to assume that seed orchards, once established, will tend to show the same irregularity in seed crops. Attempts to induce flowering and cone setting with compound fertilizers during the past four years in seed stands has so far not been successful.

Weather conditions, as MATTHEWS (1955) pointed out, have a marked effect on the occurrence and the frequency of cone crops. LOWRY (1966) found evidence of a statistical relationship between atmospheric conditions and Douglas-fir cone crops over a 40-year period in western Oregon and Washington. The present paper shows the apparent influences of temperature, precipitation and sunshine on the cone crop of Douglas-fir in the "Veluwe"[2]), the Netherlands, during the period 1931—1967.

Material and Methods

Studies dealing with initiation and development of lateral buds of Douglas-fir have been made by ALLEN (1941, 1946, 1947 a, b, 1963), BARNER and CHRISTIANSEN (1962), CHING and CHING (1962), STERLING (1946, 1947), OWENS and SMITH (1964, 1965), KISS and SZIKLAI (1966), and BARADAT (1967). The most detailed studies were made by OWENS and SMITH (1964, 1965). They studied the initiation and early development of the lateral vegetative and reproductive buds and subsequent cone development on Douglas-fir trees near Corvallis in Oregon.

Their studies revealed that the lateral reproductive and vegetative bud primordia were initiated in early April preceding the growing season when the flowers appear. They also showed that the development cycle from bud primordia initiation until seed fall lasted about 17 months.

The ovulate strobili of Douglas-fir in the Netherlands are recognizable at the end of August. Pollination occurs the following spring at the end of April or beginning of May, and cones generally start to release their seed at the end of August or early September. Close observations during the past few years have shown that ovulate strobili often tend to abort at flowering time, often on a large scale. This type of abortion has also been described by ALLEN (1941). There is also strong evidence that the continental Douglas-fir types growing in the Netherlands flower and produce cone crops at more regular intervals than the coastal types.

The crop surveys were started in 1921 (HESSELINK, 1921) and have since then been carried out each year for the most important forest tree species. The annual survey is now organized by the "Staatsbosbeheer" (State Forest Service) which depend on many cooperators throughout the country to survey the visible crop according to an arbitrary scale ranging from 0—100. A change was made in the numerical evaluation of the crop rating in 1931, and the crop figures reported in the period 1921—1930 are not comparable with those recorded later on.

The average annual rating figures for Douglas-fir cone crops of the "Veluwe" for the period 1931—1967 are shown in *table 1*. In this investigation only the rating figures of the "Veluwe" were used for the period 1931—1967 for several reasons.

Table 1. — Average Rating Figures of Douglas-fir Cone Crops in the Veluwe area, 1931—1967 (The Netherlands).*)

Year	Ratings**)	Year	Ratings**)
1931	24	1951	21
1932	25	1952	16
1933	39	1953	18
1934	24	1954	19
1935	56	1955	14
1936	16	1956	55
1937	16	1957	15
1938	19	1958	64
1939	22	1959	23
1940	28	1960	48
1941	21	1961	16
1942	64	1962	15
1943	20	1963	18
1944	15	1964	39
1945	23	1965	23
1946	37	1966	11
1947	24	1967	26
1948	66		
1949	16		
1950	31		

Source: Staatsbosbeheer (State Forest Service).

*) Rating figures based upon the arbitrary scale 0—100 as follows:

10 — failure of crop
20 — very bad crop
30 — poor crop
40 — moderate crop
50 — average crop
60 — fairly good crop
70 — good crop
80 — very good crop
90 — outstanding crop

**) Each figure is a mean of a number of independent observations.

This area contains most of the older Douglas-fir stands and more than 80 percent of the seed stand acreage. Besides, the Douglas-fir stands on the "Veluwe" are very uniform and of predominantly coastal types.

The three meteorological data used were monthly mean day temperature[3]), monthly precipitation totals and monthly hours of sunshine. The former two elements are averages for the whole country; the latter is from the Royal Meteorological Institute "De Bilt" (K. N. M. I.) located only 50 km from the area under consideration.

Correlation analyses were performed to find possible relationships between the crop rating figures and each of the three meteorological elements used. For this purpose the months prior to August, when the crop rating was made were numbered backwards from 1—31 and every possible correlation over this 2½-year period investigated. A multiple regression analysis was carried out to predict a potential Douglas-fir cone crop based on atmospheric conditions. An attempt was made to find statistical evidence of an inherent periodicity of Douglas-fir cone crops and to detect possible influences of spring frosts in the period of April 15th — May 15th. All calculations were made with an IBM 1130 computer of the "Central Organization for Applied Scientific Research in the Netherlands" (ABW-TNO) at Wageningen.

[2]) "Veluwe" is a somewhat elevated area with sandy soils located centrally in the Netherlands.

[3]) Monthly mean "day" temperature (gemiddelde dagtemperatuur) is calculated from daily readings taken at 8.00, 14.00 and 19.00 hours respectively.

Results

1. The correlation coefficients at the 5 and 1 percent level of significance are given in *tables 2 and 3*. A summary of results for apparent optimum weather requirements for a good to abundant Douglas-fir cone crop in western Oregon and Washington and the Netherlands ("Veluwe") is shown in *table 5*.

2. The "best" multiple regression formula computed for predicting Douglas-fir cone crops for the "Veluwe" in the Netherlands is shown in *table 4*. For 1968 the expectation of the average cone crop rating figure ("Veluwe") is 49 with a chance $\geqq 0.95$ that this figure will be $\geqq 33$.

Table 2. — Correlation coefficients between Douglas-fir cone crop rating figures from the "Veluwe" (the Netherlands) and meteorological factors during the period 1931—1967.

Month no. prior to crop survey	Month	Sunshine	Temperature	Precipitation
13	July	+0.59++	+0.66++	—0.36+
14	June	+0.46++	+0.34+	—0.27+
17	March			+0.45++
23	September	—n. s.	—n. s.	
24	August	—n. s.	—0.37+	
25	July	—n. s.	—n. s.	
26	June	—0.37+	—0.41++	

\+ significant at the 5 percent level.
++ significant at the 1 percent level.
n. s. not significant.

Table 3. — Simple correlation coefficients between meteorological elements (1921—1967).

sunshine	vs	temperature : r = +0.76++
sunshine	vs	precipitation : r = —0.22++
temperature	vs	precipitation : r = +0.17++

++ significant at the 1 percent level.

Table 4. — Multiple regression formula for predicting Douglas-fir cone crops for the "Veluwe", the Netherlands.

Mean crop rating figure*) =
= —38.6 + 7.27 × temperature**) (13)***) — 44.4 × precipitation (14) + 56.8 × precipitation****) (17) — 3.60 × temperature (24).

*) according to arbitrary rating scale 0—100 (see *table 1*).
**) temperature in degrees centigrade.
***) numbers between parentheses refer to months prior to the cone crop survey (see *table 4*).
****) precipitation in cm (mean daily precipitation).
R = 0.83 (significant at the 1 percent level); Residual variance = 87.20.

3. No significant statistical evidence of inherent periodicity could be found in Douglas-fir cone crops during the period 1931—1967 ($P > 0.05$).

4. No statistical evidence could be detected to connect frost damage during the flowering period and the reported cone crops during the period 1931—1967.

Table 5. — Summary of results of optimum weather requirements for a good to abundant cone crop in the USA and the Netherlands.

Month no.	Month	apparent weather requirements in western Oregon and Washington*)	apparent weather requirements in district "Veluwe" the Netherlands	Remarks
26	Jun		cool, cloudy	
25	Jul	cool		
24	Aug		cool	
23	Sep			
22	Oct			
21	Nov			
20	Dec			
19	Jan			
18	Feb			
17	Mar	moist, cloudy	moist	
16	Apr	moist, cloudy		bud primordia initiated**)
15	May			
14	Jun		sunny, warm and dry	
13	Jul		sunny, warm and dry	folial organ initiation***) (13–12)
12	Aug			
11	Sep			
10	Oct			
9	Nov			
8	Dec			
7	Jan	warm		
6	Feb			
5	Mar			
4	Apr			pollination (5–3)
3	May			
2	Jun	not cold		
1	Jul			
0	Aug			
00	Sep			seeds fall

*) Adapted from original tables. Lowry, W. P.: Apparent meteorological requirements for abundant cone crop in Douglas-fir. Forest Sci. 12: 185—192 (1966).
**) Owens, J. N. and F. H. Smith (1965).
***) From different sources.

Discussion

1. Temperature and sunshine (24—26 months)

There is a significant negative correlation between temperature in June and August and a Douglas-fir cone crop two years later. A negative value is indicated for that entire summer period for both temperature and sunshine. LOWRY (1966) found the same statistical evidence in July for Douglas-fir in western Oregon and Washington. He did not advance a physiological hypothesis to explain this apparent requirement of a cool summer, considering the period too early to have any effect on the reproductive physiology in Douglas-fir. LOWRY (1966) speculated that there might be a possible, indirect connection between the temperature requirement and the population dynamics of pests, e. g. low temperature — few pests. The new evidence requiring a cool summer from 8 to 10 months before the Douglas-fir bud primordia are initiated raises the question of whether physiological factors may be involved after all. The literature does not offer any clear suggestion which factors might be involved and this new evidence must stand on its own merit.

There is also a significant negative correlation between sunshine in June and a Douglas-fir cone crop 27 months later. This correlation need not have any independent significance since there is a relatively high positive correlation: temperature versus sunshine ($r = 0.76$).

It may be expedient at this point to note that any interpretation regarding the apparent requirement of a relative "cool" and/or "cloudy" summer two years before maturation of the cones, is closely connected with the problem of inherent periodicity (see finding nr 3, above). A positive influence of temperature and sunshine in the summer *one* year prior to yield (as in fact is evidenced in the present case, see below, could, for example by way of inherent alternation of crops (well known in fruit culture), easily cause an apparently negative influence of the same weather variables in the summer *two* years before maturation and yield. We find it necessary to make this point, because the first serial correlation coefficient of the crop-ratings, though non-significant, has a negative sign (—0.27).

2. Precipitation (17th month)

A significant positive correlation is found between precipitation in March and a cone crop 19 months later. LOWRY (1966) found the same statistical evidence for March and April as well.

OWENS and SMITH (1964) showed that flower primordia were initiated in early April and STOATE *et al.* (1961) indicated that the number of reproductive buds may be increased by fertilizing with nitrate in spring during flushing. LOWRY (1966) postulated that the correlation might indicate that biochemical reactions take place in that period for differentiation. But he did not believe that precipitation was the controlling variable, pointing out that spring in the Douglas-fir region is the period of most completely saturated soils. He suggested that the correlation might well be interpreted as a role of cloudiness. There is no evidence in the Netherlands to support this hypothesis since no correlation whatsoever could be found with sunshine during the period March — April. March has on the average the least amount of precipitation of any month in the Netherlands and moisture might therefore be a controlling variable after all. The correlation could possibly be connected with translocations of photosynthate and the growth alternation in tops and roots described by KRUEGER and TRAPPE (1967). They found that photosynthate in Douglas-fir seedlings moved from top to roots in an alternating pattern. They also cited LISTER *et al.* (1965) who found evidence in *Pinus strobus* seedlings that growth alternation may occur in conditions of high, but not of low soil moisture. The evidence found in the Netherlands does suggest that the correlation may be connected with translocation. Sufficient moisture in March may be necessary to remove certain inhibitory substances before flower initiation can take place and/or it might promote flowering by the translocation of flowering hormones and photosynthate.

The literature gives only a few references connecting precipitation with a potential cone crop. POZZERA (1959) found a significant positive correlation between rainfall in March of one year and the cone production of *Pinus pinea* thirty months later. The interesting point is that the initiation of ovulate strobili of this species unlike other regional species, starts at the beginning of the summer (FRANCINI, 1958; cited by MIROV, 1967).

3. Temperature, sunshine and precipitation (14—15 months)

There is a significant positive correlation of the temperature and sunshine in June and July and the cone crop 14 to 15 months later. This evidence supports LUDWIG's (1967) contention that a warm summer during bud development favours a good Douglas-fir cone crop in the Netherands. The importance of high summer temperatures for flower bud initiation and development has been shown for *Picea abies* (TIRÉN, 1935), *Fagus sylvatica* (MATTHEWS, 1955), *Picea glauca* (FRASER, 1958), *Pinus ponderosa* (DAUBENMIRE, 1960), *Larix leptolepis* (YANAGIKARA, 1960) and *Pinus sylvestris* (HAGEM, 1917, cited by ANDERSSON, 1965). SARVAS (1957) on the other hand, did not find conclusive evidence between high summer temperature combined with drought in the year of bud setting and a good cone crop of *Picea abies* the following year. VAN GOOR and VAN LAAR (1958) found a positive correlation between summer precipitation and height growth of Douglas-fir in the Netherlands. Conversely, little vegetative growth is made in warm and dry summers. The statistical evidence found in this investigation lends support for the notion that flower differentiation is correlated with cessation or inhibition of vegetative growth. Physiological drought, apparently has the same effect as girdling and strangulation by preventing the translocation of photosynthate downward. EBELL (1966) was able to induce flowering of potted Douglas-fir clones by giving them a minimum amount of water. Summer droughts in the year of bud setting have often been associated with bumper seed crops the following year, particularly for *Fagus sylvatica* (MATTHEWS, 1955).

Forecasting

Predicting a cone crop at an early state is based on identifying and sampling ovulate buds. By such sampling results it will generally be possible to predict a crop failure with reasonable accuracy but not necessarily forecast a good crop. Too many disturbing factors such as abortions, frost, adverse weather conditions during pollination and insects may reduce a potential crop substantially. ALLEN (1941) suggested a "cone intensity ratio" based on the number of ovulate buds and the number of vegetative buds to predict a cone crop 13 to 14 months before seeds mature. SILEN (1967), reported that still earlier forecasting was possible by correlation the female buds with early recognizable male buds. MAGUIRE (1956), and WENGER (1957) suggested that weather data might be used to predict future crops for *Pinus ponderosa* and *Pinus taeda,* respectively. The apparent weather requirements found to favour a good Douglas-fir cone crop in the Netherlands may also be used to predict a future cone crop. The method offers a quick estimate of a future Douglas-fir cone crop, but has the inherent drawback of not allowing for the disturbing factors which may take place before seeds mature.

Conclusions

The statistical analyses of meteorological data and Douglas-fir cone crops in the Netherlands over a 37-year period have indicated that weather conditions are very important for a good cone crop. Several of the optimum weather requirements found in the Netherlands for a good Douglas-fir cone crop were also reported by Lowry (1966) for western Oregon and Washington. Confirmation of the results will require closely regulated experiments and more basic research into all the aspects of the physiology of flowering.

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Untersuchungen zur Konkurrenz zwischen verschiedenen Genotypen in Pflanzenbeständen

I. Modifikation der Methode von Sakai zur Schätzung der genetischen-, Umwelt- und Konkurrenzvarianz einer Population

Von M. Hühn*)

a) Definitionen, Voraussetzungen und einleitende Bemerkungen

Seit langem ist aus vielen experimentellen Untersuchungen bekannt, daß Konkurrenz zwischen im Bestand benachbart aufwachsenden Pflanzen eine der wichtigsten Ursachen für die Variation und Kovariation konkurrenzempfindlicher Merkmale in Pflanzenbeständen darstellt und daß ihr Nichtbeachten in genetischen und züchterischen Experimenten (Nachkommenschaftsprüfung, Heritabilitätsschätzung, Plusbaumauswahl) zu verzerrten Schätzwerten und damit zu wenig effektiven Versuchsplänen führt. Ebenso ist seit langem bekannt, daß die gegenseitige Beeinflussung genetisch verschiedener Individuen, die als Nachbarn im Bestand aufwachsen, eine große Rolle spielt und das Aussehen von Pflanzenbeständen mitbestimmt.

Neben Harper (1961) gibt Stern (1969) eine ausführliche Diskussion der verschiedenen biologischen Aspekte des

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