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ON THE VARIATION OF FLOWERING AND SEED CROP IN MATURE STANDS OF *Pinus sylvestris* L.

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SELOSTE:

KUKKIMISEN JA SIEMENSADON VAIHTELUSTA VARTTUNEISSA MÄNNIKÖISSÄ

The conspicuous fluctuation in the amount of flowering and seed production of conifers has long draw the attention of researchers. Seed crop statistics, based on various types of observations, have been published since 1838 for Scots pine (GOEBEL 1886). Several papers were published in Germany and in Russia at the end of 19th and the beginning of the 20th century. Finnish researchers also began to publish observations made in Finnish forests (BLOMQVIST 1876, RENVALL 1912, LAKARI 1915, ILVESSALO 1917) at the beginning of this centure. The main emphasis was laid, right from the beginning, on the occurrence of heavy seed crops.

Two impressions are formed when one reads those early papers today: 1) The lists of good seed years given by different authors do not completely match; 2) Nothing essentially new about the periodicity of the seed crop or about the causes of variation as appeared during the last 50 years. However, our knowledge of the quantity of the seed crop as well as the whole reproductive process has increased a great deal.

The differences between the lists of good seed years are actually quite understandable. The field data were, as a rule, rather vague. Each year was scored, according to the available information, using subjective catagories such as very heavy, abundant, medium, poor. Sometimes, each case was verbally described. It is impossible to draw parallels between the evaluations made by separate persons when no absolute criterion is used.

In some cases the differences are real. We know that in certain years the cone crops in different regions may be of quite unequal magnitude. The early authors concluded that in a given locality good seed years occur at intervals of two to four years. They noticed that a good year was preceeded, two years earlier, by a warm sunny summer; which in turn had been noted for frequent forest fires.

Attempts have been made to find an inherent system that would bring trees into flowering at regular intervals. Another approach has been the search for a cosmic factor, e.g. alternations in solar activity, that would universally induce the flowering of pines. The empirical evidence does not support either of the above-mentioned hypotheses. The time series do not display any regularity that would suggest there is a constant period (except for a period of

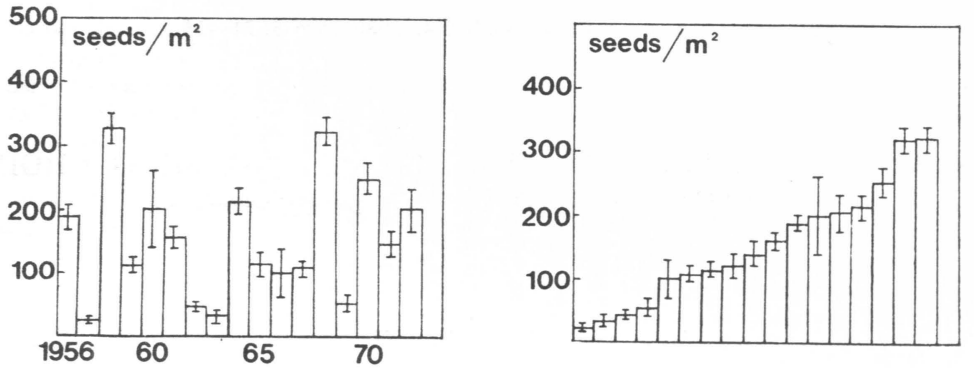

Figure 1. An example of the variation of the seed crop in a stand of *Pinus sylvestris*, sample plot XX, Kerimäki. The bars indicate the average of the measuring points and the segment lines the 95 per cent confidence limits of the average. On the left the seed crops in chronological sequence. The figures on horizontal axis refer to flowering years. The big differences between successive years give an impression of abundant and poor seed years. On the right the same data ranked by magnitude. The seed crops cannot be divided into distinct categories.

one year). The geopraphic differences with changing regional patterns clearly indicate that local factors are involved.

During the last decades comprehensive material on the variation of flowering and seed crop in forest trees has been collected by the Finnish Forest Research Institute. The work has been conducted by Heikinheimo and Sarvas. Scots pine has a dominating role among the 27 species included. The measurements were mainly directed at stands and were made by means of seed funnels. In some sample plots, observations on the flowering of individual trees were also carried out. The goal has been obtain precise numerical values with a defined accuracy. In addition to earlier investigations, the quantity of male flowering has also been studied. The measurements are closely related to the studies on flowering biology and ecological genetics of forest trees. (Sarvas 1962, 1967, 1968, 1972, 1974, Koski 1970).

Studies on reproductive behaviour have recently been of more value to the study of general adaption and population structure than to reforestation. The data collected so far have not produced any scientific surprises. However, flowering and seed production can be subjected to quantitative and statistical treament from the population biological point of view.

Seed crops have traditionally been classified into four or five categories according to magnitude. Almost every author has made a scale of his own. This tells us something about the matter. There are no natural classes, and consequently all class limits are artificial. The differences between successive years are usually so clear-cut that an impression of good and poor years is easily obtained. The situation changes if the observed values are ranked according to their absolute magnitudes. This holds true even in single stands and particularly if the results from several stands are combined. Obviously it is necessary to define a good seed crop if the fluctuation and its background are being studied.

Trees, like other flowering plants, have an inherent tendency to flower and to produce seed. Flowering is the normal behaviour of most plants after a certain developmental phase has been reached, and no exceptional external stimulus is required. Annual plants must produce a seed crop every year or else they will become extinct. The life span of an individual annual plants ends at seed ripening and the nutrients of the vegetative organs are utilized as far as possible as building materials within the seeds. Perennial plants, trees in particular, have a juvenile period when they do not flower. After maturing they produce seeds

recurrently so that they posses the ability to regenerate themselves continuously. If a new habitat becomes available species and individuals producing large numbers of seed have the advantage. When the site has once been occupied, strong vegetative growth is useful to species and individuals. Flowering and seed production, as well as vegetative growth, have to share the same pool of nutrients and energy. This kind of phenomen, reproductive–vegetative balance is familiar in fruit trees. (Barlow 1970, Luckwill 1970, Priestley 1970). Reduction in volume growth due to a heavy seed crop is generally acknowledged. Eg. Chalupka et al. (1975) report that in a Picea abies stand the reproductive parts make 9 % of the total amount of litter in an average seed year. Obviously neither of these two essential processes can be sacrificed for the other. Evolutionary processes have resulted in a compromise. In normal conditions, a specific amount of existing storage only is devoted to the reproductive processes. The limit value is of course a statistical mean within a population or species.

If we assume that the amount of material and energy devoted to the reproductive processes is a constant proportion of the whole quota, then the absolute amount of seeds is proportional to the total amount of raw material and energy available. When the quota and the limits of the proportion available for reproduction are known, it is possible to estimate the maximum amount of flowering and seed production, i.e. the capasity (Sarvas 1974 p. 73). The capacity denotes the largest amount of flowers and seeds that a population can produce in a year, under normal conditions, without endangering the existence of the present generation.

The quota remains for the time being undefined as to whether it is the amount of soluble carbohydrates and proteins, organic compounds, biomass, etc. In any case, large trees apparently possess a larger storage capacity than small trees. In other words, the capacity is likely to be proportional to the size of the trees.

A pilot test of the capacity concept was carried out by comparing the maximum values of long time-series and the size of the trees. (Koski and Tallqvist 1978). Calculations were performed in which tree size was taken as the dominant height of the stand in question. The estimates of capacity are based on the assumption that every now and then the capacity is actually realized. The maximum for each sample plot was taken from time series lasting for 12 consecutive years. Regression analysis showes obvious correlation between dominant height and maximum values.

The result encourages us to continue to search for more accurate methods of estimating the capacity. The efforts are based on pysiological and population biological factors. The concept of capacity also has consequences for seed orchard activities. Even though seed orchards are artificial genetic units, they must have a specific capasity as well. Repeated seed cops continuously exceeding the capacity due to hormonal treatments etc. may in the long run reduce seed production and even kill the trees. In pine there are not only the developing seeds but also conelets of the same year, male inflorescences and flower buds the following year, all requring share of the material and energy quota. Consequently no simple ratio, eg. between the amount of seed crop and the weather of the year of determination, can be expected.

When speaking of the occurrence of good flowering and seed years, capacity can be used as a reference value to judge whether the flowering or seed crop was abundant. The slight progress which has been made in the estimation of capacity has tempted us to try and apply it to the data which we have available. We consider, quite arbitarily, a case exceeding 50 % of the capacity as abudant a case exceeding 75 % as very heavy. In this way stands and localities can be honestly compared, independently of the impressions of different persons.

On the basis of this kind of survey we can conclude:

1. Heavy flowering does not always result in a heavy seed crop.
2. Years of heavy flowering and heavy seed crop do not occur at regular intervals.
3. Good flowering and good seed years

coincide fairly well in different stands in the same locality.

4. Even in Finland, years of heavy flowering and heavy seed crop can occur at different times in different parts of the country.

In comparison with many other tree species, the patterns of variation in flowering and seed production in Scots pine seems to be fairly regular and simple. However, the prediction of the future flowering and seed production for a certain year remains uncertain for the time being. The only definite fact is that flowering is not controlled by any single factor, but by interactions between several factors. From this point of view it is evident that all efforts to explain the variation by means of any single environmental variable or intrinsic rhythm have failed. Consequently, with the aid of our present knowledge it is not possible to predict the coming good seed years.

LITERATURE

BARLOW, H. 1970. Some aspects of morphogenis in fruit trees. In physiology of tree crops. (Ed. Luckwill and Cutting). Academic Press, London.

BLOMQVIST, A. 1976. Några iakttagelser rörande fröbildningens periodicitet hos tallen och granen samt ekorrens förekommande i Finland. Meddel. Soc. Fauna Flora Fennica 1: 47—54.

CHALUPKA, W., GIERTYCH, M. & KROLIKOWSKI, Z., 1975. The effect of cone crops on growth in Norway spruce (Picea abies (L) Karst.). Arboretum Kornickie Rocznik XX: 201—212.

ILVESSALO, L. 1917. Tutkimuksia mäntymetsien uudistumisvuosista Etelä- ja Keski-Suomessa. Referat: Studien über die verjüngunsgjahre in Süd- und Mittelfinnland. Acta For. Fenn. 6 (2). 96 p.

KOSKI, V. 1970. A study of pollen dispersal as a mechanism of gene flow in conifers. Commun. Inst. For. Fenn. 70.4 : 1—78.

— » — & TALLQVIST, R. 1978. Tuloksia monivuotisesta kukinnan ja siemensadon määrän mittauksista metsäpuilla. Summary: Result of long-time measurements of the quantity of flowering and seed crop of forest trees. Folia For. 364: 1—60.

LAKARI, O. J. 1915. Studien über die Samenjahre und Altersklassenverhältnisse der Kiefernwälder auf dem nordfinnischen Heiderboden. Acta. For. Fenn. 5 (1). 216 p.

LUCKWILL, L. 1970. The control of growth and fruitfullness of apple trees. In. physiology of tree crops (Ed. Luckwill and Cutting) Academic Press, London.

PRIESTLEY, C. 1970. Carbohydrate storage and utilization. In physiology of tree crops (Ed. Luckwill and Cutting) Academic Press, London.

SARVAS, R. 1962. Investigations on the flowering and seed crop of Pinus silvestris. Selostus: Tutkimuksia männyn kukkimisesta ja siemensadosta. Commun. Inst. For. Fenn. 53.4: 1—198.

— » — 1967. The annual period of development of forest trees. Proceedings of the Finnish Academy of science and letters. 1965: 211—231.

— » — 1968. Investigations on the flowering and seed crop of Picea abies. Selostus: Tutkimuksia kuusen kukkimisesta ja siemensadosta. Commun. Inst. For. Fenn. 67.5: 1—84.

— » — 1974. Investigations on the annual cycle of development of forest trees II. Autumn dormancy and winter dormancy. Selostus: Tutkimuksia matsäpuiden kehityksen vuotuisesta syklistä. Syys- ja talvihorros. Commun. Inst. For. Fenn. 84.1: 1—101.

SWEET, G. 1973. Shedding of reproductive structures in forest trees. In shedding of plant parts (Ed. Kozlowski) Academic Press, London.

SELOSTE:

KUKKIMISEN JA SIEMENSADON VAIHTELUSTA VARTTUNEISSA MÄNNIKÖISSÄ

Julkaistuja havaintoja havupuiden kukinnan ja siemensadon vaihteluista on 1880-luvun alkupuolelta lähtien. Suomessakin on tätä aihetta käsittelevä julkaisu vuodelta 1876. Sittemmin tuloksia on julkaistu runsaasti monessa maassa jatkuvasti tähän päivään asti. Keskeisenä asiana useimmissa tutkimuksissa on runsaiden siemenvuosien esiintyminen ja usein myös yritys selittää siemensadon vaihtelu. Kirjallisuutta lukiessa toteaa, että eri julkaisuissa esitetyt runsaat siemenvuodet eivät aina satu yksiin ja että siemenvuosien kertautumisesta ja vaihtelun syistä ei ole voitu esittää varsinaista ratkaisua. Professori Sarvaksen keräämän laajan tutkimusaineiston ja aikaisempien julkaisujen pohjalta on tultu siihen, että kaikkein ensimmäiseksi on määriteltävä, mitä runsas kukkiminen ja siemensato on. Mittaustulokset osoittavat, että vuosia ei voi siemensadon perusteella jakaa toisistaan jyrkästi erottuviin luokkiin, vaan siemensadon määrä voi saada minkä tahansa välin arvon. Ehdotetaan, että vertailuarvoksi kussakin metsikössä otetaan sen suurin mahdollinen lisääntymispotentiaali eli kapasiteetti. Siemensatoa tai kukkimista pidetään runsaana silloin, kun se on vähintään 50 % kapasiteetista ja hyvin runsaana silloin, kun se on vähintään 75 % kapasiteetista. Tältä pohjalta tarkasteltuna aineisto ei osoita siemensatojen kertautumisessa sellaista säännönmukaisuutta, että tulevien vuosien runsaat siemensadot voitaisiin etukäteen ennustaa.