

ON CONTROL OF DAILY STRUCTURAL MATTER PRODUCTION IN POPULATION OF *AVENELLA FLEXUOSA* (L.) PARL.

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SELOSTE:

EKOLOGISIA HAVAINTOJA METSÄLAUHAPOPULAATION (*AVENELLA FLEXUOSA* (L.) PARL.) PÄIVITTÄISEN KASVUN SÄÄTYMISESTÄ

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The aim of the present study was to investigate the control of structural matter production in an *Avenella flexuosa* (L.) Parl. population. Special attention was paid to the role of temperature and radiation in addition to the self regulation of the plants themselves. Temperature and self regulation explained over 90 percent of the variance in growth rate. Introduction of a variable for radiation into the analysis did not increase the explanatory power of the growth model based on temperature and self regulation.

INTRODUCTION

In the boreal zone, the environmental control of growth rate, i.e. the rate of irreversible change in shoot dimensions, is assumed to be dominated by temperature (WILSON 1972). In particular, among woody plants the role of temperature has been demonstrated for example by FARNSWORTH (1955), WHITE (1970) and READER (1975). According to HARI and LEIKOLA (1974), the introduction of solar radiation does not increase the explanatory power of the growth model for Scots pine (*Pinus silvestris* L.) based on temperature and self regulation. PROMNITZ (1975) emphasizes that in boreal and temperate zones storage of photosynthetic products is an essential part of

the growth process, and thus direct interaction between growth rate and radiation is not evident (cf. also MOONEY and BILLINGS 1960, GRACE and WOOLHOUSE 1973). The investigations carried out by VUOKKO et al. (1977) point to the fact that a similar growth pattern as that of trees might be common also among herbs and grasses.

The aim of the present study is to investigate the control of structural matter production in an *Avenella flexuosa* (L.) Parl. population. Special attention has been paid to the role of temperature and radiation in growth, in addition to the self regulation of this plant species, as based on the principles presented by HARI (1976).

STUDY APPROACH

According to WILSON (1972) growth can be divided into the following steps: photosynthesis, accumulation of assimilates and formation of structural matter as demonstrated in Fig. 1. In the present study the problems involved with photosynthesis and accumulation of assimilates are excluded. The growth rate is assumed to be dependent on environment and self regulation as presented in Fig. 2. The concept of self regulation includes the effect of varying physiological stage on the growth rate of the plant species, i.e. the effect of the

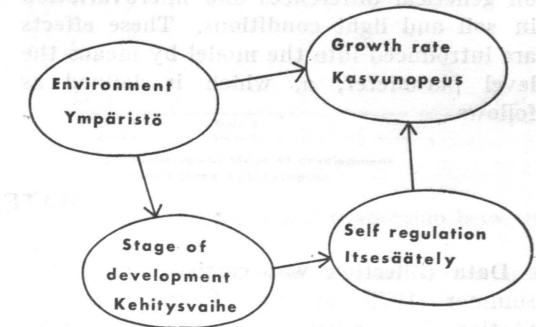


Fig. 2. Effect of external and internal factors on growth.

Kuva 2. Ulkoisten ja sisäisten tekijöiden vaikutus kasvuun.

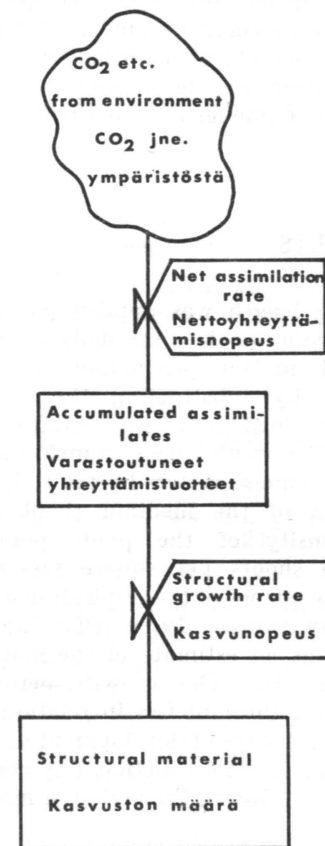


Fig. 1. Flow diagram of metabolic production and utilization of net assimilates in growth according to WILSON (1972).

Kuva 1. Metaboliatuotteiden virtaus ja yhteyttämistuotteiden käyttö kasvutapahtumassa WILSONIN (1972) mukaan.

annual cycle on the daily crop growth rate. The change in physiological stage or the rate of maturation takes place under environmental control, in particular, under the control of temperature (cf. HARI et al. 1970, SARVAS 1972, WILSON 1972).

Let M denote the rate of change in the physiological stage of a plant species and $s(t)$ the physiological stage. If environment, $x(t)$, regulates the rate of maturation then the following relationship exists between M and s

$$(1) \quad s(t) = \int_{t_0}^t M(x(t)) dt,$$

where t_0 is the initial instant of the growth period.

The effect of self regulation on height increments can be introduced into the model by means of the physiological stage of development. Let B_j denote the production of structural matter ($g m^{-2}$) on the j :th day, k_j denote the direct effect of environment on growth and $f(s_j)$ denote the effect of self regulation on growth. Let us assume that the effect of self regulation and environment is multiplicative

$$(2) \quad B_j = f(s_j) \cdot k_j.$$

The Eq. (2) determines the variation in growth rate under the control of environment

and self regulation but not the limits, within which it takes place. These limits depend on genetical differences and microvariation in soil and light conditions. These effects are introduced into the model by means the level parameter, a , which is defined as follows

$$(3) \quad B_j = f(s_j) \cdot k_j \cdot a.$$

A more detailed description of the present analytical procedure is given by HARI et al. (1977).

MATERIAL

Data collection was carried out during summer 1975 at the Forest Training Station, University of Helsinki, (60° 50' N, 24° 20' E, 150 m a.s.l.) in central Finland in a clear cut area of *Myrtillus* site type. The length of ten growing shoots in a plant population was monitored once a day (8.00 a.m.) during May and June. Measurements were carried out to an accuracy of 0.1 mm. Amounts of structural matter and the length of the growing shoots were

determined from 30 shoots in the same plant population by the harvesting method. This was performed at the same time as the shoot length measurements. Temperature was monitored with a multipoint chart recorder (model Honeywell Versaprint) and thermographs (model Lambrecht 252), the sensors being placed at a height of 30 cm. The radiation was monitored by a sphere pyranometer (model Bellani PBK 60572 N).

METHODS AND RESULTS

In order to estimate the daily values of structural matter production the regression between the amount of structural matter

and shoot length was applied (cf. Fig. 3). The regression enables the daily amounts of structural matter production (B_j) to be estimated by subtracting the sequential values obtained with the lengths of the shoots. The results were transformed into values per square meters by multiplying the production of the medium shoot by the shoot density of the plant population, i.e. 5 000 shoots per square meter.

The dependence of the respiration of shoots of Norway spruce (*Picea abies* L.) Karst. was used as an estimate of the maturation rate (Fig. 4). The growth period was divided into three phases in relation to the physiological stage of development as presented in Fig. 5. The function f is chosen so that $f(s_j) = 1$ during the period of maximum growth.

Temperature has proved to be the main environmental factor affecting growth rate. According to HARI et al. (1977) there is a time lag of six hours between temperature and its effect on growth (Fig. 7). Let h denote the height growth rate and assume that the height growth rate depends only

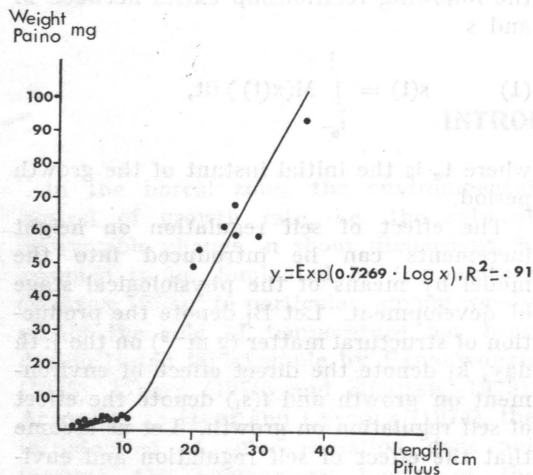


Fig. 3. Regression between shoot length and weight of *Avenella flexuosa*.

Kuva 3. Metsälauhan (*Avenella flexuosa*) verson pituuden ja painon välinen regressio.

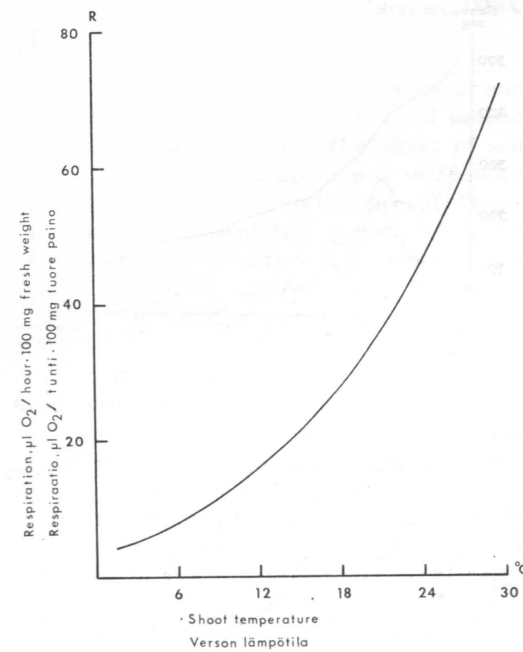


Fig. 4. Respiration function of Norway spruce (*Picea abies*) according to DAHL and MORK (1959).

Kuva 4. Kuusen (*Picea abies*) respiraatio funktio DAHLin ja MORKin (1959) mukaan.

on temperature. Then the daily weather factor k_j is obtained as follows

$$(4) \quad k_j = \int_{t_j}^{t_{j+1}} h \left(x \left(t - \frac{6}{24} \right) \right) dt.$$

The function h is approximated with the dependence of the elongation rate of runners of *Rubus saxatilis* (L.) determined by HARI et al. (1977) (cf. Fig 6).

The values of the parameters in the model (3) were estimated using the method of least squares (cf. HALD 1952, pp. 207–245) with computer iteration (HENRICINI 1964, pp. 61–97). Owing to the growth pattern of the present species, i.e. sudden onset of growth and short phases of increasing and maximum phases of growth, the monitoring of growth was possible only during the phase of decreasing growth. Therefore only the values of parameters a and s_c were estimated from the material. The values of

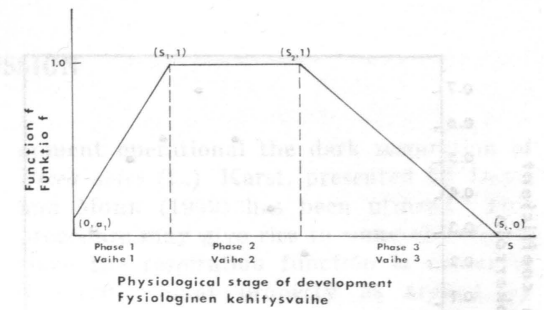


Fig. 5. The function f and relationship between its different phases.

a_1 is the level of growth at the start of structural biomass production

s_1 is the physiological stage of development in which maximum production is attained

s_2 is the physiological stage of development in which production starts to decrease

s_c is the physiological stage of development in which production ceases

Kuva 5. Funktio f ja sen eri vaiheiden väliset suhteet. a_1 on kasvun taso päivittäisen tuotannon alkajalla s_1 on fysiologisen kehityksen vaihe, jolloin maksimikasvu alkaa

s_2 on fysiologisen kehityksen vaihe, jolloin maksimikasvu päättyy

s_c on fysiologisen kehityksen vaihe, jolloin kasvu päättyy

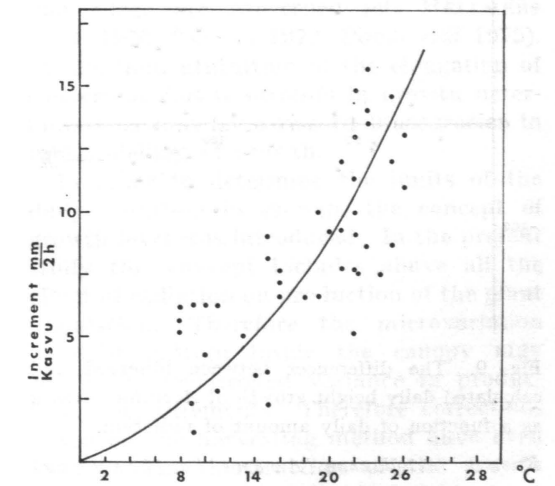


Fig. 6. The dependence of height growth of *Rubus saxatilis* on temperature according to HARI et al. (1977).

Kuva 6. Lillukan (*Rubus saxatilis*) pituuskasvun riippuvuus lämpötilasta HARIN et al. (1977) mukaan.

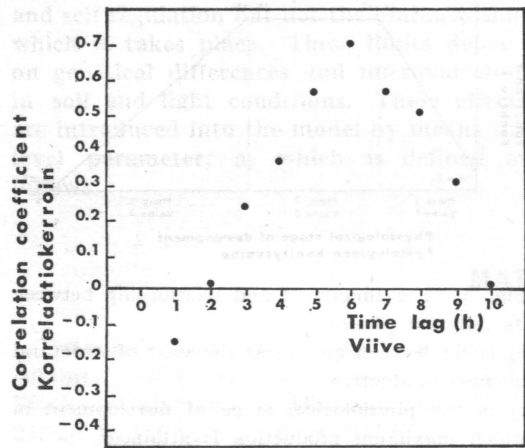


Figure 7. The time lag between height growth of *Rubus saxatilis* and temperature according to HARI et al. (1976).

Kuva 7. Lillukan (*Rubus saxatilis*) pituuskasvun ja lämpötilan välillä vallitseva viive HARIN et al. (1977) mukaan.

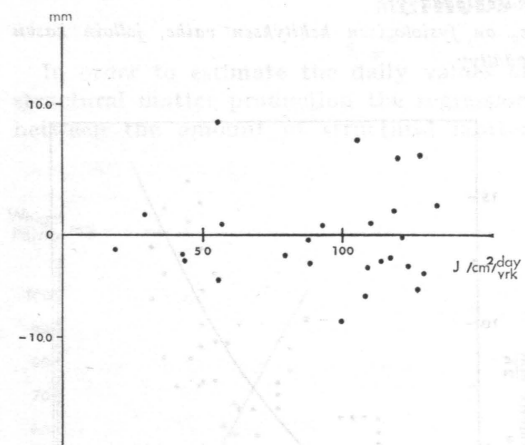


Fig. 9. The differences between observed and calculated daily height growth of *Avenella flexuosa* as a function of daily amount of radiation.

Kuva 9. Metsälauhan (*Avenella flexuosa*) havaintojen ja laskettujen pituuskasvuerojen erotus säteilyn funktiona.

the parameters were $a = 5.79$ and $s_c = 40$. The daily production of structural matter computed with self regulation and tem-

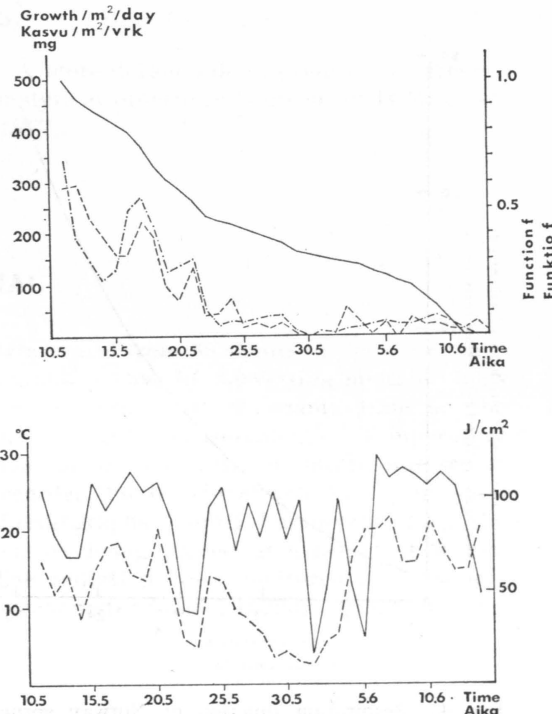


Fig. 8. Daily production of structural matter in a population of *Avenella flexuosa*.

upper part: solid line = inherent growth rhythm
single dotted line = observed values
double dotted line = calculated values

lower part: solid line = mean temperature
dotted line = radiation

Kuva 8. Metsälauhanpopulaation (*Avenella flexuosa*) päivittäinen kuiva-aineen tuotanto. ylempi kuva: yhtenäinen viiva = kasvurytmi yksinkertainen katkoviiva = todetut arvot kaksinkertainen katkoviiva = lasketut arvot

alempi kuva: yhtenäinen viiva = lämpötila katkoviiva = säteily

perature as well as the observed values has been presented in Fig. 8.

The role of radiation in the control of growth rate was investigated by analysing the difference between observed and computed values of daily structural matter production as a function of radiation. The result is presented in Fig. 9.

DISCUSSION

The correlation between measured and calculated values of daily structural matter production was .96 when the effect of self regulation and temperature was introduced into the model. The differences between observed and calculated values were not correlated with radiation and, hence it has no role in growth control within the actual range of measuring accuracy. The result agrees well with earlier findings of HARI et al. (1970) and VUOKKO et al. (1977). This result may be explained by assuming that the storage of photosynthetic products would be an essential part of growth also among grasses in a forest stand.

The sudden onset of growth refers also to the decisive role of the storage of photosynthetic products in growth (cf. KOZLOWSKI and WARD 1957 a, b, RUTTER 1957, MOONEY and BILLINGS 1960, KOZLOWSKI and WINGET 1964, FONDA and BLISS 1966, LÜTZKE 1972, PROMNITZ 1975). On the other hand, the apparent sudden onset of growth is partly a result of the monitoring technique used since the monitoring of length growth was not possible at the very beginning of the growth period.

In the present study the rate of maturation was assumed to be mainly determined by temperature as argued by HARI (1972), WILSON (1972), SARVAS (1972) and POHJONEN (1975). In principle, the rate of maturation is, however, controlled by the whole environment in which the plant is growing. For example, KISH et al. (1972) have demonstrated the importance of available soil moisture in growth and development in conditions where water resources in the soil are limited. In the boreal zone the formation of structural matter occurs, however, during a period when the effect of soil moisture stress or day length or other factors other than temperature are not evident (cf. HARI and SIREN 1972, WILLIAMS 1974). The concepts of rate of maturation and physiological stage of development and their application in growth analysis is discussed in more detail for example by WIT et al. (1970), HARI (1972), SARVAS (1972) and POHJONEN (1975).

In order to make the concept of rate of maturation and physiological stage of devel-

opment operational the dark respiration of *Picea abies* (L.) Karst. presented by DAHL and MORRIS (1959) has been utilized. This procedure may give rise to some objections, since the respiration function is evidently a specific plant property as argued by SARVAS (1972) and POHJONEN (1975). In particular, the threshold value of temperature for respiration function or rate of maturation may vary from plant to plant. In addition, the best approximation for maturation rate may be obtained by applying a logistic function. Earlier studies by HARI et al. (1970), HARI and LEIKOLA (1974) and POHJONEN (1975) give, however, evidence that no essential benefits can be obtained, if plant specific respiration function or logistic function were to be applied in analysis.

The effect of temperature on growth was assumed to be exponential in form. Evidently, this assumption is valid over the normal temperature range. The logistic function would, however, be physiologically more relevant than the exponential function as far as the lowest and highest temperature values during which growth processes may take place are concerned (cf. HELLMERS et al. 1970, SARVAS 1972, POHJONEN 1975). In addition, utilization of the elongation of runners of *Rubus saxatilis* in growth determinations may give rise to inaccuracies in the modelling of growth.

In order to determine the limits of the daily variation in growth, the concept of growth level was introduced. In the present study this concept includes above all the effect of radiation on production of the plant population. Therefore the microvariation in light pattern inside the canopy may result in uncontrolled variance in productivity measurements. Therefore corrections based on the harvesting method have been used in the construction of the growth curve of structural biomass of the current year (cf. WOODWELL and BOURDEAU 1964).

The daily production of structural matter of the plant population was $0.02 - 9.21 \text{ g} \cdot \text{m}^{-2}$ depending on the growth phase and weather. The annual production was $280 \text{ g} \cdot \text{m}^{-2}$ respectively. The result is of the same magnitude as that of earlier findings by

KJELVIK and KÄRENlampi (1975). The result is, however, based on one sample area and gives only an idea about what the

magnitude of the productivity of a population of *Avenella flexuosa* in a clear cut area of *Myrtillus* site type may be.

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SELOSTE:

EKOLOGISIA HAVAINTOJA METSÄLAUHAPOPULAATION (AVENELLA FLEXUOSA (L.) PARL.) PÄIVITTÄISEN KASVUN SÄÄTYMISESTÄ

Tutkimuksen tarkoituksena on ollut selvittää metsälauhan kasvunopeuden säätymistä. Erityisesti on selvitetty lämpötilan, säteilyn ja kasvin sisäisen säätelyn merkitystä. Havaittiin, että läm-

pötila ja itsesääteily selittivät kasvunopeudesta yli 90 prosenttia ja ettei säteilyllä ollut tapahtumaan havaittavaa vaikutusta.