

## PRODUCTION OF STRUCTURAL MATTER BY A PLANT COMMUNITY IN SUCCESSIONAL ENVIRONMENT

SEPPO KELLOMÄKI, EERO VÄISÄNEN, PEKKA KAUPPI and PERTTI HARI

### SELOSTE:

KASVIYHDYSKUNNAN KUIVA-AINETUOTOS VALAISTUKSELTAAN MUUTTUVASSA YMPÄRISTÖSSÄ

Saapunut toimitukselle 1977-09-28

The structural matter production of selected plant species of a ground cover community was determined in relation to light available for photosynthesis. The resulting functions were applied in a situation where the light reaching the ground cover was controlled by the dynamics of the tree crown strata, and the occurrence of different plant species at different stages of succession was determined on the basis of their production of structural matter in actual light conditions. The possible strategies involved in adaptation to a successional environment have been discussed.

### INTRODUCTION

The photosynthesis-respiration balance describes the status of a plant species in an actual environment in a way that can also be used in the analysis of the maintenance and development of the whole plant community (cf. HORN 1971). The environmental factors controlling the photosynthetic functions are thus of prime importance in investigations concerning successional community development. In addition to light, the effect of soil moisture, nutrient supply and several other factors which have an effect on photosynthesis, have to be considered. However, these factors work over a long time scale as secondary factors modifying the principle light photosynthetic factor in community development (cf. MONSI and SAEKI 1953,

MONSI and OSHIMA 1955, LOGAN 1965, WUENSCHER 1974). Thus, the interaction between community members through the photosynthetic system is of prime importance in community development.

A species population cannot invade an actual site already populated by a species which makes the most effective use of the available resources, as argued by GAUSE (1934). Such invasion can only take place if the environmental change favours the invading species but not the present species. Since the growth and development of a plant species takes place only if there is a positive carbon balance, the mutual shading of community members plays an important role in community development (cf. MONSI and SAEKI 1953, MONSI and OSHIMA 1955,

KUROIWA 1960, MONSI 1960). The effect of shading on community development is indicated by the production of structural dry matter by the community members and their share of the total community production.

The aim of the present paper is to study the structural matter production of a plant community in changing light conditions in order to analyse the successional mechanisms of community development. Special attention is paid to above ground production by

the ground cover and its succession under the control of the dynamics of the crown stratum.

The study was carried out in the Department of Silviculture, University of Helsinki during 1975 and 1976. We wish to express our gratitude to professor Paavo Yli-Vakkuri, Head of Department, providing the facilities which made this work possible. This paper was supported by grants from the Academy of Finland.

### STUDY APPROACH

A mature community is characterized by differentiation of the standing crop into vertical strata, for example tree storey, bush storey, and ground cover. Even though this kind of differentiation is not as evident in an immature stand as in a mature stand, the suggested assumption is considered to be valid throughout the whole course of community succession.

The light conditions in a certain stratum are determined by the standing crop above in the actual stratum. Thus, it determines the degree of penetration into the next stratum and controls its photosynthetic rate. The actual growth level of the lower stratum is hence determined by the standing crop of the upper stratum. The interaction between different strata of a stand is tentatively described in Fig. 1.

In the boreal zone, there are usually four strata in a stand: tree stratum, bush layer, field layer and bottom layer. Let us number them as follows: 1 is the trees, 2 is the bush layer, 3 is the field layer, and 4 is the bottom layer. There are different species in each stratum. The species are numbered in such a way that numbers 1, 2, . . . ,  $i_1$ , represent the different tree species; numbers  $i_1 + 1, \dots, i_2$  represent the bush species; numbers  $i_2 + 1, \dots, i_3$  represent the species in the field layer; and numbers  $i_3 + 1, \dots, i_4$  represent the species in the bottom layer.

Let  $B_i$  denote the biomass of the  $i$ th species and  $p_i$  the photosynthetic rate of the  $i$ th species. The photosynthetic light ratio,  $PLR_i$ , for the  $i$ th species is defined as the ratio between the total amount of  $CO_2$  fixed by the  $i$ th species in the actual environment and the amount of  $CO_2$  fixed by the corresponding species if there were no shading present. Let  $x$  denote temperature and  $y_k$ , ( $k = 0, 1, 2, 3, 4$ ) light intensity in the  $k$ th stratum ( $y_0$  is light intensity above the canopy). Temperature and light varies with time, thus  $x = x(t)$  and  $y_k = y_k(t)$  ( $k = 0, 1, 2, 3, 4$ ). The photosynthetic

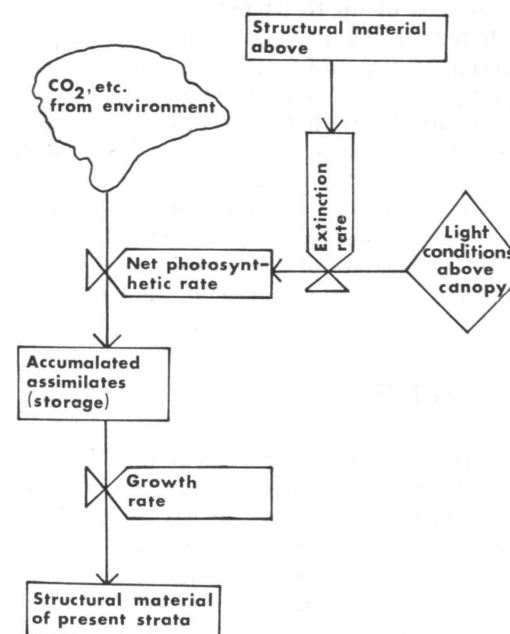


Fig. 1. Interaction between different strata in a stand.

rate is mainly determined by light and temperature, if no water stress is present, thus

$$(1) \quad P_i(t) = P_i(x(t), y_k(t)).$$

The value of the photosynthetic light ratio  $PLR_i$  can be approximated by integration

$$(2) \quad PLR_i = \frac{\int_{t_0}^t P_i(x(t), y_k(t)) dt}{\int_{t_0}^t P_i(x(t), y_0(t)) dt},$$

where  $t_0$  is the beginning instant of the photosynthetically active period and  $t_1$  is the moment at the end of photosynthetic activity.

The decrease ratio of the  $j$ :th on  $i$ :th species,  $DR_{ij}$ , is defined as the decrease in

the light ratio of the  $i$ :th species caused by the shading of the  $j$ :th species. Only those plants which are above the species  $i$ , can shade it, thus  $DR_{ij} = 0$  if  $j > i$ . The amount of biomass of the species  $j$  determines to a great extent the value of  $DR_{ij}$

$$(3) \quad DR_{ij} = DR_{ij}(B_j).$$

According to the definition of decrease ratio the following relationship exists between photosynthetic light ratio and decrease ratio for the  $i$ :th species in the  $k$ :th stratum

$$(4) \quad PLR_i = 1 - \sum_{j=1}^{i_k-1} DR_{ij}(B_j).$$

In conclusion, if the biomass and the functions in Eq. (3) are known, then the photosynthetic light ratio for each species can be approximated with Eq. (4).

## MATERIAL

The present material is partly the same as that utilized in our earlier study (VÄISÄNEN *et al.* 1977) concerning the relationship between photosynthetic production and structural matter production. It was collected in 1975–1976 at the Forest Field Station of the University of Helsinki in Central Finland (60° 50'E, 24° 20'N, 150 m a.s.l.). The following plant species typical of the *Myrtillus* site type in varying successional stages are included in the material: *Vaccinium myrtillus* L., *Vaccinium vitis-idaea* L. and

*Avenella flexuosa* (L.) Parl. Stands with a basal area of up to 34 m<sup>2</sup> per hectare were included in the material. The annual production of the structural matter for each plant species in each stand and its dependence on the photosynthetic light ratio were determined by applying the approach described by VÄISÄNEN *et al.* (1977). In addition, the succession series for tree stratum of natural spruce stand (*Picea abies* (L.) Karst) of the *Myrtillus* site type collected by KORVISTO (1959) were utilized.

## METHODS AND RESULTS

According to the basic assumption, the production of the  $i$ :th species,  $P_i$ , depends only on the light conditions in which the plant is growing. Thus, the following assumption can be made

$$(5) \quad P_i = P_i(PLR_i).$$

The dependence of production,  $P_i$ , on the photosynthetic light ratio for the plant species studied is presented in Figs. 2–4.

A plant community typical of a site of the *Myrtillus* type usually consists of Norway spruce, scattered bushes and dwarf shrubs and mosses. The shading of the ground cover is caused to a great extent by the trees. Thus, the photosynthetic light ratio of the species in the ground cover depends only on the biomass of the trees. If the stand is a pure spruce stand, the biomass of the trees can be approximated

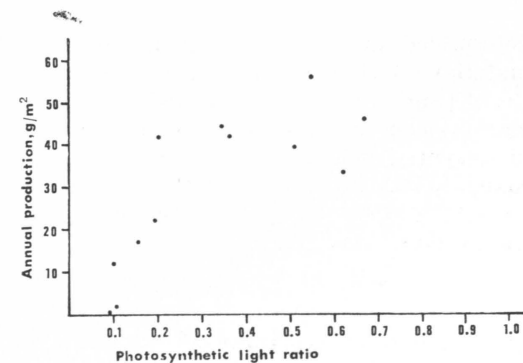


Fig. 2. Dependence of production on the photosynthetic light ratio for *Vaccinium myrtillus* according to VÄISÄNEN *et al.* (1977).

with growth and yield tables as a function of the age of the stand.

Suppose that the numbering of the species is performed in such a way that spruce is given the number one. In the present study the biomass of the tree stratum has been approximated by basal area, BA, which depends on the age,  $t$ , of the trees in the stand

$$(6) \quad BA_1 = BA_1(t).$$

The dependence of basal area on time in Eq. (6) can be approximated using the growth and yield tables collected by KORVISTO (1959) (cf. Fig. 5). This dependence

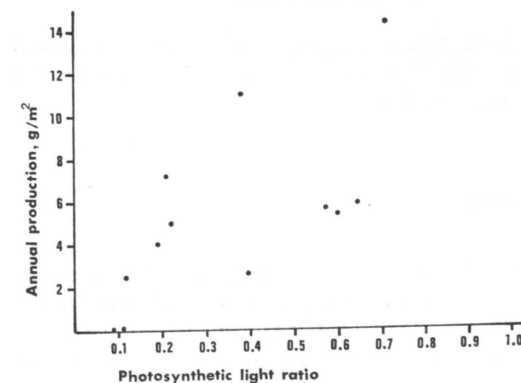


Fig. 3. Same as in Fig. 2 but for *Vaccinium vitis-idaea*.

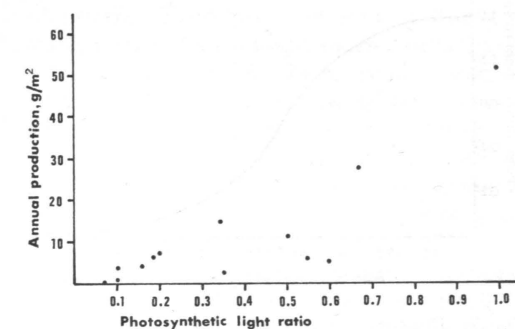


Fig. 4. Same as in Fig. 2 but for *Avenella flexuosa*.

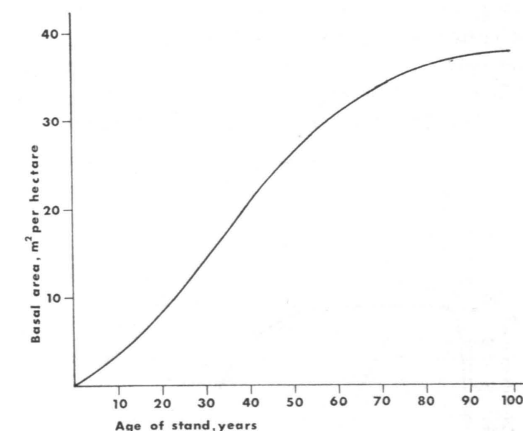


Fig. 5. Development of basal area as a function of time for Norway spruce according to KORVISTO (1959).

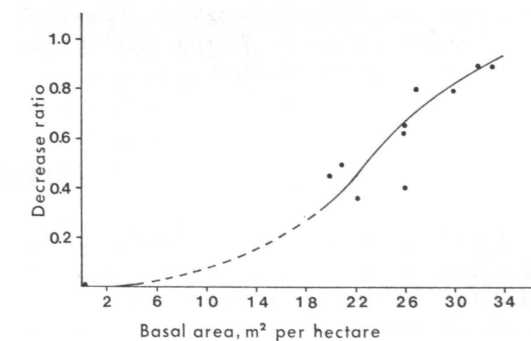


Fig. 6. Decrease ratio as a function of basal area for *Vaccinium myrtillus*.

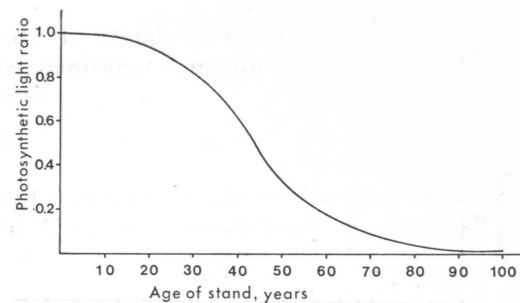


Fig. 7. Photosynthetic light ratio as a function of age of stand.

can be utilized in determining the light conditions on the forest floor during succession of the tree stratum (cf. Eq. 3). Therefore the dependence of decrease ratio on the basal area of the tree stratum was

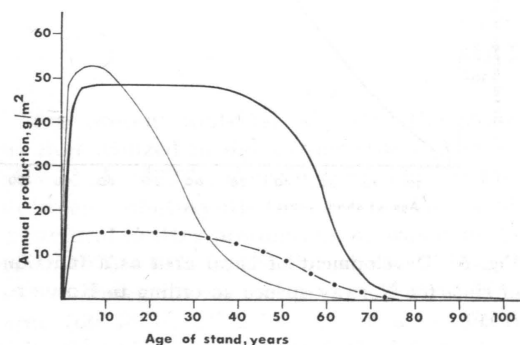


Fig. 8. Annual production of structural matter by different species in succession. Thick solid line represents *Vaccinium myrtillus*. Thin solid line represents *Avenella flexuosa*. Dotted line represents *Vaccinium vitis-idaea*.

determined on the basis of the available material (cf. Fig. 6). In the second phase the dependence of decrease ratio on stand age was computed according to Fig. 5. The photosynthetic light ratio can now be approximated as a function of the age of the trees in a stand for each of the species in the ground cover (cf. Fig. 6)

$$(7) \quad PLR_i(t) = 1 - DR_{ii}(BA_i(t)).$$

The amounts of structural matter produced annually can be approximated by compiling Eqs. (5), (6) and (7) as follows

$$(8) \quad P_i(t) = P_i(PLR_i(t)) = P_i(1 - DR_{ii}(BA_i(t))).$$

The amounts of structural matter produced annually by each species studied, computed according to Eq. (8), are presented in Fig. 8 for a period of one hundred years. The share of each plant species out of the total production of the plant community during the same period is presented in Fig. 9.

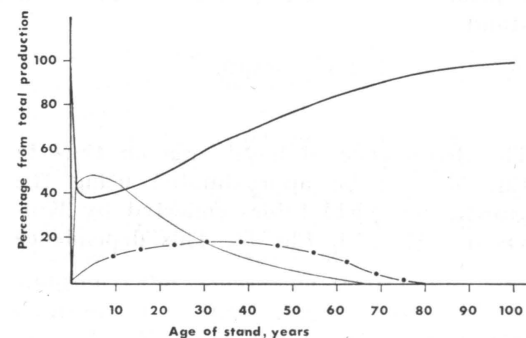


Fig. 9. Share of different species out of the total production during the course of succession. For legend see Fig. 8.

## DISCUSSION

*Avenella flexuosa* is very productive in the first twenty years during the development of a new spruce stand. Thereafter there is a strong decrease in the amount of annual production caused by the increasing shading of the tree stratum. The light conditions become crucial for this plant species after

the closure of the canopy. Since the adaptation of *Vaccinium myrtillus* and *Vaccinium vitis-idaea* to low light intensities is evident, the closure of the canopy results in an increase in the abundance of these two species at the expense of *Avenella flexuosa*. Thus, each species occurs in the community or

dominates it during a period determined by the species' response to the actual environment (cf. WUENSCHER 1974), *i.e.* in the present study to the light conditions controlled by the dynamics of the tree stratum.

The actual light conditions in a plant community were approximated using the regression between the basal area of the tree stratum and the decrease ratio. The distribution of the observations is abnormal owing to the lack of observations representing low basal area values. It may be possible that the extinction of light at low basal area values is faster than that assumed now. In particular, in young spruce stands with a closed crown system the basal area may not prove sufficient to explain the extinction of light. It is thus evident that the photosynthetic light ratio gives values which are greater than those in reality, with the result that for example *Avenella flexuosa* appears to dominate the ground cover for too long a period compared with other species. The regression between basal area and light conditions agrees, however, rather well with the results obtained by MITSCHERLICH *et al.* (1967) for the relationship between basal area and light conditions on the forest floor.

It should also be pointed out that the present results are based on the assumption that the relationship between basal area and decrease ratio can be converted into the relationship between time and decrease ratio by applying the relationship between time and basal area. By applying the regression between the decrease ratio and basal area the limited material has been expanded to cover much longer time intervals than would have been possible with the empirical material only. Since the present approach is essentially based on the role of light in the regulation of community development, not on time only the analytical procedure should not give rise to any objections.

The calculations carried out in the present study agrees with the earlier findings on the dominance of herbs and grasses in the initial stages and dwarf shrubs in the late stages of secondary succession in the ground cover (cf. for example KUJALA 1926, SIRÉN 1955, VOGL 1969, SHAFI and YARRATON 1973 a, b). The calculations, however, concern only one part of the succession of spruce stands, *i.e.* the part when the growth of spruce has just

culminated. Therefore it is evident that the relationship between plant species will change as succession proceeds. In particular, mortality in the tree stratum will decrease crown closure with the result the productivity of plant species in ground cover will increase (cf. MITSCHERLICH 1971). The present material is, however, insufficient for the consideration these phenomena.

A mosaic distribution of a species population without mutual shading is assumed in carrying out the calculations in the present study. In ground cover communities this kind of distribution is common owing to the clonal reproduction habit of vascular plants (cf. for example WITFORD 1949, OINONEN 1968, 1971). Therefore it is evident that a sufficient approximation of the field layer community may be obtained even though mutual shading of species in the field layer has been omitted in the calculations.

There are several other approaches to the analysis of community dynamics in succession as reviewed by HORN (1976). The authors have earlier presented a method based on the difference in occurrence of plant species in a successional community, *i.e.* on the stage of succession at which the species is characteristically found in the community (KAUPPI *et al.* 1977). Since this model consists of information about the successional status of community members, it gives no explanation for the interaction between community members and their adaptive mechanisms as does the present model. Since the present model takes into account the responses of community members to environmental changes from the dynamic point of view, it possesses a potentially greater area for application than the previous model. For example simulation of the behaviour of ground cover in an environment changed by repeated cuttings is possible using the present model.

Further development of the present model requires comprehensive study of the mechanisms involved in adaptation to a successional environment. MONSI and SAEKI (1953) have paid attention to the role of adaptation of the photosynthetic system in actual light conditions in community development (cf. also MONSI and OSHIMA 1955, KUROIWA 1960, LIETH and ASTON 1961, BJÖRKMAN 1970, HORN 1971). In particular, differences



in compensation and saturation of the photosynthetic process result in differences in the competition potential of community members. In addition, the consumption of carbohydrates in the different metabolic function of plant species must be taken into consideration. SCHULZE (1972) has demonstrated that high energy investment primarily above ground in the establishment of new leaves gives a plant species a high competitive potential, independent of the efficiency of photosynthesis, especially if a high turn over of carbon resources into production of structural material exists (cf. also LIETH and ASTON 1961). The basic principle in interaction between competitive plant species may be that species with the greater production of structural matter in the actual environment are strongest in competition, as suggested by the present material. Thus, the constitutional differences in photosynthetic activity are compensated by the distribution of assimilates to shoots and roots.

According to HARPER and OGDEN (1967), the energy contribution to competitive adaptation is in many cases highly correlated with energy input in addition to the intrinsic rate of an organism. For example, the maximum productivity of many forest herbs and grasses occurs at the same time as the maximum seed output, i.e. at the initial stage of secondary succession after fire or cutting. Later, the productivity of herbs and grasses decreases and their share out of the total production of the plant community decreases in favour of dwarf shrubs as in the present material. However, the climax communities also include these plant species, but their population densities are low and energy input to seed output is

exceptionally low as reported by KUJALA (1926), WITFORD (1949) and BEASLEIGH and YARRATON (1974). This kind of tactics, i.e. plasticity in the course of succession is common among vascular plants in ground cover communities represented also by the present material. Owing to this fact *Avenella flexuosa* does not disappear completely from plant community, but is ready to utilize the changing conditions, if they become favourable to it. *Vaccinium myrtillus* and *Vaccinium vitis-idaea* also seem able to utilize a similar kind of strategy in adaptation to a changing environment (cf. also OINONEN 1968, 1971, BEASLEIGH and YARRATON 1974). Thus, the tactics of plant species dominating early succession approaches those of species dominating the late succession.

An additional aspect to the study of the adaptation of community members to the successional environment is the renewal rate of the production system of community members. According to MÄLKÖNEN (1974), the annual production of structural matter by dwarf shrubs remains at 30–40 per cent of the standing crop as opposed to the total renewal of the productive system of herbs and grasses. The abundance of environmental resource in the initial stages of succession seems to favour plant species with a high turn over of productive system, as suggested also by the present material (cf. LOGAN 1973). On the other hand, the high turn over rate is commonly associated with high input formation of annual leaves and can be considered as a means of overcoming competition as discussed earlier. In habitats with sparse resources the input to perennial shoots appears to give a plant species a high competitive potential as demonstrated by MONK (1966) and LOGAN (1973).

## REFERENCES

- BEASLEIGH, W. J. & YARRATON, G. A. 1974. Ecological strategy and tactics of *Equisetum sylvaticum* during postfire succession. Can. J. Bot. 52: 2229–2318.
- BJÖRKMAN, O. 1970. Characteristics of the photosynthesis apparatus as revealed by laboratory measurements. In: Prediction and measurements of photosynthetic productivity. Proc. IBP/PP technical meeting. Trebon 1969 (ed. I. SETLIK), pp. 267–281. Centre for Agricultural Publishing & Do-

cumentation. Wageningen.

- GAUSE, G. F. 1934. The struggle for existence. Williams and Williams. Baltimore.
- HARPER, J. L. & OGDEN, J. 1970. The reproductive strategy of higher plants. I. The concept of strategy with special preference to *Senecio vulgaris* L. J. Ecol. 58: 681–698.
- HORN, H. S. 1971. The adaptive geometry of trees. Monographs in population ecology 3. Princeton University Press. Princeton.

- » — 1976. Succession. In: Theoretical ecology (ed. R. M. MAY), pp. 187–204. Blackwell Scientific Publications. Oxford, London, Edinburgh, Melbourne.
- KAUPPI, P., HARI, P. & KELLOMÄKI, S. 1977. A discrete time model for succession of ground cover communities after clear cutting. Oikos (in print).
- KOIVISTO, P. 1959. Kasvu- ja tuottotaulukoita. Growth and yield tables. Comm. Inst. For. Fenn. 51.
- KUJALA, V. 1926. Untersuchungen über den Einfluss von Waldbränden auf die Waldvegetation in Nord-Finnland. Commun. Inst. Fenn. 10.
- KUROIWA, S. 1960. Intraspecific competition in artificial sunflower communities. Bot. Mag. Tokyo 73: 300–309.
- LIETH, H. & ASHTON, D. H. 1961. The light compensation points of some herbaceous plants inside and outside deciduous woods in Germany. Can. J. Bot. 39: 1255–1259.
- LOGAN, K. T. 1965. Growth of tree seedlings as affected by light intensity. Can. Dep. For., For. Res. Publ. 1121.
- LOGAN, K. T. 1973. Growth of tree seedlings as affected by light intensity. V. White ash, beech, eastern hemlock, and general conclusions. Department of Environment. Can. For. Serv. Publ. 1323.
- MITSCHERLICH, G. 1971. Wald, Wachstum und Umwelt. Eine Einführung in die ökologischen Grundlagen des Waldwachstums. 2. Band. Waldklima und Wasserhaushalt. V. D. Sauerländer's Verlag. Frankfurt am Main.
- » —, KÜNSTLE, E. & LANG, W. 1967. Ein Beitrag zur Frage der Beleuchtungsstärke im Bestande. Allg. Forst- u. Jagtz. 138: 213–223.
- MONK, C. 1966. Ecological importance of root/shoot ratios. Bull. Torrey Bot. Club 93: 402–406.
- MONSI, M. 1960. Dry matter reproduction in plants I. Schemata of dry-matter reproduction. Bot. Mag. Tokyo 73: 81–90.
- » — & SAEKI, T. 1953. Über den Lichtfactor in den Pflanzengesellschaften und seine Bedeutung für die Stoffproduktion. Jap. Journ. Bot. 14: 22–52.
- » — OSHIMA, Y. 1955. A theoretical analysis of the succession process of plant community,

based upon the production of matter. Jap. Journ. Bot. 15: 60–82.

- MÄLKÖNEN, E. 1974. Annual primary production and nutrient cycle in some Scots pine stands. Commun. Inst. For. Fenn. 84.
- OINONEN, E. 1968. *Lycopodium clavatum* (L.) ja *L. annotinum* (L.) kasvustojen laajuus rinnastettuna samanpaikkaisiin *L. complanatum* (L.) ja *Pteridium aquilinum* (L.) esiintymiin sekä puuston ikään ja palo-aikoihin. Summary: The size of *Lycopodium clavatum* (L.) and *L. annotinum* (L.) stands as compared to that of *L. complanatum* and *Pteridium aquilinum* (L.) stands, the age of the tree stand and the dates of fire on the sites. Acta For. Fenn. 87.
- » — 1971. The time table of vegetative spreading in oak fern (*Carpogynia dryopteris* L.) and Maylily (*Maianthemum bifolium* L.) in Southern Finland. Acta For. Fenn. 118.
- SCHULZE, E.-D. 1972. Die Wirkung von Licht und Temperatur auf den CO<sub>2</sub>-Gaswechsel verschiedener Lebensformen aus der Krautschicht eines montanen Buchenwaldes. Oecologia (Berl.) 9: 235–258.
- SHAFI, M. I. & YARRATON, G. A. 1973 a. Diversity, floristic richness and species evenness during a secondary (post-fire) succession. Ecology 54: 897–902.
- » — & YARRATON, G. A. 1973 b. Vegetational heterogeneity during a secondary (post-fire) succession. Can. J. Bot. 51: 73–90.
- SIRÉN, G. 1955. The development of spruce forest on raw humus sites in northern Finland and its ecology. Acta For. Fenn. 62.4.
- WHITFORD, P. B. 1949. Distribution of woodland plants in relation to succession and clonal growth. Ecology 30: 199–208.
- VOGL, R. J. 1969. One hundred and thirty years of plant succession in a southeastern Wisconsin Lowlands. Ecology 50: 248–255.
- WUENSCHER, J. E. 1974. The ecological niche and vegetation dynamics. In: Handbook of vegetation science. Part VI. Vegetation and environment (ed. B. R. STRAIN and W. D. BILLINGS), pp. 39–45. Dr. W. Junk b.v. — Publishers. Hague.
- VÄISÄNEN, E., KELLOMÄKI, S. & HARI, P. 1977. Annual growth level of some plant species as a function of light available for photosynthesis. Silva Fenn. 11 (4): 269–275.

## SELOSTE:

### KASVIYHDYSKUNNAN KUIVA-AINETUOTOS VALAISTUKSELTAAN MUUTTUVASSA YMPÄRISTÖSSÄ

Työssä on tutkittu pintakasvillisuusyhdyskunnan kuiva-ainetuotosta olosuhteissa, joissa puuston dynamiikka säätelee pintakasvillisuuden saaman valon määrää. Kuiva-ainetuotoksen ja fotosynteesissä käyttökelpoisen valon välistä suhdetta hyväksi käyttäen on laskettu muutamien metsä-

kasvilajien esiintymisrunsautta metsikkökehityksen eri vaiheissa. Työssä on myös pohdittu erilaisia strategiavaihtoehtoja, jotka mahdollistavat kasvilajien sopeutumisen ominaisuuksiltaan muuttuviin olosuhteisiin.