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**ENERGY FLOW CHANGES RELATED  
TO THE DEVELOPMENT OF ASSIMILATORY ORGAN  
BIOMASS IN SUBOCEANIC FRESH PINE FOREST  
LEUCOBRYO-PINETUM MAT. 1962**

**ABSTRACT:** In secondary succession of the Leucobryo-Pinetum association the assimilatory apparatus dimensions of the phytocenosis were determined by means of the standing crop of green biomass and chlorophyll index. On this basis the amount of energy absorbed by the phytocenosis in the gross photosynthesis process was assessed; moreover, the magnitude of anthropogenic energy subsidy was evaluated. A tendency for stabilization of the assimilatory apparatus dimensions and an inverse correlation between these dimensions and energy subsidy were found.

**KEY WORDS:** Secondary succession, forest ecosystem, standing crop of green biomass, chlorophyll index, energy flow, energy subsidy.

**1. INTRODUCTION**

Absorption of solar energy and its transformation into chemical energy in the photosynthesis process is the main source of energy (according to, among others, Hutchinson 1970) available to phytocenoses. The amount of solar energy directly absorbed by the phytocenosis depends, among others, on the photosynthetic activity of plants, dimensions of the assimilatory apparatus and the complex effect of habitat factors. The dimensions of the assimilatory apparatus of the whole phytocenosis, most often assessed by means of the leaf area index (*LAI*, Watson 1947), chlorophyll index (*CI*, Okubo et al. 1964) or assimilatory organ biomass, in the initial period of development greatly increase, whereas at the further stages they are



relatively rapidly stabilized at the maximal level (Woodwell 1967, Whittaker 1975, Walter 1976, Bormann and Likens 1979). The dimensions of the assimilatory apparatus depend on nutrient resources of the habitat and on other physical factors whereas they are independent of the species composition of communities (Ellenberg 1939, Geyger 1964, Woodwell 1967, Covington and Aber 1980). Owing to stabilization of the assimilatory apparatus dimensions (occurring during the development of the biocenosis) on the maximal level, the amount of absorbed solar energy also becomes constant.

Apart from direct solar energy, phytocenoses as distinct systems may be supplied with allogenic energy transformed by other systems at another time and in another space. Systems in which allogenic energy significantly changes their structure and manner of functioning have been termed by Odum (1977) subsidy systems. Such biocenoses are characterized, in dependence on the amount and quality of allogenic energy, by an extremely simplified or more differentiated structure, and always by high productivity (Odum 1975).

Human activities increase the number of subsidy systems, including the subsidized phytocenoses. For high biomass production simplified phytocenoses are formed; they are most often monocultures requiring a steady energy subsidy (Pimentel et al. 1973, 1975, 1980, Pimentel 1977, Odum 1977, Collier et al. 1978, Zavitkovski 1979 and others). In these systems, e.g. in agrocenoses whose development has been artificially arrested at early stages (Montheith 1965, Jakrlova 1967, Loomis et al. 1967, Kreeb 1979), the leaf area index is decreased, as compared with natural communities.

Ecological literature affords no data on the relationships between energy subsidy and assimilatory apparatus dimensions of phytocenoses, and thus — on their potential productivity. In this connection it was attempted to determine these relationships for suboceanic fresh pine forest.

## 2. AREA AND METHODS OF STUDIES

Studies were performed in Bory Tucholskie woods, in the northern part of the Tucholska Równina plain (Lencewicz and Kondracki 1962), in sections 74 and 122 of the Przymuszewo Forest Inspectorate (Fig. 1). Geobotanically, according to Szafer (1972), this is the northern part of the Bory Tucholskie District of the Pomeranian Southern Transitional Belt Region.

Sampling stations were located in five plantations of a monoculture of Scots pine (*Pinus sylvestris* L.), of different age. They may be regarded as stage of secondary succession of the association termed by Boiński (unpublished data) Leucobryo-Pinetum, and classified by Sokołowski (1965) as a variant of the typical *Vaccinio myrtilli*-Pinetum typicum association; according to forest typology (Mastyński 1963, Alexandrowicz 1972), it is a fresh pine forest habitat. Suboceanic fresh pine forest in the Bory Tucholskie woods is a secondary association



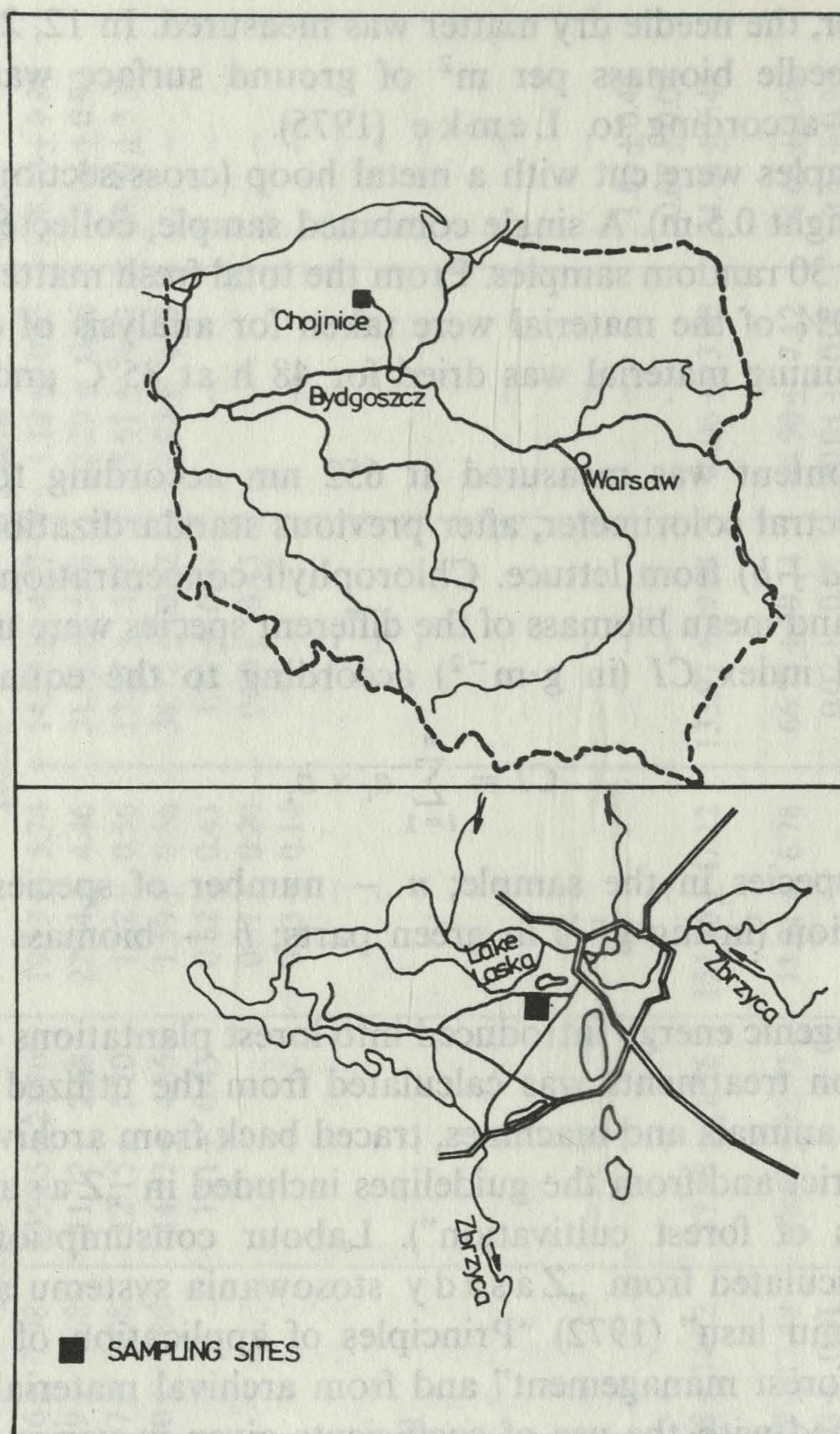


Fig. 1. Location of the area under study

of anthropogenic nature, resulting from regular and planned agricultural and other activities.

At selected sampling stations, in 3, 6, 12, 24 and 120-year old plantations, dry matter ( $\text{g}\cdot\text{m}^{-2}$ ) of pine needles, green parts of the herb layer and mosses was determined, as well as chlorophyll contents in pine needles and — for seven dominant species — in the herb layer of undergrowth and in two species of mosses were measured. Furthermore, it was attempted to evaluate the intensity of human activities by measuring the amount of anthropogenic energy introduced into the phytocenosis.

Pine needle biomass was estimated as follows: in 3 and 6-year old plantations model trees were selected according to the thickness of stem diameter at stump height and at breast height, and in accordance with the height at which needles were



collected; moreover, the needle dry matter was measured. In 12, 24 and 120-year old plantations the needle biomass per  $\text{m}^2$  of ground surface was calculated using allometric indices, according to Lemke (1975).

Herb layer samples were cut with a metal hoop (cross-section surface  $0.120 \text{ m}^2$ , diameter  $0.4 \text{ m}$ , height  $0.5 \text{ m}$ ). A single combined sample, collected from a  $3.75 \text{ m}^{-2}$  surface, comprised 30 random samples. From the total fresh matter of the green parts of each species, 10% of the material were taken for analysis of chlorophyll ( $a + b$ ) content. The remaining material was dried for 48 h at  $85^\circ\text{C}$  and weighed exact to  $0.01 \text{ g}$ .

Chlorophyll content was measured at  $652 \text{ nm}$  according to Šesták (1971), using a Specol spectral colorimeter, after previous standardization of the apparatus with chlorophyll ( $a + b$ ) from lettuce. Chlorophyll concentrations obtained for the dominant species and mean biomass of the different species were used for calculation of the chlorophyll index  $CI$  (in  $\text{g}\cdot\text{m}^{-2}$ ) according to the equation:

$$CI = \sum_{i=1}^n a_i \times b_i$$

$i$  – consecutive species in the sample;  $n$  – number of species;  $a$  – chlorophyll ( $a + b$ ) concentration (in  $\text{mg}\cdot\text{g}^{-1}$ ) in green parts;  $b$  – biomass of green parts (in  $\text{g}\cdot\text{m}^{-2}$ ).

Total anthropogenic energy introduced into forest plantations during reforestation and cultivation treatments was calculated from the utilized materials, human work and work of animals and machines, traced back from archival materials of the Laska Forest District and from the guidelines included in „Zasady hodowli lasu” (1979) (“Principles of forest cultivation”). Labour consumption of the different treatments was calculated from „Zasady stosowania systemu akordu umownego w zagospodarowaniu lasu” (1972) “Principles of application of contractual piece-work systems in forest management” and from archival materials. Energy calculations were performed with the use of coefficients given in various publications and tables (Całus 1962, Jakubowski 1973, Fibigier 1976, Kubiček 1977, Jørgensen 1979).

### 3. RESULTS

#### 3.1. BIOMASS OF PINE NEEDLES, HERB LAYER AND MOSSES

Figure 2 presents the biomass of the assimilatory organs of pine tree stand, herb layer and moss layer at different age stages of suboceanic fresh pine forest. Values of dry matter of the different species are recorded in Table 1. In the total green biomass of phytocenoses pine needles were dominant, representing (in dependence on plantation age) from 40% (6-year old plantation) to 80% (24-year old plantation). Total dry matter of the assimilatory organs increased intensively until the 24-year



Table 1. State of biomass (g dry matter · m<sup>-2</sup> ± SE) of the herb layer (c and d) and of litter of pine needles, at succession stages of the Leucobryo-Pinetum association

Age of plantation (yr)	3	6		12		24	120
Species		ploughed soil	not ploughed soil	ploughed soil	not ploughed soil		
<i>Pinus sylvestris</i> L.	42.98	218.00		263.50		525.76	419.52
<i>Vaccinium myrtillus</i> L.	0.01 ± 0.01	28.76 ± 7.98	135.85 ± 27.70	19.13 ± 5.74	14.22 ± 4.27	1.12 ± 0.45	158.43 ± 9.20
<i>V. vitis-idea</i> L.	0.75 ± 0.60	4.19 ± 1.68	11.72 ± 2.68	22.54 ± 4.46	21.32 ± 5.08	3.29 ± 0.66	5.95 ± 0.97
<i>Deschampsia flexuosa</i> (L.) Trin.	29.87 ± 14.63	1.97 ± 0.08	12.15 ± 5.10	1.62 ± 0.56	13.87 ± 4.09	5.61 ± 1.21	28.59 ± 3.36
<i>Calluna vulgaris</i> (L.) Salisb.	4.33 ± 2.60	3.10 ± 1.86	14.93 ± 4.85	1.59 ± 0.56	38.72 ± 20.62	2.94 ± 1.33	—
<i>Festuca ovina</i> L.	—	—	1.11 ± 0.43	0.62 ± 0.43	1.79 ± 0.91	—	—
<i>Veronica officinalis</i> L.	—	—	—	0.37 ± 0.20	0.60 ± 0.45	—	—
<i>Cerastium arvense</i> L.	—	—	—	0.23 ± 0.14	—	—	—
<i>Senecio sylvaticus</i> L.	3.91 ± 2.90	—	—	—	—	—	—
<i>Spergula vernalis</i> Willd.	4.19 ± 1.71	—	—	—	—	—	—
<i>Rumex acetosella</i> L.	0.22 ± 0.13	—	—	—	—	—	—
<i>Corynephorus canescens</i> (L.) P.B.	0.18 ± 0.09	—	—	—	—	—	—
<i>Calamagrostis epigeios</i> (L.) Roth	0.16 ± 0.07	—	—	—	—	—	—
<i>Melampyrum pratense</i> L.	—	—	—	—	—	—	1.85 ± 0.46
<i>Fagus silvatica</i> (seedlings) L.	—	—	—	—	—	—	0.07 ± 0.04
<i>Dicranum undulatum</i> Schrod.	<0.01	103.78 ± 34.72	87.98 ± 21.76	154.46 ± 47.12	133.97 ± 49.04	70.06 ± 13.80	34.76 ± 9.44
<i>Pleurozium schreberi</i> (Brid.) Mitt.	<0.01	38.29 ± 12.48	58.62 ± 12.72	11.91 ± 6.78	66.23 ± 39.74	44.50 ± 7.12	34.63 ± 4.09
<i>Pohlia nutans</i> (Hedw.) Lind.	<0.01	0.03 ± 0.01	—	—	0.02 ± 0.01	0.01 ± 0.01	0.43 ± 0.25
<i>Polytrichum juniperinum</i> Hedw.	0.53 ± 0.42	—	0.28 ± 0.13	—	13.75 ± 8.25	—	—
<i>Ceratodon purpureus</i> (Hedw.) Brid.	—	—	—	—	—	0.01 ± 0.01	—
<i>Ptilidium pulcherrimum</i> (G. Web.) Vainio	—	—	—	—	—	0.02 ± 0.01	—
Total state of green biomass of tree stands and herb layer	87.03	398.13	540.64	475.83	567.99	653.32	684.23



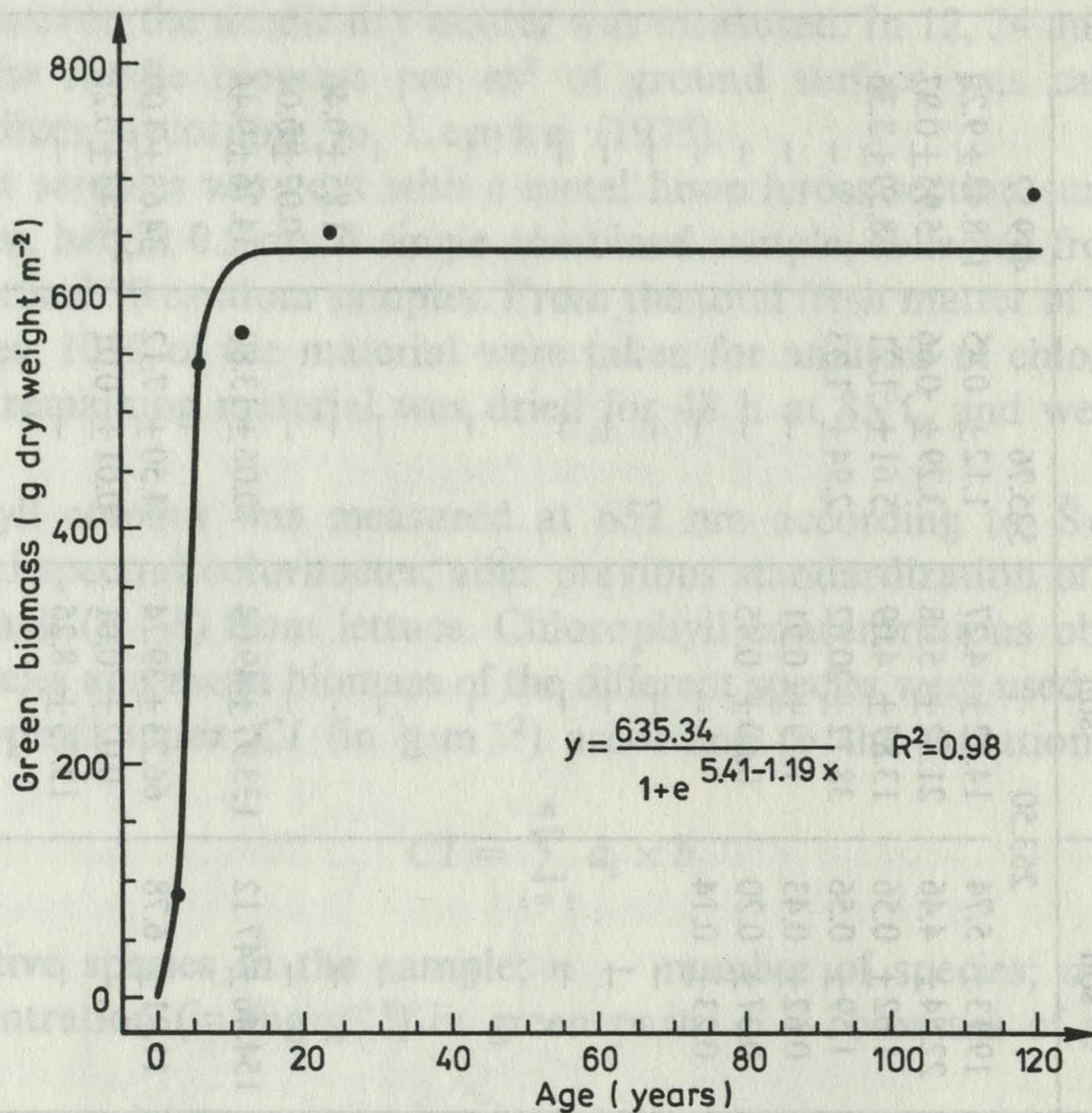


Fig. 2. State of assimilatory organ biomass in secondary succession of the Leucobryo-Pinetum association

old pole stage, in furrows and not ploughed belts; it rose more rapidly in these belts. In older tree stands the increase in biomass of the assimilatory organs was slight, and the amount of dry matter of pine needles, calculated per m<sup>2</sup> of ground surface, decreased. The biomass of the assimilatory organs of all plants remained in dynamic equilibrium owing to a correlation between the biomass of pine needles and that of the herb layers and mosses. These values compensated each other, because a great increase in pine needles biomass was associated with reduction of the herb layer and moss biomass; this was most evident in the case of 12 and 24-year old young stands. There is a feedback between plants in the different layers, and the light and moisture relationships in the forest community formed.

### 3.2. CHLOROPHYLL CONTENT

Table 2 presents the concentrations of chlorophyll ( $a + b$ ) in different plant species. Analysis of the pigments pointed to small differences in the chlorophyll ( $a + b$ ) content between the species dominant in the herb layer of a developing Scots pine monoculture. The highest concentration of chlorophyll ( $6.57 \text{ mg} \cdot \text{g}^{-1}$  dry matter) was displayed by *Deschampsia flexuosa* growing in a 120-year old Leucobryo-Pinetum association.

At the different developmental stages of fresh pine forest, light intensity exerted



Table 2. Contents of chlorophyll ( $a + b$ ) ( $\text{mg} \cdot \text{g}^{-1}$  dry matter  $\pm$  SE) in dominant plant species at succession stages of the Leucobryo-Pinetum association

Species	Age of plantation (yr)	3	6	12	24	120
<i>Pinus sylvestris</i> L.	1-yr needles	2.78 $\pm$ 0.24	2.95 $\pm$ 0.24	1.56 $\pm$ 0.06	1.85 $\pm$ 0.12	2.22 $\pm$ 0.12
<i>P. sylvestris</i> L.	2-yr needles	1.93 $\pm$ 0.12	2.24 $\pm$ 0.07	2.59 $\pm$ 0.13	3.14 $\pm$ 0.25	3.37 $\pm$ 0.30
<i>P. sylvestris</i> L.	3-yr needles	0.85 $\pm$ 0.10	2.37 $\pm$ 0.09	2.09 $\pm$ 0.23	2.84 $\pm$ 0.37	3.69 $\pm$ 0.11
<i>P. sylvestris</i> L.	4-yr needles	—	2.14 $\pm$ 0.03	1.54 $\pm$ 0.16	2.93 $\pm$ 0.26	3.97 $\pm$ 0.19
<i>Vaccinium myrtillus</i> L.		3.48 $\pm$ 0.15	3.41 $\pm$ 0.30	5.11 $\pm$ 0.27	6.02 $\pm$ 0.41	4.18 $\pm$ 0.19
<i>V. vitis-idaea</i> L.		2.92 $\pm$ 0.29	2.70 $\pm$ 0.42	3.80 $\pm$ 0.24	3.09 $\pm$ 0.18	2.62 $\pm$ 0.13
<i>Deschampsia flexuosa</i> (L.) Trin.		5.67 $\pm$ 0.23	1.85 $\pm$ 0.11	4.04 $\pm$ 0.39	5.82 $\pm$ 0.37	6.57 $\pm$ 0.54
<i>Calluna vulgaris</i> (L.) Salisb.		2.59 $\pm$ 0.25	4.08 $\pm$ 0.41	5.50 $\pm$ 0.48	5.61 $\pm$ 0.37	—
<i>Festuca ovina</i> L.		—	2.12 $\pm$ 0.19	4.92 $\pm$ 0.31	—	—
<i>Senecio sylvaticus</i> L.		6.64 $\pm$ 0.90	—	—	—	—
<i>Melampyrum pratense</i> L.		—	—	—	—	4.90 $\pm$ 0.33
<i>Pleurozium schreberi</i> (Brid.) Mitt.		2.00 $\pm$ 0.17	2.02 $\pm$ 0.13	3.22 $\pm$ 0.30	5.19 $\pm$ 0.58	4.81 $\pm$ 0.37
<i>Dicranum undulatum</i> Schrod.		1.84 $\pm$ 0.32	1.33 $\pm$ 0.15	3.13 $\pm$ 0.33	2.67 $\pm$ 0.30	4.56 $\pm$ 0.30



a significant effect on the chlorophyll concentration in plants of forest floor. This was evident in the case of *Vaccinium myrtillus*, *Calluna vulgaris* and *Pleurozium schreberi*. Chlorophyll concentration in these plants was highest in the 12 and 24-year old plantations, under conditions of greatest shading. This relationship was different in the case of *Deschampsia flexuosa* and *Dicranum undulatum*, which displayed a maximum chlorophyll concentration in the 120-year old plantation.

Chlorophyll content in pine needles rose with age of trees. This relationship could be due, among others, to an increased content of total nitrogen in plants (Falkowski and Kukułka 1964). Namely, a positive effect of the nitrogen concentration on chlorophyll content in pine needles has also been reported by Keller and Wehrmann (1963), and in poplar leaves – by Keller and Koch (1962) and by Pobiegałło (1967). This is also reflected by the needle colour intensity (Tamm 1956, Ingestad 1963, Kowalkowski 1976). According to Nowotny-Mieczysława (1976), a significant effect on the chlorophyll synthesis is exerted by nitrogen, potassium, sodium, magnesium and iron. Margajlik (1962) has observed that the chlorophyll concentration in pine needles dropped with deterioration of the habitat conditions and was dissimilar in different types of forest. This also points to the dependence of the chlorophyll concentration on the edaphic conditions of pine. In contrast, Bormann et al. (1968), and Bormann and Likens (1979) have described leaching of nitrate and of the remaining elements during reforestation after clear-cutting. In older tree stands enhancement of the

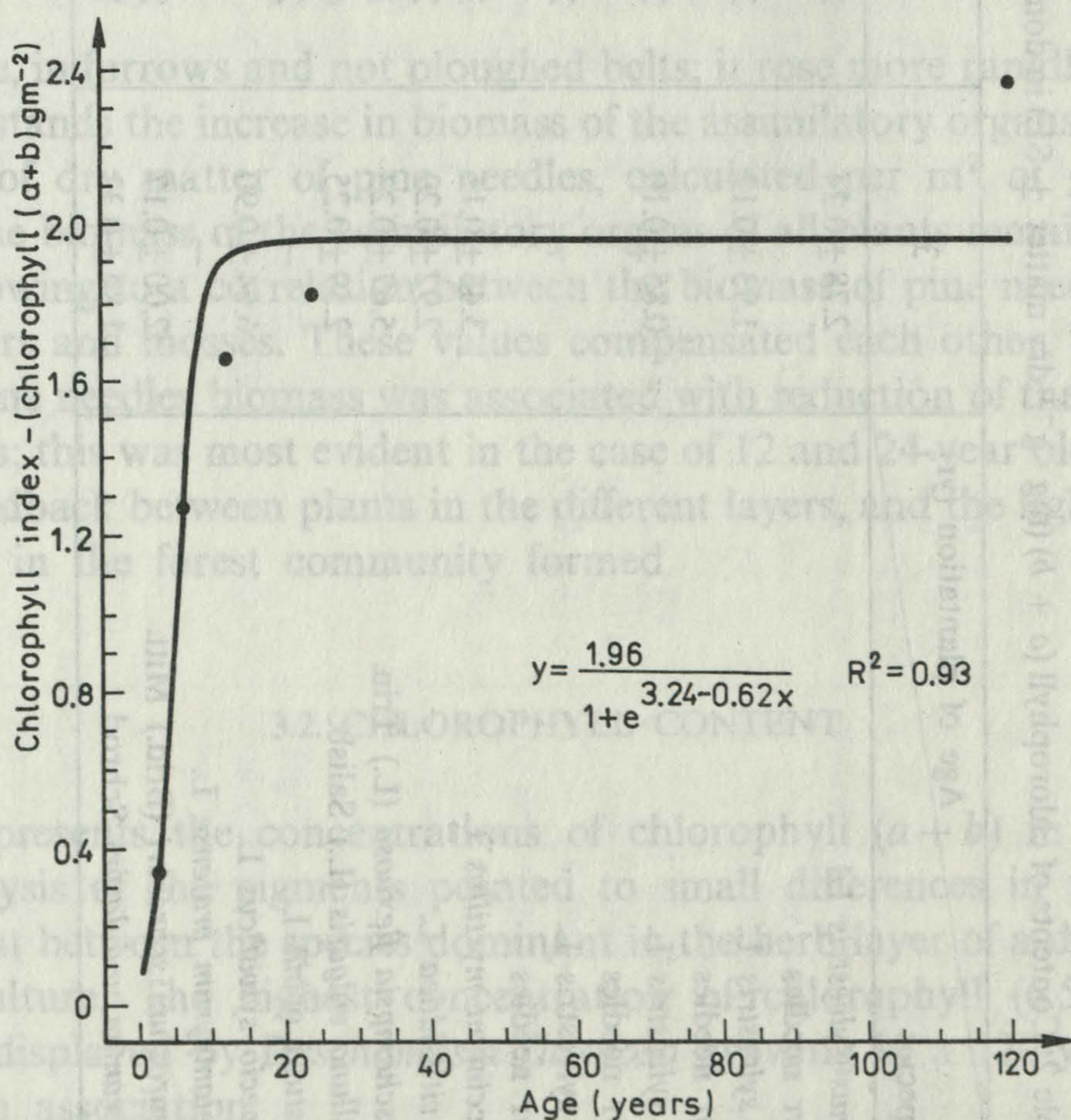


Fig. 3. Chlorophyll (a + b) index in secondary succession of the Leucobryo-Pinetum association



so-called "biological profile" leads to an increase in the participation of these nutrients in the turnover (Puchalski and Prusinkiewicz 1975). The described relationships also influence the pigment content in the herb layer plants; on forest floor, in the course of the development of the community the pigment concentration depends — apart from the trophic conditions — also on the variable light conditions.

The values of the concentration of chlorophyll ( $a + b$ ) in different species were used for calculation of the  $CI$  index whose course, shown in Figure 3, resembles the curve of the assimilatory apparatus biomass. However, in a tree stand aged ca. 120 years the increase in chlorophyll ( $a + b$ ) ( $2.36 \text{ g} \cdot \text{m}^{-2}$ ) was more clear-cut than that found for the 24-year old pole stage ( $1.82 \text{ g} \cdot \text{m}^{-2}$ ); this resulted from an increased chlorophyll concentration in needles of 120-year old pine (Table 2).

### 3.3. ENERGY FLOW

#### 3.3.1. Energy absorbed in the photosynthesis process

The value of assimilatory organ biomass, assessed in developing suboceanic fresh pine forest, allowed for estimation of solar energy absorbed by the biocenosis in the gross photosynthesis process. The energy absorbed in the photosynthesis was

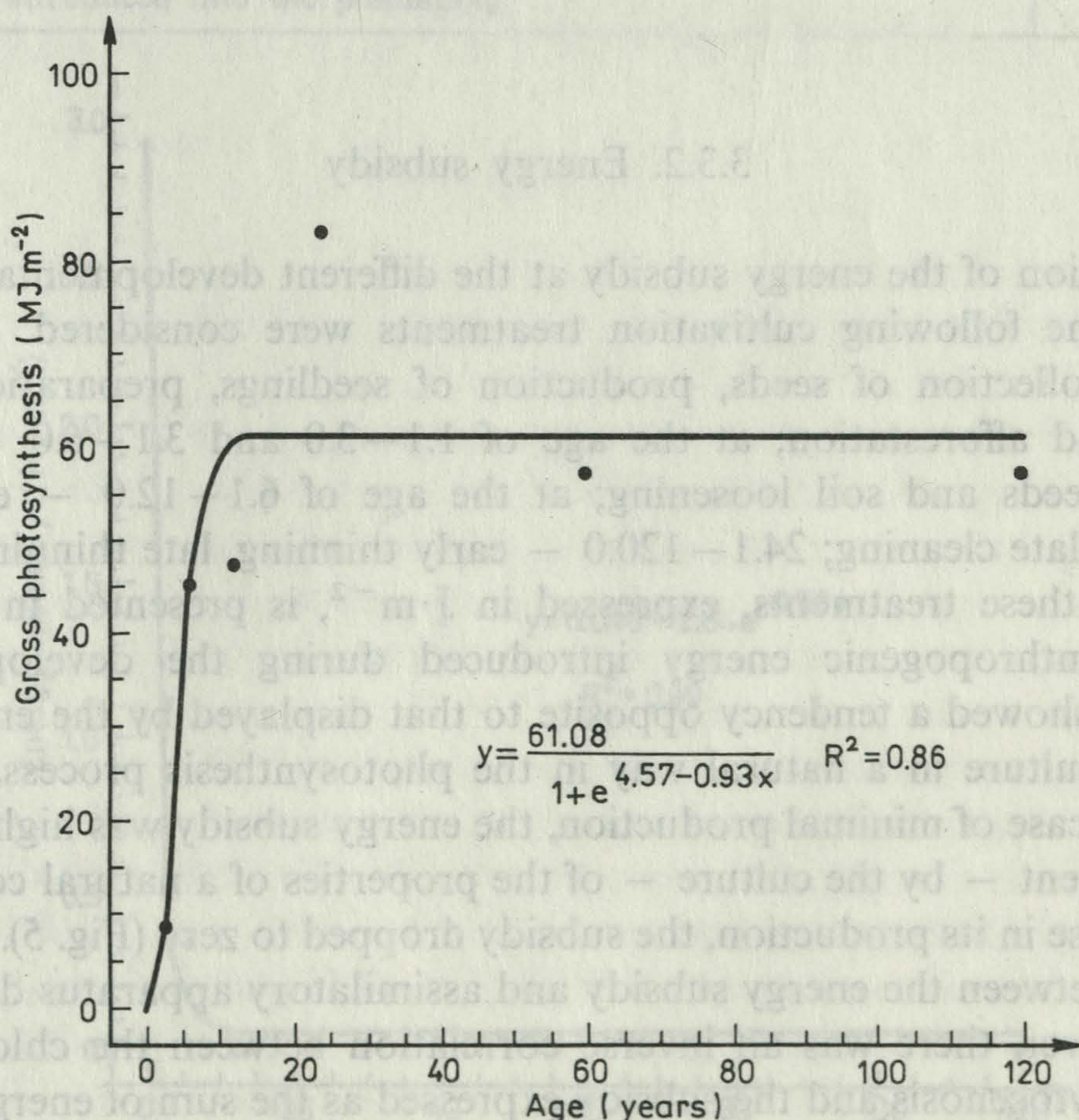


Fig. 4. Solar energy absorbed in the gross photosynthesis process in secondary succession of the Leucobryo-Pinetum association



calculated from the assimilatory organ dimensions of trees, herb layer and moss layer, according to the equation:

$$P_k = \sum_{j=1}^{n_k} (B_{zj}) \sum_{i=1}^{n'} (F_{ji} + R_{ji}) 11.33 \text{ kJ}$$

$P_k$  — yearly gross photosynthesis of the community at the selected sampling station,  $B_{zj}$  — green biomass of consecutive species in the community,  $F$  — net photosynthesis,  $R$  — respiration,  $k$  — consecutive sampling station,  $j$  — consecutive species,  $n_k$  — number of species at the selected sampling station,  $i$  — consecutive day of production in the year,  $n'$  — number of production days in the year.

In the calculations use was made of conversion coefficients based on the results reported in many papers concerning gas exchange of Scots pine, herb layer species and mosses, and dealing with undergrowth production of wood communities (e.g. Żelawski and Góral (1966), Polster (1967), W. Żelawski and B. Żelawska (1967), H. Traczyk and T. Traczyk (1967), Larcher (1969), Sesták et al. (1971), Helms (1970), Krupa (1974), Gosz et al. (1978), Bormann and Likens (1979). So obtained the energy values of gross photosynthesis displayed in the development of the phytocenosis similar tendencies as the value of assimilatory organ biomass, i.e. a rapid increase in the first 6 years after setting up of the plantation and equalized values in the later period (Fig. 4).

### 3.3.2. Energy subsidy

In calculation of the energy subsidy at the different developmental stages of the association, the following cultivation treatments were considered: at the age of 0.0–1.0 — collection of seeds, production of seedlings, preparation of soil for cultivation and afforestation; at the age of 1.1–3.0 and 3.1–6.0 — mechanical removal of weeds and soil loosening; at the age of 6.1–12.0 — early cleaning; 12.1–24.0 — late cleaning; 24.1–120.0 — early thinning, late thinning. The energy equivalent of these treatments, expressed in  $\text{J} \cdot \text{m}^{-2}$ , is presented in Table 3. The amount of anthropogenic energy introduced during the development of the phytocenosis showed a tendency opposite to that displayed by the energy obtained by the monoculture in a natural way in the photosynthesis process. In the initial period, in the case of minimal production, the energy subsidy was highest; over time, with acquirement — by the culture — of the properties of a natural community and with an increase in its production, the subsidy dropped to zero (Fig. 5). An analogous relationship between the energy subsidy and assimilatory apparatus dimensions was found. Moreover, there was an inverse correlation between the chlorophyll index ( $CI$ ) of the phytocenosis and the subsidy expressed as the sum of energy required for further development of the plantation (Fig. 6).



Table 3. Energy introduced into the plantation during 0–120 years in the form of human and animals' work and of fuels

Applied: \*Human energy expenditure during work: 180–420 (kcal · h<sup>-1</sup>) (Jakubowski 1973, Fibiger 1976); \*\*Energy expenditure of horse during work: 2500 (kcal · h<sup>-1</sup>) (Kleiber 1968); \*\*\*Combustion heat of fuel oil (FO): 9500 (kcal · kg<sup>-1</sup>); \*\*\*Combustion heat of leaded petrol (LP): 10500 (kcal · kg<sup>-1</sup>); \*\*\*Combustion heat of machine oil (MO): 9500 (kcal · kg<sup>-1</sup>) (computed from starting data of Calus 1962)

Age of plantation (yr)	Human work (h · m <sup>-2</sup> )**	Work of draft animals (h · m <sup>-2</sup> )**	Fuels (kg · m <sup>-2</sup> )***	Energy equivalent (J · m <sup>-2</sup> )
0.0–1.0	0.1352	0.0003	0.0055 FO 0.0564 LP	2.89 · 10 <sup>6</sup>
1.1–3.0	0.0451	0.0001	0.0018 FO 0.0188 LP	9.64 · 10 <sup>5</sup>
3.1–6.0	0.0047	—	0.0242 FO 0.0004 LP	9.87 · 10 <sup>5</sup>
6.1–12.0	0.0048	—	0.0004 LP	2.59 · 10 <sup>4</sup>
12.1–24.0	0.0054	—	0.0005 LP	2.86 · 10 <sup>4</sup>
24.1–120.0	0.4418	—	0.0002 FO 0.0919 LP 0.0160 MO	5.44 · 10 <sup>6</sup>
Sum of energy introduced into the plantation:				1.0342 · 10 <sup>7</sup>

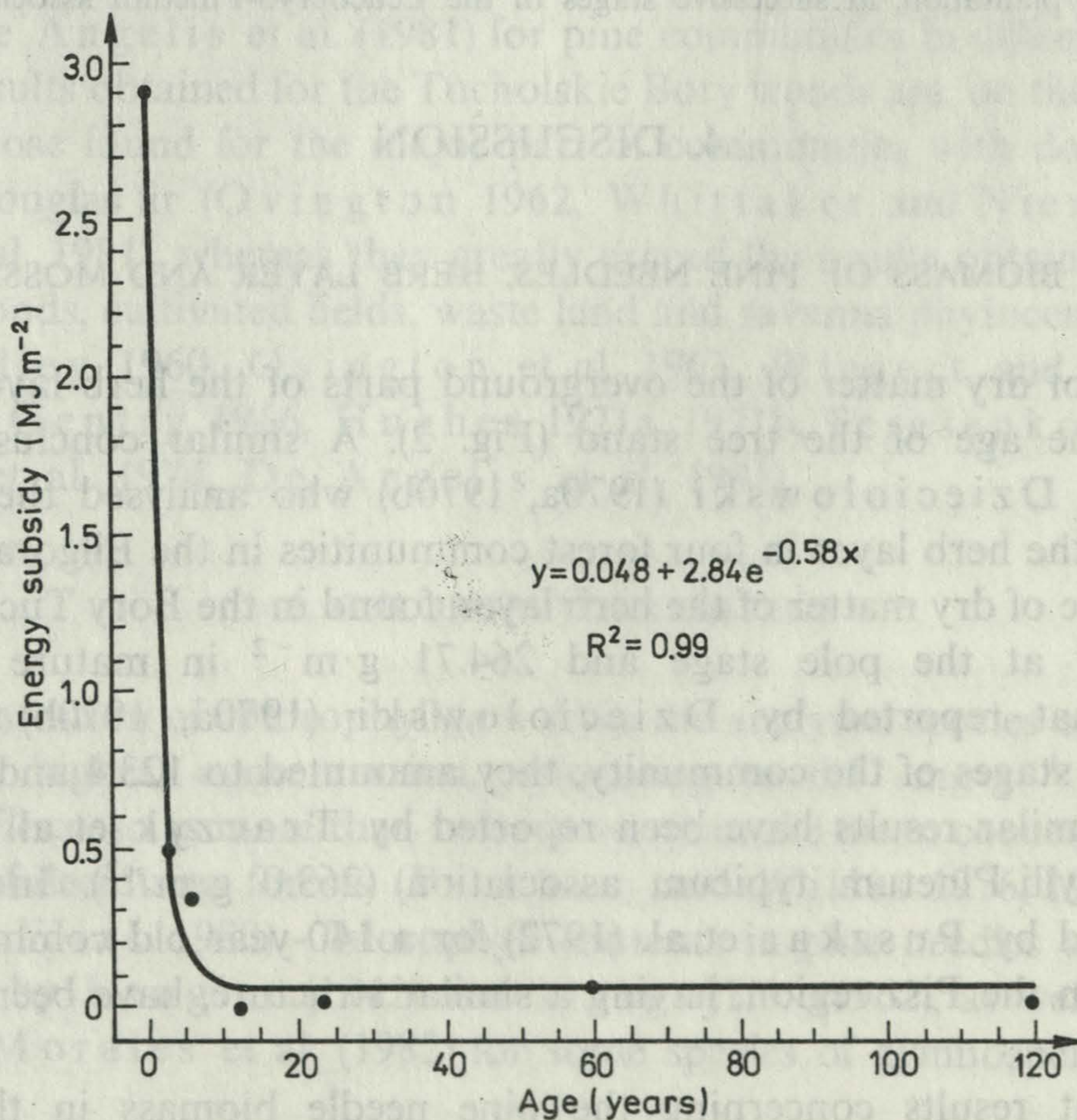


Fig. 5. Anthropogenic energy subsidy in secondary succession of the Leucobryo-Pinetum association



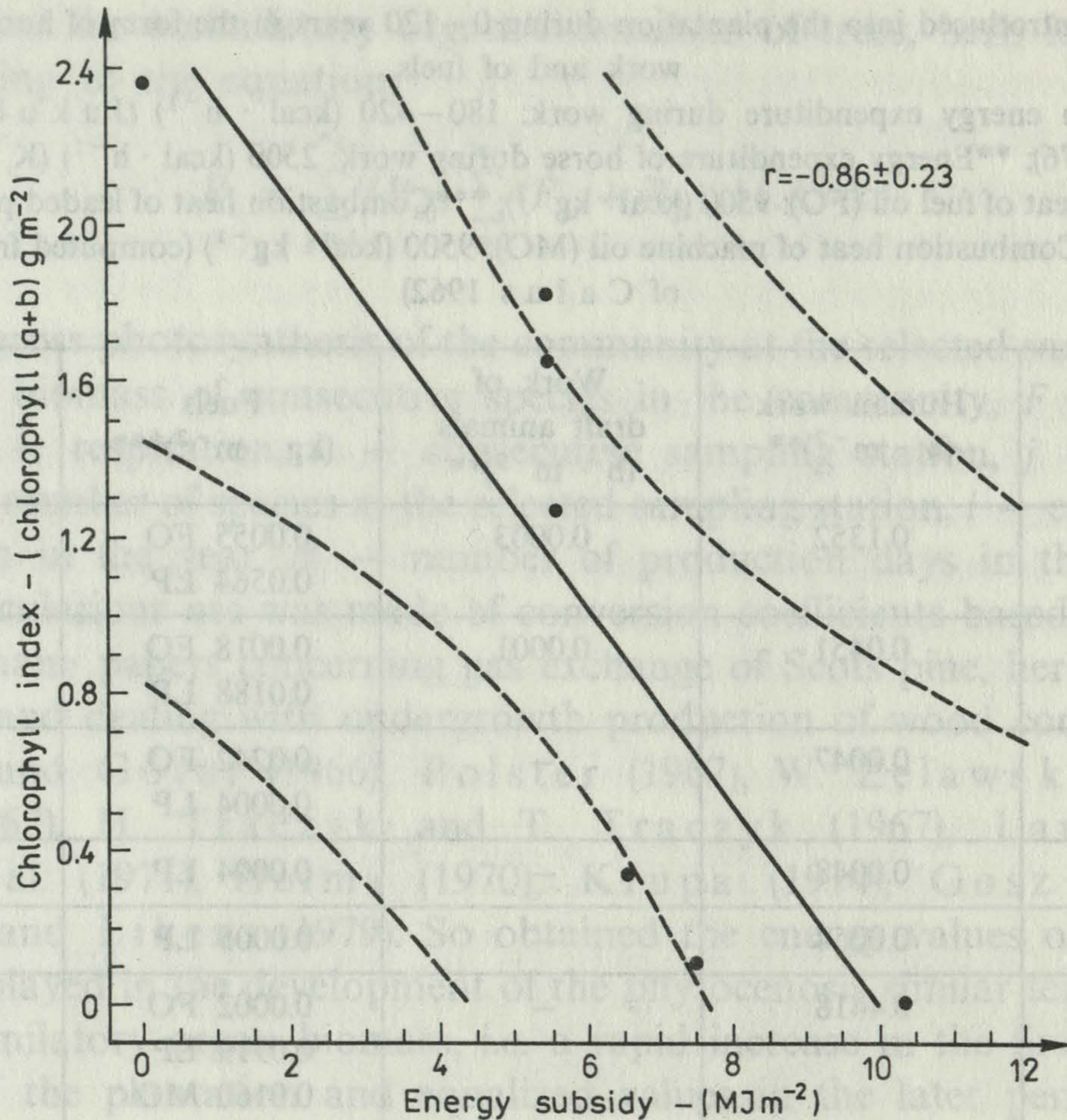


Fig. 6. Regression of chlorophyll index in dependence on energy subsidy required for further maintenance of the plantation, at successive stages of the *Leucobryo-Pinetum* association

#### 4. DISCUSSION

##### 4.1. BIOMASS OF PINE NEEDLES, HERB LAYER AND MOSSES

The value of dry matter of the overground parts of the herb layer and mosses depends on the age of the tree stand (Fig. 2). A similar conclusion has been formulated by Dzięciołowski (1970a, 1970b) who analysed the biomass and production of the herb layer in four forest communities in the Biłgorajska Równina plain. The value of dry matter of the herb layer, found in the Bory Tucholskie woods ( $127.57 \text{ g}\cdot\text{m}^{-2}$  at the pole stage and  $264.71 \text{ g}\cdot\text{m}^{-2}$  in mature forest stand) approached that reported by Dzięciołowski (1970a, 1970b) at analogous developmental stages of the community; they amounted to  $123.4$  and  $243.3 \text{ g}\cdot\text{m}^{-2}$ , respectively. Similar results have been reported by Traczyk et al. (1973) for the *Vaccinio myrtylli-Pinetum typicum* association ( $263.0 \text{ g}\cdot\text{m}^{-2}$ ). In contrast, the results obtained by Puszkar et al. (1972) for a 140-year old community of fresh pine forest from the Pisz region, having a similar structure, have been much higher ( $764.0 \text{ g}\cdot\text{m}^{-2}$ ).

The present results concerning the pine needle biomass in the developing



biocenosis approached the major part of the data reported in the literature. Values obtained for a 6-year old plantation ( $218.00 \text{ g} \cdot \text{m}^{-2}$ ) and for a 24-year old pole stage ( $526.76 \text{ g} \cdot \text{m}^{-2}$ ) were close to the results reported by Ovington (1957) for a Scots pine plantation in Great Britain; for plantations of an analogous age the latter author has obtained values of 212.0 and  $506.0 \text{ g} \cdot \text{m}^{-2}$ , respectively. Also the present data for a 120-year old plantation in the Bory Tucholskie woods resembled those reported by Tirena (1926–1927) (quoted by Żelawski 1967) from Sweden for a 105-year old monoculture. The present results remain within the range of  $470\text{--}1010 \text{ g} \cdot \text{m}^{-2}$ , reported by Ovington (1962) for plantations of different age of *Pinus densiflora*, *P. sylvestris*, *P. strobus* and *P. nigra*, from 10 sampling stations in Japan, England and Scotland. The present results also remain within the range ( $210\text{--}880 \text{ g} \cdot \text{m}^{-2}$ ) of the data obtained by Lukjanetz (1980) for young tree stands overgrowing industrial waste-dumps in the vicinity of the Ural Mountains. The quoted authors as well as Osterkov (1956) have found that the dry matter of pine needles per  $1 \text{ m}^2$  of ground surface remains — with the exception of the first 10–20 years of age of the tree stand — on a more or less constant level, with a possible tendency for a reduction of the needle litter reserve in the older tree stands.

Total biomass of pine needles, herb layer and mosses in the 6, 12, 24, and particularly in the 120-year old community (Table 1) approaches the values obtained for four pine and pine-oak forest associations from the Santa Catalina Mountains in Arizona, where the total dry matter of the assimilatory organs has been found to fluctuate between  $545\text{--}738 \text{ g} \cdot \text{m}^{-2}$  (Whittaker and Niering 1975). It also remains within the range ( $343\text{--}1160 \text{ g} \cdot \text{m}^{-2}$ ) of the results reported by Ovington (1962) and De Angelis et al. (1981) for pine communities in different parts of the world. The results obtained for the Tucholskie Bory woods are, on the average, twice lower than those found for the major part of communities with dominance of fir, spruce and Douglas fir (Ovington 1962, Whittaker and Niering 1975, De Angelis et al. 1981), whereas they greatly exceed the results obtained for oak and alder-birch woods, cultivated fields, waste land and savanna phytocenoses (Bray et al. 1959, Golley 1960, Ovington et al. 1963, Wiegert and Evans 1964, Golley and Gentry 1966, Hughes 1971a, 1971b, Terešenkova et al. 1974, Nešataev et al. 1974, De Angelis et al. 1981).

#### 4.2. CHLOROPHYLL CONTENT

The concentration of chlorophyll ( $a + b$ ) in the analysed species of the herb layer was low. The highest concentration, amounting to  $6.57 \text{ mg} \cdot \text{g}^{-1}$  dry matter in *Deschampsia flexuosa*, is more than twice lower than the mean concentration in herb layer species of deciduous forests (Packham and Willis 1976, 1977, Masarovičova and Eliaš 1980). Chlorophyll contents in pine needles approached the data reported by Langlet (1942) and Margajlik (1962), as well as the results obtained by Morales et al. (1982) for some species of gymnosperm plants from Spain.



Chlorophyll ( $a + b$ ) index obtained in the present studies for a 120-year old Leucobryo-Pinetum association ( $2.36 \text{ g}\cdot\text{m}^{-2}$ ) remained within the range of  $1.00 - 4.00 \text{ g}\cdot\text{m}^{-2}$ , reported by Aruga and Monsi (1963) for communities of terrestrial herbaceous plants. It was lower, however, than the mean chlorophyll index for the needle-leaved evergreen forests of the temperate zone, amounting to  $3.50 \text{ g}\cdot\text{m}^{-2}$  (Whittaker and Likens 1975). The *CI* index for chestnut forest ( $6.00 \text{ g}\cdot\text{m}^{-2}$  — Ford and Newbould 1971), mountain communities with fir and Douglas fir ( $5.80 - 7.00 \text{ g}\cdot\text{m}^{-2}$  — Whittaker and Niering 1975) and forest communities from the Himalayas ( $4.80 - 11.58 \text{ g}\cdot\text{m}^{-2}$  — Singh and Chaturvedi 1982) nearly twice exceeds the results obtained for the Tucholskie Bory woods. On the other hand, the data reported by Whittaker and Niering (1975) for pine and pine-oak woods ( $1.80 - 2.00 \text{ g}\cdot\text{m}^{-2}$ ) approach the present results obtained for the 24 and 120-year old plantations (Fig. 3). Likewise, the present data are close to the chlorophyll index values obtained for some communities of meadow macrophytes ( $1.00 - 2.90 \text{ g}\cdot\text{m}^{-2}$ ) (Bray 1960, Pilát 1967, Van der Valk and Bliss 1971, Boyd 1970, 1971, Boyd and Vickers 1971), and for dry deciduous forest in India ( $1.86 \text{ g}\cdot\text{m}^{-2}$ ) (Gopal and Bandhu 1972).

#### 4.3. DIMENSIONS OF THE ASSIMILATORY APPARATUS IN THE DEVELOPMENT OF THE PHYTOCENOSIS

Dimensions of the assimilatory apparatus, determined by means of total biomass of the assimilatory organs and of the chlorophyll index during succession of the Leucobryo-Pinetum association, display — after a preliminary, ca. 20-year period of rapid development — a tendency for stabilization. Similar development of the leaf area index *LAI* in succession of chestnut forest has been observed by Ford and Newbould (1971), and for eucalyptus forest — by Grove and Malajczuk (1985). Moreover, there have not been significant differences in total biomass of the assimilatory organs between an 80-year and 300-year old oak woodland ( $350.76$  and  $368.85 \text{ g}\cdot\text{m}^{-2}$ , respectively) (Nešataev et al. 1974, Terešenkova et al. 1974). Great stability of the assimilatory organ biomass in secondary succession of forest communities in the period between 30 and 150 years has been reported by Nicholson and Monk (1975), and in the succession of tropical forest — by Uhl and Jordan (1984). Covington and Aber (1980) have analysed the development of the assimilatory apparatus in secondary succession of communities according to the *LAI* index and found that — apart from the preliminary period — this index remains on a constant level and does not directly depend on age of the community; according to these authors, the value of the *LAI* index depends on the habitat conditions, and in the first place on soil nitrogen level. This relationship has been confirmed by experimental studies of Kawano and Hayashi (1977). A strong effect of nitrogen on the amount of needle biomass of pine seedlings has also been shown by Gawliński et al. (1976). Likewise, field experiments have testified to a favourable effect of multi-component mineral fertilization (N, P, K) on



an increase in pine needle biomass (Prusinkiewicz et al. 1974, Biały and Czapiewski 1980). On the other hand, Grier and Runnung (1977) have found a close correlation between the assimilatory apparatus dimensions in coniferous forests, on one hand, and the sum of precipitation and value of the water balance index.

The equilibrated values of the indices determining the assimilatory apparatus dimensions in pine monocultures of different age as well as the great similarity between the present results obtained for the Tucholskie Bory woods and the quoted data concerning different parts of the world and various types of aquatic and terrestrial phytocenoses confirm the much earlier formulated conclusions that the assimilatory apparatus dimensions of the whole phytocenosis do not depend on the structure of communities and result from the possibilities of the habitat on which the phytocenosis develops (Ellenberg 1939, Gessner 1949, Vareschi 1951).

#### 4.4. AN ANALYSIS OF ENERGY FLOW DURING SECONDARY SUCCESSION

Estimation of energy absorbed by the phytocenosis in the gross photosynthesis process, together with allogenic energy introduced by man, allowed for a more complete analysis of energy flow at the different stages of secondary succession.

The presented values of the photosynthesis, obtained by the estimation method, do not depart from the results attained by more accurate methods for communities of a similar type. The estimated amount of energy absorbed in the photosynthesis process by a 120-year old community remains within the range of the results reported by Whittaker and Likens (1975) and Boardman (1977) for needle-leaved evergreen forests of the temperate zone. The rapid increase in the amount of energy absorbed by the phytocenosis in the first years after setting up of the plantation, as well as the equalized values in the later period confirm the concept of a constant total value of primary production accompanying the succession (Peet 1981, Reiners 1988).

Total energy subsidy introduced into the plantation during the 120-year developmental period of communities was not very great, amounting to  $1.03 \cdot 10^7 \text{ J} \cdot \text{m}^{-2}$ . This result approaches those reported from North America for rapidly growing irrigated monocultures of Bank pine and poplar; in this case, during only 10 years of cultivation the subsidy has been  $1.88 \cdot 10^7$  and  $2.74 \cdot 10^7 \text{ J} \cdot \text{m}^{-2}$ , respectively (Zavitkovski 1979). Energy expenditures for maintenance of field and wood plantations in the Drwęca River catchment area have been found to average  $0.11 \cdot 10^7 \text{ J} \cdot \text{m}^{-2}$  (Barcikowski et al. 1979). Intensively cultivated agrocenoses in North America require an energy of ca.  $0.28 \cdot 10^7 \text{ J} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$  (Pimentel et al. 1973, Pimentel 1977), whereas the lawns in California call for an energy of ca.  $0.24 \cdot 10^7 \text{ J} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$  (Falk 1976).

The pine monoculture development was characterized by an inverse correlation between the amount of anthropogenic energy, on one hand, and assimilatory apparatus dimensions of the phytocenosis and the amount of energy obtained by the



phytocenosis in a natural was in the photosynthesis process. A similar relationship between the discussed parameters has been observed in natural temporal succession in a desert stream Sycamore Creek, Arizona, USA (Fisher et al. 1982). The value of natural subsidy in the form of allogenic organic matter has been found to decrease over time with a rise of the chlorophyll index value.

It seems that the described relationship between energy subsidy and assimilatory apparatus dimensions of the phytocenosis, observed during secondary succession of the Leucobryo-Pinetum association as well as in the stream Sycamore Creek, is of a general nature. This is particularly evident for anthropogenic communities. For example, the calculated average value of the leaf area index (*LAI*) for cultivated fields, meadows and woods in the temperate climate zone is as follows: cultivate fields — 3.51 (Möller 1947, Army and Greer 1967, Loomis et al. 1967, Iwaki et al. 1976, Byszewski 1977); meadows — 7.42 (Bray 1962, Medina and Lieth 1963, 1964, Geyger 1964, Redmann 1975); woods — 8.63 (Möller 1947, Kittredge 1948, Rothacher et al. 1954, Ovington 1957, Ovington and Madgwick 1959, Aruga and Monsi 1963, Kira and Shidei 1967, Satoo 1970, Art and Marks 1971, De Angelis et al. 1981).

In the total energy balance of these phytocenoses the participation of energy introduced by man is inversely correlated with the assimilatory organ dimensions. Meadows and woods, communities with a high value of the *LAI* index, do not require a high energy subsidy for maintenance, whereas into agrocenoses with a definitely lower value of *LAI* great amounts of energy are introduced (Pimentel et al. 1973, 1975, 1980, Falk 1976, Boardman 1977, Pimentel 1977).

## 5. SUMMARY

At five stages of secondary succession of the Leucobryo-Pinetum association, the assimilatory apparatus dimensions of the phytocenosis were determined. The state of green biomass and chlorophyll index (*CI*) were accepted as a measure of the assimilatory apparatus. At sampling stations in a 3, 6, 12, 24 and 120-year old monoculture of Scots pine (*Pinus sylvestris* L.) estimation was made of dry matter of pine needles, green parts of the herb layer and mosses (Table 1) as well as of chlorophyll (*a + b*) content in pine needles, dominant species of the herb layer and moss layer (Table 2). On the basis of the assimilatory organ dimensions, the amount of energy absorbed by the phytocenosis in the gross photosynthesis process was assessed (Fig. 4). Moreover, the intensity of human activities was determined by evaluating of the amount of anthropogenic energy introduced into the phytocenosis (Table 3).

Dry matter of the assimilators organs of the phytocenosis increased intensively until 24 years of the plantation's age, i.e. until the pole stage, to then attain a constant level. At the remaining stages it stayed in a dynamic equilibrium owing to a correlation between pine needle biomass and the biomass of the herb layer and mosses. A similar course in secondary succession was displayed by the chlorophyll index values (Fig. 3), with this difference that in the 120-year old plantation, as compared with the 24-year old monoculture, the rise of chlorophyll (*a + b*) was more distinct, owing to an increased chlorophyll concentration in needles of 120-year old pine.

The equilibrated values of the indices determining the assimilatory apparatus dimensions in Scots pine plantations of different age, as well as the great similarity between the present results and those reported from different parts of the world for various types of phytocenoses confirm the much earlier opinions that



the assimilatory apparatus dimensions are the result of the possibilities of the habitat on which the phytocenosis develops.

The energy values of gross photosynthesis showed during the development of the community similar tendencies as the state of assimilatory organ biomass, i.e. a rapid rise in the first years of cultivation and equalized values in the later period (Fig. 4). On the other hand, the anthropogenic energy was greatest in the initial period, at the time of minimal production. Over time, which acquiring of the properties of a natural community by the plantation, the energy subsidy dropped to zero (Fig. 5). The sum of energy introduced into the plantation during 120 years amounted to  $1.03 \cdot 10^7 \text{ J} \cdot \text{m}^{-2}$ .

## 6. POLISH SUMMARY

W pięciu stadiach sukcesji wtórnej zespołu *Leucobryo-Pinetum* określono wielkość aparatu asymilacyjnego fitocenozy. Za miarę aparatu asymilacyjnego przyjęto stan biomasy zielonej oraz wskaźnik chlorofilu (*CI*). Na wybranych stanowiskach w 3-letniej, 6-, 12-, 24- i 120-letniej monokulturze sosny zwyczajnej (*Pinus sylvestris* L.) oceniono suchą masę igieł sosny, części zielonych runa i mchów (tab. 1), ponadto zawartość chlorofilu (*a + b*) w igłach sosny, dominujących gatunkach runa i warstwy mchów (tab. 2). Na podstawie wielkości organów asymilujących oszacowano ilość energii absorbowanej przez fitocenozę w procesie fotosyntezy brutto (rys. 4). Określono również intensywność działalności ludzkiej na podstawie oceny ilości energii antropogenicznej wprowadzonej do fitocenozy (tab. 3).

Sucha masa organów asymilujących fitocenozy wzrastała intensywnie do 24 lat, tj. do fazy tyczkowiny, osiągając stały poziom. W pozostałych stadiach utrzymywała się w dynamicznej równowadze, dzięki współzależności pomiędzy masą igieł sosny a masą runa i mchów. Podobny przebieg w sukcesji wtórnej wykazały wartości wskaźnika chlorofilu (rys. 3), z tą różnicą, że w uprawie 120-letniej zaznaczył się wyraźniejszy przyrost chlorofilu (*a + b*) w stosunku do 24-letniej monokultury, co wynikało ze zwiększonej koncentracji chlorofilu w igłach sosny 120-letniej.

Zrównoważone wartości wskaźników określających wielkość aparatu asymilującego w różnowiekowych uprawach sosny zwyczajnej oraz duże podobieństwo uzyskanych wyników do rezultatów podawanych z różnych części świata dla różnych typów fitocenoz potwierdzają znacznie wcześniejsze opinie, że wielkość aparatu asymilującego jest rezultatem możliwości siedliskowych, w jakich rozwija się fitocenoza.

Energetyczne wartości fotosyntezy brutto wykazały w rozwoju zbiorowiska podobne tendencje jak stan biomasy organów asymilujących, szybki wzrost w pierwszych latach uprawy i wyrównane wartości w okresie późniejszym (rys. 4). Natomiast energia wprowadzona przez człowieka była największa w okresie początkowym przy minimalnej produkcji. Z upływem czasu, w miarę nabywania przez uprawę cech zbiorowiska naturalnego, subwencja malała do zera (rys. 5). Suma energii wprowadzona do uprawy w ciągu 120 lat wynosiła  $1,03 \cdot 10^7 \text{ J} \cdot \text{m}^{-2}$ .

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