POLISH JOURNAL OF ECOLOGY (Pol. J. Ecol.)	46	1	75–88	1998

Karol J. KRAM

Department of Plant Ecology, Institute of Ecology, Polish Academy of Sciences, Dziekanów Leśny, 05–092 Łomianki, Poland

INFLUENCE OF SPECIES COMPOSITION AND FOREST AGE ON LEAF AREA INDEX*

ABSTRACT: Investigations of leaf area index (LAI) were performed in forest stands of pine, beech as well as birch, alder, spruce, larch and oak using the LAI-2000 Plant Canopy Analyser made by American corporation LI-COR. Canopy LAI has been found to differ considerably depending on both dominant tree species and stand age. From among the species examined spruce exhibited the highest LAI amounting to 10.0 m^2 m^{-2}, where other species had much lower LAI-s (within a range 1.6–6.3 m^2 m^{-2}). Canopy LAI increased rapidly in young stands attained a peak at approximately age 20 and decreased slowly thereafter. It has been revealed that projected leaf area of an individual tree increases linearly as the tree grows older.

KEY WORDS: leaf area index (LAI), LAI-2000 Plant Canopy Analyzer, pine, beech, forest stand age.

1. INTRODUCTION

According to the original Watsons definition, leaf area index (LAI) is the ratio of one-sided (projected) foliage area to surface area of ground (Watson 1947).

Since photosynthesis, transpiration, respiration and light interception are processes directly associated with foliage area, accurate leaf area measurements are critical for estimating fluxes of solar energy, carbon and water through forest ecosystems (Pierce and Running 1988). Moreover, foliage area plays an important role in capturing aerosols from the atmosphere (Hanson et al. 1989, Hanson et al. 1992). Numerous ecological studies have pointed out leaf area index to be a good measure of productivity (Satoo 1970, Gholz 1982, Waring and Schlesinger 1985). Several

*This work was MSc. thesis at warsaw Agricultural University.

recent reports have identified the LAI as the single most important variable for characterizing vegetation energy and mass exchange for global scale research (Wittwer and Botkin, after Pierce and Running 1988).

Unfortunately, there is still little forest research on leaf area index, and those published have mainly been performed in North America so they refer to American tree species (e.g. Woods et al. 1991, Smith 1993, Deblonde et al. 1994).

The objective of this work was to assess the leaf area index for native tree species (mainly pine and beech) and to demonstrate LAI changes with stand age.

2. STUDY AREA, MATERIAL, METHODS

The studies were carried out in a forest complex in north-western Poland (Człuchów Forest) (53°53'–54°00' N and 17°05'–17°17' E), in 1996.

Investigations were performed in 34 forest stands, including:

– 13 even-aged stands of Scots pine – *Pinus sylvestris* (from 6 to 100 years);

– 8 even-aged stands of European beech – *Fagus sylvatica* (from 16 to 120 years); two of the stands were thinned between first and second measurement date;

– 6 stands of white birch – *Betula pendula* (2 stands were 7-year-old, while 4 ones – 45-year-old – the latter ones were birch clusters surrounded by pine forests);

– 3 stands of black alder – *Alnus glutinosa* (15-, 45- and 80-year-old);

– 2 stands of Norway spruce – *Picea abies* (20- and 40-year-old);

– 1 stand of European larch – *Larix decidua* (59-year-old);

– 1 stand of common oak – *Quercus robur* (105-year-old mixed deciduous forest with oak as a dominant species).

The following three dates were chosen for making measurements:

1st – in spring prior to bud sprouting – 28–29 March and 24–25 April,

2nd – after leaf development – 19–21 June,

3rd – at assumed leaf area maximum – after the leaves were fully developed, and before autumnal leaf fall – 10–17 August.

Investigations of leaf area index were performed using the LAI-2000 Plant Canopy Analyzer (referred to as LAI-2000) made by American Corporation LI-COR, the device having been accepted as the most accurate and fastest from among instruments designed for similar purposes (Zawiła-Niedźwiecki et al. 1993).

The device contains an optical sensor with "fisheye" lens projecting the image of hemispheric view onto detector arranged in five concentric rings. The data are then transferred to the control unit where, soon after readings display, the internal microcomputer calculates, among others leaf area index and its standard deviation. The calculations are made on the basis of several pairs of readings. Each pair consists of one measurement of brightness of the open sky and the reading made inside a stand beneath the plant canopy. Majority of the data in this work have been obtained from six pairs (one above- and six below-canopy readings) or more readings when some of observations were clearly incorrect.

Although measurements could practically be made anytime regardless of weather conditions, it is recommended to work when the sky is covered by an uniform layer of clouds (LI-COR 1990). To avoid an influence of direct sunlight, an additional procedure is suggested, namely making measurements just before sunrise or just after sunset (LI-COR 1989, LI-COR 1990). It is also important to place the sensor in such a way as to gather data from a given stand only, but not from neighbouring stands or open areas. This is of particular importance when the measurements are to be made in small-sized or young (short) stands adjacent to old (tall) ones. In the study region, all the stands investigated, except pine and beech forests, were relatively small in area. In order to cope with this problem, a set of view caps is provided limiting the sensors field of view. As the small-sized plots predominated, the cap reducing field of view to 1/4 (90°) have been used every time. The readings were then made from the edge or even corner of a forest looking into the stand. Such a procedure allows to cut considerably the minimum plot size required.

Another difficulty may occur when leaf area index is to assess in man-established plantations prior to canopy closure. To overcome possible errors resulting from row spacing of the trees, the measurements were made systematically along two diagonal transects instead of random distribution of readings (Fig. 1). Stand densities were determined as mean numbers of trees on two or three (in more heterogeneous stands) sample plots. The plots had different areas depending on stand density and ranged from 4 m^2 in young beech stands to 200 m^2 in the old-growth stands.

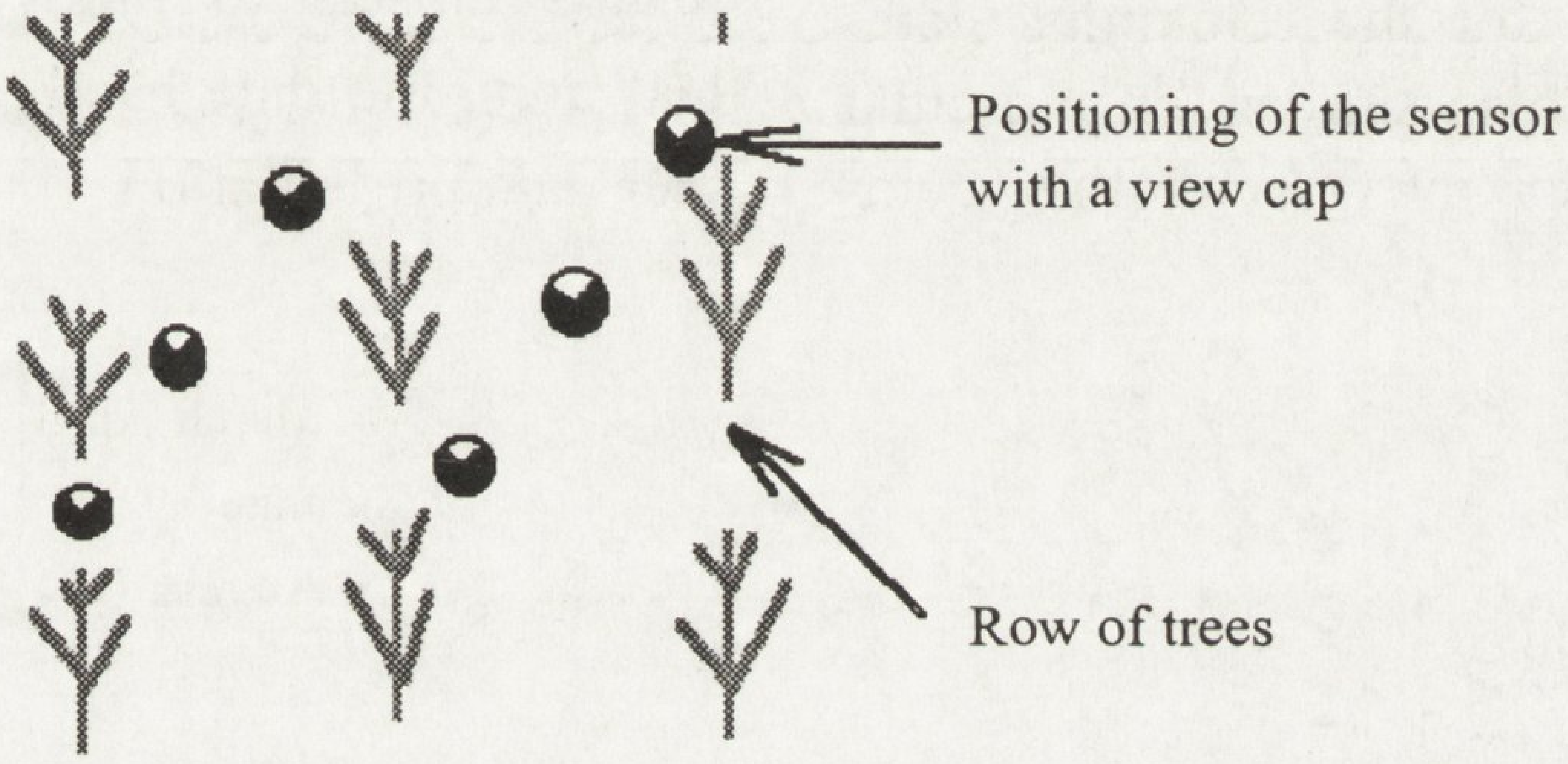

Fig. 1 Technique of making measurements in young stands with LI-COR LAI-2000 before canopy closure

G o w e r and N o r m a n (1991) found that LAI-2000 Analyzer has underestimated leaf area index by approximately 35–40% in conifer canopies due to non-random needle positioning. They also proposed a correction factor calculated for particular tree species. By multiplying the factor by the value of leaf area index predicted by LAI-2000, the error in LAI estimate is being minimalized (G o w e r and N o r m a n 1991). In this work, the conversion factor for conifers examined was assumed to be 1.60 for Norway spruce, 1.49 for European larch and 1.50 for Scots pine (the last value having been estimated by Gower and Norman for akin species, i.e. red pine).

Stand age was given according to forest management plans. Calculations of curvilinear regression coefficients were made using a software Statistica for Windows, Release 4.0.

3. RESULTS

The values of leaf area index (LAI) obtained for evergreen and deciduous species in spring (first date) are not comparable as the former have leaves (needles), whereas the latter ones are leafless in that period. In contrast, not only are the LAI values for the remaining dates comparable but also similar for particular tree species (for evergreens this comprises all the three dates) – this is exemplified by LAI-s for pine (Fig. 2). For this reason, the data from only one date will be presented below. Assuming the third measurement date (August) as producing results closest to the yearly maximum leaf area, the date has been used for further data presentation.

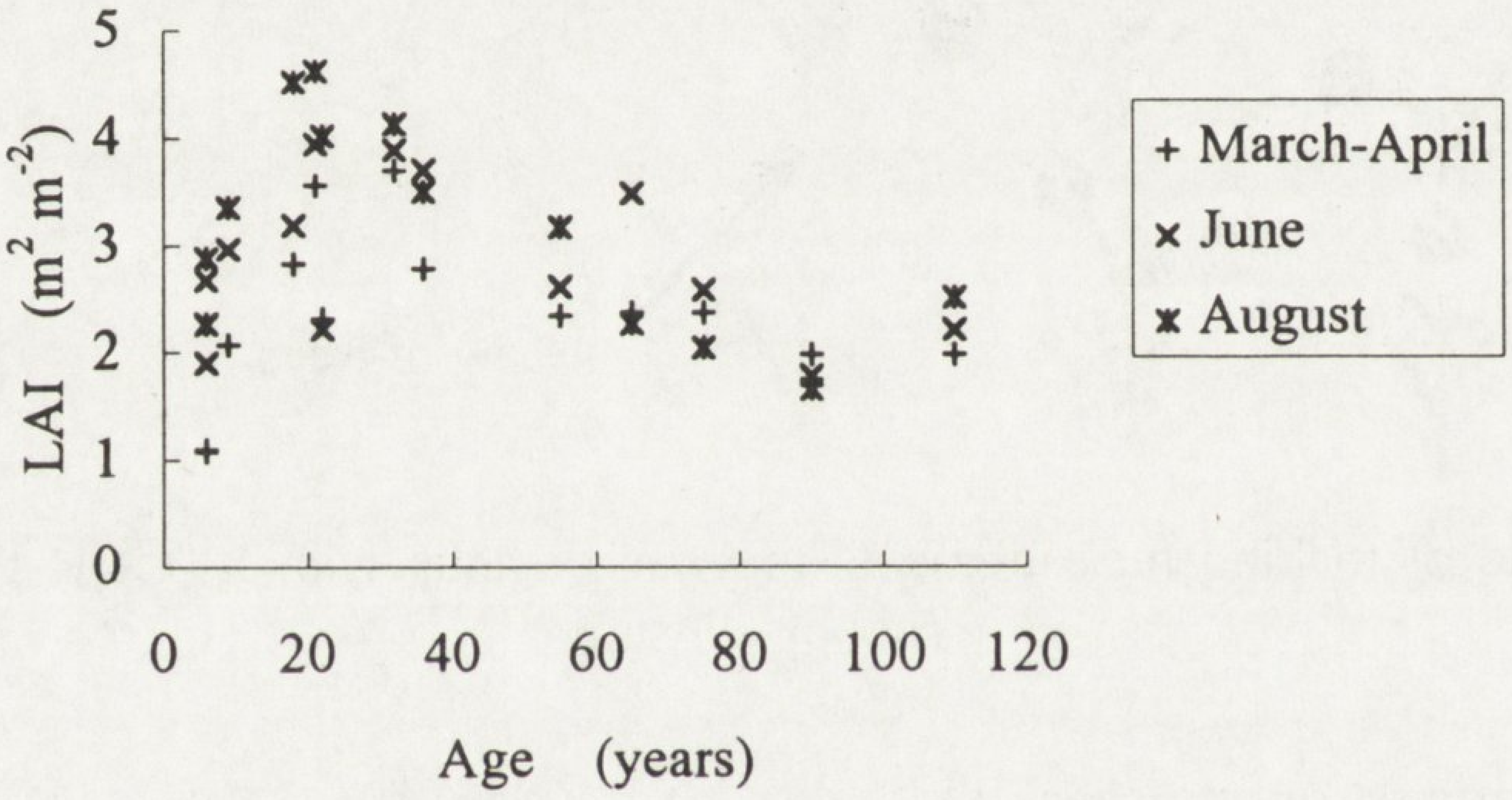

Fig. 2 A comparison of leaf area index (LAI) among pine stands of different age and among different dates of measurements

3.1. Scots pine

Scots pine is the most important species due to both its crucial importance to Polish forestry and common occurrence in the region of the studies. This is why the results obtained for that species are most comprehensive and reliable.

As expected, canopy leaf area (LAI) of pine was well correlated with stand age (r^2 = 0.826). The LAI rapidly increased in young stands up to a maximum at approximately age 20, and then begun to decrease slowly (Fig. 3).

Canopy LAI is the resultant of leaf area of an average individual tree and tree number in a stand. Therefore, changes in both LAI of an individual tree and stand density have been investigated over time. A simple linear relationship between leaf area of an individual tree and stand age has been found, with LAI increasing as the tree grows older (Fig. 4). Contrary to this, stand density dropped initially, and then tended to equilibrate (Fig. 4). Both relationships appeared to be highly significant ($p < 0.001$; at r^2 equal to 0.887 and 0.763, respectively).

The relationships described suggested that the phenomenon of decreasing leaf area index in mature pine stands did not result from limited leaf area of individual trees since the picture obtained was very clear: the older the tree, the larger its leaf area. Thus, the decline in leaf area index should rather be suspected to result from the substantial drop in tree number with stand age. To verify the above statement, stand LAI values were related to stand densities. Youngest stands (6- and 9-year-old), i.e. those with open canopies, were ignored in calcula-

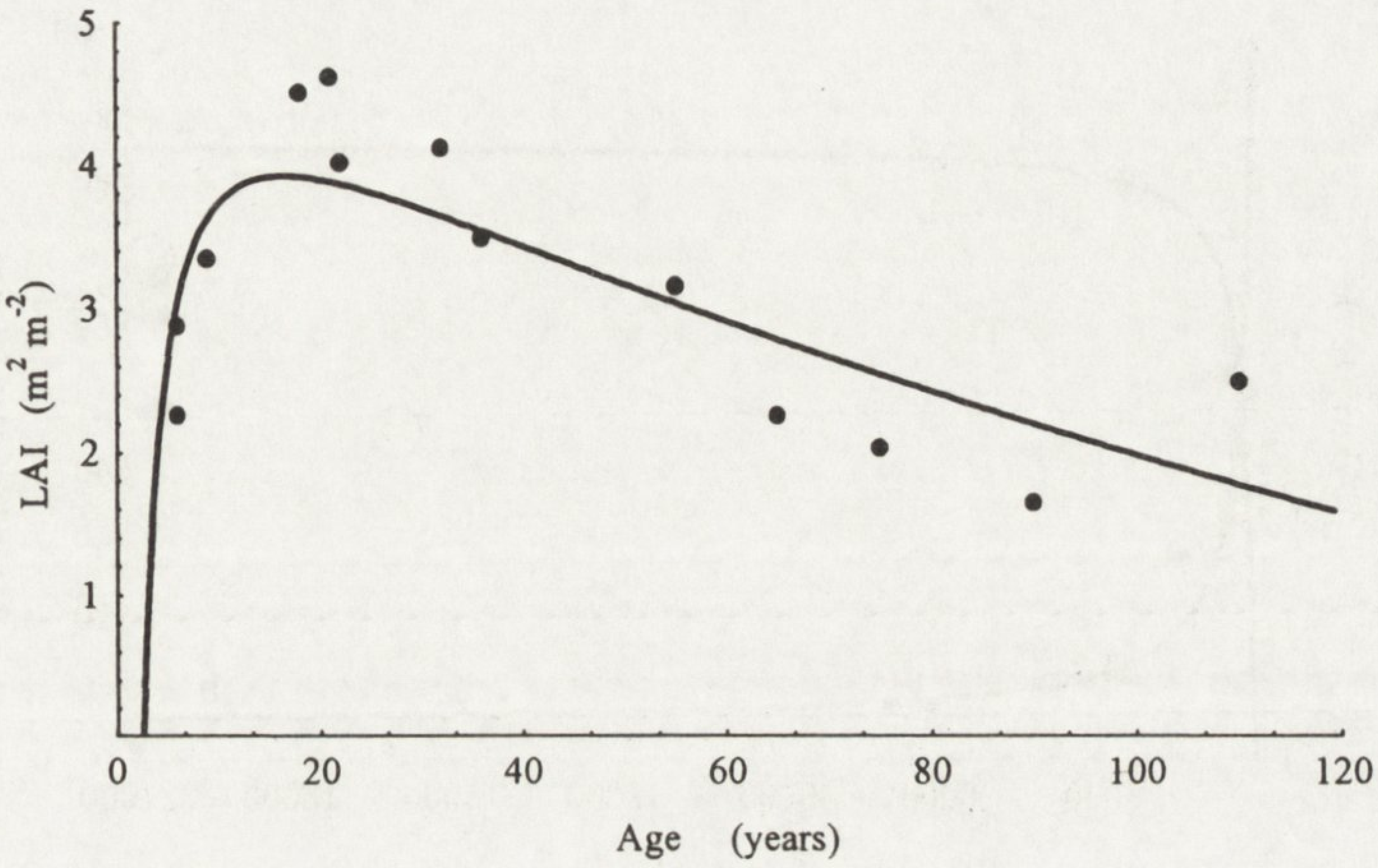

Fig. 3 The relationship between leaf area index (LAI) and stand age in Scots pine stands (August) (r^2 = 0.826, n = 13, p < 0.001)

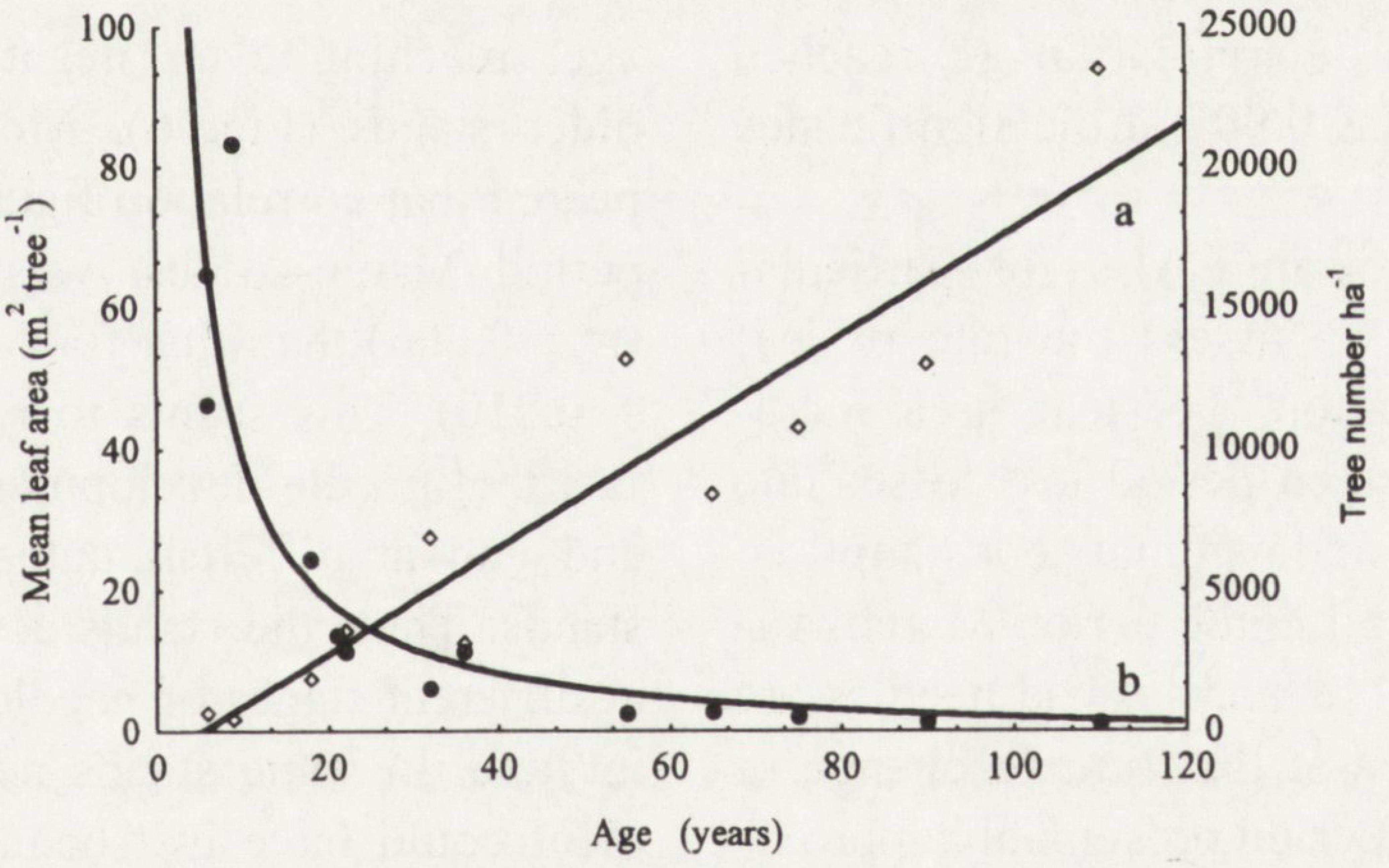

Fig. 4 The relationship between age of a pine stand and a) leaf area of an individual tree (◊; r^2 = 0.887, n = 13, p < 0.001), and b) stand density (• ; r^2 = 0.763, n = 13, p < 0.001) (August)

tions due to the fact that LAI of such stands depends on tree spacing rather (being recognized by the LAI-2000 as gaps) than canopy densities. LAI has been found to increase, at first rapidly, and then, as stand density increased, more gradually (p < 0.001) (Fig. 5). Thereby, sparse stands had much lowered LAI values than those having higher stand densities. Thus, forests do not neccessarily maintain stable leaf area over a wide range of stand densities. This result does not confirm the common observation that LAI is independent of stand density (e.g. M o h l e r et al. 1978, P e a r s o n et al. 1984).

The analysis presented points out that leaf area of an individual tree and stand density act simultaneously, provided that leaf area predominates in younger stands (increase in LAI with age), whereas stand density becomes more important when a stand reaches about 20 years (decrease in LAI). It is interesting that the two factors are closely interrelated. Leaf area of an individual tree dropped rapidly at low densities, but then a slight decrease took place (Fig. 5).

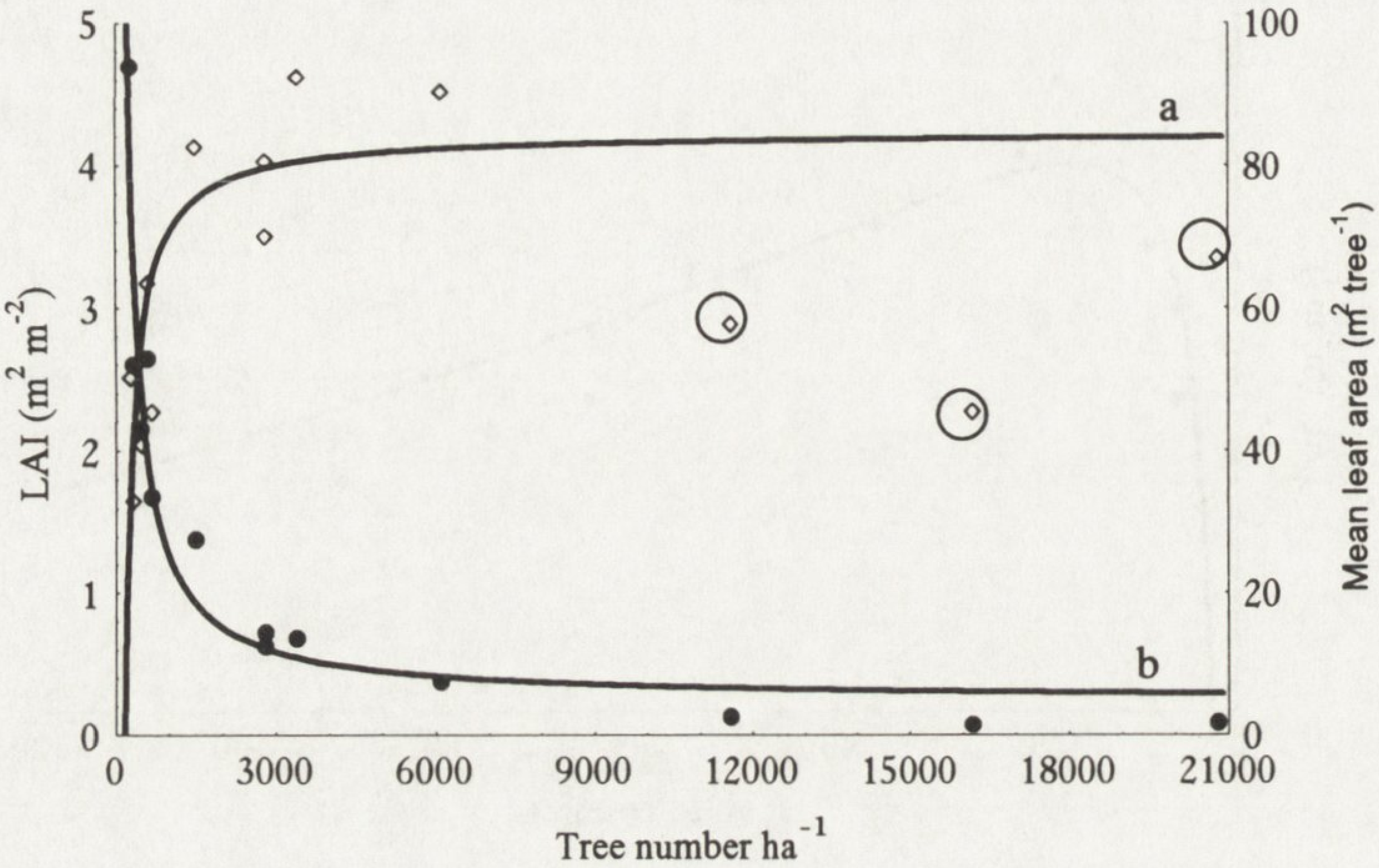

Fig. 5 The relationship between stand density of pine stands and a) leaf area index of the stand (◊; $r^2 = 0.693$, $n = 10$, $p < 0.001$), and b) leaf area of an individual tree (•; $r^2 = 0.907$, $n = 13$, $p < 0.001$) (August).

Coefficient of determination (r^2) reached here as much as 0.907 at the significance level $p < 0.001$.

Differences in LAI-s for particular dates enabled to assess the rate of leaf area accumulation, i.e. leaf area increment over a given period less losses due to leaf fall and animal consumption. Since needle fall in the period March-August is negligible, and instead needles are being produced at that time, a change in LAI over that period presumably approximates yearly needle production. It has been revealed that needle accumulation (production) tends to decrease with stand age, reaching even negative values in older stands (Fig. 6). Moreover, it appeared that correlation figured out for the period March-August was much higher ($r^2 = 0.606$) than that for March–June ($r^2 = 0.210$). This seems to result from the fact that needle development could begin and end at different dates in particular stands. Thus, the stands could have been at different stages of needle development in June. In some stands needle development could have just begun, whereas in others it could have already been completed. In August, needle development was most likely to be completed in all the

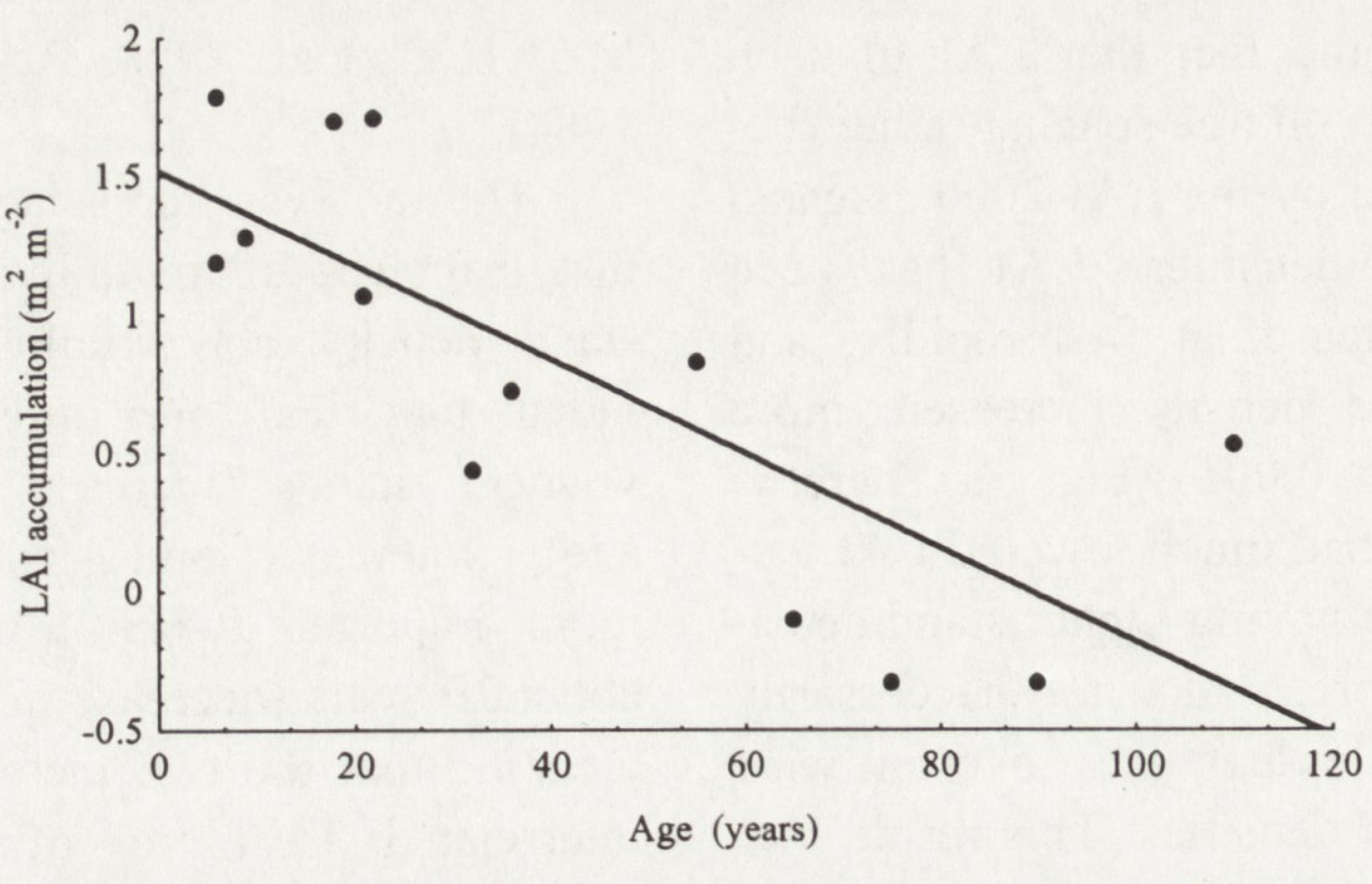

Fig. 6 The relationship between leaf area accumulation over the period March-August and stand age in Scots pine ($r^2 = 0.606$, $n = 13$, $p < 0.001$)

stands. Thus, the results obtained for that period might be more illustrative for the process considered. As the trees do not produce needles during the period Au gust–March, and needle fall, though most intensive in autumn, lasts throughout the year, annual needle accumulation is certainly lower than that figured out for the period March–August.

3.2. European beech

Beech was second most common species in the study area occurring over a wide range of stand ages and thereby investigated in detail. There are large differences between beech and pine regarding biology (leaf presence in winter) as well as silvicultural practice (pine – artificial regeneration, beech – natural regeneration). In order to find how the above differences influence leaf area of beech stands, an analogical procedure as in the case of pine has been applied.

Since beech is leafless during winter, the results for the first date served only as a basis for calculating leaf production. Interpretation of the results obtained for beech stands was complicated since thinning had been performed in two stands between 1st and 2nd measurement date. The results derived from the thinned stands differed from those for the remaining ones (LAI-s nearly two times lower) (Fig. 7).

As in the case of pine, the main relationship examined was that between leaf area index and stand age. Since the youngest beech stands were 16-year-old, only the phase of LAI decrease with age could be observed (Fig. 7). However, when extrapolating LAI values toward zero for hyphotetical zero stand age, leaf area may be expected to increase rapidly up to a maximum. If so, the relationship would resemble that found for pine. However, limited number of data gathered makes it impossible to ascertain when exactly beech stands attain their LAI maxima (although this is presumably about 20 years as in pine forests or less). Since beech is a deciduous species, it produces its foliage during the growing season and, moreover, leaf fall over the spring – summer period is almost negligible, accumulation of leaf area in beech is practically equal to annual leaf area production.

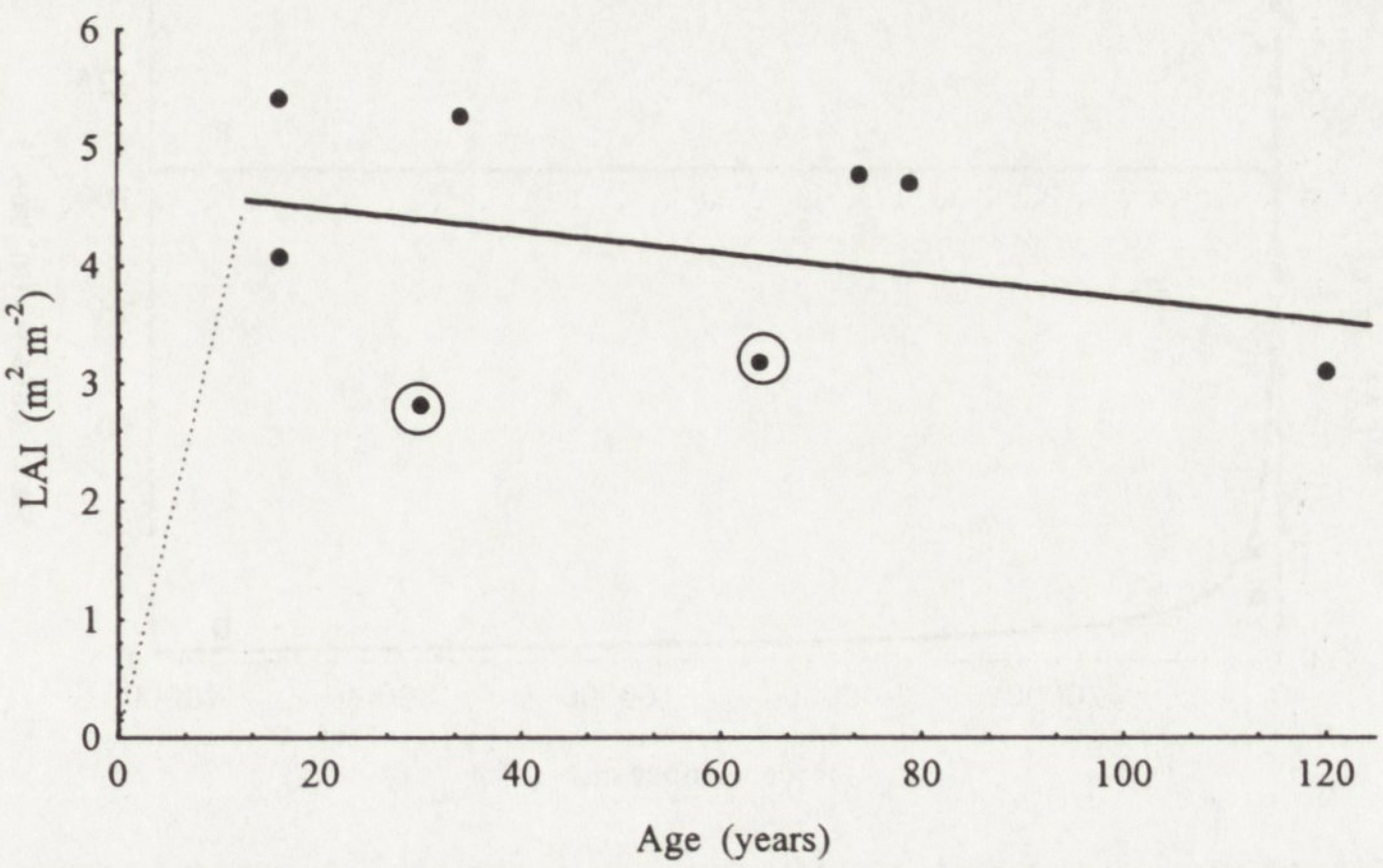

Fig. 7 The relationship between leaf area index (LAI) and stand age in European beech (August) ($r^2 = 0.656$, $n = 10$, $p < 0.02$). Dotted line indicates possible tendency in LAI in young stands. Encircled points denotes stands thinned in the year of the studies

Leaf area of an individual beech tree increased linearly with tree age (Fig. 8), provided that the relationship was slightly less significant than for pine, this being presumably an effect of beech stand thinning. The relationship between the number of beech trees per hectare and stand age also resembles that for pine stands, provided that stand density decline with age is even sharper (Fig. 8).

The relationships described hitherto point out that the pattern of changes in leaf area is almost the same for beech and pine. There are, however, differences between the two species regarding the relationship between canopy LAI and stand density. Contrary to pine, where the two factors were closely interrelated, beech forests did not exhibit any significant correlation. Canopy LAI was maintained at the level about 4.2 m^2 m^{-2} regardless of stand density ($p > 0.1$) (Fig. 9). This would confirm that LAI hardly depends on stand density (e.g. Mohler et al. 1978, Pearson et al. 1984). Beech is likely to have a greater capability of lateral growth of branches and hence to colonize gaps in the canopies more effec-

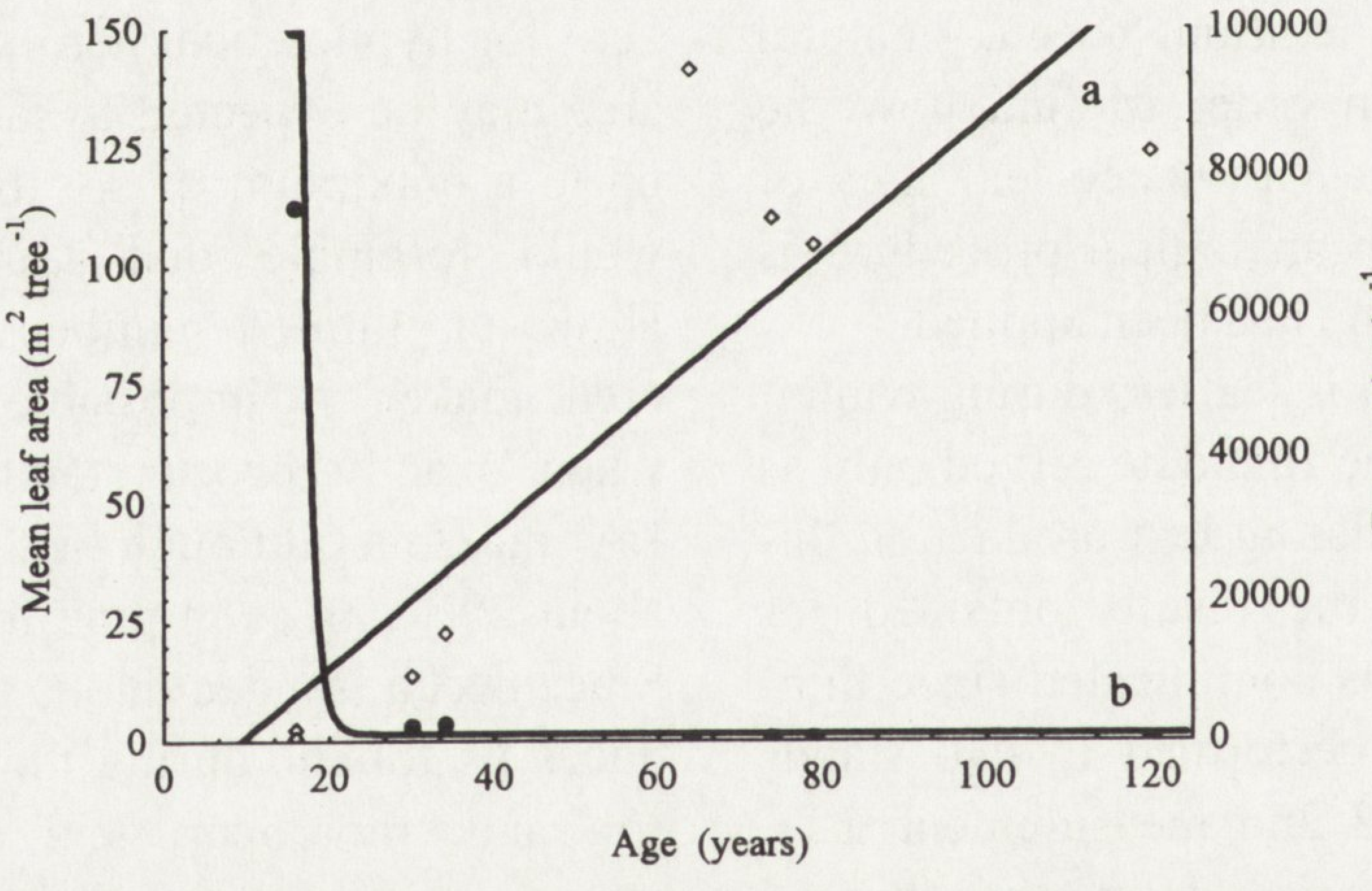

Fig. 8 The relationship between age of a beech stand and a) leaf area of an individual tree (◊; $r^2 = 0.764$, $n = 10$, $p < 0.01$), and b) stand density (•; $r^2 = 0.973$, $n = 10$, $p < 0.001$) (August)

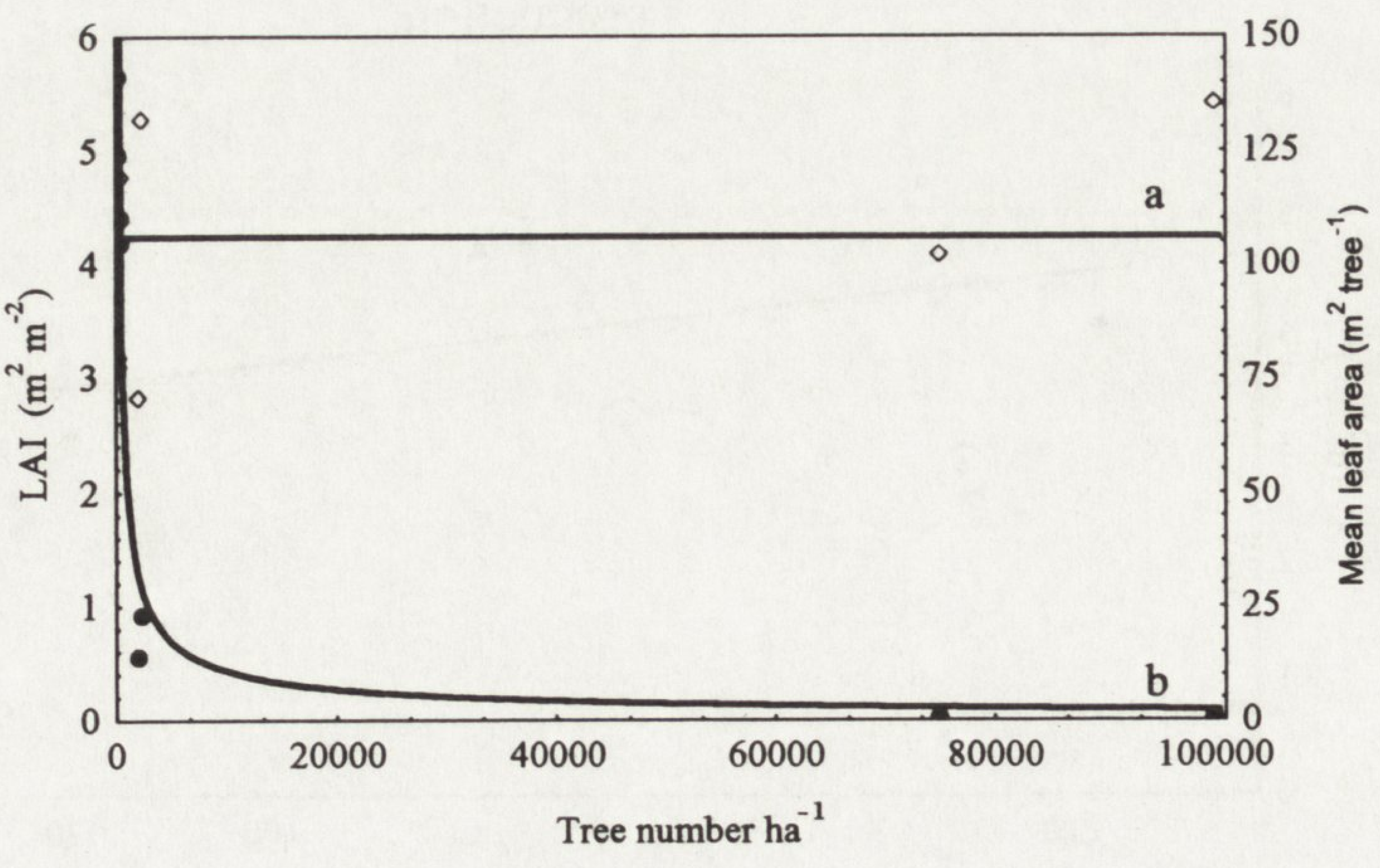

Fig. 9 The relationship between stand density of beech stands and a) leaf area index of the stand (◊; $r^2 = 0.173$, $n = 10$, $p > 0.1$), and b) leaf area of an individual tree (•; $r^2 = 0.960$, $n = 10$, $p < 0.001$) (August).

tively than pine. On the other hand, the number of beech stands examined seem to be insufficient to draw any definite conclusion.

Leaf area of an individual beech tree was closely related to tree number (r^2 = 0.960). The curve fitted to the relationship resembles that reckoned for pine, but transition between the decrease and equilibrium phase is sharper (Fig. 9). The relationship was highly significant for beech as well as for pine.

3.3. Other species

One of the objectives of this work was to find whether canopy leaf area depends on tree species. Among the species examined (pine, beech, birch, alder, spruce, larch and oak) the highest LAI-s were characteristic of spruce stands (maximum 10.0 m^2 m^{-2}). Next species carrying the largest canopy leaf area were beech and larch, with LAI values smaller than that of spruce by as much as 3–4 m^2 m^{-2}. Generally, LAI values of species other than spruce varied over a fairly wide range 1.6–6.3 m^2 m^{-2}. It should be noticed, however, that between-species variability seemed to be lower than that resulting from age differences of the stands examined. Among the species considered, beech and larch had slightly larger LAI-s, whereas birch – slightly smaller ones though LAI ranges for the above species overlapped (Table 1).

The relationship between leaf area index and stand age described formerly for pine and beech was also assessed for all the stands examined regardless of dominant tree species. Generally, canopy LAI of young stands increases, peaks at

Table 1. Variability in leaf area (LAI) of particular tree species

Species	Number of stands	LAI[a] (m^2 m^{-2})	LAI[b] range (m^2 m^{-2})
Spruce	2	7.75	5.71–9.97
Larch	1	4.93	4.63–5.22
Beech	8	4.20	2.64–6.26
Pine	13	3.01	1.65–4.62
Oak	1	2.99	2.82–3.16
Alder	3	2.93	2.60–3.32
Birch	6	2.37	1.63–3.47

[a] calculated as the mean LAI for all stands of a given species for 2nd and 3rd measurement date (June and August)
[b] minimum and maximum LAI at 2nd and 3rd measurement date.

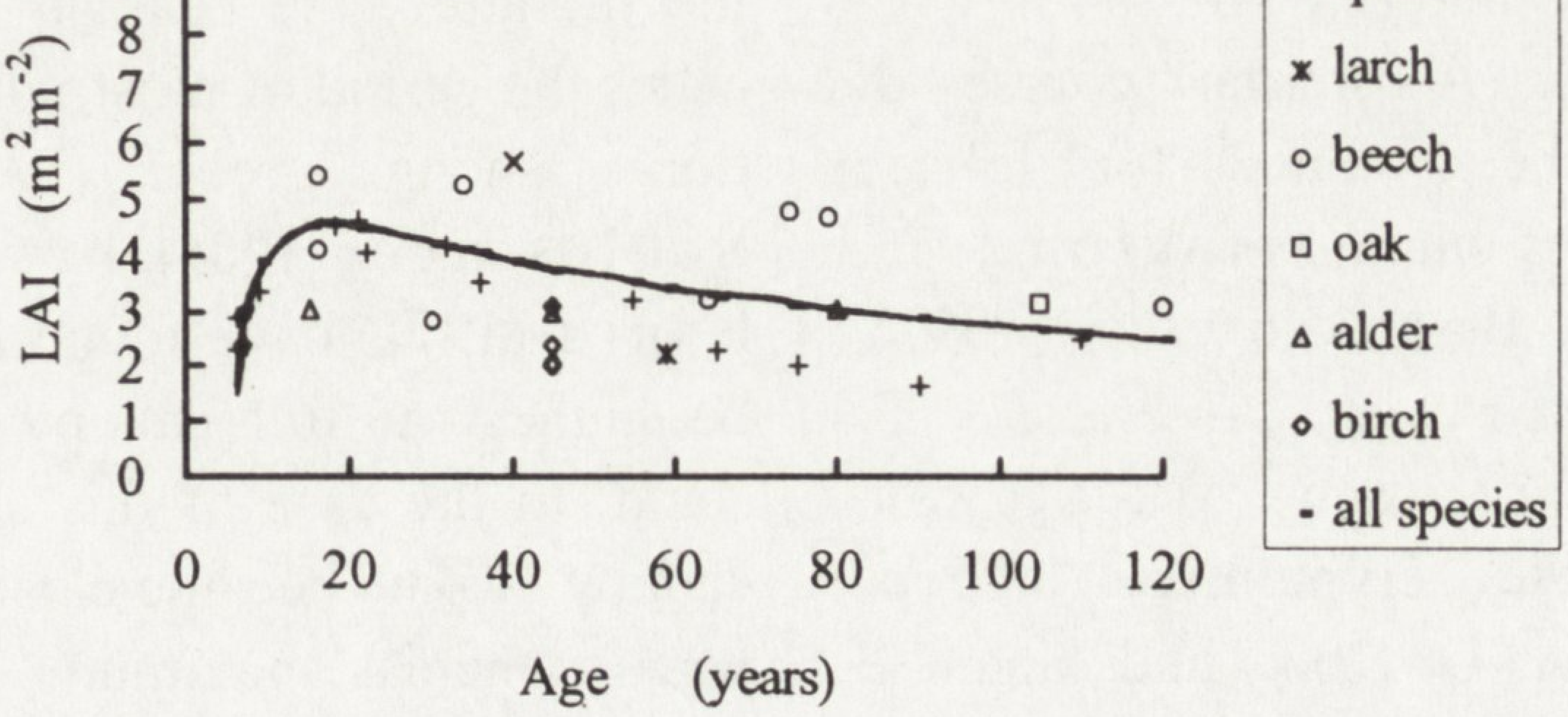

Fig. 10 A general pattern of leaf area index (LAI) dynamics derived from all the stands investigated (August) (r^2 = 0.182, n = 34, $p < 0.01$).

approximately age 20, and then decreases slowly (Fig. 10). Despite much differences in LAI among particular tree species, the relationship turned out to be significant ($p < 0.01$).

It is difficult to say something more about leaf area dynamics in spruce, larch, birch, alder or oak when considered separately, this being a result of an insufficient number of stands in the study area. Nevertheless, even so limited data allow to confirm that leaf area of an individual tree tends to increase, while stand density – to decrease with age (Table 2).

There were large differences in leaf area of an individual tree among particular tree species. The highest values were found for beech (141 m^2), and slightly lower – for oak (105 m^2) and pine (93 m^2). Alder had still lower LAI (50 m^2). Similar LAI-s were estimated for spruce and larch, whereas birch appeared to have the smallest LAI. However, as stands of the three latter species were relatively young, they could not be directly compared with the former ones.

Table 2. Stand age, density and leaf area of an average individual tree of particular tree species (except pine and beech)

Species	Age (years)	Tree number per (ha)	LAI per tree (m^2)
Alder	15	8900	3.4
	45	2500	11.9
	80	600	50.2
Spruce	20	6800	13.5
	40	1100	51.9
Larch	59	1100	47.4
Birch	7[a]	5000	5.29
	45[b]	1219	22.4
Oak	105	300	105.3

[a] means from 2 stands
[b] means from 4 stands

Table 3 presents LAI estimates given by various authors. LAI values obtained in this work correspond fairly well with those presented in Table 3. Possible differences may result from many reasons, e.g. methods applied, stand ages, site properties.

4. DISCUSSION

A pattern of leaf area index dynamics similar to that found for pine and beech in this work has previously been shown for chestnut (Ford and Newbould 1971). A similar course of changes has been found for foliage biomass of Scots pine (Ovington 1957, Miller 1986, Barcikowski 1991), eucalyptus (*Eucalyptus diversicolor* F. Muell.) (Grove and Malajczuk 1985), Japanese cryptomeria (*Cryptomeria japonica* D. Don.) and Japanese red pine (*Pinus densiflora* Sieb. and Zucc.) (Kira, after Kira and Kumara 1983). A stand may approach its LAI maximum at various age depending on species and environmental conditions (Kozlowski et al. 1991). According to the literature, the peak in LAI just precedes the period of most intense competition among trees (Waring and Schlesinger 1985). Ford and Newbould (1971) have found LAI values to be highest at full canopy closure of a stand. In the case of this study, the tree canopy of pine became closed at about 10 years, whereas maximum leaf area was attained at approximately age 20, which suggests possible leaf area increment associated with crown growth in height.

Table 3. LAI estimates by different authors

Species	LAI (m^2/m^2)	Location	Estimation method	Reference
Pinus sylvestris	1.65–4.61	Poland	LAI-2000	this study
Pinus ponderosa	1.7–3.3	Montana, USA	Sunfleck Ceptometer	Pierce, Running 1988
Pinus contorta	4.0	Montana, USA	Sunfleck Ceptometer	Pierce,Running 1988
	2.24–4,92	Utah, USA	from sapwood area	Jack, Long 1991
Pinus taeda	3–4	Tennessee, USA	?	Lindberg et al. 1990
"	2.7	N. C., USA	Decagon Instruments	Ellsworth et al. 1995
"	1.7	N. C., USA	from changes in CO_2 concentration	Ellsworth et al. 1995
Pinus banksiana	1.5–2.2	Ontario, Canada	LAI-2000	Deblonde et al. 1994
Pinus resinosa	2.9–6.2	Ontario, Canada	LAI-2000	Deblonde et al. 1994
"	6.4	Wisconsin, USA	LAI-2000	Gower, Norman 1991
Pinus strobus	7.1	Wisconsin, USA	LAI-2000	Gower, Norman 1991
Picea abies	5.71–9.97	Poland	LAI-2000	this study
"	10.4	Wisconsin, USA	LAI-2000	Gower, Norman 1991
"	8–10	Germany (RFN)	?	Lindberg et al. 1990
Picea engelmannii	4.1	Montana, USA	Sunfleck Ceptometer	Pierce, Running 1988
Picea mariana	0.48–4.26	Minnesota, USA	different	Woods et al. 1991
Abies lasiocarpa	5.02–14.16	Utah, USA	from sapwood area	Jack, Long 1991
Abies grandis	5.3	Montana, USA	Sunfleck Ceptometer	Pierce, Running 1988
Pseudotsuga menziesii	1.4–8.4	British Columbia, Canada	DIAS II Analyzer	Smith 1993
"	6.6–16.2	Oregon,USA	different methods [a]	Marshall, Waring 1986
Larix decidua	4.63–5.22	Poland	LAI-2000	this study
"	5.1	Wisconsin, USA	LAI-2000	Gower, Norman 1991
Fagus sylvatica	2.65–6.25	Poland	LAI-2000	this study
Alnus glutinosa	2.60–3.32	Poland	LAI-2000	this study
Betula pendula	1.63–3.47	Poland	LAI-2000	this study
Quercus robur	2.82–3.16	Poland	LAI-2000	this study
Quercus rubra	3.1	Wisconsin, USA	LAI-2000	Gower, Norman 1991
Populus tremuloides	1.29–3.52	Minnesota, USA	different	Woods et al. 1991

[a] – Method of light interception 6.6 and 7.9 $m^2\ m^{-2}$, literfall 8.0 $m^2\ m^{-2}$, sapwood area 8.3 $m^2\ m^{-2}$, and diameters 16.6 $m^2\ m^{-2}$.

Canopy LAI depends on many factors, with stand age and dominant tree species being especially important. Some investigators have reported leaf area index to be influenced by ground water balance rather than tree species itself (Grier and Running 1977). Other studies have pointed out that total leaf area index of the entire forest community depends on site quality, but not on species occurring in that site. Lower values of overstory leaf area are being compensated by higher LAI values of understory (shrubs and herbs) and *vice versa* (Satoo 1970).

Leaf area of an individual tree appeared to be highly dependent upon both tree age and stand density. It is difficult to assess which factor is more important especially that both of them are interrelated. A close relationship between tree number per hectare and leaf area of an individual tree or canopy LAI has been described by Jack and Long (1991). It is known that soon after stand thinning competition among trees is less intense. The rate of photosynthesis of the residual trees increases enabling the trees to produce larger crowns with larger foliage area (Kozlowski et al. 1991). Recalculating data given by Waring et al. (1981) I found that leaf area of 36-year-old Douglas fir ranged from 60.7 to 208.1 $m^2\ tree^{-1}$. It would confirm the decisive role of tree number per hectare. On the other hand, over the period between tree planting and canopy closure foliage area seems to depend upon stand age only.

When one is to compare leaf area estimates given by different authors (Table 3) large variability in LAI-s is easily noticeable. LAI values range from 0.48 $m^2 m^{-2}$ for black spruce (Woods et al. 1991) to 16.2 $m^2 m^{-2}$ for Douglas fir (Marshall and Waring 1986). The reasons of such a variability might be manifold. It seems that three of them are of outstanding importance, namely stand age, method used and location of stands examined. An effect of a method used on results has been emphasized by Marshall and Waring (1986), who considered that problem by studying Douglas fir stands. LAI estimates obtained by those authors ranged from 6.6 $m^2 m^{-2}$ (using a method based on light interception) to 16.2 $m^2 m^{-2}$ (a method based on tree diameters) (Marshall and Waring 1986). The third factor affecting greatly LAI estimates is location of study areas (e.g. type of site or altitude), which has excellently been exemplified by Smith (1993), who had measured LAI of Douglas fir canopies with DIAS II Analyzer.

Although the LAI-2000 Plant Canopy Analyzer has been accepted as the most accurate and fastest from among instruments designed for similar purposes (Zawiła-Niedźwiecki et al. 1993), it is not free from drawbacks. The results obtained in this work suggest that the analyzer measures projected area of whole trees including stems and branches, rather than leaf area index. The same was hyphotetized previously by Dufrêne and Bréda (1995). In deciduous tree stands (broad-leaved species and larch) better leaf area estimates may be obtained by subtracting LAI-s of leafless stands from those predicted after complete leaf development. In this way, leaf area produced during the growing season would be assessed. A similar procedure may also be applied to evergreens (e.g. pine, spruce), provided that leaf area production will certainly be underestimated as the difference in LAI-s between the two dates informs about leaf area accumulation, but not real production. This is emphasized by the negative values of needle accumulation obtained for old-growth pine forests.

5. CONCLUSIONS

From among all the species examined, spruce was found to have the highest LAI values (from 5.7 to 10.0 $m^2 m^{-2}$), whereas LAI-s of other species were similar and varied from 1.6 to 6.3 $m^2 m^{-2}$, with highest values being characteristic of European beech and European larch, intermediate – of common oak, Scots pine and black alder, and lowest ones – of white birch.

Leaf area index of pine canopies increases rapidly in young stands, peaks at approximately age 20 and decreases slowly thereafter. Other species are likely to follow a similar pattern of LAI dynamics, provided that the LAI maximum may be approached at different age corresponding with the period of most intense competition among trees.

Leaf area of an individual tree increases linearly with the tree age.

Leaf accumulation (and presumably leaf production) in evergreen tree canopies seems to decrease as stand age increases.

6. SUMMARY

The studies performed in forests of north-western Poland aimed at recognizing leaf area index (LAI) of main Polish forest-forming tree species (pine, beech, alder, birch, spruce, larch and oak). The LI-COR LAI-2000 plant canopy analyzer was used that predicts LAI values on the basis of a comparison between readings made above (outside) and below tree canopies. The measurements were made at three dates: once before (March–April), and twice after leaf development (June and August).

From among the species examined spruce exhibited the highest LAI amounting to 10.0 $m^2 m^{-2}$, whereas other species had much lower LAI-s (within a range 1.6-6.3 $m^2 m^{-2}$). Out of them, larch and beech had the highest, pine, oak and alder – lower, and birch – the lowest LAI values (Table 1).

LAI changes with age was analyzed for pine, beech, and all species simultaneously. Leaf area of each of the species rapidly increases in young stands, attains a maximum (at approximately age 20) and begins to decrease thereafter (Figs. 3, 7, and 10).

Leaf area of an individual tree increases linearly with tree age, the tendency being so evident that may be noticed not only in pine or beech (Figs. 4 and 8) but also in species investigated in a smaller number of stands (alder, birch, spruce) (Table 2).

A very strong relationship was found between tree number per hectare and stand age – a sharp decrease was followed by an equilibrium (Figs. 4 and 8). The strongest relationship occurred between leaf area of an individual tree and tree number – again equilibrium was preceded by a sharp decline phase (Fig. 5 and 9). A different picture was characteristic of the relationship between canopy LAI and stand density in pine – asymptotic increase (Fig. 5), and beech – constant LAI over different stand densities (Fig. 9).

Leaf accumulation and probably also leaf production of a stand decreases with stand age (Fig. 6).

The LI-COR LAI-2000 analyzer proved itself to be very useful in comparing LAI-s among different forest stands. There is, however, some uncertainty about LAI values predicted by the device, as these seem to reflect projected area of whole trees including stems and branches, rather than real projected foliage area of stands.

7. REFERENCES

1. Barcikowski A. 1991 – Energy flow changes related to the development of assimilary organ biomass in suboceanic fresh pine forest Leucobryo-Pinetum Mat. 1962 – Ekol. pol., 39(3): 403–425.
2. Deblonde G., Penner M., Royer A. 1994 – Measuring leaf area index with the LI-COR LAI-2000 in pine stands – Ecology, 75(5): 1507–1511.
3. Dufrêne E., Bréda N. 1995 – Estimation of deciduous forest leaf area index using direct and indirect methods – Oecologia, 104: 156–162.
4. Ellsworth D. S., Oren R., Huang C., Phillips N., Hendrey G. R. 1995 – Leaf and canopy responses to elevated CO_2 in pine forest under free-air CO_2 enrichment – Oecologia, 104: 139–146.
5. Ford E. D., Newbould P. J. 1971 – The leaf canopy of a coppiced deciduous woodland. I. Development and structure – J. Ecol., 59: 843–862.
6. Gholz H. L. 1982 – Enviromental limits on aboveground net primary production, leaf area, and biomass in vegetation zones of the Pacific Northwest P. J. – Ecology, 63: 469–481.
7. Gower S. T., Norman J. M. 1991 – Rapid estimation of leaf area index in conifer and broad-leaf plantations – Ecology, 72: 1896–1900.
8. Grier C. C., Running S. W. 1977 – Leaf Area of Mature Northwestern Coniferous Forests: Relation to Site Water Balance. Ecology, 58: 893–899.
9. Grove T. S., Malajczuk N. 1985 – Biomass production by trees and understorey shrubs in an age-series of Eucalyptus diversicolor F. Muell. stands – Forest Ecology and Management, 11: 59–74.

10. Hanson P. J., Rott K., Taylor G. E. Jr., Gunderson C. A., Lindberg S. E., Ross-Todd B. M. 1989 – NO_2 Deposition to Elements Representative of a Forest Landscape – Atmospheric Environment, 23: 1783–1794.

11. Hanson P. J., Taylor G. E. Jr., Vose J. 1992 – Experimental Laboratory Measurements of Reactive N Gas Deposition to Forest Landscape Surfaces: Biological and Environmental Controls (In: Atmospheric Deposition and Forest Nutrient Cycling, Eds: Johnson D. W., Lindberg S. E.) Springer-Verlag. Ecol. Stud., 91:166–177.

12. Jack S. B., Long J. N.. 1991 – Response of leaf area index to density for two contrasting tree species – Can. J. of Forest Res., 21: 1760–1764.

13. Kira T., Kumara A. 1983 – Dry matter production and efficiency in various types of plant canopies (In: Plant Research and Agroforestry, Ed. P. A. Huxley) – Pillans & Wilson, Edinburgh, 347–364.

14. Kozlowski T. T., Kramer P. J., Pallardy S. G. 1991 – The Physiological Ecology of Woody Plants – Academic Press, 657 pp.

15. LI-COR 1989 – LAI-2000 Plant Canopy Analyzer. Technical Information – LI-COR inc., Lincoln, Nebraska, USA.

16. LI-COR 1990 – LAI-2000 Plant Canopy Analyzer. Instruction Manual – LI-COR inc., Lincoln, Nebraska, USA.

17. Lindberg S. E., Bredemeier M., Schaefer D. A., Qi L. 1990 – Atmospheric Concentrations and Deposition of Nitrogen and Major Ions in Conifer Forests in the United States and Federal Republic of Germany – Atmospheric Environment, 24a (8): 2207–2220.

18. Marshall J. D., Waring R. H. 1986 – Comparison of methods of estimating leaf-area index in old-growth Douglas-fir – Ecology, 67(4): 975–979.

19. Miller H. G. 1986 – Carbon X nutrient interactions – the limitations to productivity – Tree Physiology, 2: 373–385.

20. Mohler C. L., Marks P. L., Sprugel D. G. 1978 – Stand structure and allometry of trees during self-thinning of pure stands – J. Ecol. 66: 599–614.

21. Ovington J. D. 1957 – Dry-mater Production by *Pinus sylvestris* L. – Annals of Botany, N.S. 21: 287–314.

22. Pearson J. A., Fahey T. J., Knight D. H. 1984 – Biomass and leaf area in contrasting lodgepole pine forest – Can. J. Forest Res. 14: 259–265.

23. Pierce L. L., Running S. W. 1988 – Rapid estimation of coniferous forest leaf area index using a portable integrating radiometer – Ecology, 69(6): 1762–1767.

24. Satoo T. 1970 – A Synthesis of Studies by the Harvest Method: Primary Production Relations in the Temperate Deciduous Forests of Japan. Analysis of Temperate Forest Ecosystem – Ecol. Stud., 1: 56–72.

25. Smith N. J. 1993 – Estimating leaf area index and light extinction coefficients in stands of Douglas-fir (*Pseudotsuga menziesii*). Canadian Journal of Forest Research, 23: 317–321.

26. Waring R. H., Newman K., Bell J. 1981 – Efficency of Tree Crowns and Stemwood Production at Different Canopy Leaf Densities Forestry, 54(2): 129–137.

27. Waring R. H., Schlesinger W. H. 1985 – Forest Ecosystems: Concepts and Management – Academic Press, 38–70.

28. Watson D. J. 1947 – Comparative physiological studies on the growth of field crops. I. Variation in net assimilation rate and leaf area between species and varieties, and within and between years – Annals of Botany, 11: 41–76.

29. Woods K. D., Feiveson A. H., Botkin D. B. 1991 – Statistical error analysis for biomass density and leaf area index estimation – Can. J. of Forest Res., 6: 49–57.

30. Zawiła-Niedźwiecki T., Gruszczyńska M., Strzelecki P.. 1993. Wskaźnik LAI w teledetekcyjnej ocenie kondycji lasu [LAI in Remotely Sensed Assessment of Forest Condition] – Sylwan, CXXXVII, 6: 55–59.

(Received after revising June 1997)