Variation of conducting area in stems of European larch (*Larix decidua*) growing in fresh mixed coniferous forest and fresh mixed forest sites

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ABSTRACT: The paper presents an attempt to determine conducting area (CA), relative conducting area ($CA.k^{-1}$) and mean ring conducting area (CAar) on discs cut at breast height from stems of larch trees growing in fresh mixed coniferous forest and fresh mixed forest sites, representing four age classes and the main crop according to Kraft's classification. The value of CA increases with an improvement of the social class of tree position in the community, while no such dependences were found for the value of ($CA.k^{-1}$). The parameter CAar, except for one case in age class IV in the fresh mixed coniferous forest site, increases with an improvement of the position a tree takes in the community and differentiates more markedly under the conditions of fresh mixed forest sites. Relative conducting area ($CA.k^{-1}$) decreases markedly with an increase in the age of trees, which is confirmed by high values of the coefficient of determination. Moreover, the significance of differences between individual trees in the main crop according to Kraft and forest site types was tested in terms of the values of CAar. Calculated values may be used to describe the relationships between conducting area and the size of the assimilating organ more precisely than the total sapwood zone.

Keywords: conducting area; European larch; mean ring conducting area; relative conducting area; social class of tree position

The structure and properties of wood are a consequence of genetic, environmental and anthropogenic factors acting during the formation of wood tissue (Wodzicki 2001). The general anatomical structure of tree species is constant and proves helpful in their identification. However, the structure of wood tissue falls within a relatively wide range modified by external factors (Wimmer 2002). A major function of wood is to provide the system of communication between two cooperating organs, i.e. roots and assimilatory organ. There is a close interdependence between the size of the assimilatory organ and the zone conducting water together with minerals, which has been described by numerous authors as the pipe model theory (Shinozaki et al. 1964; Warning et al. 1982; Chiba 1998; Berthier et al. 2001; McDowell et al. 2002; Jelonek et al. 2008). First of all a close dependence is assumed between the sapwood area and the area of assimilatory and transpiration organ, which also affects heartwood formation in tree stems. Hydraulic conductance of sapwood is determined, among other things, by biometric characteristics of conducting elements, assimilatory organ and several external factors. However, within the physiologically active sapwood zone rings of early and late wood are contained, the

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functions and importance of which for the life of trees are completely different. In coniferous species tracheids have the conducting and strengthening functions at the same time, thus the conducting and supporting systems merge, with the conducting function predominating in early wood and the supporting function in late wood (Hejnowicz 2002). For this reason the definition of the entire sapwood area as the conducting zone from the aspects of wood anatomy and plant physiology seems imprecise.

The aim of the study was to determine the size of conducting area (CA), relative conducting area (CA.k^{-1}) and mean ring conducting area (CAar) in stems of European larch growing in fresh mixed coniferous forest and fresh mixed forest sites, representing four age classes (II–V) and the main crop according to Kraft's biological classification.

MATERIAL AND METHODS

Investigations were conducted in stands of age classes II, III, IV and V growing in the Choszczno Forest Division (the Regional Directorate of State Forests in Szczecin), where larch was found as an admixture (in group mixtures at least) in fresh mixed coniferous forest and fresh mixed forests. The fresh mixed coniferous forest (FMCF) is a moderately poor site with relatively good moisture content. At the natural condition of the site moder or moder-mor humus is formed. Natural stands are composed of pine with an admixture of sessile oak, beech, spruce, birches, larch and other species. The forest floor vegetation is typical of coniferous forest (mosses, bilberries) with a participation of species with slightly higher site requirements. This site was formed on sandy soils or transitional peats, which are acid at least in the top horizons.

The fresh mixed forest (FMF) is quite a fertile site with advantageous moisture content. Humus takes the form of a typical moder, occasionally mull form. The stand is composed of pine, oaks, beech, spruce, with an admixture of larch, hornbeam, birches and other species. The forest floor vegetation is composed of herbs and ferns with medium trophic requirements. It is a medium fertile site with fertile, moderately acid soils (Sikorska 2006).

In selected subcompartments mean sample plots of 0.5 ha were established, where breast height diameters were measured on all trees of this species and they were listed in terms of 2 cm diameter subclasses. Next tree height was measured in proportion to the frequency of trees in the adopted diameter subclasses. The height curve was plotted, on the basis of which corresponding heights were read after breast height diameters were calculated for model trees. Based on the height and diameter characteristics of trees a total of 24 model trees were selected (with 6 in each age class) using the Hartig method (Grochowski 1973) and Kraft's biological classification (Kraft 1884), with only the first three classes, i.e. the main crop, taken into consideration. Dimensions of model trees are given in Table 1.

Table 1. Dimensions of model trees grown in site conditions of FMCF and FMF

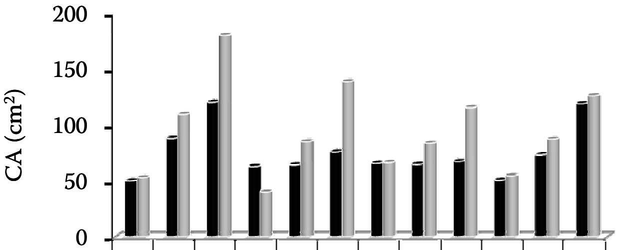
Age class	Kraft's class	FMCF		FMF	
		breast diameter (cm)	height (m)	breast diameter (cm)	height (m)
II	III	16.3	17.4	17.0	18.8
	II	21.8	19.0	23.0	21.5
	I	26.2	19.3	29.0	23.8
III	III	19.0	23.2	21.0	21.9
	II	26.0	23.8	28.0	25.2
	I	32.0	25.8	33.0	25.7
IV	III	25.0	24.9	26.0	21.0
	II	27.0	29.1	32.0	29.2
	I	35.0	31.1	39.0	29.8
V	III	28.0	24.8	27.0	31.1
	II	33.5	28.7	35.0	31.5
	I	39.0	31.6	40.0	33.8

This classification, based on the crown quality and tree evaluation, and the determination of tree height in relation to the height of adjacent trees describe quite well the crown and the social class of tree position in the community. For each model tree the crown projection radii were measured in the four principal geographical directions and after felling the length of live crown was measured. After trees were felled, discs were collected at a distance of 1 m from the bottom butt end (which corresponds roughly to the height of 1.3 m, the so-called breast height) to investigate selected macroscopic characteristics of wood. Altogether 24 discs were taken (one for each tree). Discs were used to measure the width of early and late wood on the sapwood using an electronic increment meter coupled with a computer. Measurements were taken in the four cardinal points of the compass, to the nearest 0.01 mm. Moreover, disc radii were measured in order to calculate their total area (k) from the formula for the area of a circle. The area of early wood ring was calculated as a difference of areas of circles with radii R and r:

$$P = \pi(R^2 - r^2)\ (\text{cm}^2)$$

where:
r – the radius of a circle to the beginning of early wood,
R – the radius of a circle to the beginning of late wood,
P – earlywood area in annual ring.

Total area of early wood rings within the sapwood zone constitutes the conducting area – CA. Mean area of early wood per single annual ring was defined as the conducting area of a ring – CAar. Relative conducting area ($CA.k^{-1}$) was calculated as a quotient of conducting area (CA) and total disc area (k). Crown volume of trees was calculated as an approximation by calculating the volume of a cone. Statistical analysis of measured wood elements was conducted using the STATISTICA 6.0 PL software (Kala 2002; www.statsoft.pl). Results are presented in the form of tables and figures.



	III	II	I	III	II	I	III	II	I	III	II	I
FMCF	50	88	121	63	64	76	66	65	67	51	73	119
FMF	53	110	181	40	85	139	66	84	116	55	88	126

■ FMCF ■ FMF

Fig. 1. A comparison of size of conducting area (CA) in age classes and forest site types in view of occupied social class of tree position

RESULTS

Fig. 1 presents characteristics of the size of conducting area (CA) in analyzed age classes in view of the social class of tree position in the stand. The value of CA measured at breast height is markedly higher in the youngest trees, representing age class II, while in the successive age classes it stabilizes and remains at a comparable level.

The size of conducting area (CA) changes markedly, depending on the social class of tree position. It has the highest values in Kraft's class I, while the lowest in class III (Fig. 1). In the fresh mixed forest site conducting area CA assumes higher values than in the less fertile fresh mixed coniferous forest site, which is manifested in all age classes and Kraft's biological classes, except for co-dominant trees from

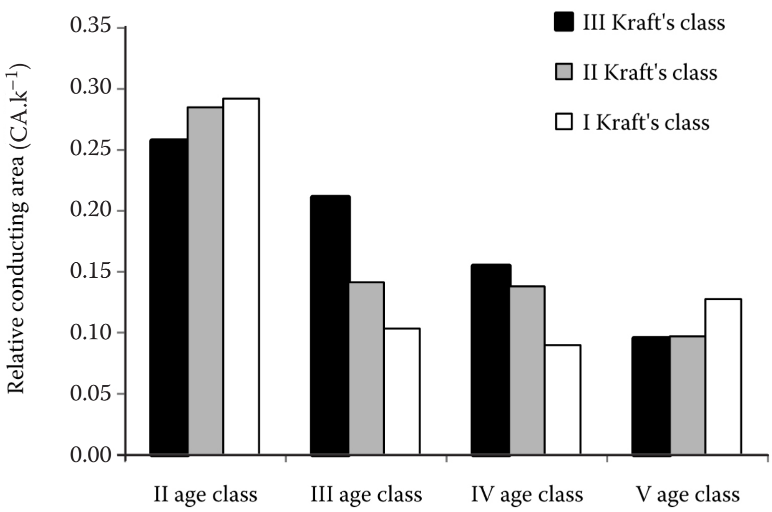


Fig. 2. The size of relative conducting area ($CA.k^{-1}$) in different age classes in view of occupied social class of tree position in the stand in FMCF

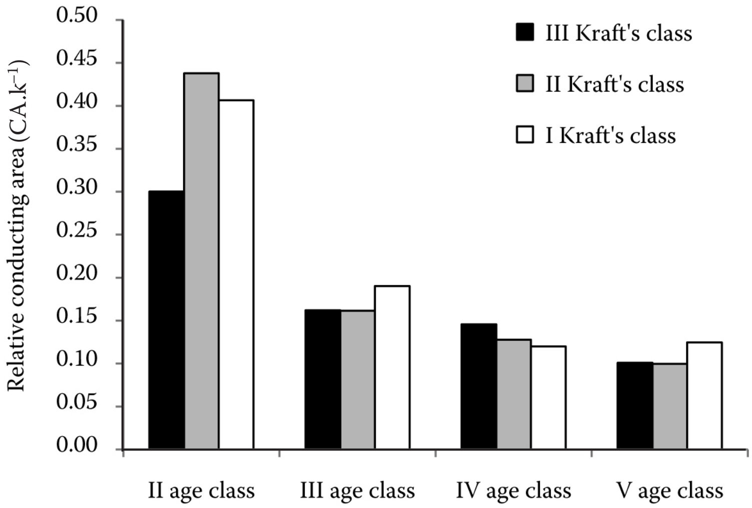


Fig. 3. The size of relative conducting area (CA.k^{-1}) in different age classes in view of occupied social class of tree position in the stand in FMF

age class III (Fig. 1). However, the comparison of absolute values does not fully reflect the investigated dependences, since it is connected with dimensions of trees, varying considerably both in age classes and in Kraft's classes. For this reason, comparing absolute values constitutes only a background for appropriate comparisons. Thus, in order to illustrate conducting area, the relative conducting area (CA.k^{-1}) and ring conducting area (CAar) were used.

The comparison of relative areas yielded completely different results. Definitely the largest relative conducting area was found in age class II, both in the fresh mixed coniferous forest and fresh mixed forest sites. In age class III the size of this area decreases rapidly and remains similar in the successive age classes (Figs. 2 and 3). A decrease in the value of relative conducting area is very clearly manifested and shows a downward trend following an exponential curve at high coefficients of determination (Fig. 4). In consistence with the trend line, the size of relative conducting area seems only to decrease. However, if we take into consideration the social class of tree position in the stand, in age class V a delicate increase is observed in conducting area in Kraft's class I in both forest site types (Figs. 2 and 3). An opposite situation was found for the youngest trees (age class II) belonging to the worst social class of tree position, as in their case the value (CA.k^{-1}) was much lower than in other Kraft's classes (Figs. 2 and 3).

A marked positive trend was observed between crown volume and conducting area (CA). This trend was expressed using the coefficient of determination fitted with exponential curves (Figs. 5A and 5B).

The size of ring conducting area (CAar) is another analyzed parameter. This parameter increases with an improvement in the social class of tree position in both forest site types (Figs. 6–9). An exception is the situation in age class IV in the fresh mixed

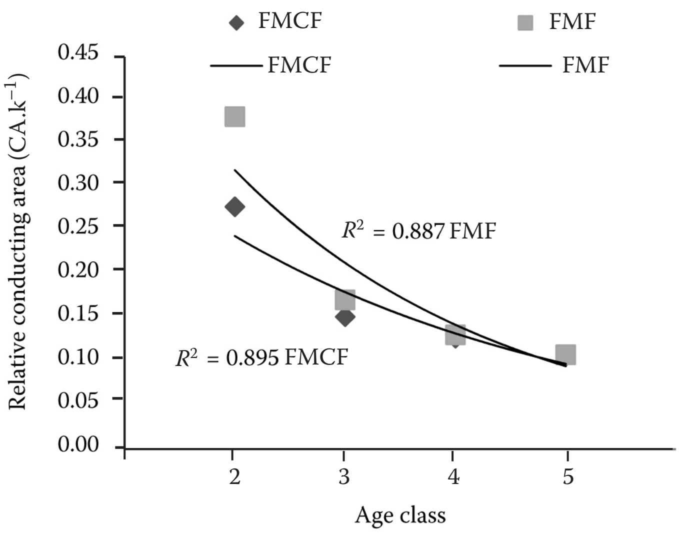


Fig. 4. A dependence of relative stem conducting area (CA.k^{-1}) on age of trees

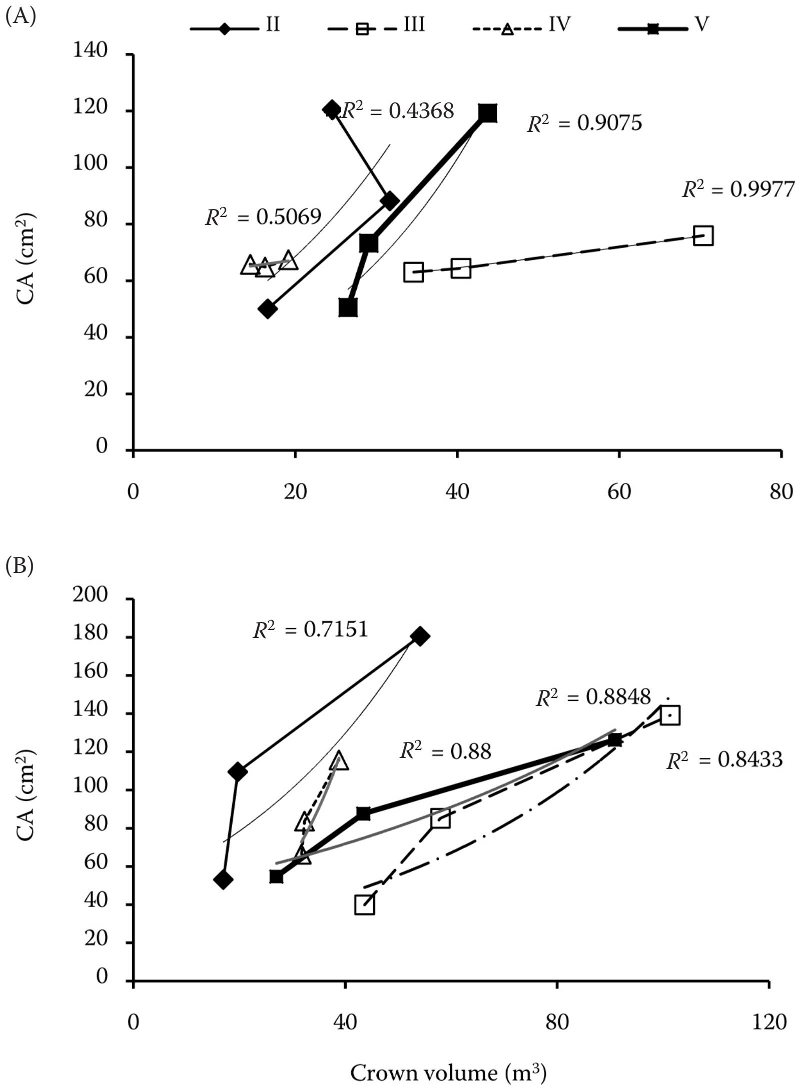


Fig. 5. Dependence between crown volume and conducting area (CA) in age classes in conditions of FMCF (A) and FMF (B)

coniferous forest site (Fig. 8A). In this case the size of ring conducting area decreases with an improvement in the social class of tree position in the stand. After the width of annual diameter increment was analyzed in trees not following the rule of an increase in CAar with an improvement in the social class of tree position, it was found that these trees exhibited a strong increment in diameter at the earlier stage of life and markedly dominated the surroundings, while in recent years under the influence of not completely identified factors they started to grow very poorly, although at the time of model tree selection and felling they took positions ascribed to them in the stand. Due to the markedly

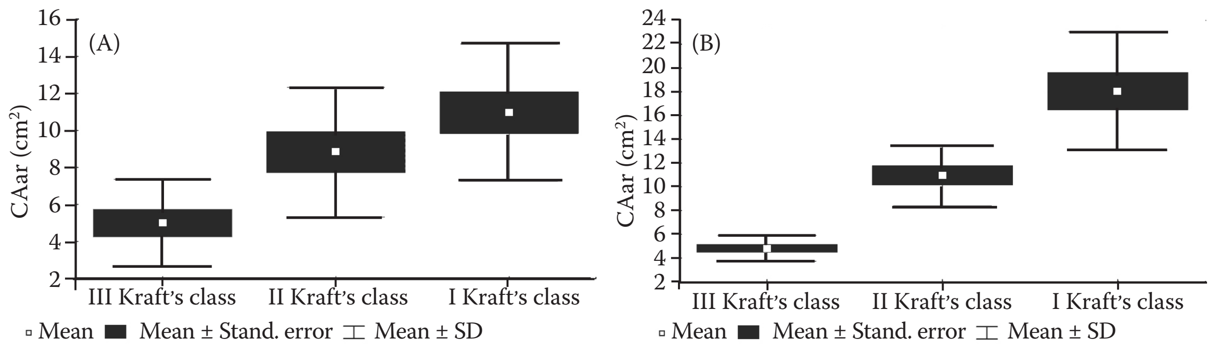


Fig. 6. A comparison of characteristics of the size of ring conducting area (CAar) in Kraft's classes in age class II in fresh mixed coniferous forest (A) and fresh mixed forest (B) sites

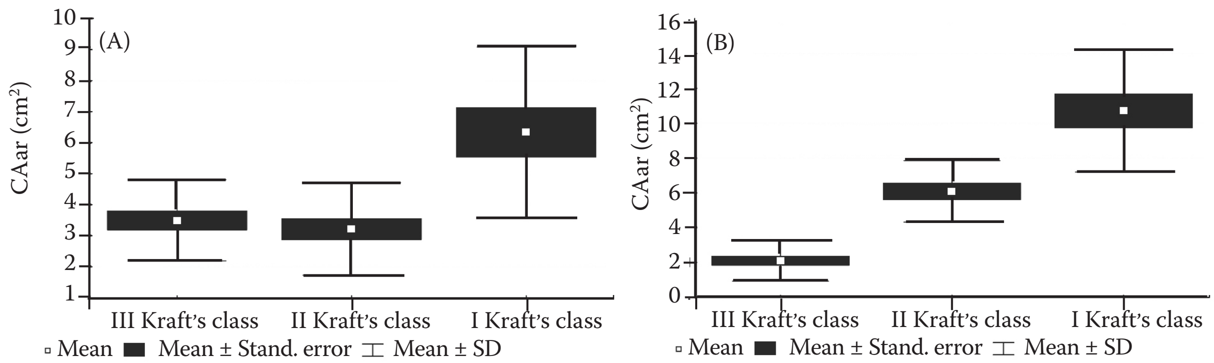


Fig. 7. A comparison of characteristics of the size of ring conducting area (CAar) in Kraft's classes in age class III in fresh mixed coniferous forest (A) and fresh mixed forest (B) sites

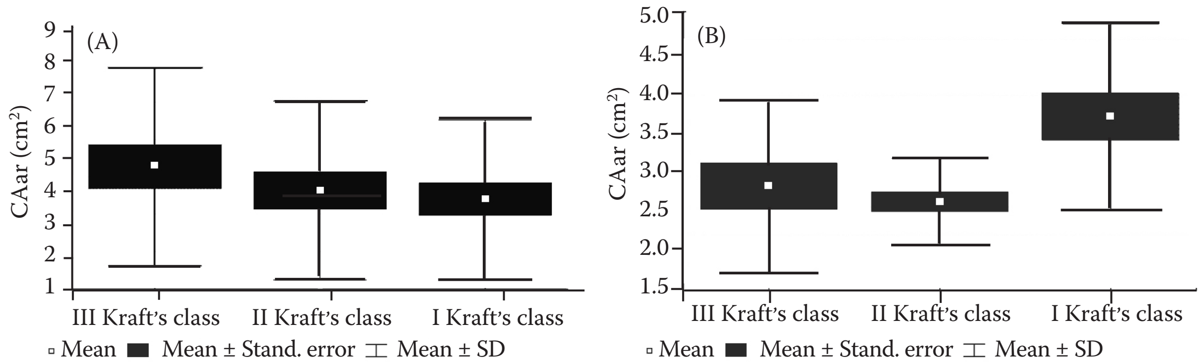


Fig. 8. A comparison of characteristics of the size of ring conducting area (CAar) in Kraft's classes in age class IV in fresh mixed coniferous forest (A) and fresh mixed forest (B) sites

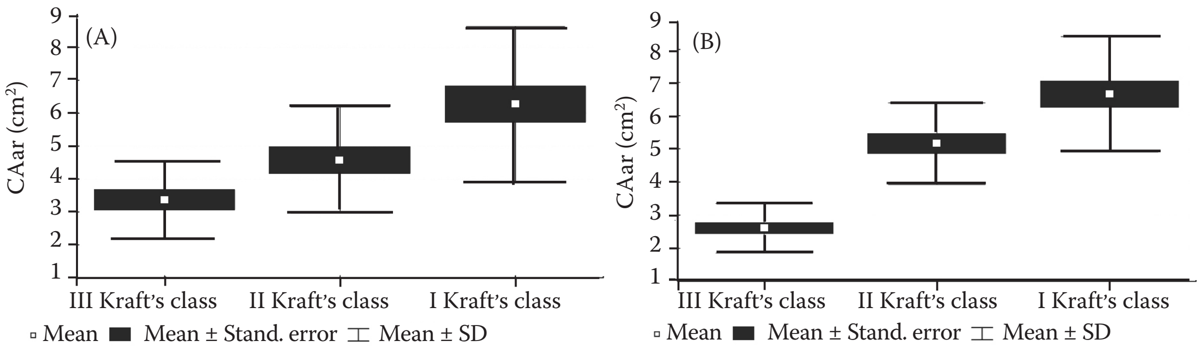


Fig. 9. A comparison of characteristics of the size of ring conducting area (CAar) in Kraft's classes in age class V in fresh mixed coniferous forest (A) and fresh mixed forest (B) sites

weaker growth in recent years it is likely that these trees would move in the stand in future by descending to lower Kraft's social classes of tree position. In age class III in the fresh mixed coniferous forest site and in age class IV class in the fresh mixed forest site a slightly larger ring conducting area would be found for trees classified to Kraft's class III than in trees from social class II (Figs. 7A and 8B), although it is only slight difference. Moreover, no significant differences were found in the discussed comparison.

Further statistical analyses of CAar were conducted in order to determine the significance of differences between the analyzed social classes of tree position and forest site types. Due to the absence of normal distribution of the investigated characteristics the non-parametric Kruskal-Wallis test was used to test these differences.

Based on the conducted tests statistically significant differences in CAar were observed between extreme trees of the main crop, i.e. predominant trees and co-dominant trees in age class II in the fresh

Tab. 2. Results of the Kruskal-Wallis test for the value of CAar in analyzed Kraft's social classes of tree position and forest site types in age class II

Dependent – CAar	Kruskal-Wallis test: H (2, *N*= 31) = 13.34659, *P* = 0.0013 (FMCF) Kruskal-Wallis test: H (2, *N*= 31) = 24.11855, *P* = 0.0000 (FMF)					
	FMCF			FMF		
	{1} R: 22.273	{2} R: 17.200	{3} R: 7.900	{1} R: 25.300	{2} R: 17.700	{3} R: 6.000
I Kraft's class {1}		0.217807	**0.000134***		0.184825	**0.000035***
II Kraft's class {2}	0.217807		0.066554	0.184825		**0.027737***
III Kraft's class {3}	**0.000134***	0.066554		**0.000035***	**0.027737***	

*Marked differences are statistically significant at $P < 0.05$

Tab. 3. Results of the Kruskal-Wallis test for the value of CAar in analyzed Kraft's social classes of tree position and in forest site types in age class III

Dependent – CAar	Kruskal-Wallis test: H (2, *N* = 50) = 12.70403, *P* = 0.0017 (FMCF) Kruskal-Wallis test: H (2, *N* = 46) = 35.91093, *P* = 0.0000 (FMF)					
	FMCF			FMF		
	{1} R: 38.250	{2} R: 19.700	{3} R: 23.444	{1} R: 38.692	{2} R: 27.214	{3} R: 10.368
I Kraft's class {1}		1.000000	1.000000		0.257562	0.000651*
II Kraft's class {2}	1.000000		1.000000	0.257562		0.078493
III Kraft's class {3}	1.000000	1.000000		0.000651*	0.078493	

*Marked differences are statistically significant at $P < 0.05$

mixed coniferous forest and in age classes III and IV in the fresh mixed forest (Tables 2–4).

Co-dominant trees from age class II growing in the fresh mixed forest differed statistically significantly from the other two social classes (Table 2). The highest variation in CAar was observed in trees representing age class V. In the fresh mixed forest site statistically significant differences were found between all trees of the main stand, while in the fresh mixed coniferous forest site predominant trees (Kraft's class I) differed statistically significantly from the other two social classes of tree position (Table 5).

No statistically significant differences in CAar at $\alpha = 0.05$ were found between trees growing in the fresh mixed coniferous forest site in age classes III and IV (Tables 3 and 4).

Moreover, the size of CAar was analyzed in the investigated forest site types. Statistically significant

Tab. 4. Results of the Kruskal-Wallis test for the value of CAar in analyzed Kraft's social classes of tree position and in forest site types in age class IV

Dependent – CAar	Kruskal-Wallis test: H (2, *N* = 69) = 1.369534, *P* = 0.5042 (FMCF) Kruskal-Wallis test: H (2, *N* = 46) = 35.91093, *P* = 0.0000 (FMF)					
	FMCF			FMF		
	{1} R: 32.280	{2} R: 34.217	{3} R: 39.095	{1} R: 34.625	{2} R: 20.700	{3}R: 21.929
I Kraft's class {1}		1.000000	1.000000		0.386655	0.004093
II Kraft's class {2}	1.000000		1.000000	0.386655		0.496183
III Kraft's class {3}	1.000000	1.000000		0.004093*	0.496183	

*Marked differences are statistically significant at $P < 0.05$

Tab. 5. Results of the Kruskal-Wallis test for the value of CAar in analyzed Kraft's social classes of tree position and in forest site types in age class V

Dependent – CAar	Kruskal-Wallis test: H (2, N = 50) = 14.85423, P = 0.0006 (FMCF) Kruskal-Wallis test: H (2, N = 57) = 40.14657, P = 0.0000(FMF)					
	FMCF			FMF		
	{1} R: 34.316	{2} R: 24.938	{3} R: 14.933	{1} R: 34.625	{2} R: 20.700	{3} R: 21.929
I Kraft's class {1}		0.006463*	0.000000*		0.019131*	0.000000*
II Kraft's class {2}	0.006463*		0.085185	0.019131*		0.006469*
III Kraft's class {3}	0.000000*	0.085185		0.000000*	0.006469*	

*Marked differences are statistically significant at $P < 0.05$

differences in CAar between the fresh mixed coniferous forest and fresh mixed forest were found only for trees representing age class IV. In the other age classes no statistically significant differences were found in the value of CAar between the two forest site types at $\alpha = 0.05$.

DISCUSSION

The area of sapwood ring is frequently calculated by researchers as a value used to describe conducting area and relate it to biometric traits of tree crowns (Ganskopp, Miller 1986; Dean et al. 1988; Margolis et al. 1988; Mörling, Valinger 1999; McDowell et al. 2002; Medhurst, Beadle 2002; Sellin, Kupper 2003; Stancioiu, O'Hara 2005; Longuetaud et al. 2006). However, the areas of late wood ring contained within sapwood, neither participating nor involved in water conduction to a limited extent, result in a situation when the sapwood area reduced by the area of late wood, i.e. the total area within this wood zone, should be considered to be the conducting area. The sapwood area with the deducted late wood area was calculated by Eckmüllner and Sterba (2000), who called it early sapwood area, referring to the area of early wood within the sapwood zone. In the opinion of these authors such a calculated conducting area is a very good estimator of the assimilating and transpiring organ, useful in the assessment of needle biomass in Norway spruce (*Picea abies* [L.] Karst.). Conducting area (CA) showed the highest values in the youngest age class. This results probably from the immaturity of parenchymal cells initiating the heartwood formation. According to Hejnowicz (2002), as long as the age of the stem does not exceed the limit of life for parenchymal cells, wood is composed solely of sapwood. Starting from age class III the value of CA remains more or less identical, to increase slightly in age class V. We need to ask a question whether the heartwood area is regulated in the process of conducting area optimization, or maybe heartwood plays an active role in the regulation of sapwood area. Most probably the process of heartwood formation initiated by the death of parenchymal cell stabilizes the size of conducting area in trees of younger age classes, and then the cause and effect of the interrelationship in the transpiring organ – conducting area dependence plays a primary role in the optimization of conducting area, thus affecting proportions of sapwood and heartwood. The process which inhibits conductive functions of sapwood has not been truly clarified yet (Spicer, Gartner 2001). In the opinion of Pazdrowski (1994), genotypic and phenotypic variation in tree crowns may be interdependent with wood quality, i.e. it may be an indicator of quality characteristics such as the proportion of sapwood and heartwood in the stem. Heartwood and sapwood have different properties and their proportion within the stem has a decisive effect on the rational utilization of timber (Duda, Pazdrowski 1975; Nawrot et al. 2008).

In this study in the analysis of conducting area the relative conducting area ($CA.k^{-1}$) and the respective index (CAar) were used. This index relates CA to the number of rings in sapwood, containing two components at the same time: ring increment response and ring conducting area (early wood). In one case (age class IV, fresh mixed coniferous forest site) the analysis of the value of CAar showed a deviation from the trend to increase ring conducting area with an improvement of the social class of tree position in the stand (Fig. 8A). Since the index is based on rings originating from sapwood, it always shows the current increment trend.

In the analysis of relative conducting area ($CA.k^{-1}$) two deviations from the trend were surprising which manifested themselves after illustrating CA.–1 in different Kraft's classes. The first of these deviations was an increase in the value of ($CA.k^{-1}$) in age class V in trees with the best social class of tree position (Kraft's class I). Since the phenomenon was not observed in younger specimens, it may hardly be explained solely by the tree position in the stand. It may only be assumed that the competition of a tree for a position in the stand already ceased and trees with larger crowns and better access to light continue to stimulate the increase in conducting area. The other deviation is the low value of ($CA.k^{-1}$) in the youngest trees (age class II) classified to Kraft's class III. The relative conducting area is smaller than in other Kraft's classes, and it results probably from the inferior crown access to light, thus resulting in an inadequate stimulation of the increase in conducting area.

In the opinion of Jaworski (2004) a characteristic trait of stand growth and development processes is the natural movement of trees within their layers. This change in the stand social hierarchy of individual trees may be either positive, i.e. attainment of a higher social position, or negative at their descending to socially lower classes. According to Leibundgut et al. 1971 (see Jaworski 2002), at the age of 40–66 years (age class III and the beginning of age class IV) more trees show a negative movement (7–12%) rather than a positive one (1–11%), which seems to be confirmed by situations observed in this study, where trees from Kraft's class III (co-dominant) were characterized by the higher CAar value than dominant trees. Probably the trees, taking the position of co-dominant trees at the time of felling, existed earlier in the stand as predominant or dominant trees, losing the position they had previously taken for unknown reasons.

It is also of some importance that the European larch as a definitely light-demanding forest-forming species, dynamically responding to any changes in the stand crown closure caused by tending interventions or forces of nature, at older age classes forming stands composed only of the first three Kraft's classes of social position, which frequently exchange positions in the stand in the course of life in response to changes, particularly in light conditions. In the opinion of Borowski (1974), the course of section-area increment does not exhibit an identical trend to that found for increment in height. The course of section-area increment of a tree, in contrast to the course of increment in height, is a reflection of changing environmental conditions to a larger extent rather than of species-specific traits.

The subject discussed in this paper is of importance not only for pure science but also for forestry and wood industry practice. However, due to the complexity of this problem numerous additional tests are required to confirm the inferred assumptions.

CONCLUSIONS

- Relative conducting area ($CA.k^{-1}$), being a quotient of conducting area (CA) and total disc area (k), exhibits a marked downward trend with age.
- High coefficients of determination were found between relative conducting area and the age of trees and between calculated crown volumes and conducting area.
- The size of conducting area (CA) increases with an improvement of the social class of tree position in the stand, while relative conducting area ($CA.k^{-1}$) does not show any distinct trends depending on the social class of tree position in the stand.
- The calculated index CAar seems to be a good indicator of the current growth trend for a given tree, containing two pieces of information: the current increment trend and ring conducting area. Statistically significant differences were found in the size of CAar between all Kraft's social classes in age classes II and V for both analyzed sites and between forest site types in age class III.
- A more distinct variation in the size of CAar between social classes of tree position within age classes was recorded in fresh mixed forest site types.
- Conducting area (CA) and ring conducting area (CAar) seem to be the values that may describe the relationships between conducting area and the size of the assimilating and transpiration organ more precisely than the total sapwood area.
- In-depth knowledge of relationships between the conducting area of sapwood and the social class of tree position in the stand as well as crown volume may be used for the assessment of the size and proportions of macroscopic wood characteristics and thus for the optimization of its utilization in view of different chemical, physical and mechanical properties of sapwood and heartwood.

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