Effect of intra-specific competition on tree architecture and aboveground dry matter allocation in Scots pine

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Abstract

The study was carried out in a 25 year old Scots pine spacing trial, established with grafted clones. The oven-dry weight of the different aboveground parts of the tree (i.e. stem, large and small branches, needles and cones) has been assessed separately. With increasing competition, the relative proportion of generative parts and of large branches per tree decreased, while the dry matter increment allocated to stemwood increased gradually from 11.7 to 28.5 percents. In solitary, i.e. no-competition condition, the dry matter allocated to generative parts was nearly similar to that of current stemwood increment. On a unit area basis, the dry matter weight allocated to cones did not change significantly at different density levels and remained between 0.6 and 1.0 tons per ha. The highest total biomass per unit area was measured at maximum stand density (98.2 t/ha), where stem number is regulated by natural mortality (self-thinning). A slightly positive effect of competition on height growth was detectable only at early ages.

Introduction

Trees have an important role in generating biodiversity in ecosystems first of all due to their complex, long lasting structure that has a modulating effect on the environment. Organs and parts of a mature tree, such as flowers, fruits, leaves, shoots, branches, stem, bark, sapwood and roots offer not only a variety of consumable tissues of various types, but also a multitude of microhabitats and hiding-places.

In a forest ecosystem, the density and architecture of the crown layer is a major component of the structural diversity, and determines to a large extent the living condition and species composition of lower plant strata (shrubs, grasses, mosses).

In principle tree growth and crown architecture is determined by heredity, including the appearance and profusion of flowers (Bánó 1971). Competition by neighbours will cause changes in the crown structure and influence allocation of dry matter to different parts and organs (Peszlen at al. 1998).

Biomass allocation is decisive for the quantity of exploitable dendromass (timber yield) in a forest. Through regulation of stand density, silviculturists intend to influence the quantity and quality of harvestable timber. The total quantity of produced biomass per unit area is determined by external factors, i.e. by the “reciprocal yield law” (Shinozaki and Kira 1961), which means that gross biomass yield cannot be increased, only the ratio of dry matter increment allocated to selected trees can be improved by silvicultural treatments. An option to increase yields is through genetic selection for higher harvestable ratio of produced dry matter.

The effect of growing space changes on allocation rates can be studied only in even-aged, monospecific forest stands. While the 'harvest index' concept is effectively utilised in agricultural breeding, in forestry there are relatively few studies on architectural characteristics of trees, respectively on the genetic component in allocating biomass (Cannell et al. 1983). The study of biomass allocation and tree architecture is a precondition to formulate an 'ideotype' for tree breeding. Along with other desirable traits (i.e. vigorous growth, narrow crown, well-developed root system, prolonged active growth period) harvest index is nevertheless of high importance. The analysis of allocation ratios needs destructive sampling which can not be carried out on a large scale, so even available studies are based on relatively small sample sizes (Wu & Yeh 1997).

Matthews et al. (1975 cited in Cannell 1983) investigated a Virginia pine (*Pinus virginiana*) progeny test and found that the ratio between the dry matter accumulated in the stem and in the branches showed significant between-family differences, the calculated heritabilities were high. However, there was no significant correlation between allocation rates, tree height and total dry matter mass per tree, which indicates good possibilities for individual selection to improve harvest index.

Van Buijtenen (1978 cited in Cannell 1983) analysed 14 years old loblolly pine *(Pinus taeda)* half-sib families and grafted slash pine *(Pinus elliottii)* clones from a seed orchard. He stated that the stem ratios of the loblolly families showed no significant differences; however, the slash pine clones differed considerably in stem dry mass allocation (30-47%). Also in this case, no correlation was found with tree dimensions.

Numerous studies indicate that narrow crown form and small branches are genetically determined e.g. in Sitka and Norway spruce, lodgepole and Scots pine, and selection to improve harvest index can provide a basis for significant volume gains (Cannell 1983, Thompson 1985).

Although the genetic control of dry matter allocation seems to be evident from the cited and other studies, the competitive environment, especially growing space conditions have strong modifying effects. The experiment conducted in Acsád, Hungary offered favourable preconditions to assess these factors on clonally identic material.

The original aim of the experiment laid out nearly thirty years ago was to study the effect of spacing on the cone and seed yield, for the purpose of finding optimal planting distances in seed orchards. The experiment was established with grafts to eliminate the effect of genetic variability between individuals. The applied initial spacings were unusually broad, as compared to standard yield experiments. This experiment has been utilised for the present study, with the aim to investigate the effect of intraspecific competition on the allometric ratios between organs and parts ("sinks"), as well as on the reproductive ability, i.e. cone and seed crop. Originally the comparison of environmental and genetic effects was also planned, but the low number of replicates made it impossible to significantly prove genetic differences between the investigated clones.

Materials and methods

The analysed experiment was established in 1971 by I. Bánó and J. Retkes on a loamy brown forest soil in West Hungary (Acsád, Vas county). In each of four spacing variants (2x2 m, 8x2 m, 8x6 m, and 8x16 m - 2500, 625, 210 and 75 trees/ha, respectively) a set of 20 grafted Scots pine clones were outplanted in one-tree plots in randomised arrangement with three replications.

Three clones of different cone yielding capacity ('1-20', '6-10', and '6-25') have been selected for this study to assess the effect of growing space on dry matter allocation. Three sample trees per clone and spacing variant were felled in late autumn 1996 at the age of 25 years and the following traits were measured: total height, crown width and height, length and diameter of stem sections at branch whorls and at breast height, branch diameter (measured 5 cm from the stem), volume of branch parts over 5 cm in diameter, weight of small branches (all branch parts < 5 cm), shoots + needles (shoots of the last two years, bearing dense needle growth), quantity and weight of cones (including seeds). Due to natural mortality in the plantation, the three replicates per treatment were not available in all cases. All of the samples were oven-dried at 105°C until weight was stable to determine dry matter weight. Regarding increment analysis, the dry matter weight produced in stem and branches in the current year of investigation was utilised as well as the dry matter weight of the current cone crop. For shoots and needles simply the half of the dry weight of the two year old shoots was taken as the current year's allocation into green parts.

Results and discussion

Production and allocation of biomass

In the first decade of the plantation the annual height increment and the average height of the trees in the narrowest spacing (2×2 m) was higher than that of the ones grown in wider spacings. After canopy closure and with increasing competition, height growth decreased and in the 25th year the trees in the 2×2 m spacing variant were nearly 2 m lower than the trees grown under less competition pressure (Figure 1.), but these differences were not significant at p = 0,05 level (except between 8×6 and 8×16 m spacing variants). The average height was the lowest in the widest spacing (8×16), where the relatively greatest sink of the assimilates is the canopy (needles+shoots, Figure 2.) and neighbouring trees are not competitors at this age yet.

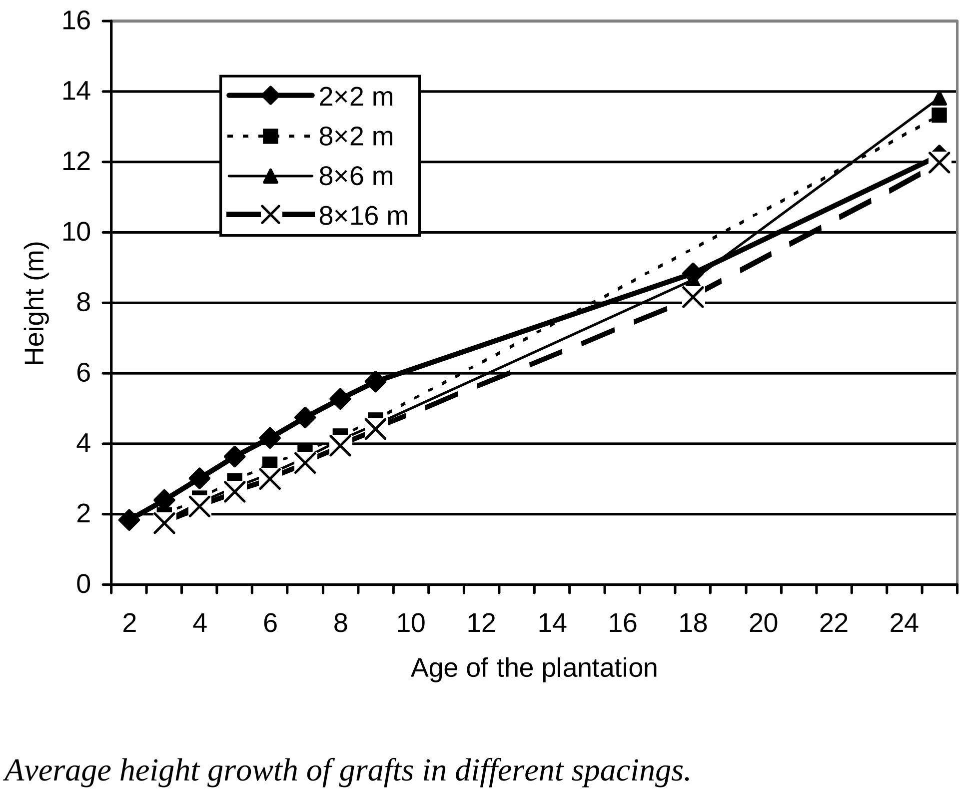
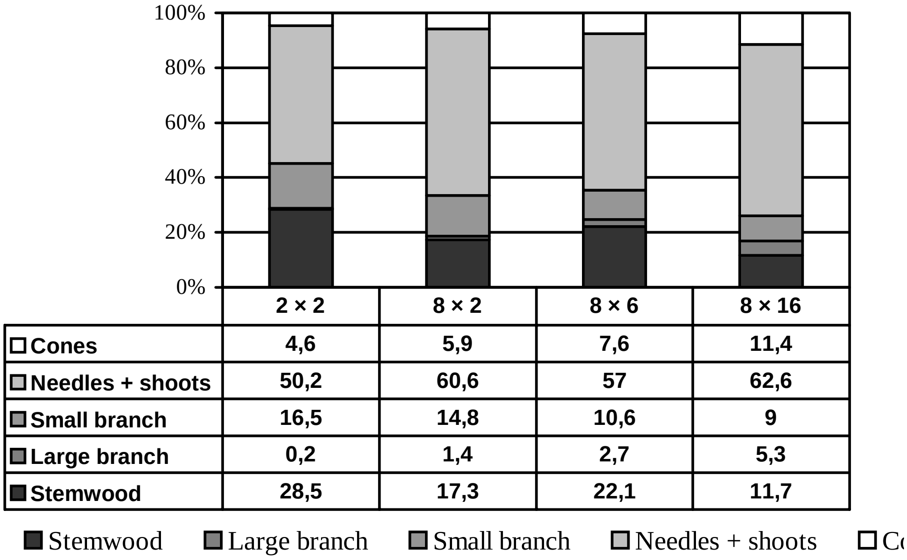


Figure 1: Average height growth of grafts in different spacings.

Comparing the dry matter ratios for stemwood, large branches (>5cm), small branches, needles + shoots and cones, the allocation of the dry matter in the year of the sampling (age 25) shows clear trends: the dry matter percentage allocated in the stem and small branches is decreasing towards wider spacings, while the ratio of large branches, needles + shoots, and cones is increasing (Figure 2).



	2 × 2	8 × 2	8 × 6	8 × 16
Cones	4,6	5,9	7,6	11,4
Needles + shoots	50,2	60,6	57	62,6
Small branch	16,5	14,8	10,6	9
Large branch	0,2	1,4	2,7	5,3
Stemwood	28,5	17,3	22,1	11,7

Figure 2: Percentage of dry matter current increment at age 25, allocated per tree in stemwood, large branches, small branches, needles + shoots and cones. (Average of all grafts per spacing variant.)

There were significant differences between spacing variants when comparing the dry matter produced in the year of sampling. The accumulated wood in the stem (annual volume increment) seems to respond somewhat less to larger spacings as compared to large branches and especially needles and cones. The total dry matter production per year showed very pronounced differences: trees growing in the widest spacing (8x16m) produced 7 times more dry matter than the ones in the narrowest spacing (2x2m) (Table 1). The strong horizontal development of the crown in the wide spacings ('bushy' growth) increases significantly the accumulation of dry matter in the large branches, while in the closest spacing large branches are practically missing.

Table 1: Mean of current allocation of dry matter per tree in the year of sampling (kg/tree)

Spacing (m × m)	Stem-wood	Large branches	Small branches	Needles + shoots	Cones	**Total**
2 × 2	3.78	0.03	2.18	6.65	0.61	**13.25**
8 × 2	5.22	0.41	4.46	18.26	1.77	**30.11**
8 × 6	12.32	1.48	5.89	31.73	4.23	**55.64**
8 × 16	11.34	5.09	8.73	60.45	10.97	**96.58**

In spite of strongly increasing dry matter production per tree towards wider spacings, the productivity per unit area is still the highest in the narrowest spacing of 2x2m (Table 2, Figure 3). Although mortality was highest (50%) in the narrowest spacing (Figure 6), the highest stem dry weight and total dry weight per ha was reached in this treatment.

Table 2: Total dry matter allocated in the phytomass components per unit area (in tons per ha) at the age of 25 years

Tree parts	Spacing							
	2 × 2 m		8 × 2 m		8 × 6 m		8 × 16 m	
	tons/ha	%	tons/ha	%	tons/ha	%	tons/ha	%
Stem-wood	58.3	59.4	37.0	44.9	18.9	43.2	6.9	30.3
Large branch	0.6	0.6	3.4	4.1	3.3	7.5	4.1	18.0
Small branch	20.8	21.2	21.8	26.5	10.1	23.1	5.3	23.2
Needles + shoots	17.7	18.0	19.2	23.3	10.8	24.7	5.9	25.9
Cones	0.8	0.8	1.0	1.2	0.7	1.6	0.6	2.6
Total	98.2	100.0	82.4	100.0	43.8	100.0	22.8	100.0

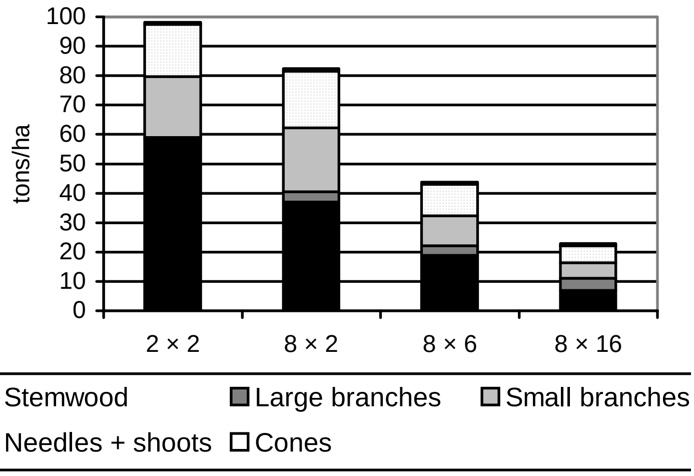


Figure 3: Total dry matter allocated in phytomass components per unit area at the age of 25 years (t/ha)

Comparing the allocated dry matter of the different phytomass components (tree parts) to each other, the needle mass per tree correlates strongly with crown volume (m^3), cone crop (kg) and the total amount of woody parts of the tree, respectively (Figure 4).

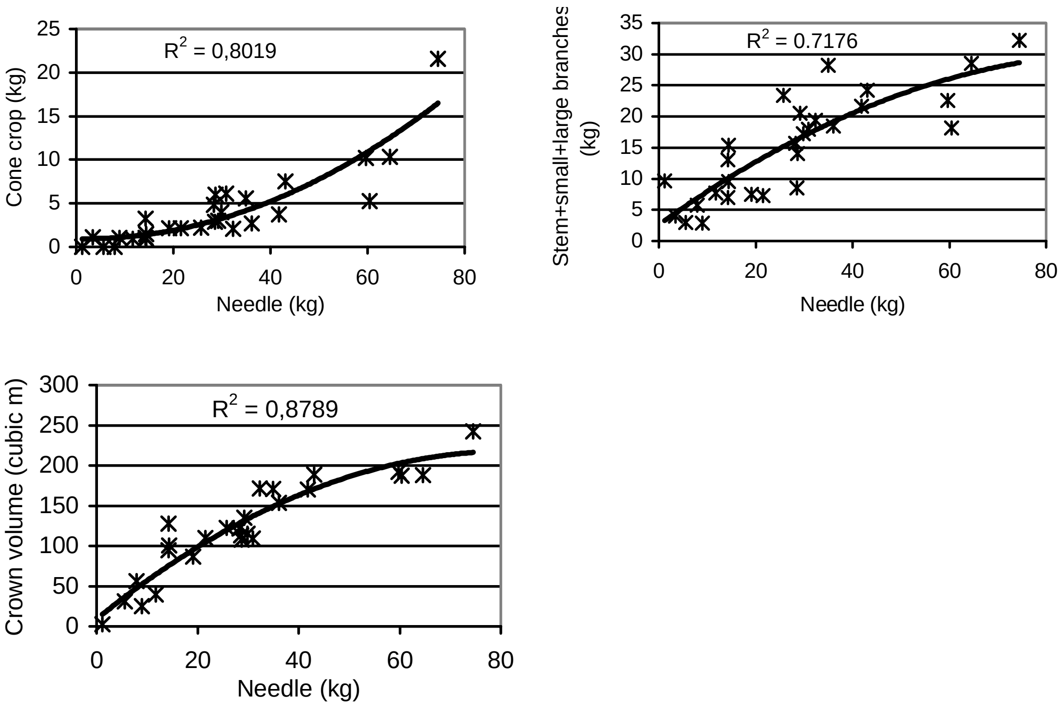


Figure 4: Relations between needle mass, cone crop, woody parts and crown volume at age 25.

Canopy closure and ability of reproduction

The cone production increased with age, but after the trees reached full canopy closure, the crop per tree diminished, depending on year (Figure 5). After canopy closure, mortality also increased, for example in the 2×2 m spacing only 50% of the planted trees survived until age 25 (Figure 6). Mortality in this spacing (2×2 m) followed normal stem number decrease tendencies as described in Central European yield tables (Erteld 1963). Mortality in wide spacings can not be explained by competition effects. It is suspected that the relatively severe mortality in the spacing variant 8×16 m was caused by serious snow-brake damages, a recurrent problem of wide-spacing plantations.

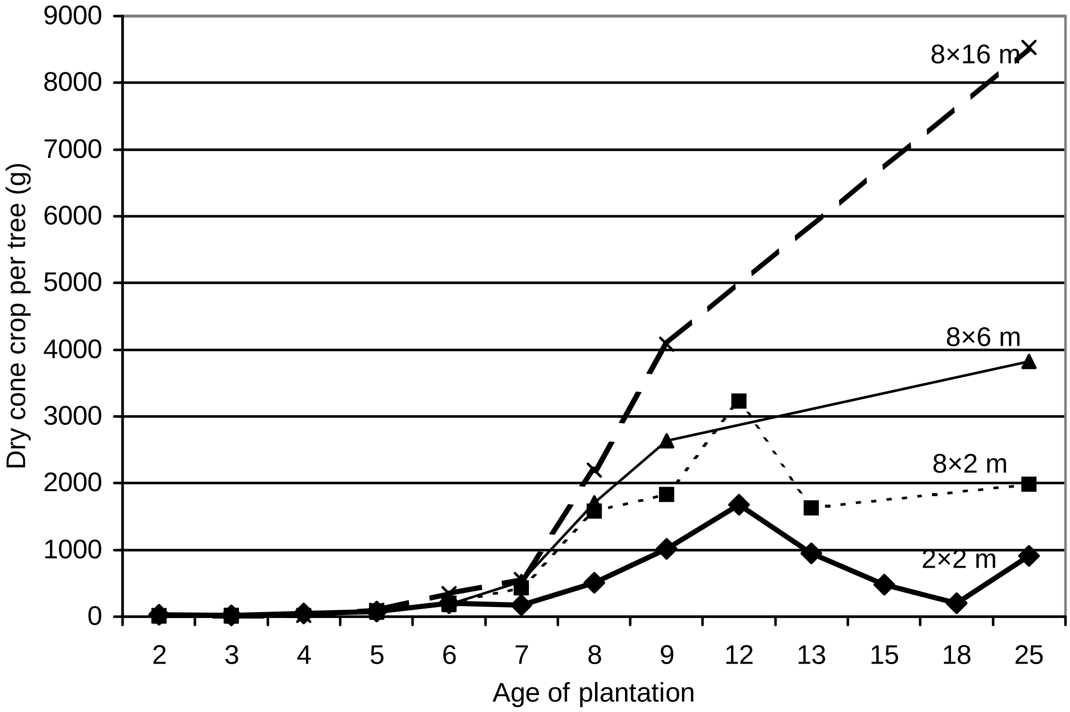


Figure 5: Development of cone production per tree until age 25 in the different spacings.

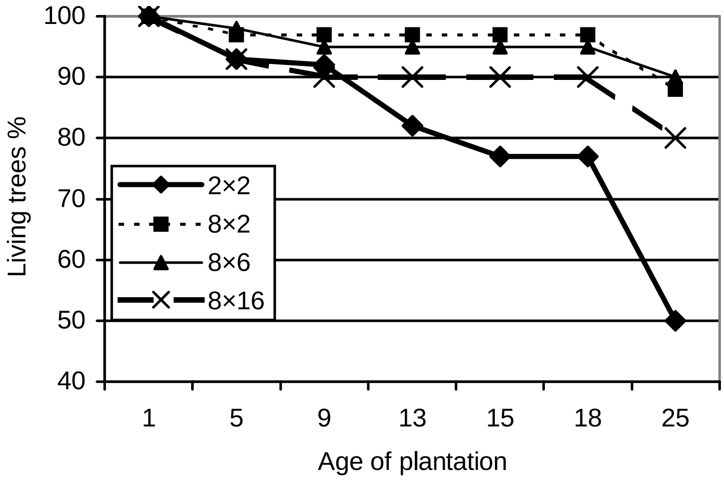


Figure 6: Mortality of trees observed in different spacings.

Regarding the cone crop at age 25, it is somewhat surprising, that although the quantity of cone produced per tree was the lowest in the narrow spacing variants, the amount of the cones per unit area (ha) was higher in these spacings (2×2 and 8×2 m) than in the wide ones.

Conclusions

Intraspecific competition in even-aged Scots pine stands has an effect on tree growth and on allocation rates of both the aboveground vegetative parts and of the quantity of cones and seeds.

The few available studies on allocation of dry matter in conifers usually found genetic components in allocation ratios. However, none of the studies have dealt with the effect of various levels of competition, as well as with the partitioning of assimilates into vegetative (stem, branch, shoot, and needles) and generative organs. In the present study, genetic components of allocation rates could not be traced, due to high within-clonal variation and low number of replicates. A high within-clonal variation is not unusual in Scots pine grafts, the suspected main cause of which is rootstock-scion interaction and partial incompatibility.

Regarding the reproductive input of the trees, it is surprising to note that there is only a negligible difference in seed crop per unit area (i.e. reproductive capacity) when comparing maximum-density and extreme wide spacings. This means that Scots pine at this age reacts to the ease of competition with excessive cone and seed production. In fact, the percentage of assimilates allocated to cones is nearly the same as the current stem increment in the widest spacing (11.4 and 11.7 percent respectively). The per tree difference between narrowest and widest spacing is only threefold for current stem increment, but 18-fold for cone crop.

Although generally assumed, reproductive capacity of a high-density plantation is not inferior to lower density situations.

Most (50 to 60 percent) of the dry matter is allocated to needle and shoot growth. In percentages, the differences between spacing variants are minor. In dry matter weight, however, free standing trees (8×16 m spacing) produce ten times more green substance than trees at maximum density, which certainly provide improved living conditions for inhabiting birds and insects of this forest type.

Increasing crown size needs stronger branches. The dry matter allocated to the formation of branches above 5 cm diameter in the year of sampling was only 0.03 kg/tree in the densest, but 5.09 kg/tree in the widest spacing.

From forestry point of view, the dry matter allocated to stem formation is an important value. It is no surprise that at age 25 the stemwood proportion of the total aboveground biomass is 60 percent at maximum density as compared to 30 percent in the widest spacing. The harvestable biomass in tons per hectare is nearly a magnitude higher in the maximum-density variant as in the widest spacing (58.3 tons and 6.9 tons of stemwood, respectively): a strong argument for foresters to transform open woodlands into dense forests.

References

1. Bánó I. (1971): Conifer seed orchards in Hungary. (15 year results of observations of flowering and seeding of Scots pine clones.) *Erdészeti Kutatások* 1971. Vol. 67. II. p. 81-109.
2. Cannel, M. G. R., Sheppard, L. J., Ford, E. D. and Wilson, R. H. F. (1983): Clonal differences in dry matter distribution, wood specific gravity and foliage "efficiency" in *Picea sitchensis* and *Pinus contorta*. *Silvae Genet*., 32: 195-202.
3. Erteld, W. (1963): Ertragstafel-Auszüge. Neumann Verlag, Radebeul
4. Matthews, J. A., Feret, P. P., Magdewick, H. A. I. and Bramlett, D. L. (1975): Genetic control of dry matter distribution in twenty half-sib families of Virginia pine. In: Proc.Thirteenth Southern Forest Tree Improvement Conference. p. 234-241.
5. Peszlen I., Mátyás Cs., Varga G. and Szojákné-Török K. (1998): Dry matter allocation and wood quality in relation to spacing in a Scots pine (*Pinus sylvestris* L.) clone trial. In Peszlen I. (ed.): Environment and Wood Science, *Acta Facultatis Ligniensis*, 1998, pp. 15-22. University of Sopron., Hungary.
6. Shinozaki, K. and Kira, T. (1961): The C-D rule, its theory and practical uses (Intraspecific competition among higher plants. X.) Journ. Biol., Osaka City University, 12: 69-82.
7. Thompson, S. (1985): Branching habit and dry matter distribution in *Pinus contorta*. In Tigerstedt, P. M. A. (ed.): Crop physiology of forest trees. Helsinki, Univ. p. 285-293.
8. Van Buijtenen, J. P. (1979): Genetic differences in dry matter distribution between stems, branches and foliage in loblolly and slash pine. In: Holiis, C. A. and A. E. Squillace (ed.): Proceedings of the Fifth North American Forest Biology Workshop. p. 235-241. School of Forest Resources, University of Florida, Gainsville, Fl., U.S.A.
9. Wu, H. X. and Yeh, F. C. (1997): Genetic effect on biomass partition and tree architecture in seedlings *Pinus contorta ssp. latifolia*, in Alberta, Canada. *Forest Genetics* 4 (3): 123-130.