

## The influence of age and crown position on growth efficiency along a Scots pine chronosequence

Mieczysław Turski,  
Hanna Kwaśna,  
Cezary Beker,  
Roman Jaszczak,  
Katarzyna Kaźmierczak,  
Tomasz Najgrakowski,  
Wojciech Borzyszkowski

The study deals with the effects of age and crown position (either dominant or intermediate, as determined by Kraft's social class) on stemwood growth efficiency ( $GE$ ), which is viewed as the ratio of annual stemwood volume increment of the previous five years to needle volume of the entire tree, in eight even-aged pure stands of Scots pine (*Pinus sylvestris* L.). The highest  $GE$  was observed in the youngest stands, and the lowest in the oldest ones. There was no clear interdependence of  $GE$  on the age of intermediate stands.  $GE$  was most variable in the youngest, the 25-year-old stand, and was the least variable in the 74-year-old stand.  $GE$  in dominant trees was lower in 25-, 74- and 85-year-old stands and higher in 33-, 44-, 56-, 64- and 93-year-old stands. The  $GE$  ratios of dominant trees to intermediate trees in 25-, 33-, 44-, 56-, 64-, 74-, 85- and 93-year-old stands were 0.47:1, 1:0.93, 1:0.87, 1:0.81, 1:0.86, 0.88:1, 0.90:1 and 1:0.61, respectively. Tree age had a statistically significant effect on  $GE$ ; however, the contribution of the age factor to  $GE$  was assessed as weak. Generally, the position of trees (whether dominant or intermediate) had no effect on  $GE$ , while age  $\times$  position of trees had a statistically significant effect on  $GE$ , which means that the two factors interacted. The correlation between  $GE$  and tree height, diameter at breast height (DBH), and the needle volume of the entire empirical material was statistically significant with a negative sign; however, the situation varied among the particular stands.

**Keywords:** Pine, Needle Volume, Growth Efficiency, Dominant Trees, Intermediate Trees

### Introduction

The growth of forests is a function of resource supply, the proportion of resources used by trees, and the efficiency with which the resources are used for carbon dioxide fixation. Growth efficiency ( $GE$ ) estimated as the ratio between biomass production and resource supply is an indicator of forest productivity. It can be determined as either gross or net primary production. Gross primary production refers to the total biomass produced at a certain time and area. Net primary production is defined as the biomass that remains after the elimination of respiration losses. Light, water or nutrient supply can be used as a denominator. Light (or proxies for light) was found to be most closely related to wood production, as it is the main driver for photosyn-

thesis (Monteith 1972). The production of wood depends on the absorption of light, and the efficiency with which it is used. Larger trees absorb more light and use it more efficiently (Binkley et al. 2013). Their greater growth results from a combination of increased light absorption and increased efficiency.

The  $GE$  index may be determined in various ways depending on the available volume increments and the measured elements of the crown. Dengler (1937) defined it as the ratio of increment in stem volume to dry needle mass. Schmidt (1953) defined it as the mass of annual increment in the absolute dry matter of wood per unit of dry needle mass. Mayer (1958) introduced the concept of assimilation intensity or assimilation energy, defined on the basis

of annual increment in tree volume per unit area of crown projection or crown mantle. A similar approach was adopted by Borowski (1966). Lemke (1968) proposed determining the  $GE$  in Scots pine (*Pinus sylvestris* L.) as the ratio of increment in stem volume to volume of leafy twigs. Waring et al. (1980) calculated  $GE$  from the ratio of stemwood volume increment ( $v_i$ ,  $\text{dm}^3$ ) to projected leaf area. The index proposed by Waring et al. (1980) is the one most commonly used nowadays.

There are three relationship patterns between growth efficiency ( $GE$ ) and projected leaf area ( $LA$ ): monotonic increasing, peaking, or monotonic decreasing. All of them arise from a strong relationship between the increment of stemwood volume and the area of projected leaves. The graphs display concave, sigmoid or convex shapes (Seymour & Kenefic 2002). Interestingly, the monotonically decreasing  $GE$  pattern appears to gather strong empirical support (Roberts et al. 1993, Gilmore & Seymour 1996, Maguire et al. 1998).

The variation in  $GE$  is relatively well scrutinized among the even-aged stands of a single species. However, it is less evident in cases of varied structural characteristics, i.e., a history of past suppression (Maguire et al. 1998) or specific forest management (Vose & Allen 1988, Velazquez-Martinez et al. 1992), site quality, stand structure, canopy strata, age and tree size or crown

□ Department of Forest Management, Faculty of Forestry, Poznań University of Life Sciences, Poznań (Poland)

@ Mieczysław Turski ([mieczyslaw.turski@up.poznan.pl](mailto:mieczyslaw.turski@up.poznan.pl))

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class (O'Hara 1988, 1996, Long & Smith 1990, Roberts & Long 1992, Gilmore & Seymour 1996, Sterba & Amateis 1998, Seymour & Kenefic 2002, Burkes et al. 2003, Reid et al. 2004, Berrill & O'Hara 2007), as well as shade tolerance (Roberts et al. 1993, Gersonde & O'Hara 2005).

The aim of this study was to investigate the effects of age and different positions of the crown (dominant or intermediate, as determined by Kraft's social class) on growth efficiency in eight even-aged and pure stands of Scots pine (*P. sylvestris*) which grew in one location in western Poland. The study evaluates differences in productivity potential in the naturally variable *P. sylvestris* chronosequence.

Owing to concerns expressed by Waring et al. (1980) about their own *GE* index, which proved to be inconsistent with suppressed trees and may be sensitive to environment and the influence of competition, *GE* in this study was calculated following the model of Lemke (1968) with modification introduced by the authors. The *GE* used in the study is viewed as a ratio of annual increment in stemwood volume of the last five years to volume of twigs with needles which come from the entire tree. A similar approach has recently been proposed by Burkes et al. (2003), who calculated growth efficiency as an annual increment in stemwood volume to needle biomass. Therefore, the following two hypotheses were considered: (i) both tree age and biosocial position are factors which influence growth efficiency; and what is more (ii) growth efficiency depends on the size of the tree (breast height and height) and the volume of needles.

## Material and methods

The empirical material was comprised of measurements taken from 200 sample trees, which were selected from among eight Scots pine stands, according to the Draudt scheme.

### Study site

The sampling process was carried out in

eight pure stands of the Scots pine (*P. sylvestris*) growing in a fresh mixed forest, close to Murowana Goslina (52° 34' N, 17° 00' E) in western Poland. The stands were even-aged (25-, 33-, 44-, 56-, 64- 74-, 85- and 93-years-old) and were characterized by irregular canopies. In each stand one plot with 200-350 trees was chosen. The reasoning behind choosing the particular plot locations in each stand was in order to minimize the non-age-related differences between the trees. All plots created a trajectory of changes resulting from the chronosequence. The volume-based stand density was 0.81-1.23 and the number of trees per hectare was 402-2927 (Tab. 1). The average temperature in the five years prior to the study was 8.02 °C, with average annual rainfall at 544.2 mm.

### Sample tree selection

All trees in each plot were numbered. The height (*h*, m) and diameter at breast height (*d*<sub>1.3</sub>, cm) of each of the standing trees was determined. The mean stand height (*H*, m) was calculated following Lorey's model. The mean diameter at breast height (*D*<sub>g</sub>, cm) of the stand was calculated as DBH of the tree with mean basal area. In each plot, 25 sample trees (200 in total, from all of the eight stands) were selected according to the Draudt method.

### Measurements on the sample trees

The social position of each tree within the stand was assessed according to Kraft's classification. The sample trees were felled and divided into one-meter-long sections. Stemwood discs which were 5-cm thick were cut at the heights of 0.0, 0.5, 1.3 (breast height), 1.5, 2.5 m, and upwards to the top. All twigs with needles were trimmed from the crown of each tree, and their mass (*M*, kg) was determined immediately afterwards. The samples of fresh twigs with needles were collected for laboratory analyses; 20% of twigs were collected for laboratory analyses from the trees aged between 25 and 56 years, whereas in the group aged 64-93 years

only 10% of twigs were collected. The sample mass of twigs with needles (*M*<sub>s</sub>, kg) was not lower than 2 kg and its weight depended on the stand's age.

### Laboratory procedure

Stemwood discs were used to estimate the stemwood volume and to calculate the mean annual stemwood volume increment in the previous five years (*i*<sub>v1</sub>, m<sup>3</sup>). The twig samples with needles were used to estimate the volume of needles from one tree (*v*<sub>n</sub>, m<sup>3</sup>). Next, the needles were separated from the twigs and then the total volume of needles in each sample was measured by means of xylometry, and this was used to determine the volume of needles of the entire tree (*v*<sub>n</sub>, m<sup>3</sup>) according to the formula (eqn. 1):

$$v_n = \frac{v_i M}{M_s} \quad (1)$$

*GE* was estimated from the ratio of annual stemwood volume increment in the previous five years (*i*<sub>v1</sub>) to needle volume of the entire tree (*v*<sub>n</sub>). *GE* indicates the volume of stemwood produced within one year per needle volume of the entire tree.

### Statistical analysis

The *GE* of each of 200 sampled trees allowed the calculation of the arithmetic means and coefficients of variation (*CV*) for each of the eight examined stands. Both measures were calculated for dominant (Kraft's classes 1, 2, 3) and intermediate trees (Kraft's classes 4, 5). The assumptions of normality and the equal variance of *GE* were assessed using the Shapiro-Wilk test in order to adopt the appropriate tests and procedures necessary for further analysis. The relationship between *GE* and height (*h*), diameter at breast height (*d*), and needle volume of the trees (*v*<sub>n</sub>) in each stand was assessed using the Pearson's correlation coefficient. The differences in *GE* between the eight stands and the contribution of the independent variables (age, dominant or intermediate trees, age × dominant or intermediate trees) to *GE*

**Tab. 1** - Structural characteristics of stands and sample trees. (*D*<sub>g</sub>): mean diameter at breast height; (*H*): mean stand height; (*d*<sub>1.3</sub>): diameter at breast height; (*h*): tree height; (*v*<sub>n</sub>): needle volume of the whole tree; (*i*<sub>v1</sub>): mean annual stemwood volume increment in the previous 5 years; (*CV*): coefficient of variation.

Stand		Sample trees													
Age (yrs)	Density	Trees ha <sup>-1</sup>	<i>D</i> <sub>g</sub> (cm)	<i>H</i> (m)	<i>d</i> <sub>1.3</sub> (cm)		<i>h</i> (m)		<i>v</i> <sub>n</sub> (m <sup>3</sup> )		<i>i</i> <sub>v1</sub> (m <sup>3</sup> )		Number of sample trees		
					Mean	CV (%)	Mean	CV (%)	Mean	CV (%)	Mean	CV (%)	Dominant trees	Intermediate trees	
25	1.17	2590	13.4	15.49	12.9	24.4	13.4	9	0.0094	100.1	0.0067	71.8	19	6	
33	1.2	2927	13.7	16	12.2	29.5	14.6	7.9	0.0082	77.5	0.0055	83.3	17	8	
44	1.23	1225	20.4	21.23	19	22.4	20.4	7.1	0.0151	69.8	0.0138	64.1	18	7	
56	1.1	1160	20	21.65	17.8	25.7	20	8.9	0.0139	73.7	0.0119	73	17	8	
64	0.94	766	23.7	24.74	21.9	21.7	23.2	8	0.0204	62	0.0155	66.9	17	8	
74	0.81	537	25.5	24.46	24.8	21.3	23.4	7	0.0197	64.2	0.0156	57.2	19	6	
85	0.88	419	30.8	28.32	30.2	17.9	26.8	6.3	0.0293	54.9	0.0234	51.3	20	5	
93	0.91	402	31.4	26.12	29.4	17.6	25.6	5.9	0.0334	53.5	0.0162	59.2	19	6	

**Tab. 2** - Growth efficiency (GE) of all sample trees and of dominant and intermediate trees.

Age of stand (yrs)	All sample trees				Dominant trees		Intermediate trees		Contribution of dominant trees (%)
	Mean	Min	Max	CV (%)	Mean	CV (%)	Mean	CV (%)	
25	0.9515	0.4854	2.6286	57.6	0.7493	27.8	1.5919	50.1	-53
33	0.6713	0.4912	0.888	19	0.6867	16.5	0.6386	24.8	+7.5
44	0.9116	0.3292	1.3099	24.1	0.9444	18.4	0.8271	37.5	+14
56	0.8478	0.4883	1.2347	21.2	0.9028	18.6	0.7308	21	+23.5
64	0.7299	0.4432	0.952	17.9	0.7628	14.6	0.6599	22.6	+15.5
74	0.8317	0.5473	1.06	17.1	0.8047	18.3	0.9174	9.4	-12
85	0.8377	0.3508	1.3421	29	0.8193	31.1	0.9113	20.9	-10
93	0.4789	0.2086	0.8701	33.7	0.5279	27.8	0.3239	29.5	+63

were analyzed using a two-way ANOVA. The significance of the difference between GE in the eight stands was calculated using the non-parametric Kruskal-Wallis test. The computed probability level for this test was  $<0.0001$ . The extent of the influence of age and position on growth efficiency was analyzed with coefficients  $\eta^2$  and  $\omega^2$  (Stanisz 2007).  $\eta^2$  is the proportion of variance associated with one or more main effects, errors or interactions in ANOVA, while  $\omega^2$  is a measure of effect size, or the degree of association for a population.

## Results

The structural characteristics of each stand (density, number of trees per hectare, average diameter at breast height and mean stand height) and of the sample trees are presented in Tab. 1. In the sample trees: (i) diameter at breast height ( $d_{1.3}$ ) and the tree height ( $h$ ) were smallest in, respectively, the 33- and 25-year-old stands (12.2 cm and 13.4 m) and they increased with age (30.2 cm and 26.8 m in the 85-year-old stand); (ii) needle volume ( $v_n$ ) and annual stemwood volume increment ( $i_v$ ) were lowest in the 33-year-old stand (0.0082 m<sup>3</sup> and 0.0055 m<sup>3</sup>, respectively) and highest in the 85- and 93-year-old stands (0.0293 m<sup>3</sup> and 0.0334 m<sup>3</sup>, and 0.0162 m<sup>3</sup> and 0.0234 m<sup>3</sup>); (iii) trees with a dominant crown position accounted for 68% in the 33-, 56- and 64-year-old stands and up to 80% in the 85-year-old stand. The smallest variation was observed in the tree diameter at breast height (17.6-29.5%) and the tree height (5.9-9.0%). A much greater variation occurred in the needle volume (53.5-100.1%) and the annual stemwood volume increment (51.3-83.3%). The variability of the individual characteristics was most noticeable in the two youngest stands, and smallest in the two oldest stands.

In the sample trees, GE was: (i) highest in the youngest, 25-year-old stand (0.9515) and smallest in the oldest, 93-year-old stand (0.4789 – Tab. 2); (ii) similar in the 56-, 74- and 85-year-old stands (0.8317-0.8478); (iii) variable between 33- and 85-year-old-stands; (iv) most variable (5.4-fold, CV = 57.6%) and least variable (1.8-fold, CV = 17.1%) in, respectively, the 25- and 74-year-old stands; (v) higher in dominant trees than in the intermediate trees of the 33-,

**Tab. 3** - Results of ANOVA tests for the effect of age and position on growth efficiency (GE). (df): degrees of freedom.

Effect	SS	df	MS	F	p
Intercept	98.81039	1	98.81039	2103.699	<0.0001
Age	5.92625	7	0.84661	18.024	<0.0001
Dominant and intermediate trees	0.09795	1	0.09795	2.085	0.1504
Age × dominant and intermediate trees	3.76578	7	0.53797	11.453	<0.0001
Error	8.64245	184	0.04697		

**Tab. 4** - Contribution of age and position to growth efficiency (GE, %).

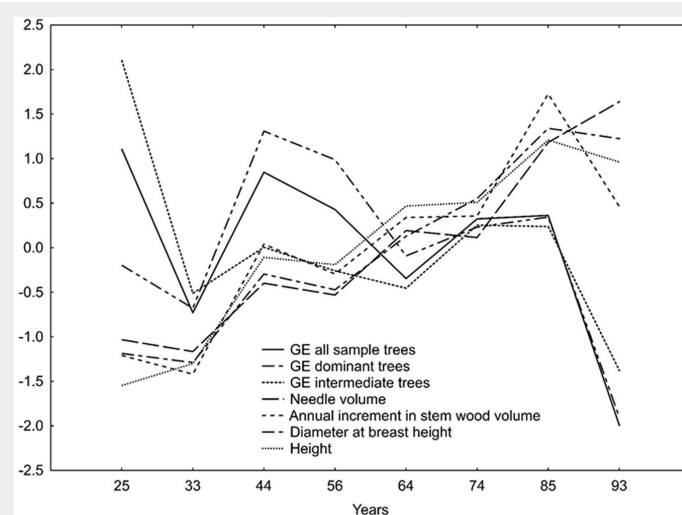
Independent variable	$\eta^2$	$\omega^2$
Age	40.68	30.29
Dominant and intermediate trees	1.12	0.28
Age × dominant and intermediate trees	30.35	18.60

44-, 56-, 64- and 93-year-old stands (from 7.5 to 63%); (vi) lower in the dominant trees than in the intermediate trees of the 25-, 74- and 85-year-old stands (over twofold in the youngest stand). In the dominant trees, GE varied most in the 85-year-old stand (CV = 31.1%) and least in the 64-year-old stand (CV = 14.6%). In intermediate trees, GE was most variable in the 25-year-old stand (CV = 50.1%).

The age of trees had a statistically significant effect on GE ( $F_{Age} = MS_{Age} / MS_{Error} = 18.024$  (Tab. 3). The contribution of age to

GE was 40.68% (see  $\eta^2_{Age}$  in Tab. 4). The sum of the partial variance  $\omega^2$  was 49.17%.

In comparison to the intermediate trees, GE in the dominant trees was lower in 25- 74- and 85-old stands (10-53%) and greater in 33- 44-, 56- 64- and 93-old-stands (7.5- 63% – Tab. 2). The ratios of the GE of dominant trees to the GE of intermediate trees in 25-, 33-, 44-, 56-, 64-, 74-, 85- and 93-year-old stands were 0.47:1, 1:0.93, 1:0.87, 1:0.81, 1:0.86, 0.88:1, 0.90:1, and 1:0.61. Generally, however, the position of trees (whether dominant or intermediate) had no signifi-

**Fig. 1** - Growth efficiency (GE) in sample trees in association with mean height, mean diameter at breast height, annual stemwood volume increment and needle volume (standardized values – Statistica® ver. 13.1, Tulsa, OK, USA).

**Tab. 5** – Pearson's correlation coefficients between growth efficiency (GE) and diameter at breast height ( $d_{1.3}$ ), tree height ( $h$ ) and needle volume ( $v_n$ ). (\*):  $p < 0.05$ .

Age of stand (years)	$d_{1.3}$	$h$	$v_n$
25	-0.528*	-0.505*	-0.460*
33	0.180	0.234	-0.023
44	0.283	0.526*	0.014
56	0.350	0.388	0.064
64	0.451*	0.477*	0.401*
74	-0.295	-0.166	-0.484*
85	-0.131	0.005	-0.321
93	0.430*	0.548*	0.095
25-93 (all sample trees)	-0.144*	-0.155*	-0.195*

**Tab. 6** - Assessment of normality of distribution of growth efficiency using the Shapiro-Wilk test.

Shapiro-Wilk test	Stand (years)							
	25	33	44	56	64	74	85	93
W	0.70328	0.92582	0.97733	0.95761	0.96254	0.96259	0.97887	0.95334
p-value	0.00001	0.06964	0.82769	0.36887	0.46727	0.46838	0.86172	0.29774

cant effect on GE ( $p = 0.1504$ ,  $\eta^2_{\text{Dominant and intermediate trees}} = 1.12$  – Tab. 3, Tab. 4).

Age  $\times$  position of trees had a statistically significant effect on GE, which means that the two factors interacted ( $\eta^2_{\text{Age} \times \text{dominant and intermediate trees}} = 30.35$  – Tab. 4). The contribution of other factors (including any that were not part of this study) was 50.83% (Tab. 4).

GE was negatively correlated with tree height, diameter at breast height, and needle volume at the ages of 25 and 74 (partly), and positively correlated at the ages of 44, 64, and 93 years (partly – Tab. 5). A long-lasting GE decline was, however, associated with the independent, possibly confounding, effects of a moderate but continuous increase in mean tree height, mean diameter at breast height, annual stemwood volume increment, and needle volume (Fig. 1).

The Shapiro-Wilk test indicated that the GE of 25-year-old trees was not normally distributed. Thus, the non-parametric Krus-

kal-Wallis test was used to compare the mean GE of the sample trees from the eight stands. The results showed that the GE of trees was not significantly different among the majority of stands. Multiple comparison analyses showed that the GE of trees in the 93-year-old stand differs significantly from all the others, except the 33-year-old one. Another significant difference occurs between 33- and 44-year-old trees; the differences in GE among trees of other ages were statistically insignificant (Tab. 6, Tab. 7).

## Discussion

The growth of individual forest trees declines with age and, furthermore, the decline stems from their reduced resource-use efficiency (Ryan et al. 1997).

We observed that the GE of a *P. sylvestris* forest in even-aged plantations varied with age. Generally, in the long term, between the ages 25-93, there was a slow but continuous decline, with temporary fluctua-

tions observed as the stand was aging. The highest GE value was observed relatively early, in the 25-year-olds. This was followed by a substantial aberration between 30- and 85-year-olds and a sudden decline afterwards (GE = 0.4789 at 93 years). The high GE in the youngest plantation resulted largely from the contribution of the intermediate trees.

Such or similar age-related GE patterns have also occurred in other coniferous and deciduous forests (Long & Smith 1990, Gower et al. 1996, Kira & Shidei 1967, Ryan et al. 1997, 2004). *P. sylvestris* is the most widely distributed pine species in the world, found in many, ecologically diverse habitats, and has become very important commercially, socially and culturally. Only recently its growth has been studied by numerous authors (Vanninen & Mäkelä 2000, Martínez-Vilalta et al. 2007, Riofrío et al. 2016).

Although the growth efficiency was calculated as a ratio of annual increment in the stemwood volume to the volume of needles, and not to the projected leaf area as proposed by Seymour & Kenefic (2002), we still observed the monotonically decreasing pattern, which is the most common one. In Poland similar monotonically decreasing patterns of GE in *P. sylvestris* were earlier observed by Lemke (1974). A similar pattern among *Abies balsamea* (L.) Mill., *Picea rubens* Sarg., *Pinus contorta* Dougl. ex Loud, and *Pinus strobus* L. was observed in Europe and the USA by Roberts et al. (1993), Maguire et al. (1998), and DeRose & Seymour (2009).

We also analyzed fluctuations in GE in dominant vs. intermediate trees and the results were connected with age. A higher GE of dominant trees was observed in most stands and ages; however, it declined with age. The ratio of the GE of dominant trees to the GE of intermediate trees was only partly in agreement with Lemke's estimates (Lemke 1968), who observed that in a 35-year-old stand of *P. sylvestris* the ratios of the GE of class 1 trees to the GE of class 2, 3, 4 and 5 trees were 1:1.18, 1:1.13, 1:0.94 and 1:0.67, and in a 50-year-old stand the

**Tab. 7** - Significance of differences in growth efficiency (GE) among the eight studied stands. Multiple comparisons p-values (Kruskal-Wallis test, 2-tailed) are shown. Independent (grouping) variable: Age (years); Kruskal-Wallis  $H_{[7,200]} = 63.82966$ ,  $p < 0.0001$ . (R): mean rank value.

Stand Age (years)	Stand Age (years)							
	25 (R=108.76)	33 (R=71.920)	44 (R=138.04)	56 (R=122.00)	64 (R=91.520)	74 (R=122.76)	85 (R=118.48)	93 (R=30.520)
25	-	0.683929	1.000000	1.000000	1.000000	1.000000	1.000000	0.000049
33	0.683929	-	0.001504	0.062156	1.000000	0.053180	0.124702	0.320371
44	1.000000	0.001504	-	1.000000	0.125662	1.000000	1.000000	<0.000001
56	1.000000	0.062156	1.000000	-	1.000000	1.000000	1.000000	0.000001
64	1.000000	1.000000	0.125662	1.000000	-	1.000000	1.000000	0.005444
74	1.000000	0.053180	1.000000	1.000000	1.000000	-	1.000000	<0.000001
85	1.000000	0.124702	1.000000	1.000000	1.000000	1.000000	-	0.000002
93	0.000049	0.320371	<0.000001	0.000001	0.005444	<0.000001	0.000002	-

ratios were 1:1.10, 1:1.02, 1:0.77 (with no class 5).

The fluctuations in age-related GE agree with the hypothesis put forward by Binkley (2004), who observed regular and continuous changes in contribution of dominant and non-dominant trees to productivity of forest. In younger stands, prior to canopy closure, the dominance is usually low, and resource-use efficiency for all trees is high. In older stands near canopy closure, however, the increasing dominance reduced resource-use efficiency by non-dominant trees, which decreased forest productivity. Furthermore, in older stands the resource-use efficiency continuously declined in the largest trees and reduced the level of dominance. The growth dominance pattern has been observed in stands of native forest co-dominated by *Pseudotsuga menziesii* Carrière, *Tsuga heterophylla* (Raf.) Sarg. and *Picea sitchensis* (Bong.) Carr. (Binkley 2004), *Pinus elliottii* Engelm. and *Pinus taeda* L. (Martin & Jokela 2004), and *Pinus resinosa* Sol. ex Aiton (Bradford et al. 2010).

An increasing GE in trees with more dominant crown classes of the same species has been observed by Waring et al. (1980), O'Hara (1988), and Sterba (2005). However, Reid et al. (2004) found an opposed pattern. The differences resulted from stand structure, ecological conditions, species-specific effects, methods used to evaluate tree increment and crown projection area, and variations in assimilation efficiency. The history of past suppression, planting density, canopy/strata class, age, size, availability of light, and tolerance to shade have significant effects on the crown leaf area, contributing to growth efficiency (Assmann 1961, Schulze et al. 1977, Chen et al. 1996, O'Hara 1996, 1988, Maguire et al. 1998, Sterba & Amateis 1998, Seymour & Kenefic 2002, Burkes et al. 2003, Reid et al. 2004, Gersonde & O'Hara 2005). It is vital to observe that (i) greater past suppression diminished growth efficiency in *Picea rubens*; (ii) shade significantly decreased (50%) growth efficiency in intermediate trees of *Betula* and *Picea*, compared to dominant trees growing under advantageous light conditions; (iii) low density of planting decreased growth efficiency in *Pinus taeda* and *Pinus elliottii*.

This study was conducted on sites which were considered as having a high productivity potential. A better site quality usually positively influences GE. The effect may, however, be species-specific; GE increased significantly in shade-intolerant *Abies balsamea*, moderately in shade-tolerant *Abies lasiocarpa* (Hook.) Nutt. and *Picea engelmannii* Parry ex Engelm., and was stable in shade-tolerant *Picea rubens* and shade-intolerant *Pinus contorta* (Meng & Seymour 1992, Reid et al. 2004, Seymour & Kenefic 2002). It is possible that the GE response depends on site quality. However, the reaction depends also on the species. DeRose & Seymour (2009) observed that a higher site index caused an increase in growth ef-

iciency in *Abies balsamea*, but not in *Picea rubens*.

## Conclusion

The long-term productivity of *P. sylvestris* forest declines with age. The greatest mean growth efficiency in the Scots pine was found in the youngest trees, while it was lowest for the oldest trees. This may result from the fact that the analyses did not include increment in the biomass of branches or roots, increasing with age.

The mean growth efficiency of the youngest intermediate trees was over 2-fold greater than for the dominant trees. An opposite situation was found in the oldest trees, in which mean growth efficiency for dominant trees was over 1.6-fold greater than for intermediate trees.

The greatest variation in growth efficiency was observed for the youngest trees. Regarding tree social position, variation in the growth efficiency of intermediate trees is greater than that of dominant trees in six out of eight analyzed stands.

Only in the youngest stand and in the 64-year-old stand we found a significant dependence of growth efficiency (GE) on diameter at breast height ( $d_{1.3}$ ), tree height ( $h$ ), and needle volume ( $v_n$ ) observed. An increase in each of the three traits in the case of the youngest trees resulted in a reduction of growth efficiency, while for 64-year-old trees it led to its increase. The two-way analysis of variance indicated a significant effect of the tree age on growth efficiency. However, the affiliation of trees to the group either as dominant or intermediate trees caused no such effect.

According to the arbitrary scale of effects of the analysis of variance given by Cohen (1988), the effect of the age on the growth efficiency needs to be considered as weak (30.29%), that of the social class of tree position (dominant vs. intermediate trees) very small (0.28%), while that of the interaction of factors dominant or intermediate trees as small (18.60%).

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## References

- Assmann E (1961). Waldertragskunde. [Forest Yield Science]. BLV-Verlagsgesellschaft, München-Bonn-Wien, pp. 490. [in German]
- Berrill JP, O'Hara KL (2007). Patterns of leaf area and growing space efficiency in young even aged and multiaged coast redwood stands. *Canadian Journal of Forest Research* 37 (3): 617-626. - doi: [10.1139/X06-271](https://doi.org/10.1139/X06-271)
- Binkley D (2004). A hypothesis about the interaction of tree dominance and stand production through stand development. *Forest Ecology and Management* 190: 265-271. - doi: [10.1016/j.foreco.2003.10.018](https://doi.org/10.1016/j.foreco.2003.10.018)
- Binkley D, Laclau JP, Sterba H (2013). Why one

tree grows faster than another: patterns of light use and light use efficiency at the scale of individual trees and stands. *Forest Ecology and Management* 288: 1-4. - doi: [10.1016/j.foreco.2012.08.009](https://doi.org/10.1016/j.foreco.2012.08.009)

- Borowski M (1966). Über den Zuwachs der sozialen Baumklassen in Kiefernbeständen. [About the growth of social tree classes in pine stands]. *Archiv für Forstwesen* 3: 233-241. [in German]
- Bradford JB, D'Amato AW, Palik BJ, Fraver S (2010). A new method for evaluating forest thinning: growth dominance in managed *Pinus resinosa* stands. *Canadian Journal of Forest Research* 40 (5): 843-849. - doi: [10.1139/X10-039](https://doi.org/10.1139/X10-039)
- Burkes EC, Will RE, Barron Gafford GA, Teskey RO, Shiver B (2003). Biomass partitioning and growth efficiency of intensively managed *Pinus taeda* and *Pinus elliottii* stands of different planting densities. *Forest Science* 49 (2): 224-234. [online] URL: <http://academic.oup.com/forestscience/article/49/2/224/4617479/>
- Chen HYH, Klinka K, Kayahara GJ (1996). Effect of light on growth, crown architecture, and specific leaf area for naturally established *Pinus contorta* var. *latifolia* and *Pseudotsuga menziesii* var. *glauca* saplings. *Canadian Journal of Forest Research* 26 (7): 1149-1157. - doi: [10.1139/X26-128](https://doi.org/10.1139/X26-128)
- Cohen J (1988). *Statistical power analysis for behavioral sciences* (2<sup>nd</sup> edn). Lawrence Erlbaum Associates, Hillsdale, NJ, USA, pp. 567.
- Dengler A (1937). Kronengröße, Nadelmenge und Zuwachsleistung von Altkiefern [Crown size, needle quantity and increment performance of old pines]. *Zeitschrift für das Forst- und Jagdwesen* 69: 321-336. [in German]
- DeRose RJ, Seymour RS (2009). The effect of site quality on growth efficiency of upper crown class *Picea rubens* and *Abies balsamea* in Maine, USA. *Canadian Journal of Forest Research* 39 (4): 777-784. - doi: [10.1139/X09-012](https://doi.org/10.1139/X09-012)
- Gersonde RF, O'Hara KL (2005). Comparative tree growth efficiency in Sierra Nevada mixed-conifer forests. *Forest Ecology and Management* 219 (1): 95-108. - doi: [10.1016/j.foreco.2005.09.002](https://doi.org/10.1016/j.foreco.2005.09.002)
- Gilmore DW, Seymour RS (1996). Alternative measures of stem growth efficiency applied to *Abies balsamea* from four canopy positions in central Maine, USA. *Forest Ecology and Management* 84 (1-3): 209-218. - doi: [10.1016/0378-1127\(96\)03728-0](https://doi.org/10.1016/0378-1127(96)03728-0)
- Gower ST, McMurtrie RE, Murty D (1996). Above ground net primary production decline with stand age: potential causes. *Trees* 11 (9): 378-382.
- Kira T, Shidei T (1967). Primary production and turnover of organic matter in different forest ecosystems of the western Pacific. *Japanese Journal of Ecology* 17 (2): 70-87. - doi: [10.1896/0/seitai.17.2\\_70](https://doi.org/10.1896/0/seitai.17.2_70)
- Lemke J (1968). Związek pomiędzy wielkoscia korony a przyrostem drzew w drzewostanach sosnowych [The dependence of the crown size and tree increment in the Pine stands]. *Prace Komisji Nauk Rolniczych i Komisji Nauk Lesnych PTPN* 25: 1-48. [in Polish]
- Lemke J (1974). Wydajność igliwia sosny zwyczajnej w produkcji drewna strzały. [Efficiency of Scots pine needles in stemwood production]. *Sylwan* 118 (9): 33-38. [in Polish]

- Long JN, Smith FW (1990). Determinants of stemwood production in *Pinus contorta* var. *latifolia* forests: the influence of site quality and stand structure. *Journal of Applied Ecology* 27 (3): 847-856. - doi: [10.2307/2404381](https://doi.org/10.2307/2404381)
- Maguire DA, Brissette JC, LianHong G (1998). Crown structure and growth efficiency of red spruce in uneven-aged, mixed-species stands in Maine. *Canadian Journal of Forest Research* 28: 1233-1240. - doi: [10.1139/x98-093](https://doi.org/10.1139/x98-093)
- Martin TA, Jokela EJ (2004). Developmental patterns and nutrition impact radiation use efficiency components in southern pine stands. *Ecological Applications* 14 (6): 1839-1854. - doi: [10.1890/03-5262](https://doi.org/10.1890/03-5262)
- Martínez-Vilalta J, Vanderklein D, Mencuccini M (2007). Tree height and age-related decline in growth in Scots pine (*Pinus sylvestris* L.). *Oecologia* 150 (4): 529-44. - doi: [10.1007/s00442-006-0552-7](https://doi.org/10.1007/s00442-006-0552-7)
- Mayer R (1958). Kronengröße und Zuwachsleistung der Traubeneiche auf süddeutschen Standorten [Crown size and productivity of sessile oak on sites in southern Germany]. *Allgemeine Forst- und Jagdzeitung* 129 (114): 151-163. [in German]
- Meng X, Seymour RS (1992). Influence of soil drainage on early development and biomass production of young, herbicide released fir-spruce stands in north central Maine. *Canadian Journal of Forest Research* 22: 955-967. - doi: [10.1139/x92-128](https://doi.org/10.1139/x92-128)
- Monteith JL (1972). Solar radiation and productivity in tropical ecosystems. *Journal of Applied Ecology* 9: 747-766. - doi: [10.2307/2401901](https://doi.org/10.2307/2401901)
- O'Hara KL (1988). Stand structure and growing space efficiency following thinning in an even aged Douglas fir stand. *Canadian Journal of Forest Research* 18 (7): 859-866. - doi: [10.1139/x88-132](https://doi.org/10.1139/x88-132)
- O'Hara KL (1996). Dynamics and stocking-level relationships of multi-aged ponderosa pine stands. *Forest Science* 42 (2): 1-34. [online] URL: [http://academic.oup.com/forestsience/article/42/suppl\\_2/a0001/4627269/](http://academic.oup.com/forestsience/article/42/suppl_2/a0001/4627269/)
- Reid DEB, Lieffers VJ, Silins U (2004). Growth and crown efficiency of height repressed lodgepole pine: are suppressed trees more efficient? *Trees* 18: 390-398. - doi: [10.1007/s00468-003-0317-4](https://doi.org/10.1007/s00468-003-0317-4)
- Riofrío J, Del Río M, Bravo F (2016). Mixing effects on growth efficiency in mixed pine forests. *Forestry* 90 (3): 381-392. - doi: [10.1093/forestry/cpw056](https://doi.org/10.1093/forestry/cpw056)
- Roberts SD, Long JN (1992). Production efficiency of *Abies lasiocarpa*: influence of vertical distribution of leaf area. *Canadian Journal of Forest Research* 22 (9): 1230-1234. - doi: [10.1139/x92-164](https://doi.org/10.1139/x92-164)
- Roberts SD, Long JN, Smith FW (1993). Canopy stratification and leaf area efficiency: a conceptualization. *Forest Ecology and Management* 60 (1-2): 143-156. - doi: [10.1016/0378-1127\(93\)90028-L](https://doi.org/10.1016/0378-1127(93)90028-L)
- Ryan MG, Binkley D, Fownes HJ (1997). Age-related decline in forest productivity: pattern and process. *Advances in Ecological Research* 27: 213-262. - doi: [10.1016/S0065-2504\(08\)60009-4](https://doi.org/10.1016/S0065-2504(08)60009-4)
- Ryan MG, Binkley D, Fownes HJ, Giardina CP, Senock RS (2004). An experimental test of the causes of forest growth decline with stand age. *Ecological Monographs* 74: 393-414. - doi: [10.1890/03-4037](https://doi.org/10.1890/03-4037)
- Schmidt H (1953). Kronen- und Zuwachsuntersuchungen an Fichten des bayerischen Alpenvorlandes [Crown and increment studies on spruce trees of the Bavarian Alpine foothills]. *Forstwissenschaftliches Zentralblatt* 72 (9-10): 276-286. [in German]
- Schulze ED, Fuchs M, Fuchs MI (1977). Spatial distribution of photosynthetic capacity and performance in a mountain spruce forest of northern Germany. *Oecologia* 30: 239-248. - doi: [10.1007/BF01833630](https://doi.org/10.1007/BF01833630)
- Seymour RS, Kenefic LS (2002). Influence of age on growth efficiency of *Tsuga canadensis* and *Picea rubens* trees in mixed-species, multi-aged northern conifer stands. *Canadian Journal of Forest Research* 32 (11): 2032-2042. - doi: [10.1139/x02-120](https://doi.org/10.1139/x02-120)
- Stanisz A (2007). Przystępny kurs statystyki z zastosowaniem STATISTICA PL na przykładach z medycyny [The intelligible statistics course using STATISTICA PL on examples from medicine]. StatSoft, Kraków, Poland, pp. 868. [in Polish]
- Sterba H (2005). Gibt es eine baumindividuelle Zuwachsoptimale Überschirmung - ein Beitrag zur Theorie des Einzelbaumwachstums [Is there a tree-specific growth-optimal shielding - a contribution to the theory of individual tree growth]. *Austrian Journal of Forest Science* 2: 55-68. [in German]
- Sterba H, Amateis RL (1998). Crown efficiency in a loblolly pine (*Pinus taeda*) spacing experiment. *Canadian Journal of Forest Research* 28: 1344-1351. - doi: [10.1139/x98-115](https://doi.org/10.1139/x98-115)
- Vanninen P, Mäkelä A (2000). Needle and stem wood production in Scots pine (*Pinus sylvestris*) trees of different age, size and competitive status. *Tree Physiology* 20 (8): 527-533. - doi: [10.1093/treephys/20.8.527](https://doi.org/10.1093/treephys/20.8.527)
- Velazquez-Martinez A, Perry DA, Bell TE (1992). Response of aboveground biomass increment, growth efficiency, and foliar nutrients to thinning, fertilization, and pruning in young Douglas-fir plantations in the central Oregon Cascades. *Canadian Journal of Forest Research* 22: 1278-1289. - doi: [10.1139/x92-170](https://doi.org/10.1139/x92-170)
- Vose JM, Allen HL (1988). Leaf area, stemwood growth, and nutrition relationships in loblolly pine. *Forest Science* 34: 546-563. [online] URL: <http://academic.oup.com/forestsience/article-abstract/34/3/547/4642485/>
- Waring RH, Thies WG, Muscato D (1980). Stem growth per unit of leaf area: a measure of tree vigor. *Forest Science* 26: 112-117. [online] URL: <http://academic.oup.com/forestsience/article-abstract/26/1/112/4656392/>