Transformation of solar radiation in Norway spruce stands into produced biomass – the effect of stand density

I. Marková[1], R. Pokorný[2,3], M. V. Marek[1,2]

[1]*Department of Forest Ecology, Faculty of Forestry and Wood Technology, Mendel University in Brno, Brno, Czech Republic*
[2]*Laboratory of Plant Ecological Physiology, CzechGlobe – Centre for Global Change Impact Studies, Brno, Czech Republic*
[3]*Department of Silviculture, Faculty of Forestry and Wood Technology, Mendel University in Brno, Brno, Czech Republic*

ABSTRACT: The present paper is focused on an assessment of the effects of stand density and leaf area development on radiation use efficiency in the mountain cultivated Norway spruce stand. The young even-aged (17-years-old in 1998) plantation of Norway spruce was divided into two experimental plots differing in their stand density in 1995. During the late spring of 2001 next cultivating high-type of thinning of 15% intensity in a reduction of stocking density was performed. The PAR regime of investigated stands was continually measured since 1992. Total aboveground biomass (TBa) and TBa increment (ΔTBa) were obtained on the basis of stand inventory. The dynamic of LAI development showed a tendency to be saturated, i.e. the LAI value close to 11 seems to be maximal for the local conditions of the investigated mountain cultivated Norway spruce stand in the Beskids Mts. Remarkable stimuli (up to 17%) of LAI formation were started in 2002, i.e. as an immediate response to realized thinning. Thus, the positive effect of thinning on LAI increase was confirmed. The data set of absorbed PAR and produced TBa in the period 1998–2003 was processed by the linear regression of Monteith's model, which provided the values of the coefficient of solar energy conversion efficiency into biomass formation (ε). The differences in ε values between the dense and sparse plot after realized thinning amounted to 18%.

Keywords: biomass production; LAI; Norway spruce; PAR absorption; solar energy conversion

Biomass production of forest stands is determined by the assimilation activity and allocation of assimilates. These processes are strongly affected by the climatic conditions of the local stand environment. Especially, the assimilation activity is strongly dependent on the accessibility of solar radiation, and its absorption plays a key role in a set of physiological processes connected with forest stand biomass production. Thus, the final amount of the absorbed solar radiation during the growing season determines the upper limit of forest stand biomass production (Linder 1985). The real production of a forest stand at a particular locality is determined not only by the absorbed solar radiation but also by the efficiency of conversion of this radiation energy into biomass (significantly determined by the stand structure) and by the "quality" of the locality (water and nutrition availability).

To quantify the forest stand ability to absorb photosynthetically active radiation (PAR) and to convert this

Supported by the Ministry of Education, Youth and Sports of the Czech Republic, Project No. MSM 6215648902, by the Ministry of Environment of the Czech Republic, Project No. SP/2d1/70/08, and by the Governmental Research Intention No. AV0Z60870520. This article is an output of the CzechGlobe Centre that is developed within the OP RDI and co-financed from EU funds and the State Budget of the Czech Republic, Project CzechGlobe – Centre for Global Climate Change Impacts Studies, Reg. No. CZ.1.05/1.1.00/02.0073.

energy into biomass, the term radiation use efficiency – RUE ($g \cdot MJ^{-1}$) was introduced (Goyne et al. 1993). RUE provides a useful approach to the observation of biomass formation by terrestrial plant communities for its relatively easy estimation. The real estimation of RUE is dependent on an appropriate measurement of absorbed PAR and accurate measurement of the biomass increment. The main advantage of this approach arises from the fundament of the relationship between biomass formation and absorbed solar radiation, especially for the PAR. This relation is formally described on the basis of the light-conversion analysis introduced for the first time by Monteith (1977). He reported a linear relationship between PAR which is absorbed (intercepted) by the stand (PARa) and aboveground dry matter production (ΔTBa) over relatively short time spans (i.e. day – growing season): $\Delta TBa = \varepsilon \times PARa$, where ε is the coefficient of efficiency of solar energy conversion into produced biomass ($g\ DW \cdot MJ^{-1}$ PARa). The linear character of this relation is a great advantage, i.e. the interpretation of its angular coefficient (slope) is very easy. A lot of empirical studies have supported this assumption (Cannell et al. 1987; Grace et al. 1987; McIntyre et al. 1993; Monteith 1994; Madakadze et al. 1998). The mentioned equation has formed the basis for a number of studies concerning carbon accumulation by terrestrial plants at a regional and global scale using satellite data (Malstrom et al. 1997).

The above-mentioned relation is strongly dependent on two main driving factors: (*i*) the ability of a given stand structure to absorb incident PAR (PARi), and (*ii*) the efficiency of assimilate conversion into biomass. The PARi represents an integral of irradiance over the stand leaf area in time. Therefore, the final amount of PARi absorbed by the given stand structure results from: (*i*) the amount of incident solar radiation, (*ii*) effectiveness of leaf area absorbed PARi, or (*iii*) the considered time period, e.g. the length of the growing season. Any of these parameters can be changed separately, assuming the others remain unchanged (Stenberg et al. 1994). Increased incident PAR simply escalates the potential amount of absorbed PAR (Oker-Blom et al. 1989). Considering the light response function for leaf/stand photosynthesis to be a non-rectangular hyperbola, Haxeltine and Prentice (1996) showed analytically that daily canopy photosynthesis is proportional to absorbed PAR.

The spatial structure of forest stand canopy plays a key role in the absorbing process of incident radiation. Because of the role of active leaf area in PAR absorption and PAR energy utilization, the crown structure, which is a result of the stand architecture simply represented by the density of individuals and leaf area distribution, is of great importance (Ford et al. 1990; Ford 1992). The duration of PAR absorption by active leaf area affects the final biomass formation, and thus differences between individual seasons are obvious. The growth of the biomass responsible for PARa will be dependent on the efficiency of the assimilate conversion into biomass and biomass allocation. Thus, all external factors regulating the stand structure, architecture of tree crowns and photosynthetic activity have a potential to affect the efficiency of solar energy conversion at the scale of tree – stand.

The objective of the present paper is to assess the effects of stand density and leaf area development on the radiation use efficiency and relationship between absorbed PAR and aboveground biomass production in the mountain cultivated Norway spruce stand.

MATERIAL AND METHODS

Plant material and experimental design

All observations were performed in a young Norway spruce (*Picea abies* [L.] Karst.) stand located at the Experimental Research Site of Bílý Kříž in the Moravian-Silesian Beskids Mts. (NE Moravia, Czech Republic, 49°30'N, 18°32'E, 908 m a.s.l.). A detailed description of this experimental site was published by Kratochvílová et al. (1989). The seasonally averaged (i.e. from May to October) air temperature and sum of precipitation in 1998–2003 are shown in Table 1.

The investigated mountain cultivated even-aged plantation of Norway spruce was 17 years old and its mean tree height was 6.5 m (in autumn 1998, i.e. in the season when the investigation was started). It was divided into two experimental plots 0.25 ha in size differing in their tree density in 1995. One of the two plots (denoted as FD) represented a high tree density (2,650 $trees \cdot ha^{-1}$, LAI = 9.7). The other plot (denoted as FS) represented a medium stand density (2,100 $trees \cdot ha^{-1}$, LAI = 7.2). During the late spring 2001, the second cultivating high-type thinning was performed in the FS plot in order to reach the final tree density of 1,800 $trees \cdot ha^{-1}$. Therefore, the stocking reduction of 300 $trees \cdot ha^{-1}$ represented thinning intensity of 15%.

Photosynthetically active radiation observation

The PAR regime of the investigated stand has been measured continually since 1992. The LI-190S Quantum Sensor (LI-COR, Lincoln, USA) was located four

Table 1. Mean seasonal (May–October) air temperature and sum of precipitation at the study site of Bílý Kříž in 1998–2003

	Air temperature (°C)	Sum of precipitation (mm)
1998	11.9	797
1999	12.6	631
2000	15.4	659
2001	16.0	900
2002	15.4	796
2003	13.2	566

meters above the stand canopy on a meteorological steel mast and was used for a long-term measurement of the incident PAR (PARi). A set of five pieces of a special linear holder system (the length of one holder was 2.5 m) equipped with quantum sensors (placed every 10 cm) was located at ca 10% of the stand height in the east-west direction, i.e. transversally through the plot along the altitudinal level line, and it was used for the measurement of the stand canopy transmitted PAR (PARt). One linear holder system equipped with quantum sensors was oriented in the opposite direction and was placed one meter above the stand canopy on a meteorological steel mast. PAR reflected by the stand canopy (PARr) was measured in this way. The final PAR absorbed by the stand canopy (PARa) was calculated as follows:

PARa = PARi – PARr – PARt.

The self-made quantum sensors (wave range 400–700 nm) used for the PAR measurements were based on the BPW-21 photocell (Siemens, Germany). The sensors were cosine-corrected, and the maximum sensitivity was peaking at 550 nm. Possible differences in sensor sensitivity were accounted for a calibration routine based on a linear regression between the raw volt output of BPW-21 quantum sensors and the standard LI-190S Quantum Sensor (LI-COR, Lincoln, USA). The routine was performed twice per growing season. The record of incident, transmitted and reflected PAR values was carried out at 30-s intervals, and 30-min average values of these records were automatically stored by a DL-3000 data-logger (Delta-T, Cambridge, England). The measurements were carried out simultaneously in both investigated plots which were equipped with a meteorological steel mast which was used as a holder of a set of meteorological sensors (PAR, global radiation, net radiation, wind speed, CO_2 concentration, air temperature and relative humidity profiles).

Forest stand biomass estimation

The total aboveground biomass (TBa) and the total aboveground biomass increment (ΔTBa) were obtained on the basis of stand inventory realized at the end of each growing season. The procedure of the stand inventory consisted of measurements of stem circumference at the height of 1.3 m above the ground (SC) and tree height (H) of each individual located in the experimental plots. SC was measured using a metal meter (accuracy 0.1 cm), and H using a special height-meter (Forestor Vertex, I. Haglöf, Sweden, accuracy 0.1 m). From the SC the final value of stem diameter at breast height (dbh) was calculated. TBa was obtained on the basis of the local site-specific allometric relation with dbh (Pokorný, Tomášková 2007):

$TBa = 0.1301 \times dbh^{2.2586}$ ($r^2 = 0.98$)

The total aboveground biomass increment formed during the investigated periods of individual growing seasons was estimated as a difference in TBa values of the current and previous year. However, tree dendrometric parameters (i.e. dbh, H, crown length and width, crown projection, crown surface area and volume) and biomass significantly correlated with the index of competition (Pokorný 2002) while the allometric relations between dbh and TBa did not significantly differ ($\alpha = 0.05$) between sampled trees in FS and FD after thinning. The values of radiation use efficiency (RUE) were calculated for each growing season as follows:

RUE = TBa/PARa.

RESULTS

A huge amount of photosynthetically active radiation (PARi), i.e. 7,302 $MJ \cdot m^{-2}$, was incident on the investigated plots during the period of six growing seasons (1998–2003). The individual plots differed in the amount of absorbed PAR (PARa), i.e. 6,326 $MJ \cdot m^{-2}$ for the FD and 5,417 $MJ \cdot m^{-2}$ for the FS plot. Thus, the FD stand absorbed 86% and the FS stand 74% of the total incident PARi during the investigated period (Fig. 1). The stand-canopy-surface reflected PARr slightly differed between FD and FS plots (Fig. 1) and amounted to 3% and 2% for FD and FS plot, respectively. The residual transmitted PARt value quantifies PAR reaching the soil surface. This part of irradiance was higher in FS (24%) compared to FD (11%). The amount of absorbed PARa was strongly dependent on the stand development phase, which can be documented on

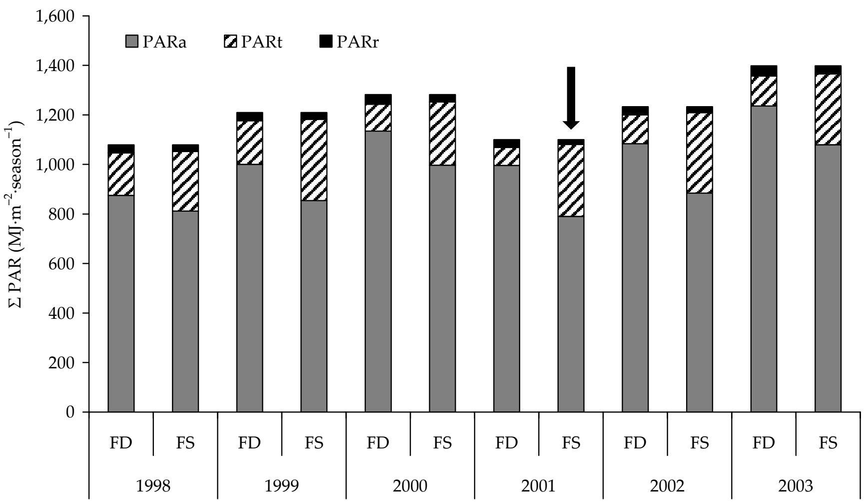

Fig. 1. Amount of transmitted (PARt), absorbed (PARa) and reflected (PARr) photosynthetically active radiation measured on dense (FD) and sparse (FS) Norway spruce stands during the growing seasons (May–October) 1998–2003. Arrow indicates the year of thinning realization

the scale of the leaf area index (LAI) changes. During the investigated years the LAI value on the FD plot increased up to 11%. The change in the LAI value on the FS plot amounted to 17% despite the LAI reduction (up to 20%) in the year 2001 caused by thinning (Fig. 2).

The aboveground biomass formation on both investigated plots was related to the absorbed PAR and to the LAI development (Fig. 3). The thinning and the subsequent LAI development were related to the new biomass formation increase on the thinned plot compared to the biomass increment stagnation on the dense plot. The high value of LAI in the FD plot, which was responsible for the huge amount of absorbed PAR, did not predetermine high biomass production.

The development of the stand LAI was responsible for the final values of the absorbed PAR. In FS compared to FD, a higher slope of the linear relationship between LAI and PARa (117.9 vs 98.8), when fitted the zero, indicated higher absorption of PAR by similar leaf areas. In other words, it indicated a similar amount of absorbed PAR by the smaller leaf area in FS compared to FD. The efficiency of PAR absorption per unit change of the LAI value was higher for the lower LAI values between 6 and 9 on the FS plot compared to 9–12 on the FD plot. It was documented by the logarithmic fitting (r^2 = 0.58) when an increasing tendency of PARa started to saturate over LAI of 9 (Fig. 4).

The seasonal value of radiation use efficiency, i.e. the stand structure ability to transform radiation energy into biomass, can be regarded as the final result of absorbed PAR and spatial arrangement and the amount of the leaf area. To be able to evaluate the importance of these two basic parameters the relationship between seasonal values of RUE and absorbed PAR and LAI was determined (Fig. 5). From the aspect of radiation use efficiency, LAI values close to 9 ($m^2 \cdot m^{-2}$) appeared to be optimal.

The increased value of LAI, which was not related to the increased biomass production despite the huge amount of absorbed PAR, was not accompanied by the increased value of seasonal RUE on the dense plot. The positive effect of thinning on the FS plot was documented on the level of the seasonal course of RUE values. A comparison of the years 2001 and 2002, i.e. the season of thinning re-

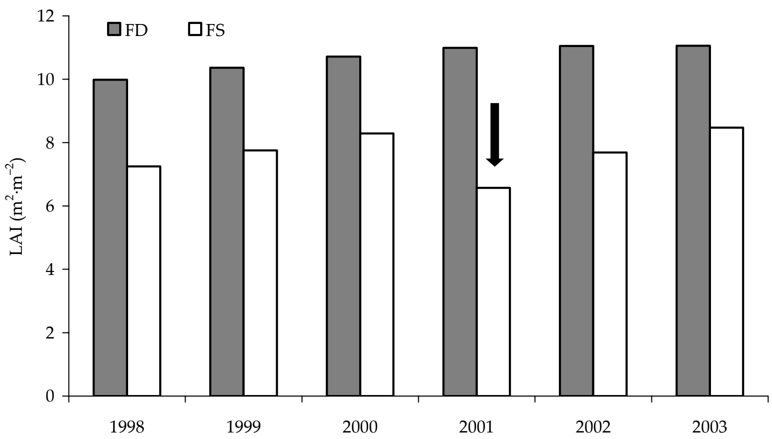

Fig. 2. Development of leaf area index (LAI; seasonal maximum) on dense (FD) and sparse (FS) Norway spruce stands during the growing seasons (May–October) 1998–2003. Arrow indicates the year of thinning realization

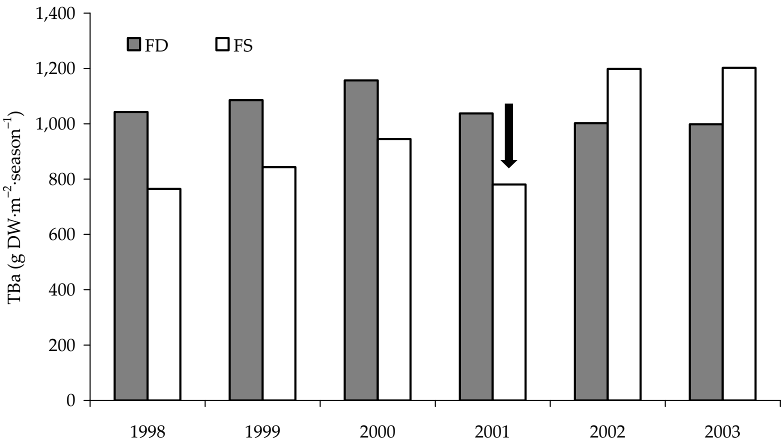

Fig. 3. Total aboveground biomass (TBa) increment on dense (FD) and sparse (FS) Norway spruce stands during the growing seasons (May–October) 1998–2003. Arrow indicates the year of thinning realization

alization and subsequent growing seasons (Fig. 6), showed a trend for one-peak trajectory of RUE as an effect of thinning.

The data set of absorbed PAR and produced biomass in the period 1998–2003 was processed by the linear regression of Monteith's model which provided the values of the coefficient of solar energy conversion efficiency into formed biomass ε (Fig. 7). The thinning exhibited a positive effect on the efficiency of solar energy transformation.

DISCUSSION

The final reached amounts of canopy absorbed PAR are not dependent only on the amount of incident PAR, which is a seasonally variable factor determined by the length of the growing season (determined by temperature), duration of the sunshine (depending on geographic position, terrain orography), number of sunny and cloudy days etc. Moreover, the stand and canopy structure represented by the number of trees on the stand area, crown body architecture and the amount of active foliage are also of great importance (Stenberg et al. 1994). Thus, the forest stand structure characteristics are crucial for the final interaction of stand and PARi. Hence, the lower ratio of PARa and PARr to PARi in the sparse FS stand was the result of smaller leaf area and higher amount of PARt which was incident upon the stand soil surface and therefore was not absorbed by the canopy (Fig. 1).

The development of stand LAI is basically a result of the initial number of trees on the site area and the network of planted individuals. On the investigated plots, the basal spacing network at the time of planting was 2 × 1 m – as it is a common forestry practice in mountain managed spruce monocultures. In 1995, the first schematic thinning was performed to segregate the plot with lower density of 0.25 ha area. The dynamics of LAI development increase in time was related to the stand density. During the investigated period 1998–2003 the FD plot exhibited permanently higher values of LAI compared to the FS plot. Consequently, it was about 37%, 34%, 34%, 68%, 56% and 36% per year, resp. For both investigated plots it was possible to observe a trajectory of the LAI increase (Fig. 2).

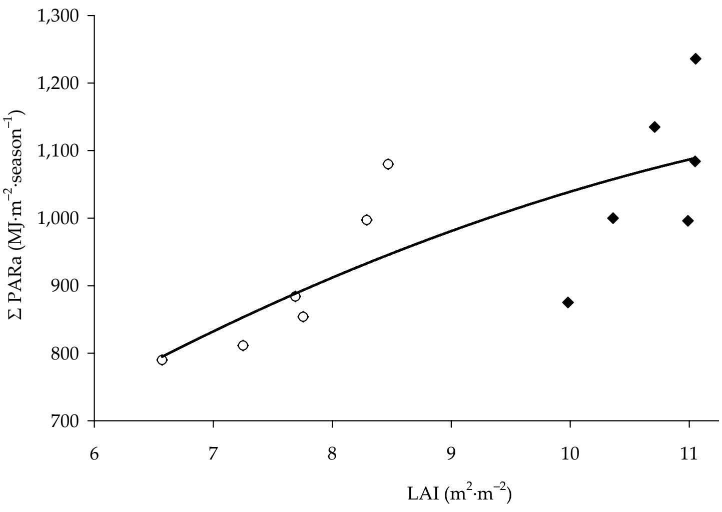

Fig. 4. Relationship between absorbed photosynthetically active radiation (PARa) and leaf area index (LAI) values on dense (FD- full diamonds) and sparse (FS – open circles) Norway spruce stands

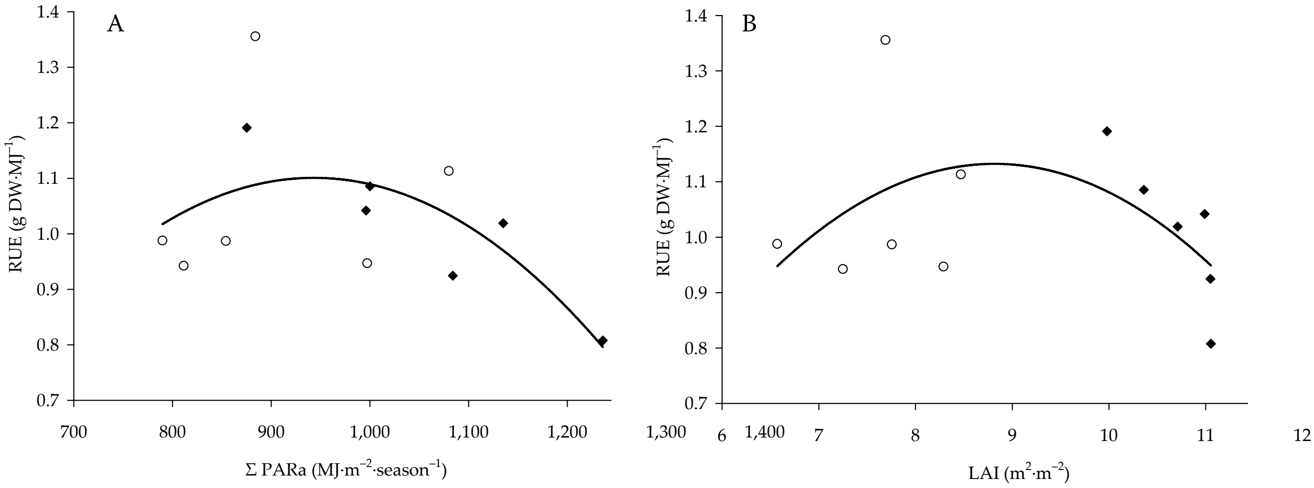

Fig. 5. Relationship between seasonal values of radiation use efficiency (RUE) and (A) seasonal amount of absorbed photosynthetically active radiation (PARa), (B) leaf area index (LAI) values on dense (FD – full diamonds) and sparse (FS – open circles) Norway spruce stands

From 1998 to 2000 the LAI values increased proportionally in both plots. After thinning in spring 2001, highly reduced LAI (by 23%) in FS started to increase rapidly, and the LAI values between FS and FD became different similarly like in previous years in 2003. The reason was not only the rapid increase of leaf area in FS, but also starting LAI saturation over LAI of 11 in FD. The annual difference between seasonally maximum LAI values was about 3% in FD. The dynamics of LAI development in spruce monoculture showed a tendency to be saturated, i.e. the maximal value of LAI was reached (Wang 1988). Hence, the LAI value close to 11 seems to be maximal (equilibrated) for the local conditions of the investigated mountain cultivated Norway spruce stand in the Beskids Mts. In the sparse plot (FS) the seasonal maximum of LAI increased by 7%, remarkable stimuli (up to 17%) for LAI formation were started in this plot in the year 2002, i.e. as an immediate response to the realized thinning. Thus, the positive effect of the thinning on LAI growth and stimulation of biomass formation (Fig. 3) was confirmed as a general phenomenon (Harrington, Reukema 1983; Wang 1988). Interactions between PARa and physiological activity of foliage resulted in the final formation of new biomass (Fig. 3). Anatomical and chemical characteristics of foliage as well as its physiological activity are adjusted to the light regime (Niinemets 1997). On the basis of these adjustments, sun and shade types of foliage with different qualitative characteristics can be distinguished. Higher "maintenance" costs of the dense FD canopy influenced the biomass increment. Annual biomass increment amounted to 5% on average, when the LAI values were below 10 in FD. After overreaching this LAI value, the annual biomass increment dropped down to/by 1–2%.

When certain critical LAI values were reached, they documented the relation between LAI and PARa (Fig. 4). The efficiency of solar radia-

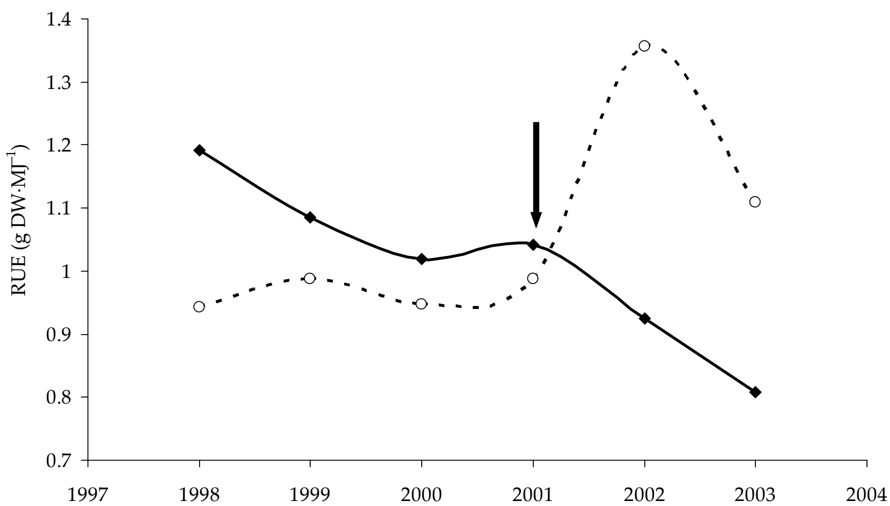

Fig. 6. Seasonal values of the radiation use efficiency (RUE) on dense (FD- full diamonds) and sparse (FS – open circles) Norway spruce stands. Arrow indicates the year of thinning realization

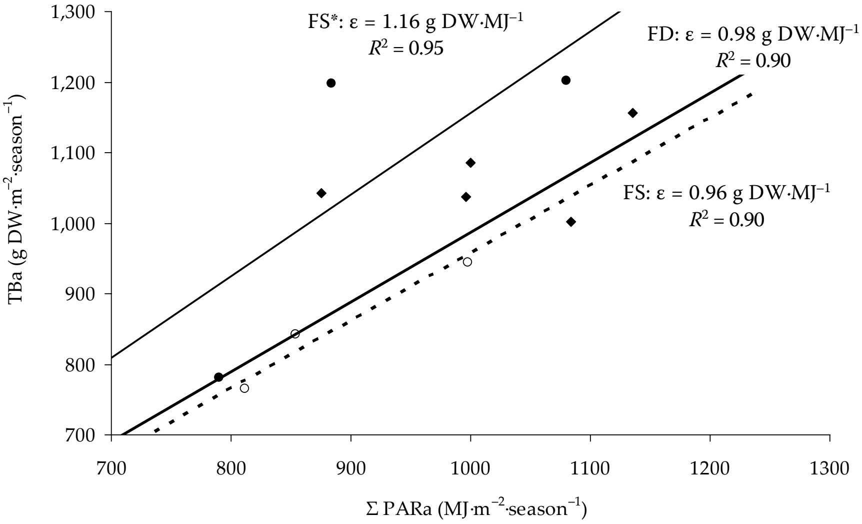

Fig. 7. Aboveground biomass production (TBa) as related to seasonally absorbed photosynthetically active radiation PARa on dense (FD- full diamonds), sparse before thinning (FS – open circles) and sparse after thinning (FS* – closed circles) Norway spruce stands (ε – coefficient of solar energy conversion efficiency into formed biomass)

tion absorption per unit change of LAI increases only within a certain optimal range of LAI values (Linder 1985; Čermák 1998; Madakadze et al. 1998). In fact, the increase of PAR absorption per LAI unit was higher (up to 19%) in the sparse plot (LAI value interval 7–8.5) compared to the dense one. Thus, the subsequent increments of the foliage amount did not result in the increased solar radiation absorption as it was conjoined with foliage quality.

According to Linder (1985) and Stenberg et al. (1994), radiation use efficiency is in principle affected: (*i*) by the amount of solar radiation absorbed by the stand canopy, and (*ii*) by the leaf area which is able to capture solar radiation. A relationship between RUE and PARa and/or LAI (Fig. 5) shows the importance of both, and the final effect of the leaf area amount is evident. The increased amount of foliage in FD plot implies the increasing amount of absorbed PAR. However, the RUE decrease was observed in relation to the increasing amount of absorbed PAR because the increased LAI clearly shows a lower ability of the dense canopy foliage to transform solar energy into the formation of biomass. Mutual shading within the dense canopy is responsible for a decrease in the efficiency of solar energy conversion into biomass due to a prevailing amount of the shade type of foliage with high maintenance costs.

The importance of the amount of leaf area and particularly its spatial distribution on the RUE supports a comparison of its annual values between FD and FS plots during the investigated years (Fig. 6). Realized thinning, i.e. modification of the spatial arrangement of individual trees within the stand, induced the formation of new physiologically active leaf area (Helms 1964; Harrington, Reukema 1983; Wang 1988; Marek et al. 1997). Positive effects of thinning in 2001 were reflected in the 17% increase of LAI in 2002. Reaching or exceeding of the critical LAI value was responsible for a decrease in the radiation use efficiency (Jarvis et al. 1976; Jarvis, Leverenz 1983) because the considerable amount of absorbed PAR is not directly involved in solar energy transformation into the formation of new biomass. The increased amount of foliage is not involved in effective assimilate production and utilization because of the effects of mutual shading of shoots, increased dark respiration of foliage and increased transpiration as a function of increased foliage mass (Stenberg et al. 1994). Thus, the reached maximal LAI value of 11 seems to be close to a threshold. The dense stand structure, i.e. dense crown canopy space, is not an advantage. Whereas a permanent annual decrease in RUE values was observed in FD plot, the newly formed sun-type leaf area extremely enhanced annual RUE values in FS. Thus, the immediate positive effect of thinning on the level of assimilation performance and thus on the solar radiation energy transformation into aboveground biomass was confirmed. The impact of this classical forestry practice on biomass increment is undisputable.

When the relationship between absorbed PAR and dry matter production is analyzed, the key question is whether and under what conditions this relation is acceptable to be useful for quantifying relations between stand structure, absorbed PAR and biomass productivity. A strong linear relationship with zero intercept between absorbed PAR and aboveground biomass production was found for example by Grace et al. (1987) for *Pinus radiata* and by DallaTea and Jokella (1991) for slash and loblolly pine. The study of Linder (1985) supported the strong linear relationship between annual aboveground biomass increment and absorbed PAR of different tree species. Unfortunately, his regression lines had a large negative intercept to the contrary of general assumption of zero biomass increment when zero PAR absorption. Linder's value of e varied between 0.27 and 1.60 g $DW \cdot MJ^{-1}$. Moreover, a large variation among the species, i.e. 0.36–1.70 g $DW \cdot MJ^{-1}$, was reported (Linder 1985; Grace at al. 1987; DallaTea, Jokella 1991; McIntyre et al. 1993; McMurtrie et al. 1994; Madakadze et al. 1998). This variation is very often explained by latitudinal variation in intercepted PAR. The values of e obtained for the investigated spruce stand are in the range of published reports. The differences in e values obtained in the dense and sparse plot after realized thinning amounted to 18%. Before the thinning the solar radiation transformation was higher in the dense plot. The differences between the absorbed PAR and LAI value amounted to 18 and 30% in the FD and FS plots, respectively. The biomass increment was higher in the thinned plot and the difference at the end of the period of investigated years amounted to 20%. Thus, it is evident that reaching the super-threshold amount of foliage does not mean higher solar energy transformation into formed biomass.

Regardless of the reported results of a strong linear relation between the seasonal amount of absorbed solar radiation and dry matter production under favourable environmental conditions (Stenberg et al. 1994; Tsubo, Walker 2002), the presentation of a wide range in slope greatly reduced a possibility to use them for growth prediction from absorbed radiation. These variations are caused by the fact that only the aboveground biomass increment is mostly used. Other reasons for variations can be found in the accuracy of PARa estimation on a seasonal basis. The use of the horizontally placed integration sensors does not fully correspond to the real situation of PAR absorption by the crown body. Some improvement can be expected by the use of small sensors located perpendicularly to the shoot axis. However, the main thinning effect on a discussed relation is attributed to the stand structure, mainly to the foliage amount and distribution. Thus, the thinning impacts and the existence of the threshold value of LAI on the final values of RUE and ε are of great importance.

CONCLUSION

Two Norway spruce stands with different densities were investigated from the aspect of absorbed PAR and conversion of this energy into newly formed biomass as the spatial structure of forest stand canopy plays a key role in the intercepting process of incident radiation. The efficiency of PAR absorption per unit change of LAI value was higher for the sparse stand (FS) with LAI values between 6 and 9 compared to the dense stand (FD) with LAI values ranging from 9 to 12. From 1998 to 2000 the LAI values increased proportionally in both plots. In FS, LAI highly reduced (by 23%) due to the high-type thinning started to immediately increase rapidly and LAI values between FS and FD were different two years after the thinning similarly like in previous years. Positive effects of the high-type thinning in 2001 were reflected in the 17% increase of LAI in 2002. The realized thinning exhibited positive effects on the efficiency (ε) of solar energy transformation into produced aboveground biomass. The newly formed sun-type leaf area extremely enhanced annual RUE values in FS whereas a permanent annual decrease of RUE values was observed in FD. The differences in ε values between the dense and sparse plot after the realized thinning amounted to 18%. However, the RUE decrease was observed in relation to the increasing amount of absorbed PAR, the increased LAI clearly showed a lower ability of the dense canopy foliage to transform solar energy into the formation of biomass. Resulting from the presented data of both stands PAR absorption by the spruce canopy started to decrease with LAI increasing over 9 ($m^2 \cdot m^{-2}$) and this LAI value appeared also to be optimal for reaching the maximal values of radiation use efficiency. The high-type thinning of medium intensity (15% reduction in the number of trees, and 23% reduction in LAI) led to the enhancement of the radiation transformation process into aboveground biomass and fast LAI recovering.

References

Cannell M.G.R, Milne R., Scheppard I.J., Unsworth M.H. (1987): Radiation interception and productivity of willow. Journal of Applied Ecology, ***24***: 261–278.

Čermák J. (1998): Leaf distribution in large trees and stands of the floodplain forest in southern Moravia. Tree Physiology, ***18***: 727–737.

DallaTea F., Jokella E.J. (1991): Needlefall, canopy light interception, and productivity of young intensively managed slash and loblolly pine stand. Forest Science, ***37***: 1298–1313.

Ford E.D. (1992): The control of tree structure and productivity through the interaction of morphological development and physiological processes. International Journal of Plant Science, ***153***: S147–S162.

Ford E.D., Avery A., Ford R. (1990): Simulation of branch growth in the *Pinaceae*: interactions of morphology, phenology, foliage productivity, and the requirement for structural support, on the export of carbon. Journal of Tudor Biology, ***146***: 15–36.

Goyne P.J., Milroy S.P., Lilley J.M., Hare J.M. (1993): Radiation interception radiation use efficiency and growth of barley cultivars. Australian Journal of Agriculture Research, ***44***: 1351–1366.

Grace J.C., Jarvis P.G., Norman J.M. (1987): Modelling the interception of solar energy in intensively managed stands. New Zealand Journal of Forest Science, ***17***: 193–209.

Harrington C.A., Reukema D.L. (1983): Initial shock and long-term stand development following thinning in a Douglas-fir plantation. Forest Science, ***29***: 33–44.

Haxeltine A., Prentice I.C. (1996): A general model for light-use efficiency of primary production. Functional Ecology, ***10***: 551–561.

Helms J.A. (1964): Apparent photosynthesis of Douglas-fir in relation to silvicultural treatment. Forest Science, ***10***: 432–442.

Jarvis P.G., James G.B., Landsberg J.J. (1976): Coniferous forest. In: Monteith J.L. (ed.): Vegetation and the Atmosphere. Academic Press, London – New York – San Francisco: 171–240.

Jarvis P.G., Leverenz J.W. (1983): Productivity of temperate, deciduous and evergreen forests. In: Lange O.L., Nobel P.S., Osmond C.B., Ziegler H. (eds): Physiological Plant Ecology IV New Series. Vol. 12D. Springer, Berlin – Heidelberg – New York: 223–280.

Kratochvílová I., Janouš D., Marek M., Barták M., Říha L. (1989): Production activity mountain cultivated Norway spruce stands under the impact of air pollution. I. General description of problems. Ekológia (CSFR), ***4***: 407–419.

Linder S. (1985): Potential and actual production in Australian forest stands. In: Landsberg J.J., Parson W. (eds): Research for Forest Management. CSIRO, Melbourne: 11–35.

Madakadze I.C., Stewart K., Peterson P.R., Coulman B.E., Samson R., Smith D.L. (1998): Light interception, use-efficiency and energy yield of switchgrass (*Panicum virgatum* L.) grown in a short season area. Biomass & Bioenergy, ***15***: 475–482.

Malstrom C.M., Thompson M.V., Juday G.P., Los S.O., Randerson J.T., Field C.B. (1997): Interannual variation in global-scale net primary production: testing model estimates. Global Biogeochemical Cycle, ***11***: 367–392.

Marek M.V., Marková I., Kalina J., Janouš D. (1997): Effect of thinning on parameters of photosynthesis characteristics of Norway spruce canopy. I. Light penetration and photosynthesis. Lesnictví-Forestry, ***43***: 141–153.

McIntyre B.D., Flower D.J., Riha S.J. (1993): Temperature and soil water status effects on radiation use and growth of pearl-millet in a semi-arid environment. Agricultural and Forest Meteorology, ***66***: 211–227.

McMurtrie R.E., Gholz H.L., Linder S., Gower S.T. (1994): Climatic factors controlling productivity of pines stand a model-based analysis. In: Gholz H.L., Linder S., McMurtie R.E. (eds): Environmental Constrains on the Structure and Productivity of Pine Forest Ecosystems: A Comparative Analysis. Ecological Bulletins (Copenhagen), ***43***: 173–188

Monteith J.L. (1977): Climate and efficiency of crop production in Britain. Philosophical Transactions of the Royal Society London B, ***281***: 227–294.

Monteith J.L. (1994): Validity of the correlation between intercepted radiation and biomass. Agricultural and Forest Meteorology, ***68***: 213–220.

Niinemets U. (1997): Acclimation to low irradiance in *Picea abies*: influences of past and present light climate on foliage structure and function. Tree Physiology, ***17***: 723–732.

Oker-Blom P., Pukkala T., Kuuluvainen T. (1989): Relationship between radiation interception and photosynthesis in forest canopies: effect of stand structure and latitude. Ecological Modelling, ***49***: 73–97.

Pokorný R. (2002): Leaf area index in forest stands. [Dissertation.] Brno, Faculty of Forestry and Wood Technology, Mendel University of Agriculture and Forestry. (in Czech)

Pokorný R., Tomášková I. (2007): Allometric relationships for surface area and dry mass of Norway spruce aboveground organs. Journal of Forest Science, ***53***: 548–554.

Stenberg P., Kuuluvainen T., Kellomaki S., Grace J.C., Jokella E.J., Gholz H.L. (1994): Crown structure, light interception and productivity of pine trees and stands. In: Gholz H.L., Linder S., McMurtie R.E. (eds): Environmental Constrains on the Structure and Productivity of Pine Forest Ecosystems: A Comparative Analysis. Ecological Bulletins (Copenhagen), ***43***: 20–34.

Tsubo M., Walker S. (2002): A model of radiation interception and use by a maize-bean intercrop canopy. Agricultural and Forest Meteorology, ***110***: 203–215.

Wang Y.P. (1988): Crown structure, radiation, absorption, photosynthesis and transpiration. [Ph.D. Thesis.] Edinburgh, University of Edinburgh.

Received for publication May 17, 2010
Accepted after corrections March 23, 2011

Corresponding author:
RNDr. Ida Marková, CSc., Mendel University in Brno, Faculty of Forestry and Wood Technology,
Department of Forest Ecology, Zemědělská 3, 613 00 Brno, Czech Republic
e-mail: markova@mendelu.cz