



Air temperature is the main driving factor of radiation use efficiency and carbon storage of mature Norway spruce stands under global climate change

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Abstract

Plant growth is affected by light availability, light capture, and the efficiency of light energy utilisation within the photosynthetic uptake processes. The radiation use efficiency (RUE) of four even-aged, fully stocked mature Norway spruce stands along a temperature, precipitation, and altitudinal gradient of the Czech Republic was investigated. A new straightforward, methodological approach involving an analysis of digital hemispherical photographs for RUE estimation was applied. The highest annual RUE value (0.72 g MJ^{-1}) was observed in the stand characterised by the lowest mean annual air temperature, the highest annual amount of precipitation, located at the highest altitude, and with the lowest site index reflecting site fertility. From the viewpoint of global climate change mitigation, this stand fixed 4.14 Mg ha^{-1} and 13.93 Mg ha^{-1} of carbon units and CO_2 molecules into above-ground biomass, respectively. The lowest RUE value (0.21 g MJ^{-1}) within the studied growing season was found in the stand located at the lowest altitude representing the site with the highest mean air temperature and the lowest amount of precipitation where 1.27 Mg ha^{-1} and 4.28 Mg ha^{-1} of carbon units and CO_2 molecules, respectively, were fixed. From the tested meteorological variables (mean air temperature, the monthly sums of temperature, precipitation, and air humidity), RUE was only significantly dependent on air temperature. Therefore, global warming can lead to diminishing RUE and carbon sequestration in Norway spruce stands, especially at low altitudes.

Keywords Carbon sequestration · Hemispherical photography · *Picea abies* · Solar radiation · Above-ground biomass

Highlights

- RUE is significantly dependent on air temperature
- The RUE value decreased with increasing air temperature
- The new straightforward method involving digital hemispherical photographs analysis for RUE estimation was applied
- Stand growth, as well as carbon storage, increased with higher RUE values

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Introduction

Resource availability for green autotrophic terrestrial plants, including forest stands, impacts its foliage production, which in turn affects light interception needed for photosynthesis processes and subsequent plant growth (Vose and Allen 1988; Landsberg and Sands 2011). In many production studies, a linear relationship between absorbed photosynthetically active radiation (APAR, wavelength from 380 to 720 nm; Larcher 2003) and plant biomass production has been tested for various tree species (Jarvis and Leverenz 1983; Grace et al. 1987; Cannell et al. 1988; Dallatea and Jokella 1991) and crops (Stockle and Kiniry 1990; McIntyre et al. 1993; Madakadze et al. 1998). The biomass production of plant communities at a particular site is determined not only by APAR, but also by the efficiency of the conversion of this light energy into biomass, which is reliant on both the structure of the plant community (density, leaf area index) and the site conditions (water and soil nutrient availability e.g. Marková et al. 2011; Binkley et al. 2013; Forrester and Albrecht 2014). Efficiency is defined as the ratio

between any measure of biomass production and the measure of the resource supply or use (Gspaltl et al. 2013). Light (or proxies for light) was found to be the most closely related factor to wood biomass production (Monteith 1972) since it is the main driver for photosynthesis (Gspaltl et al. 2013), through which atmospheric CO₂ fixation into biomass occurs (Monteith 1977). Typically, an efficiency estimate using light as a resource is either related to short-term light use efficiency (LUE; g MJ⁻¹; e.g. Soudani et al. 2014; Albaugh et al. 2016; Nelson et al. 2016) or long-term RUE (g MJ⁻¹; e.g. DeLucia et al. 2002; Broeckx et al. 2015; Krupková et al. 2017).

In previous decades, the leaf area (LA) or sapwood area as proxies of the light resource were applied (Shinozaki et al. 1964). Foliage is a production unit of primary assimilates forming biomass, whereas sapwood connecting root systems with leaves deliver water and nutrients as another primary biomass component. Alternatively, from the economical point of view in forestry, above-ground biomass and/or only the stem wood volume or biomass increment to LA ratio were examined and called growth efficiency (GE; Waring et al. 1980; Omari et al. 2016) or leaf area efficiency (LAE; Pokorný et al. 2008; Gspaltl et al. 2013). The canopy production index (CPI; Taylor 1993; Norby 1996) was introduced as an equivalent to GE. Recently, several models for calculating APAR used by trees or entire stand canopies have been developed (e.g. Wang and Jarvis 1990; Brunner 1998; Brunner and Nigh 2000). Given that wood volume is attaining great interest in forest production because of CO₂ fixation into woody biomass from the atmosphere under global climate change (GCC), RUE (or LUE) is now very frequently expressed as the wood volume increment per unit of APAR (Albaugh et al. 2016; Nelson et al. 2016).

Pioneer work quantifying RUE in crop plants began in the 1970s (Monteith 1977). RUE focuses on the fundamental relationships in plant growth, where plants use the sun's energy (photon flux density; PPFD) to fix carbon from the atmosphere and then allocate the carbon into various plant components (Cannell 1989). Despite seasonal variability, this parameter is deemed to be stable over long time frames (e.g. on an annual base, Cannell 1989; Jarvis and Leverenz 1983) and provides a useful tool for observing biomass formation by terrestrial plant communities for its relatively simple estimation (Marková et al. 2011). Assessing RUE is directly reliant on having a suitable APAR estimation and a precise measurement of the amount of fixed carbon or produced biomass, usually above-ground biomass, as a more easily measurable equivalent. As mentioned above, the above-ground biomass increment using site-specific allometric equations is widely used for quantifying RUE, but it must be noted that below-ground biomass production should be taken into account. Some authors (Niklas 2005; Hendricks et al. 2006; Jarčuška and Barna 2011) presume proportional root growth to above-ground biomass, although this is not entirely valid, especially over time. Nowadays, an eddy covariance

technique, which involves direct quantification of a fixed amount of carbon through net primary production for the whole ecosystem, is used because it is more reliable (e.g. Krupková et al. 2017). Dissimilarities in productivity among plants or plant communities growing on similar sites are primarily the result of differences in the amount of APAR (Monteith 1977). Stand structure strongly determines the leaf area index (LAI) and the proportion between sun- and shade-adapted foliage differing in anatomy, morphology, chemical composition, and mainly in physiological activity; hence, the amount of APAR and RUE can be distinct at sites with different nutrient (e.g. Knecht and Gönarsson 2004; Fox et al. 2007; Albaugh et al. 2016) or soil water availability (e.g. Albaugh et al. 1998; Coyle et al. 2016; Albaugh et al. 2016).

The world's forests significantly contribute to the overall carbon balance of the Earth (Malhi et al. 1999), and forest ecosystems are among the most critical components of the global carbon cycle and are currently thought to be a significant atmospheric CO₂ sink (DeLucia et al. 2002; Bonan 2008; Pan et al. 2011). Thus, knowledge and comprehension of RUE remain an immense challenge for engaging in a perennial investigation under GCC. This is especially true in Norway spruce (*Picea abies* L.) stands, because spruce is an ecologically and economically significant tree species, not only in the Czech Republic (Green Report 2018), but also in Boreal biome, as it covers 11% of the Earth's terrestrial surface (Bonan and Shugart 1989). Therefore, emphasis has been placed on carbon fixation to mitigate current GCC effects (IPCC 2018), where increasing forest production area and the silvicultural intensity of forested land have been suggested as ways to increase global carbon sequestration (Woodbury et al. 2007). Furthermore, improvement treatments such as thinning and shifting tree species composition can alter tree crown growth and enhance light capture (Forrester et al. 2013).

Presently, many empirical studies are engaged in issues concerning RUE within forest stands (e.g. Albaugh et al. 2016; Nelson et al. 2016, and others). However, only a few studies have been devoted to the RUE of mature Norway spruce stands as one of the most represented and industrially essential tree species in the northern hemisphere. APAR is obtained either from modelled values (e.g. Gspaltl et al. 2013; Forrester and Albrecht 2014) or calculated from directly estimated incident radiation measured by sensors located both above and beneath the canopy (Marková et al. 2011; Krupková et al. 2017). Thus, more effort and more extensive long-term work within these forest stands are necessary owing to the reasons mentioned above. When LA substitutes APAR as a proxy, the amount of shade might cause deviations in the actual measurement of APAR. For simplicity, one unit of LA can receive a different amount of light as a consequence of self-shading (i.e. leaves from the upper crown shade leaves in the lower parts of the crown) and competition (shading from adjacent trees or trees at higher canopy layers; Gspaltl et al.

2013). Therefore, a new simple and straightforward approach for measuring RUE, combining global radiation measurement, the analysis of digital hemispherical photographs and noting seasonal changes in total above-ground dry mass production, was applied in this study.

We hypothesised that:

- I. RUE will be significantly dependent on all tested meteorological variables (air temperature, precipitation, and air humidity) and calculated meteorological indices (Lang's rain factor, the Angström index, the de Martonne aridity index, and their inverse eigenvalues).
- II. The highest annual RUE and the highest monthly values of RUE occur in the investigated mature Norway spruce stand with the highest site index.

The aims of the study were as follows: (1) to examine the seasonal course of RUE at monthly resolutions in mature Norway spruce stands; (2) to compare the amount of sequestered carbon in the above-ground dry mass of the studied stands; (3) to compare the RUE values in the different investigated Norway spruce stands for the whole studied growing season (i.e. May–October) based on site index along altitudinal, temperature, and precipitation gradients; (4) to investigate the effect of the tested meteorological variables and calculated meteorological indices on RUE; and (5) to evaluate the potential of the studied forest stands from the viewpoint of GCC mitigation.

Materials and methods

Study sites

In 2018, all measurements were performed in four mature Norway spruce stands (see Supplementary material 1). All studied plots belong to the international ICP Forests—level II research network (www.icp-forests.net). The plots were selected to represent the dominant production range of Norway spruce stands with a similar defoliation rate (see PAIe in Supplementary material 3) along the temperature, precipitation, and altitudinal gradients in the Czech Republic. It could be presumed that fully stocked and fully leaved stands have a similar ratio between sun- and shade-adapted foliage. The fundamental site characteristics are listed in Supplementary material 2.

Dendrometric and structural characteristics of all investigated forest stands in the forest inventory performed at the end of the 2018 growing season (at the end of November) are summarised in Supplementary material 3.

Forest inventory

Before the beginning of the 2010 growing season, DB20 manual band dendrometers (EMS, Czech Republic) were installed on

selected sample trees for making a detailed observation of the annual growth dynamic. The sample trees were selected based on the regular forest inventory from the previous year (i.e. 2009) to represent the whole diameter range of spruce trees on each of the investigated plots. In total, 15, 21, 15, and 20 manual band dendrometers were installed at KL, LA, LU, and ZE, respectively. In each of the studied stands, an annual stem increment of each present tree in the stand was calculated based on the data obtained from manual band dendrometers for each particular diameter class. In the 2018 growing season, all manual band dendrometers were read at regular monthly intervals. Based on the exact monthly increment of the sample trees, monthly increments of the remaining live trees in each of the studied stands were calculated within the corresponding diameter classes. Afterwards, the exact dry mass weight of the total above-ground biomass of each tree measured within the forest inventory was proportionally calculated according to specific allometric relationships reported by Vejvustková et al. (2017), Vejvustková et al. (2013), and Muukonen and Mäkipää (2006) for Norway spruce, European beech, and European silver fir, respectively.

As the mature stands were also evaluated from the viewpoint of GCC mitigation, monthly weight changes in the total above-ground dry mass of each investigated plot were subsequently divided by two to determine the amount of carbon accumulated by the particular stand within each observed month (i.e. May–October) and throughout the whole above-mentioned 2018 growing season (Krupková et al. 2017). Furthermore, the amount of sequestered carbon was recalculated to the equivalent amount of CO₂ molecules fixed by the specific stand structure related to the release of greenhouse gases (emissions) into the atmosphere (or more precisely their fixation from the atmosphere by forest ecosystems). It was calculated as the product of the amount of sequestered carbon by the total above-ground dry mass and 3.667 (N'Gbala et al. 2017; USEPA 2005).

RUE estimation

In the 2018 growing season (May–October), incident global solar radiation was measured using LI-200R sensors (LI-COR, NE, USA) according to Raspe et al. (2016). The sensors were placed at 2 m above the ground on a sufficiently large clearing situated in close proximity to each investigated stand. LI-200R sensors measured the energy of the global solar radiation ($W\ m^{-2}$) at 30-s intervals, and dataloggers automatically stored the average 10-min values. For each day of the studied growing season (i.e. within the May–October period) and each investigated stand, daily sums of the energy of incident global solar radiation ($MJ\ m^{-2}$) in the clearing (i.e. above the canopy) were calculated from the average daily values of the global solar radiation energy ($W\ m^{-2}$) recorded by the LI-200R sensors. The daily sums of incident global solar radiation energy ($MJ\ m^{-2}$) were calculated according to the ICP

Forests manual for taking meteorological measurements (Raspe et al. 2016) as the product of the average daily value of the global solar radiation energy ($W\ m^{-2}$) and a conversion factor of 0.0864 (Raspe et al. 2016, pp. 9):

$$E_{gr} = P_{gr} * 0.0864 \quad (1)$$

where E_{gr} is the daily energy sum of the incident global solar radiation per $1\ m^2$ ($MJ\ m^{-2}$); and P_{gr} is the average daily value of the incident global solar radiation energy ($W\ m^{-2}$) recorded by LI-200R sensors.

Subsequently, the sums of global solar radiation energy ($MJ\ m^{-2}$) were calculated for each month of the investigated 2018 growing season (May–October) as the total of the daily sums of global solar radiation energy (E_{gr}) for each corresponding month. The monthly sums of global solar radiation energy ($MJ\ m^{-2}$) were then multiplied by the exact area of each investigated stand. The amount of APAR was calculated according to Bartelink et al. (1997) as 50% of the incident global solar radiation in the clearings mentioned above (i.e. above the canopy of each studied stand; Eq. 2):

$$E = \Sigma E_{gr} * A * 0.5 \quad (2)$$

where E equals the total energy of APAR over the entire area of each investigated stand for a particular month within the observed 2018 growing season ($MJ\ month^{-1}\ stand\ area^{-1}$), ΣE_{gr} is the total of the daily energy sums of the incident global solar radiation per $1\ m^2$ for a particular month ($MJ\ m^{-2}\ month^{-1}$), and A is the precise area of the investigated stand (m^2).

To determine the structure of each studied stand, 16 digital hemispherical photographs were acquired within a regular grid at 1.3 m above the ground (i.e. above natural regeneration) in the same way as Fleck et al. (2016) under standard overcast and windless conditions to avoid light intensity underestimation and penumbra effect (Čater et al. 2013; Černý et al. 2019). Based on digital hemispherical photographs, total site factors (TSF) and values of effective plant area index (PAIe) were obtained. TSF expresses the ratio between incident solar radiation above and below the canopy of each investigated stand. PAIe is defined as the total one-sided area of all above-ground plant compartments per unit of ground surface. All digital hemispherical photographs were evaluated using WinsCANOPY® software, version 2009 (Régent Instruments Inc., Canada) where PAIe as LAI(2000)-Lin were calculated based on Miller's theorem (Miller 1967). The total energy of APAR fixed (accumulated) by each studied Norway spruce stand was calculated according to Eq. 3:

$$E_c = (1 - TSF) * E \quad (3)$$

where E_c is the amount of APAR energy fixed by the total above-ground dry mass of the studied stand, TSF is the median of 16 TSF values of each analysed Norway spruce stand, and E is the total energy of APAR over the entire area of each

investigated stand for a particular month within the observed 2018 growing season ($MJ\ month^{-1}\ stand\ area^{-1}$).

For each studied Norway spruce stand and each month within the 2018 growing season (May–October), RUE ($g\ MJ^{-1}$) by the assimilation apparatus within photosynthetic uptake was calculated as the ratio between the monthly value of the weight change in the total above-ground biomass expressed in grammes of dry matter per unit area of the stand and the value of total APAR energy fixed by the stand:

$$RUE = TAB_{inc} E_c^{-1} \quad (4)$$

where RUE is the radiation use efficiency ($g\ MJ^{-1}$), TAB_{inc} is the weight change of the total above-ground dry mass for a particular month ($g\ month^{-1}$), and E_c is the amount of APAR energy fixed by the total above-ground dry mass of the studied stand for a particular month ($MJ\ month^{-1}$).

Field meteorological measurements

Mean daily air temperatures with air humidity and daily precipitation were measured using EMS 32A sensors (EMS, Czech Republic) and MetOne 370 rainfall gauges (Met One Instruments Inc., OR, USA), respectively, in the clearings mentioned above at 2 m above the ground (see Raspe et al. 2016) to study the effect of the measured meteorological variables on RUE. Mean monthly air temperatures, monthly sums of air temperatures, the monthly sum of precipitation, and mean monthly air humidity were used to study the influence of the meteorological variables on RUE for corresponding months. Moreover, relationships between RUE and monthly precipitation shifted by 1 month (i.e. April precipitation with May RUE etc.) and 2 months back (i.e. March precipitation with May RUE etc.) were tested.

Furthermore, the following meteorological indices characterising the availability of water, moisture and thus the amount of accessible nutrients dissolved in the water solution for plant development: (i) Lang's rain factor (L) as monthly precipitation (Pr) and mean monthly air temperature (Ta) ratio ($mm\ ^\circ C^{-1}$; $L = Pr\ Ta^{-1}$; Oury 1965), (ii) Angström index (A ; $mm\ ^\circ C^{-1}$; $A = Pr\ (1,07^{Ta})^{-1}$; Oury 1965), and (iii) de Martonne aridity index (M ; $mm\ ^\circ C^{-1}$; $M = Pr\ (Ta + 10)^{-1}$; de Martonne 1926), and their inverse eigenvalues were calculated and tested to assess their effect on RUE for each observed month (May–October) within the 2018 growing season.

Statistical data processing

All statistical analyses were conducted with the SigmaPlot® software, version 13.0 (Systat Software Inc., CA, USA), using a confidence level of 0.95 ($p < 0.05$) throughout the whole study. Shapiro-Wilk's test was applied to test the normality of

data distribution. The coefficient of determination (R^2) was used to quantify the tightness of the fit of the linear function.

Results

Seasonal course of RUE and sequestered carbon related to RUE

For the analysed 2018 growing season, the seasonal course of RUE determined based on changes in the weight of total above-ground dry mass is depicted in Fig. 1a. Monthly RUE values ranged within intervals from -0.08 to 1.18 g MJ^{-1} , from -0.18 to 0.94 g MJ^{-1} , from -0.29 to 1.56 g MJ^{-1} , and from -0.24 to 0.64 g MJ^{-1} in KL, LA, LU, and ZE, respectively; whereas the RUE values for the whole observed 2018 growing season (May–October) reached 0.41 g MJ^{-1} , 0.32 g MJ^{-1} , 0.72 g MJ^{-1} , and 0.21 g MJ^{-1} in KL, LA, LU, and ZE, respectively (Fig. 1b). The highest seasonal RUE value was observed in LU. It is characterised by the highest altitude, the lowest mean air temperatures, the highest amount of precipitation, and the lowest site index of all the studied Norway

spruce stands. On the contrary, the lowest seasonal RUE value was found in ZE located at the lowest altitude, representing the site with the highest mean air temperatures and the lowest amount of precipitation (cf. Supplementary material 2).

Monthly changes in the total above-ground dry mass within the observed 2018 growing season expressed as the amount of sequestered carbon per hectare of the studied mature Norway spruce stands are shown in Fig. 1c. Monthly changes in the total above-ground dry mass (Fig. 1c) corresponded with the RUE values (cf. Fig. 1a). Carbon sequestration is functionally reliant on the growth of the biomass, which is an integrated variable in RUE. Therefore, the highest amount of annual carbon sequestration was also found in LU (4.14 Mg ha^{-1} ; Fig. 1d) when analysing the amount of carbon fixed by mature Norway spruce stands. It was followed (same as with RUE) by KL, LA, and ZE with 2.48 Mg ha^{-1} , 2.08 Mg ha^{-1} , and 1.27 Mg ha^{-1} , respectively. From the viewpoint of the importance of forests in mitigating the impact of GCC, the volume of CO_2 (as a greenhouse gas) fixed from the atmosphere is a significant equivalent of the findings mentioned above. In this case, 13.93 Mg ha^{-1} of CO_2 molecules, 8.36 Mg ha^{-1} of CO_2 molecules, 7.02 Mg ha^{-1} of CO_2 molecules, and

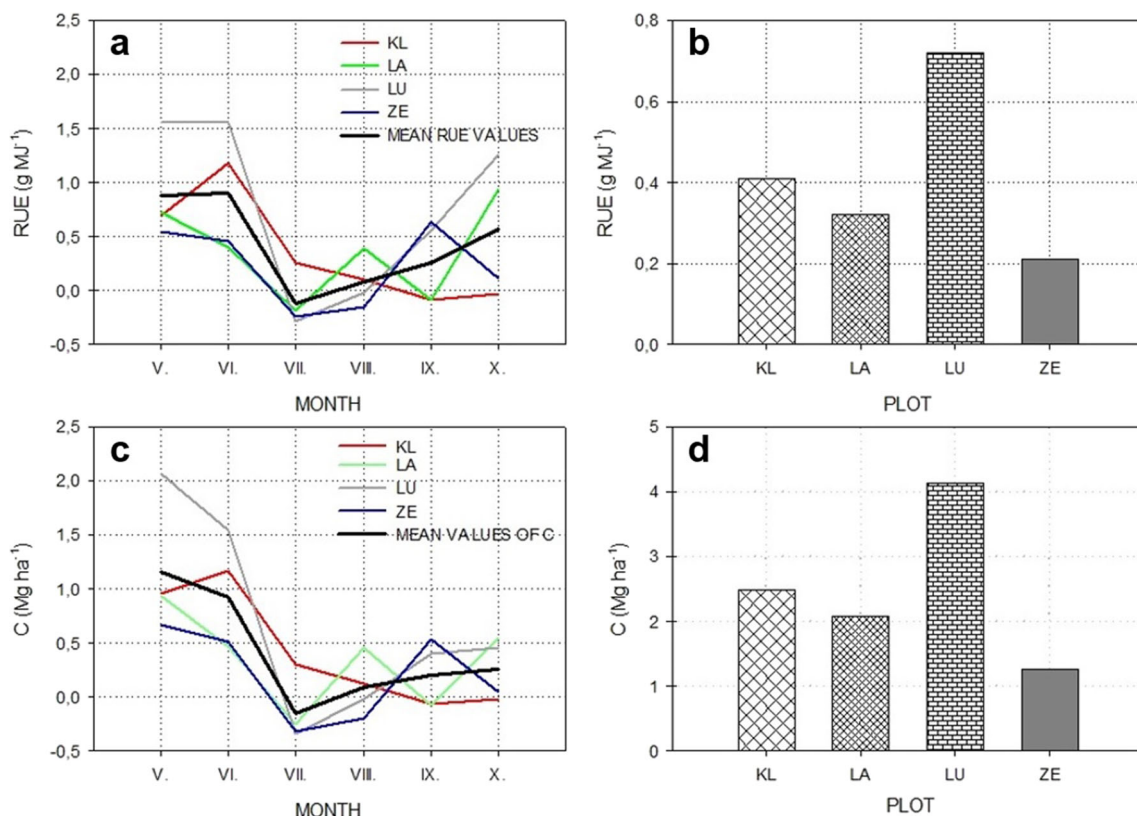


Fig. 1 The seasonal course of RUE determined based on changes in the total above-ground dry mass weight of all investigated Norway spruce stands in the 2018 growing season (a); the RUE values for the whole observed growing season (May–October) (b); the amount of sequestered carbon in the studied mature Norway spruce stands within individual months (c) and for the entire 2018 growing season (d). RUE, radiation

use efficiency; KL, Klepacka; LA, Lazy; LU, Luisino udoli; ZE, Zelivka. Negative values are also presented (c) since the amount of sequestered carbon is based on weight changes in the total above-ground dry mass. Bold lines in a and c depict the mean RUE values of all analysed mature Norway spruce stands and the mean values of fixed carbon of all analysed mature Norway spruce stands, respectively

4.28 Mg ha⁻¹ of CO₂ molecules in LU, KL, LA, and ZE, respectively, were accumulated within the observed 2018 growing season (May–October).

A significant linear relationship was found between monthly changes in total above-ground dry mass expressed by the amount of fixed carbon and RUE ($y = 0.99x - 0.0103$; $R^2 = 0.85$; $p < 0.001$), where the amount of fixed carbon in the total above-ground dry mass increased with enhancing RUE (see Supplementary material 4).

The relationship between RUE and tested meteorological variables

Within the testing of significant dependency among monthly RUE values of the studied mature Norway spruce stands and tested meteorological variables, as well as the calculated meteorological indices, significant linear regressions between RUE and mean monthly air temperatures; RUE and values of the inverse Lang's rain factor; RUE and the inverse Angström index; RUE and the inverse de Martonne aridity index were found (Fig. 2; Supplementary material 5). On the contrary, no significant linear regressions were observed between RUE and the sum of monthly air temperatures, nor between RUE and precipitation, air humidity, Lang's rain factor, the Angström index, and the de Martonne aridity index, respectively.

Discussion

Seasonal course of RUE

Seasonal RUE values of tree species generally range from 0.20 (Gower et al. 1999) to 1.58 g MJ⁻¹ (Cannell et al. 1987). In this study, seasonal RUE values of four mature Norway spruce stands varying between 0.21 and 0.72 g MJ⁻¹ (Fig. 1b) were observed over the whole 2018 growing season defined as the period from the beginning of May to the end of October, which entirely corresponds to RUE values compiled by other authors (Cannell et al. 1987; Gower et al. 1999). Similar ranges of RUE values (0.46–0.78 g MJ⁻¹; and 0.59–0.79 g MJ⁻¹) were recorded by Vajda (2012) and Volná (2008), respectively, within 6-year (2005–2011) observation periods in pure Norway spruce pole stands in the mountainous altitudinal zone (the eastern part of the Czech Republic, on the Czech-Slovakian border). These results correspond to the LU spruce stand (RUE = 0.72 g MJ⁻¹) also located at the mountainous site. Comparable RUE values (0.56–1.21 g MJ⁻¹) were noted by Dvořák and Opluštilová (1996), who analysed the RUE of mature Norway spruce stands related to stand density in the Czech Republic. Higher RUE values in the upper part of the interval (i.e. ~ above 0.90) recorded by Dvořák and Opluštilová (1996) were mainly affected by stand

density and more benign climatic conditions (lower mean annual air temperatures, higher annual precipitation) than in the growing season analysed in this study. For 2014 and 2015, Bellan et al. (2017) studied seasonal RUE values in pure even-aged Norway spruce pole stands (33- and 36-year-old) situated in middle and mountainous altitudinal zones in the Czech Republic. The authors observed seasonal RUE values ranging from 0.45 to 0.65 g MJ⁻¹ there. Since Gspaltl et al. (2013) and Binkley et al. (2010) found an increased RUE in individual trees with rising tree dimension (i.e. also with increasing age) in Norway spruce stands along age gradient (pole stands, immature, mature), the seasonal RUE values of mature spruce stands analysed in this study should be generally higher compared with the values obtained by Volná (2008), Vajda (2012), and Bellan et al. (2017). However, this assumption was confirmed only at the LU stand, with the highest altitude where the seasonal RUE value of 0.72 g MJ⁻¹ was reached. In the remaining three studied stands (KL, LA, ZE), lower values of seasonal RUE were noted. Those results may have been caused by the fact that net primary production of trees and stands become lower with age as respiration losses increase due to maintaining a considerable amount of living biomass, as hydraulic conductivity coupling with stomatal feedback become limiting, and surface area of assimilation apparatus decrease as well (Landsberg and Waring 1997) and by the course of air temperatures within the 2018 growing season as discussed in more detail in the part entitled “The Relationship between RUE and Tested Meteorological Variables”.

However, if RUE values related to particular months of the observed 2018 growing season (May–October) were taken into account, the RUE values of the studied spruce stands ranged between -0.29 and 1.56 g MJ⁻¹ (Fig. 1a). Nevertheless, monthly RUE values were characterised by high variability in all analysed spruce stands. Bartelink et al. (1997) observed a similarly high variability of monthly RUE values in coniferous tree species (especially in Douglas-fir stands), where the FORGRO growing model generated monthly RUE values. The authors also noted negative monthly values of RUE in some months. Bartelink et al. (1997) attributed this fact to the maintaining expenditure of energy in individual trees. This means certain individuals (ecosystem) release (respire) more carbon in the form of CO₂ than they can fix into biomass through photosynthetic uptake (i.e. dissimilation exceeds the assimilation process).

Nonetheless, the primary causation may be seen both in changes in transpiration and mainly in contemporaneously decreased water content within biomass due to insufficient soil water supply, which may subsequently cause stem shrinkage. Thus, this is most likely the main reason for the recorded negative values of RUE in some months of the studied 2018 growing season. This phenomenon can occur especially in arid months when the shortage of precipitation (low soil

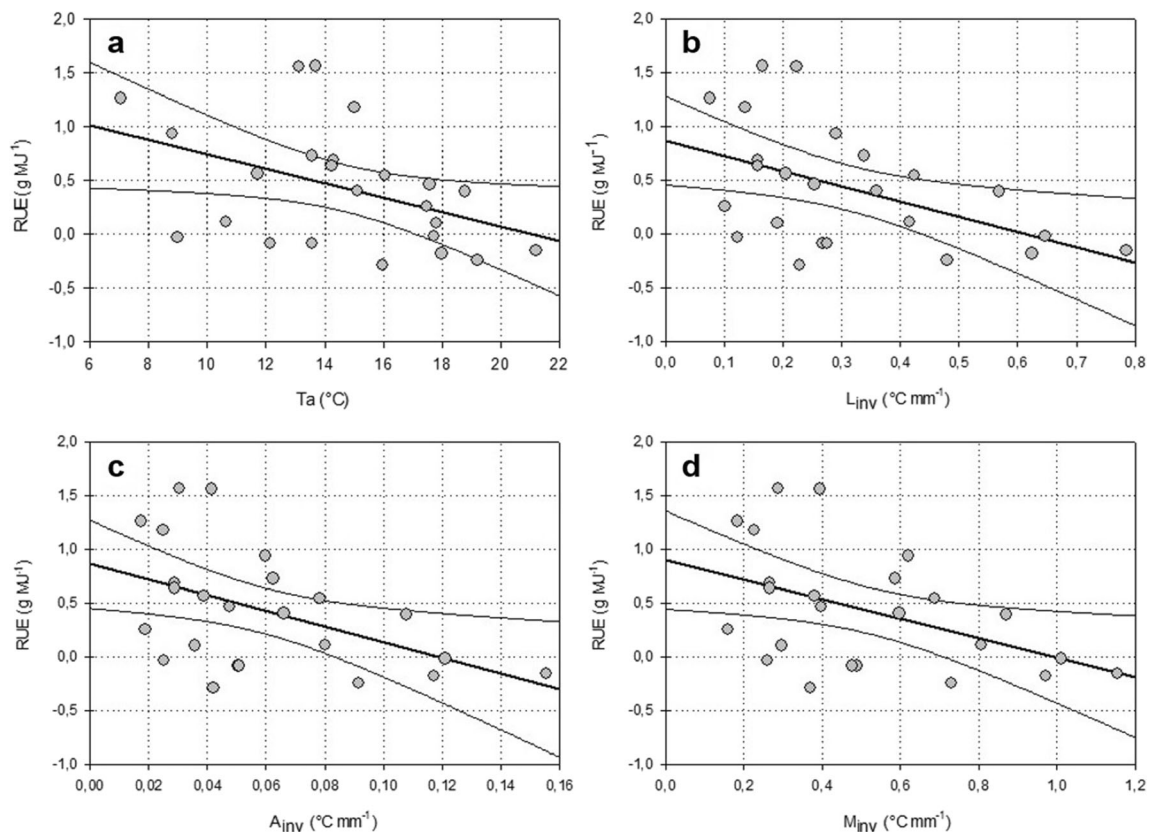


Fig. 2 The significant linear regression between monthly RUE values and mean air temperatures (**a**), inverse Lang's rain factor (**b**), inverse Angström index (**c**), and inverse de Martonne aridity index (**d**). RUE, radiation use efficiency (g MJ^{-1}); T_a , mean monthly air temperatures

($^{\circ}\text{C}$); L_{inv} , inverse Lang's rain factor ($^{\circ}\text{C mm}^{-1}$); A_{inv} , inverse Angström index ($^{\circ}\text{C mm}^{-1}$); M_{inv} , inverse de Martonne aridity index ($^{\circ}\text{C mm}^{-1}$). Bold lines show the trend of dependency. Thin shaded lines depict confidence intervals of 95% ($p < 0.05$)

moisture) along with high air temperature and low humidity (i.e. a high saturation deficit) lead to volume changes in stems due to water scarcity, i.e. volume changes at both the cellular and intercellular levels (i.e. the biomass of individual stems decrease in volume due to the water deficit), which are noted but do not reflect incremental changes of the total above-ground biomass. The second factor leading to negative RUE values could be preferential biomass allocation (and carbon sequestration) in the root system. That fact is not reflected in standard RUE calculations (see Eq. 4). Therefore, different growth dynamics (phenology) of tree organs can lead to variations and differences seen over time, as well as among various sites. Besides forest stand structure, the different proportion between diffuse and direct light and a combination of all these factors could be another factor causing the differences among the sites.

Sequestered carbon related to RUE

In this study, mature Norway spruce stands were also evaluated for carbon sequestration and from the viewpoint of the amount of fixed CO_2 from the atmosphere, which is an essential role played by forest ecosystems in mitigating GCC. In

each investigated spruce stand, the monthly and total annual (for the whole studied growing season) changes in the total above-ground dry mass were recalculated to the amount of carbon accumulated by the given stand structure (Figs. 1c, d). Since CO_2 is a greenhouse gas that is significantly emitted by human activity, the equivalent amount of atmospheric CO_2 fixed by a particular stand structure was subsequently calculated from the amount of sequestered carbon.

There are two main factors as a driving force for photosynthesis and respiration, as a reciprocal process, resulting in biomass production. The first factor is light. Light intensity has several effects on plants, among them are photo-cybernetic effects (including photoperiod), photo-energetic effect (i.e. the source of energy for photosynthesis), and even photo-destructive effect when the amount of incident solar energy is too high. Variation in photosynthetic rates among individual leaves, light distribution within the leaf canopy, and respiratory activity all complicate attempts to make exact calculations of RUE (Sinclair and Horie 1989). Sinclair and Horie (1989) also noted that those leaves that are photosynthetically light saturated are less efficient than those in the shade. It is clearly shown by Jarvis and Leverenz (1983) that the assimilation rates on individual needles, shoot, and forest

canopy level differ and become higher on the canopy level as the effect of leaf area distribution and efficiency of light utilisation. Moreover, the energy of solar radiation in the form of diffuse light is used more efficiently in CO₂ assimilation (Urban et al. 2007a). Specific role can play sun-flecks reaching the canopy layer with the high leaf area density as there are differences in photosynthetic induction etc. (Urban et al. 2007b; Kubásek et al. 2013). The second factor is temperature. Both processes, i.e. photosynthesis and respiration, are enzymatic and thus temperature dependent, but in a slightly different functional relationship (Larcher 2003). Respiration is extremely exponentially dependent, whereas photosynthesis has shown optimum for C3 plants at temperate zone close to 25–30 °C, and presumably close to 30–35 °C under elevated atmospheric CO₂ concentration (Sinclair et al. 1992), and then dropped down. Both environmental factors' effects can explain the higher RUE values found at mountain forest stand, where the higher proportion of diffuse to direct radiation, as well as presumably higher air humidity (as there is collinearity between elevation and precipitation), comparing with lower elevation leads to higher stomatal conductance and efficiency of net primary production reflecting on RUE.

Since the significant relationship between RUE and carbon sequestration ($p < 0.001$; $R^2 = 0.85$) is caused by the functional dependency of carbon fixation on the total intensity of photosynthetic uptake (Grace et al. 1987), both sequestered carbon and fixed CO₂ from the atmosphere are also reflected in the RUE values within the given stand structure at each particular site. Thus, the higher the RUE within a particular stand, the higher carbon sequestration of the ecosystem and the interannual changes on the level of RUE affected by the weather of the given year (significantly by air temperature; Fig. 2a; Supplementary material 5) are naturally involved in total carbon sequestration. Based on the results of the presented study and as discussed in more detail below, RUE shows a downward trend with increasing air temperatures (within the observed range of temperatures). Moreover, the maximum value of RUE for Norway spruce stands was achieved according to Lagergren et al. (2005) at a mean air temperature during the growing season around 15 °C (in Sweden), corresponding to the maximum chemical efficiency of photosystem II there, which was also proven for Norway spruce stands (Lundmark et al. 1998). The findings obtained by Lagergren et al. (2005) were also confirmed by Bartelink et al. (1997). These results are entirely in line with the measurements taken by Lindroth et al. (1998), who measured the respiration of mixed pine-spruce stands using the eddy covariance method in close connection with air temperature in Sweden. The authors found a significant exponential increase in stand respiration (released CO₂) at air temperatures exceeding 10–12 °C. Based on these results, it is evident that a significant decrease in RUE with increasing air temperature (which occurs in the growing season according to Bartelink et al. 1997 and

Lagergren et al. 2005 just around a mean air temperature of 15 °C) is caused by both a decrease in the rate of photosynthetic uptake (particularly the chemical efficiency of photosystem II, as proven Lundmark et al. 1998) on the one hand, and a concomitant increase in respiration as a dissimilation process on the other hand (Lindroth et al. 1998).

Moreover, sun- and shade-adapted leaves and their proportion can also influence carbon sequestration, as this distinguishing factor plays a crucial role both in assimilation and dissimilation processes. Air temperature affects carbon gain when the temperature increment increases the photorespiration (through the enhanced oxygenase activity of Rubisco). Therefore, leaves exposed to the sun are predisposed to higher rates of photorespiration despite those losses being covered by a higher gross photosynthesis rate (and higher points of gross photosynthesis saturation- I_s) easily. Furthermore, carbon losses can be influenced, for instance, by isoprene emission, which is significantly affected by temperature where leaves exposed to the sun emit greater amount of isoprene than leaves in the shade under the same temperature (especially at higher temperatures), as was found by Harley et al. (1996).

The relationship between RUE and tested meteorological variables

The seasonal RUE values (i.e. for the May–October period) varied among the studied Norway spruce stands. In central Europe, Norway spruce naturally occurs on sites with a mean annual air temperature below 6 °C and with mean annual precipitation greater than 800 mm (Souček and Tesař 2008). The highest annual RUE values were recorded at the LU site, which has the lowest mean annual air temperature and the highest annual amount of precipitation (3.7 °C; 1373 mm). This result very closely corresponds to the growth optimum of Norway spruce under central European conditions. From the viewpoint of annual RUE values, the LU site was followed in descending order by KL, LA, and ZE, with mean annual temperatures of 7.2 °C, 5.5 °C, and 7.9 °C, respectively. Although the mean annual air temperature at KL was higher than at LA, a higher RUE value was found at KL. These findings can be explained either by the significantly higher annual amount of precipitation at KL than at LA (1137 vs 745 mm; see Supplementary material 2), or by the presence of shade-tolerant European beech in the understorey (Supplementary material 3), which can lead to higher RUE under the shelter of the stand's upper layer (i.e. in its growth optimum). This was also indicated in findings obtained by Bartelink et al. (1997), who tested RUE under varying proportions between Douglas fir and European beech in the different social statuses of individuals within studied stands. The contribution of the European beech growing below the upper canopy as individually mixed was also confirmed by

Pretzsch et al. (2012). The authors found the highest level of RUE within a stand mixture of Norway spruce and European beech in the case of individual mixing (the RUE value of the grouped mixed form did not differ much from the pure stand). The importance of the beech admixture or a generally deciduous tree species on higher RUE values as demonstrated Pretzsch et al. (2012) was also shown in this study (albeit to a minimal extent since the admixture of beech in the understorey represented only a small tree species representation in the KL stand). Under these circumstances, this fact could also be caused by the positive effect of deciduous tree species on the stand's microclimate related to the different evaporation rate of deciduous and coniferous tree species (e.g. Catovsky et al. 2002), and is discussed in more detail below.

Furthermore, Bartelink et al. (1997) observed high variability in daily RUE values, which reached up to 2.3 g MJ^{-1} in Douglas fir stands. They also found that RUE decreases with air temperatures higher than $15 \text{ }^{\circ}\text{C}$ ($T_a > 15 \text{ }^{\circ}\text{C}$). The finding of this decreasing trend within the relationship between RUE and mean air temperatures is utterly in line with the conclusions reached in this study, where a significant linear dependence between RUE values and mean air temperatures was found in pure mature Norway spruce stands along their production gradient in the Czech Republic (Fig. 2a; cf. Supplementary material 2).

The fact that a lower RUE value in three mature Norway spruce stands was found in this study compared with the RUE values of spruce pole stands observed by Bellan et al. (2017) in the Czech Republic could have been caused by the specific course of the weather and differences within individual years, since 2018 was characterised by warm periods, and a generally higher mean annual air temperature compared with 2014 and 2015, even though these 2 years also typified above-average air temperatures (Lubojacký, unpublished data). If a significant negative correlation between RUE and mean monthly air temperatures was shown in this study, the above-average temperatures of 2018 could be the causation of lower RUE levels in those mature spruce stands where the temperature extremes of 2018 were more evident in three spruce stands located at lower altitudes. Even compared with spruce pole stands analysed under temperatures that were less extreme, yet still above average, the pole stands should attain lower RUE values under comparable temperature conditions (Gspaltl et al. 2013). The fact that the interannual dynamics of RUE may differ within the same stand was also proven by Marková et al. (2011). This results not only in interannual RUE changes within the same stand (without stand tending), but also in a significant initiation of RUE in the year following stand tending (and partly still evident in the following year). Although the effect of silvicultural treatment leading to a sudden increase of RUE after the treatment may be neglected in this study because no silvicultural treatments were performed

in the observed stands within the 5 years preceding the study, a different course of mean annual air temperatures over the particular years cannot be omitted. This must always be taken into account when comparing various RUE values from different growing seasons.

Moreover, the findings mentioned above were fully confirmed in a detailed study by Pretzsch et al. (2012) in which the course of RUE was monitored in two different research plots for a long time (for 9 years) where three various forms of stand mixing of Norway spruce and European beech were observed (pure stand, group mixed, individually mixed). In both plots and all three forms of stand mixture, RUE trends coincided throughout the whole observation period (i.e. an increase in RUE within 1999–2002; a steep decline in 2003 with a gradual increase in 2004 and 2005 followed by a marked decrease in 2006 and a significant increase in 2007). However, despite the same trends, the RUE values (the position of curves) of the particular stand types differed and the highest RUE value was observed in an individually mixed stand.

Thus, no significant inhibitory role of lower temperatures (within the analysed temperature range) in the Czech Republic was evident (see Fig. 2a). If the mean air temperature of the whole growing season (i.e., May–October) were taken into account, the above-mentioned maximum RUE value attained around $15 \text{ }^{\circ}\text{C}$ would very closely correspond to the maximum chemical efficiency of photosystem II (Bartelink et al. 1997; Lagergren et al. 2005) which Lundmark et al. (1998) found in Norway spruce seedlings (also in Sweden). Therefore, it is likely that RUE is affected by air temperature within a functional context. The effect is obviously directly caused by changes in the rate of photosynthetic processes (i.e. photosynthetic assimilation) which immediately enter into the RUE value through increased total above-ground biomass. If we compare the results of this study with Lagergren et al. (2005), who performed a detailed analysis of the influence of air temperature on RUE within particular periods of the growing season (May–June, July–August, September–October), we find out that a continual decrease of RUE values with increasing air temperatures in May–June and July–August entirely coincides with the course of RUE observed in this study, where the effect of monthly mean air temperatures on RUE was found (Fig. 2a). On the contrary, Lagergren et al. (2005) found a positive relationship in the September–October period and hence a gradual increase of RUE with rising mean air temperatures.

Some authors (e.g. Goetz et al. 1999; Running et al. 2000) generally suppose that RUE is affected by air temperature and air humidity (saturation deficit). However, the fact that no significant effect of either monthly amount of precipitation or air humidity on RUE was found in this study corresponds to other studies. In particular, Albaugh et al. (2016) proved on a wide range of tree species (including Norway spruce) and

site conditions that even controlled artificial irrigation conditions did not lead to any demonstrable changes in the RUE level. They also showed the same in the case of nutrient effects under controlled conditions of different fertilisation regimes.

The findings that the amount of precipitation had no significant influence on RUE was found (despite the general assumption that precipitation would also affect RUE since water availability is a crucial factor for sufficient photosynthetic uptake, transpiration, vitality, and plant production) can be explained by the fact that air temperature significantly affects the water operation of plants as well as stress caused by water scarcity (i.e. drought stress is considerably integrated into eigenvalue) through the saturation of water vapour in the air. As shown, for instance, by Horáček et al. (2018), the transpiration stream increases proportionally to the gradient of the water potential (its absolute value) between the soil and the air of the crown layer and its close surroundings: if we admit that trees just “overbridge” these two environments with different water potential. The low value of this gradient (in an absolute value), the low real transpiration, and the small risk of stress caused by water scarcity occur not only when the soil is adequately supplied with water, but also in the case the soil conditions are unfavourable from the viewpoint of water supply; however, if there is, the air is sufficiently humid. This presumption of high saturation of air by water vapour (i.e. a high water potential and low saturation deficit) can more easily occur in air at low temperatures than in air at higher temperatures (which can include a higher volume of water vapour than colder air). This fact can be considered crucial when we observe a significant influence of air temperature on RUE where air temperature plays such an essential role in the water balance of trees. This is even greater than the role of the current water content in the soil, which is determined mainly by the amount of precipitation.

Conclusions

Based on changes in total above-ground dry mass weight, RUE (g MJ^{-1}) was evaluated and compared in fully stocked mature Norway spruce stands covering the dominant production range of spruce in the Czech Republic (site index 20–38) along the temperature, precipitation and altitudinal gradients. In this study, an innovative methodological approach combining digital hemispherical photographs and sensors recording incident global radiation in a sufficiently large open area was used to determine the amount of absorbed solar radiation by the canopy. Furthermore, the effect of selected climate variables on RUE was analysed. It was found that mean air temperature significantly affects RUE, where the value of RUE decreased with increasing mean annual and/or monthly air temperature. This fact was also confirmed from the viewpoint of the amount of sequestered carbon by stand structure, where

the most carbon with the highest RUE value was fixed in the stand with the lowest site index and the lowest monitored air temperature, as well as the highest amount of precipitation; it confirms the hypothesis that air temperature affects RUE more than just the production potential of a site (site index). A high degree of RUE dependence on the inverse Lang’s rain factor, the inverse Angström index and inverse values of the de Martone index of aridity was also found; however, a fundamental influence of air temperature entering into the calculations of these indices can again be assumed. The significant dependence of the amount of sequestered carbon (or the CO_2 molecules) fixed by forest ecosystems on RUE was also found in the presented study. Therefore, GCC accompanied by global warming can lead to diminishing RUE and carbon sequestration in spruce stands at low altitude sites.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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