MENDEL UNIVERSITY IN BRNO
Faculty of Forestry and Wood Technology
Department of Forest Ecology

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Net balance of production gains and respiration losses of the forest ecosystem

BACHELOR THESIS

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Guides to writing a thesis:

1. Elaboration of an overview of the measurement of greenhouse gas fluxes between the ecosystem and the atmosphere. Description of the methods used, their advantages and limitations.
2. Acquisition of CO2 flux data between forest ecosystems and the atmosphere and meteorological measurements. Data will be obtained free of charge from the stations of the CzeCOS network operated by GCRI CAS and possibly from the FLUXNET database.
3. Processing the obtained data to identify the situations when the studied ecosystem is the receiver and when it is the source of CO2. Focusing on situations in which the ecosystem loses carbon during the growing season. Description of the typical situations and try to identify the main drivers that control the CO2 sink/source by the forest ecosystem.
   The student will acquire techniques of Forest ecology and will understand Forest ecology from a wider perspective.

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Net balance of production gains and respiration losses of the forest ecosystem

Čistá bilance produkčních zisků a respiračních ztrát lesního ekosystému

Pavol Klimo

Abstract

This thesis deals with the carbon fixing ability of forest ecosystems. It describes the methodology and instruments, mainly eddy covariance, used to measure fluxes of greenhouse gases between forests and the atmosphere, as well as their advantages and limitations. By processing and analyzing flux and meteorological data measured throughout the year obtained from the ecosystem station of CzeCOS/FLUXNET networks it was possible to determine precise time windows during which forest ecosystems receive and emit greenhouse gases, most importantly carbon dioxide. The analysis is focused on identifying situations which drive these ecophysiological processes, carbon loss during growing season in particular.

Keywords: Eddy covariance, ecosystem production, carbon sink, meteorological variables, plant ecophysiology

Abstrakt

Tato práce se zabývá schopností lesních ekosystémů fixovat uhlík. Popisuje metodiku a nástroje, zejména eddy kovarianci, používané k měření toků skleníkových plynů mezi lesy a atmosférou, jakož i jejich výhody a omezení. Zpracováním a analýzou meteorologických dat a dat toků plynů měřených po celý rok získaných z ekosystémových stanic sítě CzeCOS/FLUXNET bylo možné určit přesná časová okna, během nichž lesní ekosystémy přijímají a emitují skleníkové plyny, především oxid uhličitý. Analýza je zaměřena na identifikaci situací, které řídí tyto ekofyziologické procesy, zejména ztráty uhlíku během vegetačního období.

Klíčová slova: Eddy kovariance, ekosystémová produkce, propad uhlíku, meteorologické proměnné, ekofyziologie rostlin

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Introduction

Carbon is the most important and abundant element in living organisms and ecosystems on planet Earth. Its ability to form energy-rich compounds is the basis of life and the food chain. It also is the primary building material for every living thing, and it plays a very important role in the greenhouse effect of our planet, which makes conditions for life itself possible. Natures primary producers, called autotrophs, turn inorganic carbon into organic compounds, the vast majority of them using solar energy in the process of photosynthesis with a few species, called chemotrophs, utilizing oxidation as an energy source. Although, because of their cells requiring energy like every other organism, plants, and other autotrophs have to break down carbon compounds in the process of respiration as well. Carbon dioxide is the only source of carbon for plants that use photosynthesis. It is also one of the most important carbonaceous greenhouse gases. Concentrations of greenhouse gases (GHG) in the atmosphere change the climate of the Earth, affecting some areas more than others. The ability of plants to photosynthesize and remove carbon dioxide from the atmosphere is affected by many conditions: climate, weather, species, the plant health and age being significant. Measuring meteorological conditions is essential for the analysis of their influence on photosynthesis and respiration. Measuring carbon flux, the amount of carbon received and lost by an area, can be accomplished by numerous methods *e.g.*, allometric, chamber and relaxed eddy accumulation methods. However, the eddy covariance method provides estimates of fluxes over a large area based on high frequency data. It relies on direct, fast, and precise measurements of gas concentrations, but also heat, transported by turbulent airflow in and out of an area, which can be integrated over bigger areas correspondingly. While deploying this method there are many important assumptions to be made and large amounts of data to process and correct. Nevertheless, when done correctly, using modern instruments, it can achieve accurate measurements and flux estimates. Measuring meteorological conditions together with fluxes is crucial for analyzing carbon removal. By subsequent comparison of these data, typical and atypical situations of carbon dioxide fluxes are identified, along with the meteorological drivers responsible for them. This thesis focuses on identifying and describing situations of forest ecosystem carbon losses during the growing season, which decrease the net productivity of studied ecosystems to various extent.

Thesis objectives

This work is focused on the mainly description of measured CO_2 fluxes between three forest ecosystems and the atmosphere, along with the meteorological variables that drive their dynamics in time. After a theoretical part describing the carbon cycle, plant ecophysiology and various methods of flux measuring, and data processing, ecosystem production data obtained from the ecosystem stations of the CzeCOS network will be analysed together with meteorological data. The main objective is to characterize the situations that occur in the carbon exchange between forests and the atmosphere throughout a year, while assessing their carbon respective carbon sink potentials. By the comparison of situations which occurred during two years with contrasting climatic conditions, it is possible to identify the main drivers which have an effect on this exchange situations and the scope of this effect in different ecosystems. The secondary objective is to identify situations of severely decreased ecosystem production, during which the forest acts as a source of CO_2 to the atmosphere, along with the factors causing these phenomena.

1. Literature review

1.1. The carbon cycle, climate change and forests

The global carbon cycle is a biogeochemical cycle, a pathway by which carbon in various forms circulates and is exchanged between the Earths biosphere, atmosphere, lithosphere, pedosphere and hydrosphere. The main processes in this cycle are photosynthesis, respiration, decomposition and mineralization. Atmospheric carbon, existing mainly in the form of CO_2, is a very small but the more important constituent of total terrestrial carbon (Pulselli, 2008).

Over the course of hundreds of thousands of years, the global carbon cycle maintains consistence in carbon concentrations, preventing carbon emissions into the atmosphere or carbon sedimentation. This maintenance is a part of the slow carbon cycle, in which carbon takes 100-200 million years to cycle between the atmosphere, rocks and oceans. In the slow cycle approximately 0.01 to 0.1 gigatons of carbon (GtC) are transported and transformed yearly, and its main mechanisms are weathering of rocks and sedimentation in the oceans, volcanoes, and ocean-atmosphere carbon exchange. It is based on chemical reactions and tectonic activity.

On the other hand, the fast carbon cycle is measured in decades. It is the movement of carbon though the biosphere, in which 1 to 100 gigatons of carbon are cycled yearly. Since plants and phytoplankton are the principal components of this cycle, photosynthesis, respiration and decomposition are its mechanisms (Riebeek, 2011).

Cyclic variations in the orbit of Earth cause changes in its climate, called glacial and interglacial periods. These consistent climate changes affect the carbon cycle and atmospheric CO_2 concentrations (Lüthi *et al.*, 2008, Jouzel *et al.*, 2007).

The concentration of atmospheric CO_2 has increased by 48% (277-410 ppm) due to human activity since the industrial revolution (Dlugokencky and Tans, 2020). Fossil fuel usage as an energy source, cement manufacturing and deforestation are the main sources of CO_2 emissions (Ciasis *et al.*, 2013). This anthropogenic perturbation of the carbon cycle has caused changes in Earths energy balance. Since CO_2 is a greenhouse gas (GHG) which absorbs energy and heats the atmosphere, its increased concentrations (along with other GHGs such as CH_4 and N_2O) in the atmosphere result in the change of global climate.

These human-induced changes have led to a global warming of 1 °C, exceeding 1.5 °C in some regions and increasing at 0.2 °C per decade (Allen *et al.*, 2018). Climate change substantially affects terrestrial ecosystems, causing biome shifts, phenology changes, species range and abundance, changes in precipitation *etc.*, due to the changing conditions (Hoegh-Guldberg *et al.*, 2018). Forest ecosystems are an important component of the carbon cycle and are recognized as one of the key factors contributing to the mitigation and adaptation to global climate change, reducing desertification, land degradation and providing food security (IPCC 2019; Paris agreement).

1.1.1. Forests as carbon sinks

The United Nations Framework Convention on Climate Change refers to a sink as "any process, activity or mechanism which removes a greenhouse gas, an aerosol or a precursor of a greenhouse gas from the atmosphere." A carbon source consequently releases any of the above (UNFCCC, 1992). It is thus a component of the carbon cycle which accumulates carbon annually.

The intergovernmental Panel on Climate Change (IPCC) defines carbon dioxide removal as "anthropogenic activities removing CO_2 from the atmosphere and durably storing it in geological, terrestrial, or ocean reservoirs, or in products. It includes existing and potential anthropogenic enhancement of biological or geochemical sinks and direct air capture and storage but excludes natural CO_2 uptake not directly caused by human activities" and carbon sequestration as "the process of storing carbon in a carbon pool" (IPCC, 2019).

During the decade of 2009-2019, the terrestrial CO_2 sink accounted for approximately a third of anthropogenic carbon emissions, equaling to 3.4 ± 0.9 GtC yr^{-1} out of 9.4 ± 0.5 GtC yr^{-1} plus 1.6 ± 0.7 GtC yr^{-1} of fossil fuel emissions and land use emissions (consisting mostly of deforestation), respectively (Friedlingstein *et al.*, 2020). Forests are one of the most prominent and important terrestrial carbon sinks. (Malhi *et al.*, 2002; Luyssaert *et al.*, 2007; Pan *et al.*, 2011; Harris *et al.*, 2021). The main reason behind this is the ability of woody species, of which forests consist, to remove and store carbon in their vascular and structural tissue – wood – for long periods of time up to hundreds of years. Another substantial forest component containing large amounts of carbon is forest soil, the ratio of soil to biomass carbon increasing with latitude (Lal, 2005). While sources and authors agree on the significance of forests as carbon sinks and on the necessity of reforestation, afforestation, conservation, and proper forestry management to counter climate change effects (Bastin *et al.*, 2019), global forest carbon flux estimates differ greatly in publications. This discrepancy occurs due to the multitude of flux estimate calculations methods used, variable data quality, lack of spatial detail and overall complexity in measuring systems. These shortcoming cause uncertainties in the degree of climate mitigation by forests and discourage actions required in the forest sector to improve global climate mitigation. It is thus crucial to specify forest GHG fluxes in order to support future decisions and goals regarding climate (Harris *et al.*, 2021, Pan *et al.*, 2011). Uncertainties in the changes and trends of global carbon cycle and land carbon sinks also need to be assessed (Le Quéré *et al.*, 2013).

Almost all forests are net carbon negative, removing more carbon from the atmosphere than emitting into it. Tropical and subtropical forests are responsible for the majority of carbon fluxes, though due to their high carbon emissions they are not the most effective carbon sink. Temperate and boreal forests account for two-thirds of the global forest net carbon sink, thanks to their lower carbon emissions compared to removals. This is partially a result of forest management by logging and regeneration in temperate forests (Harris et al., 2021). Multiple factors affect the carbon sink of forest ecosystems. Forest regrowth after disturbance plays a role in the global forest carbon sink. The carbon sink in stands regrowing after natural disturbances, land use changes or management practices could be higher than in old-growth boreal and tropical stands. This study likewise claims that most of the carbon sink is in mid-high latitudes, not tropics (Pugh *et al.*, 2019). Although with uncertainties in the roles of other effects of climate change and in the magnitude, the increase of atmospheric CO_2 concentration increases photosynthesis and the terrestrial carbon sink (Walker *et al.*, 2021). Some evidence suggests that up to 60% of the terrestrial carbon sink is caused by increased atmospheric CO_2 (Schimel *et al.*, 2015). Regarding trees, contrasting conclusions on the effects of higher CO_2 concentrations can be found in study cases. While some claim its positive effect on their growth (Ainsworth and Long, 2004), other report no related growth increase attributed to CO_2 levels in trees around the globe during the last century (Peñuelas *et al.*, 2011).

Climate has a prominent effect on forest disturbances and forest carbon sink. The severity and frequency of abiotic factors such as drought, wind, snow and biotic factors like insects and pathogens has increased in recent years due to the changing climate, resulting in higher forest disturbance occurrence. Drought especially is one of the most relevant emerging factors threatening forest ecosystems (Allen *et al*., 2010).

Climate induced change in the disturbance regime of forests is thought to be a very significant climate change effect on forest ecosystems, potentially strongly impacting its socially valued services. Vulnerability to these disturbances varies in different regions and forests in Europe, as does their potential severity. Adaptive actions in forest management can help mitigate the effects of climates change (Linder *et al*., 2008; Seidl *et al*., 2017).

1.1.2. Climate-Smart Forestry

Our understanding of how all the drivers affecting global forest carbon sink add up in sync is lacking, and so are the predictions of their future changes. Models radically disagree on the potential change in forest carbon sink throughout this century, ranging from predictions of sink becoming multiple times higher to forest turning into a carbon source. The future potential of forests as carbon sinks paves the way for incorporating management strategies for climate mitigation. Depending on the forest behaving as a carbon sink or source, conservation or increased wood harvest would be preferred, respectively. To establish global forest climate mitigation strategies, there should arise a general assumption about the carbon balance of unmanaged forests, as they are a vital part of the world forests. Most past literature reports their ultimate carbon neutrality, but new studies do not record the cease in their carbon uptake (Luyssaert *et al*., 2008; Paw U *et al*., 2004; Zhang *et al*., 2006; Baldocchi, 2008). Data sourced from multiple methods (forest inventories, flux measurements) should be combined and their quality should satisfy established criteria, such as being able to reproduce trends in large data sets, so uncertainties of forest sinks can be assessed. Forest management methods that increase both wood production and carbon allocation with efficient wood uses that do not release carbon back into the atmosphere will provide climate change mitigation regardless of global carbon sink evolution (Bellassen and Luyssaert, 2014).

Climate-Smart Forestry (CSF) is an emerging European branch of forestry management, which aims to implement management strategies in response to global climate change. It is, by definition, a sustainable adaptive forest management to enhance and protect forest potential of adapting to and mitigating climate change, while ensuring constant delivery of forest goods and services (Bowditch *et al*., 2020). Its goal is to find the optimal combination of measures to increase climate mitigation *etc*. in regard to regional conditions. It builds on the concept of sustainable forest management, increasing climate benefits while creating synergies with other ecosystem functions like biodiversity. Nabuurs *et al*. (2018) describes three basic pillars of CSF, which require very different approaches depending on the region:

- removing or reducing GHG emissions to mitigate climate change
- changing forest management to build forest resiliency to changing climate
- sustainably increasing productivity while providing all other forest benefits

Verkerk *et al*. (2020) mentions another component of sustainable wood use as a substitute to non-renewable materials in products such as chemicals, construction, plastic, *etc.* The work also highlights finding balance between short and long-term goals, but also wood production and biodiversity conservation and their policy implications.

Measuring the production of various forest ecosystems and its drivers is thus a necessary process in addressing uncertainties of forest carbon sink and its predictions in the changing climate, as well as in the implementation of forest management techniques for climate mitigation and increased productivity such as CSF.

1.2. Plant ecophysiology

This discipline examines relationships between the internal and external environments of plants, clarifying physiological responses of plants to ambient conditions and pressures (Ferry-Graham and Gibb, 2008). Considering the changes in climate and atmospheric chemistry, good understanding of plant and ecosystem responses is much needed. Assessing how environmental stresses jointly affect productivity is required to make predictions about the future of vegetation (Waring, 1993).

1.2.1. Photosynthesis

Photosynthesis is a physiological process of converting light energy into chemical energy, characteristic mainly for plants, algae, and cyanobacteria. It is a crucial process for life on Earth as it provides most of the energy to the food chain.

During the most common type of photosynthesis called oxygenic, carbon dioxide and water are converted into energy-rich carbohydrates with oxygen split from the water being a byproduct. The oxygen produced this way is a main factor in maintaining the oxygen content of our atmosphere (Petsch, 2003). The sugars produced for energy storage are also converted into other compounds, which make up about 95% of plant dry mass (Chapin and Eviner, 2007).

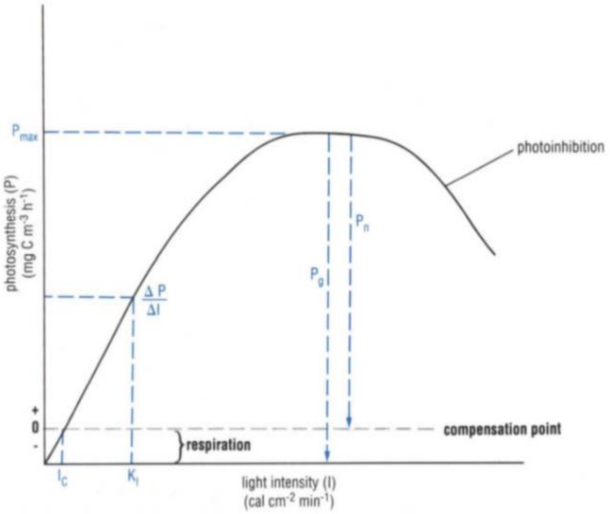
Photosynthesis is a two-stage process, consisting of the light and dark reactions. In the light reactions, light energy is converted into chemical energy and water is split into hydrogens protons oxygen molecules and electrons.

Conversion of inorganic carbon into organic compounds, called carbon assimilation, is carried out by the Calvin cycle, which is a part of the dark reactions. These processes do not require radiation. The enzyme RuBisCO catalyzes reduction of CO_2 into a precursor of the final carbohydrate product. Plant types are named depending on the number of carbon atoms in this precursor, with most trees belonging to the C_3 type. This catalyzation is, though, carried out with a relatively low efficiency because RuBisCO also binds oxygen. To compensate for this, plants use metabolic pathways which ultimately produce CO_2. During this process called photorespiration 25% of the fixed CO_2 is released back into the atmosphere in C_3 plants (Sharkey, 1988), with hot and dry conditions causing it to increase at higher rates than photosynthesis (Long, 1991), due to more O_2 captured by RuBisCO at higher temperatures (Petsch, 2003 oxygen cycle; Dusenge *et al.*, 2019).

Light

Radiation is the source of energy for photosynthesis, having a vital effect on its amount and rate. Photosynthetic organisms can use the light within a wavelength of 400-700 nanometers, termed photosynthetically active radiation (PAR). Irradiance increases photosynthesis until a saturation point, after which additional increase in light intensity can cause a decrease called photoinhibition, potentially damaging the plant photosynthetic tissues (Aro *et al.*, 1992). This correlation is expressed by the photosynthesis-irradiance (PI) curve (**Figure 1.1**), which differs within species. Shade leaves reach the saturation point at lower irradiance than sun leaves. Other factors like temperature, CO_2 concentrations, leaf shape and chlorophyll content also affect the shape of this curve (Teskey *et al.*, 1995).

Figure 1.1 PI curve
I_C – compensation light intensity, photosynthesis equal to respiration
K_I – half-saturation constant, photosynthesis equal to half of P_{max}
P_{max} – maximal photosynthesis
P_g – gross photosynthesis
P_n – net photosynthesis
(From Lalli and Parsons, 1993)



Temperature

Photosynthesis response to temperature can be described by a parabolic curve, being limited by both too low and too high temperatures and having an optimum. Optimal temperature for photosynthesis varies between species (**Figure 1.2**), plant types (**Figure 1.3**) and growing conditions. For C_3 plants the optimum range is 10-35 °C, for most temperate zone plants it is 25-30 °C (Gates, 2003). C_3 plants have comparable photosynthetic activity at both higher and lower temperatures, unlike C_4 plants for which higher temperatures substantially increase photosynthetic rates, by more than twofold. This increase is also manifested in annual and deciduous woody C_3 plants, though only by 20-30%. Perennial and evergreen woody C_3 plants exhibit little change in photosynthetic rates at higher compared to lower temperatures. This shows the acclimation of C_3 plants to wider ranges of temperatures (Yamori *et al.*, 2014; Sage and Kubien, 2007).

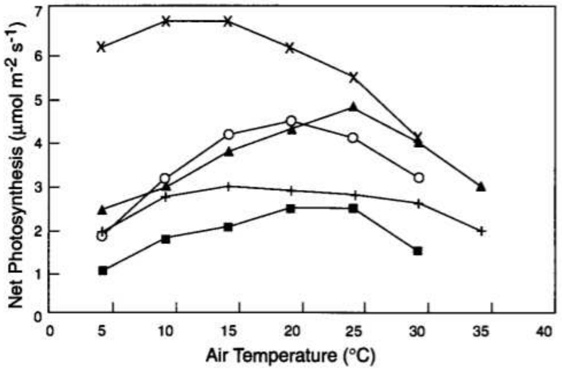


Figure 1.2 Response of photosynthetic rates of various C_3 conifer species to air temperature. ×*Pinus ponderosa,* ▲*Pinus taeda,* ○*Pinus strobus,* +*Pinus sylvestris,* ■ *Picea engelmanii* (From Teskey *et al.*, 1995)

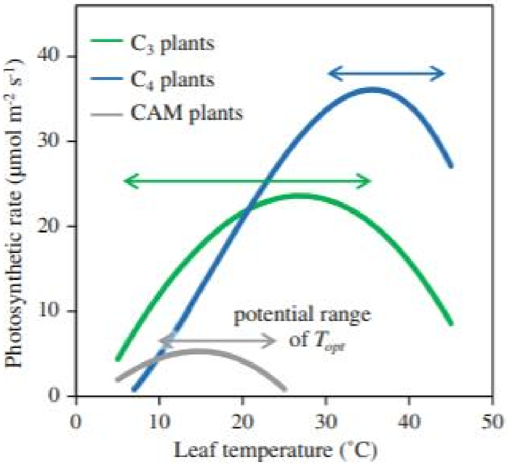


Figure 1.3 Response of photosynthetic rates of photosynthetic pathway plant types to temperature.
(From Yamori *et al.*, 2014)

CO_2

Elevated CO_2 concentrations directly increase photosynthetic activity by providing more CO_2 available for RuBisCO saturation and suppressing photorespiration. (Drake *et al.*, 1997). As CO_2 concentrations increase and RuBisCO is saturated, the rate of photosynthesis becomes limited by regenerating abilities of photosynthetic metabolism pathways and processes. Thus, the effect of rising CO_2 levels on photosynthesis is not linear (**Figure 1.4**) (Dusenge *et al.*, 2019).

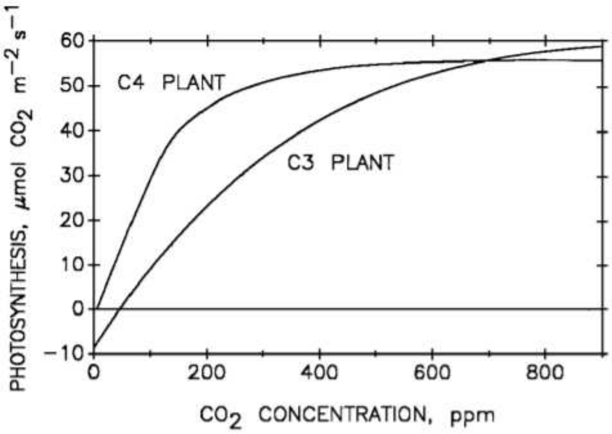


Figure 1.4 The rate of photosynthesis of C_3 and C_4 plants in response to increasing air CO_2 concentrations measured in saturated light conditions. (From Allen and Prasad, 2004)

1.2.2. Ecosystem production

Biomass is the mass of all living organisms of a certain area. It usually refers to living material only, unless stated otherwise (Houghton, 2008 Encycl. of ecology). Since biomass is composed of approximately 50% carbon (Petrokofsky *et al.*, 2012) it is generally reported by the mass of carbon (*e.g.*: 1 gigaton of carbon = 10^{15} g of carbon) per area unit in most of the current literature, being independent of water content (Bar-On *et al.*, 2018).

The total amount of energy fixed and created by primary producers over a certain time length, mostly in the process of photosynthesis, is called gross primary production (GPP). A part of this energy is further utilized since plants, like all living organisms, require energy to grow and maintain their tissues. Organisms obtain this energy via cellular respiration, termed autotrophic for primary producers, the process opposite to photosynthesis. Net primary production (NPP) refers to the difference between carbon uptake during photosynthesis (GPP) and emissions during autotrophic respiration. Having said that, the total carbon balance or flux of the whole ecosystem (area) also includes the heterotrophic respiration of other organisms in addition to primary producers (**Figure 1.5**).

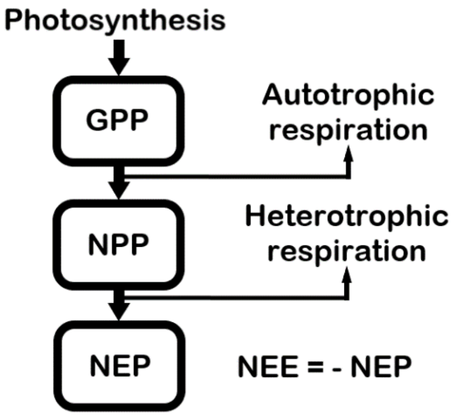


Figure 1.5

Ecosystem production diagram, arrows represent the flux of CO_2

Production is also typically expressed as carbon mass per unit area, though in this case per time unit, *e.g.*: gC m^{-2} yr^{-1} (Landsberg and Gower, 1997). Ecosystem CO_2 flux can be also expressed as net ecosystem exchange (NEE), the carbon flux from the ecosystem to the atmosphere (Chapin *et al.*, 2006), which is equal to NEP in opposite sign when not involving inorganic carbon fluxes (Lovett *et al.*, 2006) *e.g.*: negative net ecosystem exchange represents positive net production, rendering the studied ecosystem as carbon sink.

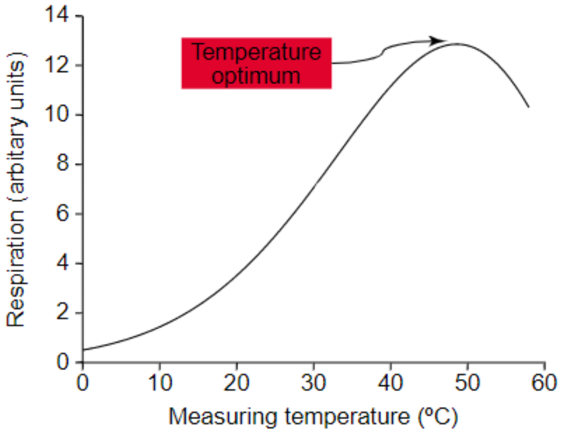
Carbon use efficiency (CUE) quantifies the capacity of vegetation to relocate carbon from the atmosphere into biomass. It refers to the ratio of NPP to GPP of ecosystems. Across different forest types, its value varies from 0.23 to 0.83, with the slope of the relationship being 0.53 (DeLucia *et al.*, 2007).

1.2.3. Respiration

Aerobic respiration is a process common to almost all eukaryotic organisms. During this process energy is released by oxidation of organic compounds, most commonly glucose, and stored in ATP. In phototrophic plants glucose is sourced from photosynthesis and respiration is fundamentally an opposite reaction to it. Glucose and oxygen are consumed for energy, with water and carbon dioxide being byproducts. Photorespiration also consumes O_2 and releases CO_2, but it only occurs in light conditions, while mitochondrial respiration operates throughout both day and night (Taiz and Zeiger, 2006). Temperature is the main external driving factor of respiration because it increases enzymatic rates (Arcus *et al.*, 2016). It is known that respiration rates rise with temperature to a certain optimal point around 45 °C above which enzymes cannot function. This relationship is often thought to be exponential, although research has shown that the rise in respiration due to increasing temperature decelerates. This reflects a declining sensitivity of plant respiration to higher temperature (**Figure 1.6**) (Heskel *et al.*, 2016; Atkin and Tjoelker, 2003). Studies have also found that respiration response time to temperature is short and that short-term (hourly) response slopes are more exponential than long-term (daily), which are linear (Landsberg and Sands, 2011).

Figure 1.6

Response of respiration to temperature (From Atkin and Tjoelker, 2003).



1.2.4. Water

Even though Central Europe has a generally humid climate, water availability is a very important limiting factor for tree vitality and tree species range of distribution. Studies show that annual tree ring growth in Central Europe is mainly limited by summer droughts, and symptoms of worsened forest stand vitality seen throughout the last decades in this region have been attributed to low precipitation.

Trees react to water deficit in various ways by changes on the physiological, chemical and morphological levels. Long term adaptations to water scarcity consist of reduced height, lower leaf area index, the growth of fewer and/or smaller stomata *etc*. Short term effects of drought are connected to decreasing water potential. At first, this decrease inhibits cell expansion and the synthesis of cell walls and proteins. Subsequently, it causes gradual stomatal closure, which results in reduced transpiration and CO_2 acquisition and thus production. Limited transpiration then causes overheating of plant tissues. It is worth mentioning that besides soil moisture, air humidity also has an important effect on plant water status and growth (**Figure 1.7**). Although trees can store significant amounts of water in their stems and branches, which can be used for transpiration during short term water deficit, prolonged drought periods cause substantially decreased tree productivity and vitality. This makes trees more vulnerable to additional stressors and can result in various damages to the plants assimilation and structural parts or eventually its demise (Brázdil *et* al., 2015; Leuschner and Ellenberg 2017).

The most important of the actual mechanisms behind tree mortality caused by drought is thought to be the hydraulic failure of xylem (water conductive wood cells) resulting in the inability of transpiration. Another factor is carbon starvation, or the depletion of carbohydrates required for a functioning metabolism, although it has not proven to be as universal causing more problems in coniferous species (Adams *et al.*, 2017).

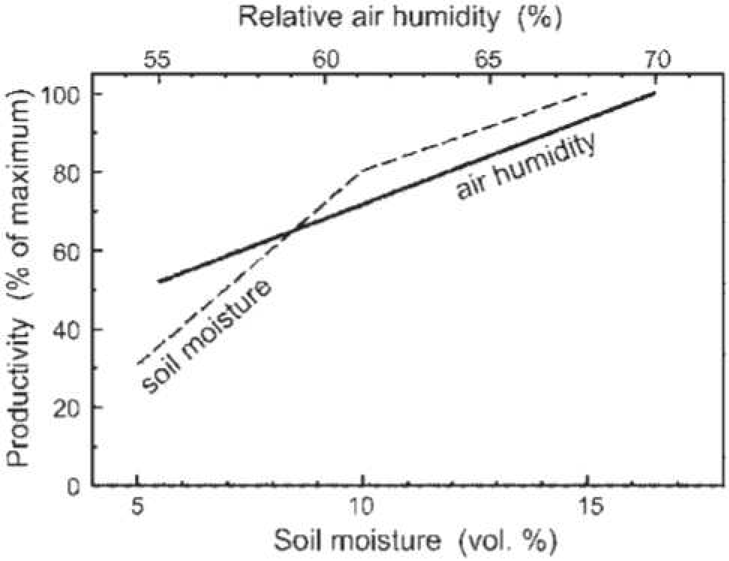


Figure 1.7

The effect of soil moisture and air humidity on beech seedling growth.

(From Leuschner and Ellenberg 2017)

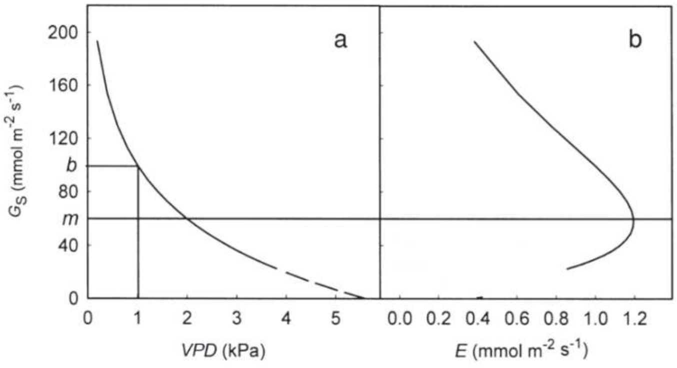
1.2.5. Transpiration

Terrestrial plants absorb and lose water throughout their life. Water supplies hydrogen and electrons for photosynthesis. Yet less than 1% of the water roots absorb is directly used in this process. Most of the remaining absorbed water is lost by evaporation from leaves or needles in the process called transpiration. It is the only significant year-long loss of water by plants (Gutschick, 1997). Through this process plants lose more than 95% of the water absorbed, losing on average 400 molecules of water for every molecule of CO_2 they gain across all plant species (McElrone *et al.*, 2013). Transpiration also acts as an effective cooling agent, keeping the plant tissues at a temperature suitable for metabolic processes and the water brought from the roots to the stomata to evaporate carries nutrients while helping roots absorb more of them (Taiz and Zeiger, 2006).

The exchange is carried out by stomata, small opening on the surface of leaves or needles and is regarded as a basic principle of ecophysiology. Both water loss and carbon gain are thus coupled and regulated by stomata and the degree by which they mediate the exchange.

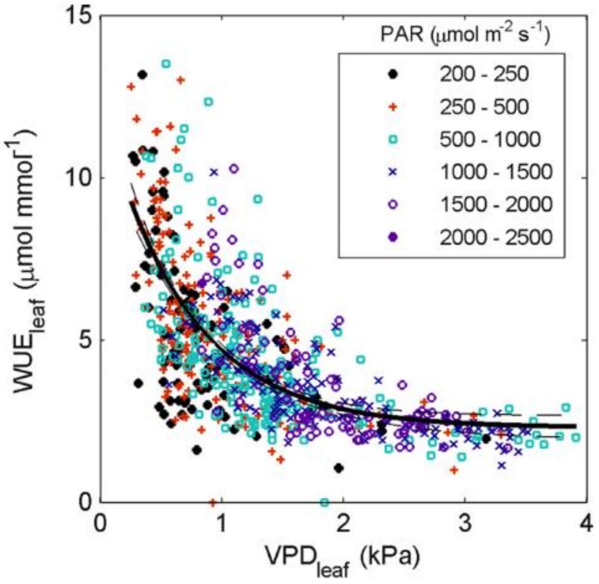
Stomatal conductance represents the rate of transport of gaseous molecules through the stomata. It affects the acquisition of CO2 into or the water loss from the leaves, therefore the rate of photosynthesis and transpiration. As a molar flux, it is usually measured in mmol m^{-2} s^{-1}. It positively correlates with the plant assimilation rate. Multiple factors integrated together affect the rate of stomatal conductance. Higher irradiance and temperature cause its higher rates and increasing CO_2 concentration causes its linear decline to a minimum at the concentration of of 1000 ppm (Landsberg and Sands, 2011). However, one of the most important factors influencing stomatal conductance and transpiration is vapour pressure deficit or difference (VPD). Atmospheric water content can be expressed by the partial pressure of its vapour in kPa. VPD reflects the drying power of the air, it is the difference between actual instantaneous vapour pressure of the atmosphere and the atmospheric vapour pressure under saturated conditions. The rate of water diffusion out of the stoma depends on the difference between atmospheric vapour pressure and vapour pressure the inside the leaf, i.e., inside the cavity behind the stoma, which is assumed to be saturated with vapour. Since warmer air can hold more moisture content, it depends on temperature (Gates, 2003). With higher VPD stomatal conductance universally declines, although various species exhibit different rates of decline. Simultaneously, transpiration increases with increasing VPD to a certain point, after which it plateaus or begins to decrease (**Figure 1.8**). This transpiration increase can substantially stress out plants, being a major factor in recent drought episodes (Landsberg and Sands, 2011; Oren *et al.*, 1999; Grossiord *et al.*, 2020).

Figure 1.8
Representation of the relationship between stomatal conductance and vapour pressure deficit and transpiration, respectively.
VPD – vapour pressure deficit
G_S – stomatal conductance
E – transpiration rate
(From Oren *et al.*, 1999)



Insufficient water at the root system will cause a decrease in stomatal conductance to minimize water losses, but also in photosynthesis (Teskey *et al.*, 1995). Plant water use efficiency (WUE) commonly describes the ratio of the amount of carbon gain to water loss (Bacon, 2004). WUE is generally higher in C4 and CAM plants compared to C3 plants. Along with greater WUE, C4 plants are also more productive than C3 plants during the same conditions. CAM plants have very high WUE but are the least productive (Hartzell *et al.*, 2018). The WUE of European beech (*Fagus sylvatica* L.) is higher than that of Norway spruce (*Picea abies* (L.) H. Karst.) (Rötzer *et al.*, 2017). Higher amount of available CO_2 increases WUE. Some authors report it both directly increases photosynthesis and reduces stomatal conductance and transpiration, resulting in higher productivity thanks to more efficient carbon acquisition and assimilation (Drake *et al.*, 1997). Other researchers claim this increase is mostly caused by enhanced photosynthetic rates, reduced stomatal conductance only having a minor effect (Mathias *et al.*, 2021). WUE also significantly depends on VPD (**Figure 1.9**) (Linderson *et al.*, 2012). Evapotranspiration refers to the sum of transpiration and evaporation rates.

Figure 1.9
The effect of VPD on WUE measured during multiple wavelenth ranges of PAR (From Linderson *et al*., 2012)



1.2.6. Tree ecological requirements

Tree species of Central Europe have their own ecological and physiological optimums, at which they display the highest vitality and growth. These optimal conditions differ between young and mature trees and include light, temperature, soil characteristics and water availability among others.

Spruce

Norway spruce (*Picea abies* (L.) H. Karst.) is relatively indifferent to temperature and has little requirements for soil quality and nutrient content, although it is outcompeted by beech on limestone substrates. Spruce tolerates shade during its youth but requires a lot of sunlight at maturity. It can put up with redundant soil water or even waterlogged stands but since it has a shallow root system, it is at maturity one of the most drought-sensitive tree of Central Europe. It also very poorly tolerates low air humidity. Some sources assign the drought sensitivity of spruce to its inability to reduce water uptake in order to produce assimilates (Modrzyński, 2007). The optimal precipitation amount for spruce is 700-800 mm or more per year (Brázdil *et* al., 2015). Mean annual transpiration sum of a spruce forest stand in Central Europe based on soil water content is reported to be 403 mm yr^{-1}, increasing to 465 mm yr^{-1} during drought years such as 2003. Drought affects big spruce trees more than small ones (Rötzer *et al*., 2017).

In Leuschner and Ellenberg (2017) it is written that spruce has a productivity optimum of 600 m a.s.l. in Central Europe (Germany), but the study cited is more than 60 years old. In Central European mountains, it is naturally outcompeted by European beech (*Fagus sylvatica* L.) and silver fir (*Abies alba* Mill.) at these altitudes, being pushed into the coldest and most nutrient-poor areas. In the last 200 years, spruce forest stands have been anthropogenically expanded to non-optimal conditions and altitudes thanks to its growth properties being suitable for forestry management (Úradníček *et al.*, 2009, 2014).

In a recent study from Krejza *et al.* (2021) the altitude of 900 m a.s.l. has been determined as the threshold below which spruce stands of the Czech Republic displayed significantly lowered productivity. This suggests the shift of Spruce optimum of growth to higher altitudes due to the changing climate, since the forest stands above this altitude showed a increase in productivity while stands below it showed a substantial, even severe, decrease.

Beech

European beech (*Fagus sylvatica* L.) is a species which tolerates shade very well. This property is the main reason why it creates natural near monocultures in the conditions of Central Europe at altitudes *ca* from 400 to 800 m a.s.l. Beech has medium soil moisture requirements; it avoids both water extremes and thrives the most at deep humous soils of limestone origins. It needs substantial rainfall and high air humidity during the summer, that is why it requires approximately 900 mm of precipitation in warm areas, but 500 mm of rain is enough for it in the colder parts of its distribution (Úradníček *et al.*, 2009, 2014). Annual transpiration of beech trees in Central Europe is estimated to be 324 mm yr^{-1} on average, increasing to 379 mm yr^{-1} during years of drought. Unlike with spruce, drought does not seem to affect big beech trees more than young ones (Rötzer *et al.*, 2017). Another publication from Schipka *et al.* (2005) states the mean yearly transpiration value of mature beech stands in Central Europe at 289 mm yr^{-1}.

Beech is considered a drought sensitive species; it displays reduced vitality at the warm edges of its distribution range (Leuschner and Ellenberg 2017). Although beech has a large leaf area index, the leaves have a relatively low water vapour conductance and a big portion of them are in shade, making the amount of water spent by this species relatively low. The fine root system of this species is intensive, but most those roots are typically present in the uppermost part of the soil, making it susceptible to droughts. Nevertheless, beech has a big drought acclimation and adaptation potential (Leuschner, 2020).

Floodplain hardwoods

Numerous tree species grow in the biodiverse floodplain forest ecosystems, this chapter describes species which are dominant at Lanžhot - one of the experimental sites.

English oak (*Quercus robur* L.) has a big area of distribution growing in both oceanic and continental climate. It thus thrives at a wide range of temperatures, but it requires a lot of sunlight. Regarding soil water needs, there exist two contrasting ecotypes, first of them is accustomed to growth on shallow soils which dry out during summer. The second floodplain ecotype has higher water requirements, though it also grows on loess. This species displays such drought resistance thanks to its prominent taproot, which can reach the groundwater and develops early in its life.

Narrow leaved ash (*Fraxinus angustifolia* Vahl.) is a species common for the warm south area of Mediterranean Europe. It requires a lot of sunlight, high groundwater levels and deep humous soils. In Czech Republic it only grows continuously in the southern edges of Moravia, and it is tolerable to floods.

Hornbeam (*Carpinus betulus* L.) is, even if not as much as beech, a shade tolerant species. It is thus able to grow in the understory of oaks and other trees. As for soil, it prefers moister and nutrient richer areas, though it also grows in areas which dry out. In floodplains, it reaches the edges of regularly flooded areas, but otherwise does not tolerate the floods themselves (Úradníček *et al.*, 2009, 2014).

1.3. Flux measuring methods

Flux can be technically described as the amount of an entity passing through an area per time unit. (Reifsnyder *et al.,* 1991). There are many uses of flux measurements, for instance when dealing with emissions of greenhouse gases for the purpose of their regulation, with this work focusing on their use in ecology and ecophysiology. Analyzing fluxes of gases and heat energy between an ecosystem and the atmosphere can be very useful as it provides information on ecosystem health, quantifies primary production, and reveals how an ecosystem reacts physiologically to various environmental conditions (Baldocchi, 2014). With properly measured and processed flux data, we can describe an investigated area as being a source or a sink of monitored GHG, depending on the net flux being in the direction away from the surface or into it, respectively.

The first methods of quantifying a carbon flux of an ecosystem consisted of stand inventory, mensuration, harvest and subsequent allometric scaling to determine changes in accessible above ground biomass. When concerning the measuring of trees, they are a part of dendrometry and tree allometry. They remain popular because of their simplicity, low cost and applicability in many terrains (Clark *et al*., 2001). Regardless, there are limitations to these methods. Field tree sampling is labor intensive, so the samples of different species, ages and structure types can be inadequate and so can be soil carbon concentrations and root biomass (Yanai et al., 2003). These methods also work best at seasonal to annual time scales, not reflecting the changes in carbon flux during shorter time scales.

When studying the ecophysiology of plants, it is possible to use enclosure and chamber methods to measure gas exchange of individual leaves, branches, and plants with resulting flux information in hourly, daily, or longer time scales. The main problem with these methods is their difficult upscaling, from leaves to canopy and to ecosystem scale. It is necessary to sample representatively, to minimize measurement artefacts transfer into the dataset. For example, leaves throughout the canopy experience different fluxes based on their different position resulting in their different microclimates, their orientation to the sun and their respective illumination and obscuration (Rayment et al., 2000). In practice, it is almost impossible to make enough measurements using this method without introducing artefacts. It is preferred to measure the response of leaves to different environmental factors and drivers with this method, then upscale it with canopy models (Collatz et al., 1991).

Another method consists of systems wholly enclosing the studied plants. Being possible only for species of smaller size and affecting the microclimate of the plant and soil among others, it is not suited for the research of forest ecosystems. There is also a requirement of 10-20 chambers for the measurements to be statistically representative, which is rarely achieved. Nevertheless, whole plant chambers are considered a suitable alternative of measuring plant flux data and the effect of different CO_2 concentrations, temperatures, *etc* on plant growth (Barton *et al.,* 2010, Medhurst *et al.,* 2006) if all the necessary micrometeorological factors are assessed (Lindroth and Cienciala 1995).

Concerning studying soil gas effluxes, mainly respiration, chamber systems are the most suitable and used way of measurements (Luo and Zhou, 2006; Pavelka *et al.*, 2018).

Various methods and types of chambers are available, with studies being done regardning the reliability of different techniques (Pumpanen *et al.*, 2004) and different commercially available models (Görres *et al.*, 2016).

Chamber methods are relatively inexpensive and simple to use, being suitable for a wide range of studies ranging from laboratory and in-situ measurements to projects on a global scale. They are thus an important part of flux measuring networks such as the Integrated Carbon Observation System (ICOS). The methodic, standards and quality checks for the employment of manual chambers and various types of automatic chambers in flux measuring in the ICOS network are described in detail by Pavelka *et al.* (2018).

There have been long-term continuous measurements of soil efflux and its responses to biotic and abiotic factors, seasonal changes, *etc,* carried out in forest ecosystems (Jassal *et al.*, 2012, Pumpanen *et al.*, 2015).

Eddy accumulation technique is micrometeorological method related to eddy covariance method (EC), which is described later in this work. Since EC has its limitations when measuring trace gases (CH_4, N_2O, O_3 *etc.*) due to the higher financial costs or possibly high power requirements of analysers, eddy accumulation (EA) offers a different way of measuring turbulent gas fluxes suitable for some applications. Unlike EC, eddy accumulation utilizes sensors (analysers) with much slower response time, allowing for the use of gas or mass spectrometry (Bowling et al., 1998). The idea behind this method is that upwards and downwards moving air drafts is continuously collected into separate reservoirs. After a set sampling period, these are analysed by the slow gas analyser, and from the difference in their gas contents, flux approximation is calculated. Depending on the approach to air sampling, this method divides into true and relaxed eddy accumulation.

With the true EA method air parcels are sampled proportionally to their vertical wind velocity. While this is a technical challenge, new technologies are helping in progressing this method further, mainly aimed on measuring trace gases, *e.g.*: (Siebicke and Emad, 2019).

Relaxed EA method does not require the collected air parcels to be proportional to their respective wind velocities and instead uses a constant flow rate. As well as the true EA, this method is being actively worked and improved on, with new, affordable and accurate (agreement with EC data) systems being developed (Grelle and Keck, 2021).

1.4. Eddy covariance

Methods described above have many substantial limitations, which make measuring and studying the gas flux on the ecosystem level very difficult. Micrometeorological methods like the eddy covariance method, although having numerous limitations themselves, provide a way to circumvent these obstacles. Eddy covariance is a statistical method based on direct measurements of turbulent air flow in the boundary layer of the atmosphere. This layer is characterized by developed turbulent flow mainly during daytime, which consists of many rotating air currents varying in size, speed, directions, and gas concentrations, called eddies. An eddy is a current with its flow direction different from the direction of the general flow, or in this case, wind. Energy is transferred from large to small eddies until it dissipates. This can be observed in many cases in nature, for example the eddies breaking off the gulf stream and transferring energy. Turbulent air flow is also the mechanism of atmospheric eddy transport. Although eddies vary in size and speed, smaller ones rotating at higher frequencies are more common closer to the ground where they are responsible for most of the flux transport, the same applying to larger ones further from the ground rotating at lower frequencies making up most of the transport there. As said, each of the rotating eddies has its own speed and is characterized by its temperature, gas of interest concentration, humidity, etc. By measuring these properties of multiple eddies at the same spot, we get to know the vertical flux of our interest. If eddies carry more molecules or heat energy upwards or downwards, we can conclude the monitored area, or footprint, as a source or a sink at the measured time, respectively. Thus, the basic principle of eddy covariance is the covariance between the vertical wind speed, and the concentration of the gas of interest. In the case of a negative covariance, when upwards (positive speed) wind carries less gas molecules or downwards (negative speed) wind carries more gas molecules, the flux is directed towards the ground, which is also the case with CO_2 molecules during the process of photosynthesis. The eddy covariance technique provides substantial amount of data about gas fluxes of a surface, measuring wind speed, direction, and gas concentrations at frequencies of at least 10 Hz, averaged and scaled into 30-minute flux datasets. This way, we only measure turbulent transport, meaning mechanisms of transport like molecular diffusion, advection, etc. are negligible compared to turbulence. This occurs during the day and during nights with wind speeds exceeding 1 meter per second (Burba, 2013), which are not common. Turbulence is more developed during the day thanks to heat being supplied to the atmosphere and ground, resulting in warmer air parcels becoming buoyant and accelerating upwards (Venkatram and Schulte, 2018). The impact of other than turbulent mechanisms of transport can be also estimated or measured using wind speed and gas concentration profiles. Because turbulent fluctuations occur very rapidly and changes in concentrations are miniscule, the measurements need to be done rapidly and sensitively as well, requiring proper and often costly instruments. Nevertheless, this method can provide direct measurements of fluxes on a half-hourly basis integrated over an area of interest and produces continuous data for years on end, resulting in an advantage over other methods in many aspects (Baldocchi, 2003).

1.4.1. Mathematical principles

In this part the math formulas are edited, and important assumptions are made to arrive to the standard eddy flux equation.

Vertical flux in turbulent flow: $F = \overline{\rho_d w s}$

ρ_d = air density

w = vertical wind speed

s = dry mole fraction of the gas of interest

Dry mole fraction (s) in micrometeorology describes the ratio of the component (gas) to the dry air (air with the component). It can also be called the mixing ratio.

Using Reynolds decomposition, we break terms into means and deviations from the means:

$$F = \overline{(\overline{\rho_d} + \rho_d')(\overline{w} + w')(\overline{s} + s')}$$

Means marked with a macron or a vinculum (overline) represent the average of air density, wind speed, and dry mole fraction over some time e.g., 30 minutes.

Marked with a prime are instantaneous deviations from these means in very short intervals e.g., every 0,1 seconds.

After opening the parentheses average deviations from the average, marked in grey, are removed as they equal 0. The equation is simplified.

$$F = \overline{(\overline{\rho_d}\,\overline{w}\,\overline{s} + \overline{\rho_d}\,\overline{w}\,s' + \overline{\rho_d}\,w'\,\overline{s} + \overline{\rho_d}\,w'\,s' + \rho_d'\,\overline{w}\,\overline{s} + \rho_d'\,\overline{w}\,s' + \rho_d'\,w'\,\overline{s} + \rho_d'\,w'\,s')}$$

$$F = (\overline{\rho_d}\,\overline{w}\,\overline{s} + \overline{\rho_d}\,\overline{w' s'} + \overline{w}\,\overline{\rho_d' s'} + \overline{s}\,\overline{\rho_d' w'} + \overline{\rho_d' w' s'})$$

The first important assumption that air density fluctuations are negligible is made, marked in grey. This can be safely assumed over flat and vast terrain.

Secondly, we assume that mean vertical flow is also negligible for flat terrain, marked in dark grey. There is a need to assess the specific site of the experiment when making this assumption, as the evidence suggests even a small slope resulting in flow divergence and convergence can make this claim implausible and needing corrections.

$$F = (\overline{\rho_d}\,\overline{w}\,\overline{s} + \overline{\rho_d}\,\overline{w' s'} + \overline{w}\,\overline{\rho_d' s'} + \overline{s}\,\overline{\rho_d' w'} + \overline{\rho_d' w' s'})$$

$$\boldsymbol{F \approx \overline{\rho_d}\,\overline{w's'}}$$

After these assumptions we are left with the classical equation for an eddy flux, which is equal to the product of mean air density and mean covariance between instantaneous deviations of vertical wind speed and mixing ratio.

This is the classical formula of the eddy flux of gases like CO_2, CO, H_2O, CH_4, SO_4, *etc*. Other fluxes like sensible heat flux or H_2O (latent heat) fluxes by their own variations of this formula (Burba, 2013).

1.4.2. Measuring instruments

As written above, measurements of turbulent transport are necessary for all types of stations and so are the devices for obtaining them. In most cases, the devices are situated on a tower, above the area of interest. Three dimensions of wind speed are measured by a sonic anemometer, gas concentrations by an open-path or closed-path gas analyser. To achieve accurate results, the sonic anemometer and gas analyser should not be horizontally separated by more than 15 cm, and the positioning of instruments cannot distort the natural flow of air, as it is the subject of measurement. The adequate placement of instruments should be located at least 1.5 – 2 canopy heights above the surface and depends on the desired footprint or area of measurement.

Sonic anemometers

Three dimensional sonic anemometers use the speed of sound to measure all three vectors of wind speed. They consist of six nodes, divided into three pairs. These transducer pairs send bursts of sound between themselves, one way and the other between pairs. One vector component is calculated from each pair, using the measured speed of sound in moving air and the known speed in still air or by the time difference in between the paired transducers in opposite directions. As the wind speed components are the basis for essential calculations and corrections in this method, the measurements are very fast and sensitive, operating at 10-20 Hz and recording small fluctuations of vertical wind speed (w), which is used in the calculations. Nevertheless, the aim to minimize airflow distortions is difficult to execute when employing these devices, as they intercept the flow by having a frame.

Multiple arrangements of transducers can be used, each having a different airflow distortion magnitude from different angles. Using the speed of sounds and making the necessary corrections, the sonic temperature is calculated as well.

Gas analysers

A multitude of gas analyser types exists, using chemical, optical, or electrical gas detection technology. As not all of these are sufficient for application in the eddy covariance method, which requires a high frequency of sampling (at least 10 Hz) and high resolution, suitable options will be described. Optical analysers fast and sensitive enough can be used, being divided into broadband and narrowband types. Both measure light transformation by gas of interest molecules in a certain volume, providing gas density measurements.

Broadband optical analysers measure absorbed light over a wider range of wavelengths of the electromagnetic spectrum, gathering data by registering light absorption at wavelengths characteristic for carbon dioxide or water. This technology is based on the Lambert-Beer law which mathematically describes light absorbance or attenuation by a material of known properties. Broadband analysers are appropriate for CO_2 and H_2O measuring, providing fast and precise data. They are mostly based on non-dispersive infrared (NDIR) sensor technology. There are different designs of these instruments, based on technological principles of their operation, like using an optical or a mechanical reference. While differing slightly, their capabilities of measuring speeds of hundreds of Hz provide fast data of gas concentration averaged into 10-20 Hz. Narrowband devices usually employ a laser, which is in a very narrow band of wavelengths, making measuring of other greenhouse gases (*e.g.:* CH_4,N_2O) possible. There are many varieties of laser-based measuring, the gas concentration being calculated from the expected and transformed feature of the laser, for example the waveform feature, not from the light absorption itself.

Optical gas analysers were originally physically designed either as open or closed-path. Open-path analysers do not need enclosure, they have an open cell, and the sampled air moves freely through it. Their advantages are very good frequency response, no pressure drop and lower power requirements and disadvantages consist of bad measurements during rain or snow and the need for density corrections as they are exposed to fluctuations in temperature, pressure and humidity. On the other hand, closed-path design needs enclosure, they can thus operate during rain. Due to their long intake tube, they have greater frequency loss and temperature attenuation and require more power supply for their pump, but they also need smaller density corrections. Combining the advantages of both designs, enclosed gas analyser design has short intake tube can operate in bad weather with relatively low power consumption and better frequency response. It is able to compute fast dry mole fraction directly without the need for density corrections as it measures air temperature and pressure inside the call along with gas concentrations (Burba *et al*., 2010). Even though its frequency losses also need correcting (Fratini *et al*., 2012), these conveniences make it a preferred choice in standards of measurement such as (Rebmann *et al*., 2018).

As written above, optical gas analysers provide measurements of gas density – the number of molecules in a known volume transforms light to a certain degree. Gas density is fundamentally not the same as mole fraction or dry mole fraction, which represent gas content per mole of air and mole of dry air respectively. Dry mole fraction (s), used in flux calculations, differs from gas density due to gas pressure, temperature, and water mole fraction. Enclosed designs can calculate s right away (Burba, 2013).

1.4.3. Major assumptions and sources of errors

Measurements can never be perfect, due to assumptions, physical atmospheric phenomena, particular geomorphology and instrument and setup specifics. Proper site selection and station setup are necessary for assumptions to be plausible. Next to the mentioned negligible air density fluctuations and divergences, convergences, the most important ones are:

- Measurements represent a certain area, and flux is fully turbulent
- Measurements are done inside the atmospheric boundary layer
- The terrain is flat and homogenous
- Flux is measured from the area of interest
- Instruments used are sensitive enough and able to operate at high frequencies
- The station structure and/or the instruments do not alter air flow

Footprint

Fluxes generated over a certain area, called footprint, are registered by the measuring instruments of eddy covariance technique. The term fetch means the distance from the measuring tower to the edge of the area of interest. Fluxes coming from the outside of this area need to be assessed, which will be discussed later. Size of the footprint area depends on the height of measurement, surface roughness and thermal stability. Increased height of measurement and reduced surface roughness increase the footprint area while also increasing the size of an area around the instruments that did not contribute flux data (Burba, 2013).

Nonturbulent transport

Since the eddy covariance method measures turbulent transport only, well developed turbulent flow is a necessary condition for correct measurements. Turbulence is linked with wind shear and buoyancy, which is an outcome of heating at the ground, it is thus much more developed during daytime (Venkatram and Schulte, 2018). At night, atmospheric conditions are more stable, less turbulent and fluxes are generally smaller. These conditions cause various atmospheric phenomena, which greatly affect flux measurement ability of EC, mainly intermittent turbulence and advection (Aubinet, 2008), but also storage changes, stratification, drainage flows, flow divergence and convergence *etc*. As a result, most EC stations in many measured ecosystems are unable to meet the requirements for proper measurements and produce nighttime datasets of low quality, namely underestimating CO_2 fluxes (Aubinet, 2012). Ways of nighttime flux data acquisitions by correcting are described later.

Advection

Advection occurs during periods of low turbulence, mostly at night. It is one of the most important factors in nighttime flux corrections (Aubinet *et al*., 2012). Horizontal and vertical advection extents varied within different forest sites in the study of Aubinet *et al*. (2010). Substantial horizontal advection variation occurred on the sites in this study. Vertical advection varied less within sites, reaching highest values during stable conditions

Katabatic flow, also called drainage or gravity flow, stands for downslope advection near the ground. This flow can also be decoupled from above canopy airmass, depending on the leaf area density of the particular forest stand and the height of the flow vertical profile, which increases with distance from a mountaintop (Aubinet *et al*., 2005).

Decoupling

This phenomenon occurs at forested measuring sites, mainly during nighttime, but also daytime. Decoupling of below and above canopy air masses is a result of divergence in atmospheric stratification during low wind conditions and the dense canopy itself obstructing turbulent flow. In such cases, the measured efflux of the area of interest can be biased as sub-canopy respiration is often removed by advection, which results in the overestimation of ecosystem carbon uptake (Jocher *et al.*, 2017, Thomas *et al.*, 2013). Above and below canopy wind velocity measurements are required to reveal decoupling. Two level filtering is recommended to address decoupling and new approaches are being developed (Jocher *et al.*, 2018, 2020). Decoupling also occurs in less dense canopy forest stands but does not considerably affect total ecosystem efflux probably due to flat terrain (Kowalska *et al.*, 2022).

Storage flux

Also occurring during calm, low wind conditions, such as nighttime or under a tall canopy, storage is another possible phenomenon, which can affect EC measurements. Below the height at which the flux is being recorded, concentration of gas, mainly CO_2 can decrease or more commonly increase. Measuring gas concentration profiles by slow response gas analysers at multiple heights below the flux measurement height can detect and address this concentration buildup. Storage term is thus calculated and added to the EC flux for total flux values (Burba, 2013). High frequency, good resolution and shorter averaging periods are needed to capture the sudden removal of stored gas after a calm period (Aubinet, 2008). Yet, addressing storage only is not sufficient for flux correction, although it has to be considered when applying filters (Aubinet *et al.*, 2012). It is significant during periods with low turbulence and low advection at flat terrains. Storage and subsequent draining of CO_2 by advection is the main process responsible for biased EC measurements during stable conditions (Aubinet *et al.*, 2005).

Instrument shortcomings

When trying to achieve the highest possible quality of data on precise flux measurements there are numerous potential error sources, which can affect some or all fluxes in different extents, respectively. These can be prevented or corrected during the planning and designing of the station or during data processing. As they can affect the flux measurements substantially, possibly by over 100%, it is of major importance to avoid them. The first group of errors are frequency errors like instrument time response, sensor separation, tube attenuation, *etc*. When instruments do not operate fast enough it is not possible for them to register all the significant immediate changes. With the wind speed and mixing ratio measuring points separated in space their covariance is computed for data of uneven time origin. Tube attenuation occurs in closed-path analysers being caused by the tube diminishing fluctuations in concentrations. Frequency response error can affect all fluxes up to 50% in closed-path analysers.

Besides that, other error sources occur; unleveled anemometer, wind angle of attack, sensor time delay in closed-path systems, spikes and noise, density fluctuations, *etc*. For example, all fluxes are affected by an unleveled sonic anemometer as the horizontal wind component is included in the vertical wind speed, altering its magnitude. Most of it is readily reduced by steading the tower and levelling the anemometer, with the remainder being fixable during data processing. With proper station setup, experimental design, instrument choice, and maintenance, it is possible to minimize many of the potential errors. Modern instrument designs aim to reduce error potential by implementing new sophisticated technology and methods, such as sonic anemometers utilizing an inclinometer and closed path analysers having much shorter intake tubes. The remaining errors can be corrected during data processing. This makes the selection of mentioned station and instrument specifics an important step in achieving precise flux measurements (Burba, 2013).

1.4.4. Other measured variables

Eddy covariance measurements can be used in various fields for various purposes, *e.g.*, regulatory,, agricultural, scientific *etc*. Depending on the purpose, selecting the measured variables and, subsequently, instruments selection is vital for achieving sufficient data. When working with a scientific application of this method, more variables and instruments are needed to interpret measurement results than in, for example, a regulatory application. Variables describing the turbulent transport are necessary for every application and consist of all three dimensions of wind speed (u, v, w), sonic temperature (T_s), and concentrations of the gas of interest and water. Typically, they are accompanied by weather variables like air temperature, precipitation rates, relative air humidity, air pressure, soil moisture, *etc*., which make the processing and interpretation of the flux data possible. In scientific applications, more variables are included to describe the studied ecosystem or area in more detail and help interpret and explain different situations and ecosystem responses. These include vapour pressure deficit, other gas concentrations, soil temperature, water fluxes, heat fluxes, incoming direct and diffuse photosynthetically active radiation, canopy dimensions like leaf area index *etc.*, and are often chosen specifically for a particular project (Burba, 2013).

1.4.5. Data acquisitions standards

As stated before, proper understanding of how climate factors affect GHG fluxes between ecosystems and the atmosphere is necessary when assessing predictions about climate, atmospheric GHG content, ecosystems, and their mutual relations. Multiple networks situated around the world such as Euroflux, FLUXNET, NEON and other aim to provide high quality data of these fluxes with their own standards and protocols (Aubinet *et* al., 2000; Pastorello *et* al., 2020; Keller *et al.*, 2008).

Integrated Carbon Observation System (ICOS) is one of these networks, operating across the European continent, CzeCOS being its national component of the Czech Republic. Eddy covariance is the main method used to study ecosystem-atmosphere exchanges in ICOS. In order to conduct precise harmonized long-term measurements and gather high quality data with this method, experts from around the globe have composed a standard for station setup, instrument models and data acquisition hardware.

Each EC tower station in the ICOS network should measure fluxes of a specific ecosystem, so that as many ecosystem types as possible are covered. The site should be situated in a location that makes it possible to determinate the area of interest or fetch from which fluxes are measured, so that the ecosystem is represented. Height of the measurement above the canopy is also specified, along with suitable instrument placement on the tower. Regarding instruments, the models HS-100 or HS-50 (Gill Instruments Ltd, Lymington, UK) were chosen as the best overall option for sonic anemometers, heating and an additional backup anemometer being recommended. Thanks to the advantages of enclosed gas analysers described in the instruments chapter, the most recent model of LI-7200 (LI-COR Biosciences, Lincoln, USA) with enclosed design has been chosen as the standard after field tests. Measurement protocol and a specific layout are also required for the analyser. It is crucial to collect data and diagnostics in an aligned manner, making fully digital data acquisition system capable of synchronizing them obligatory. Additional data of air temperature, relative humidity and air pressure necessary for flux data processing and their respective instruments are also described (Rebbman *et al.*, 2018).

1.4.6. Data corrections and processing

Proper processing of measured EC flux data is necessary for all stations and projects, as its goal is to provide results which represent the course of natural events at the point of measurement. This ensures correct interpretation of the information obtained by a station. There are some universal standards for this which are applied universally. However, each measurement site has own characteristics, thus every research group can use different details in their approach to processing, fitting their specific needs. Yet it is most important to stick to standards and protocols which ensure proper qualities of the final data. Groups of processing steps consists of data pre-conditioning, correcting, quality control and gap-filling.

Pre-conditioning

The first step in pre-conditioning is usually the conversion of voltages to physical units and the removal of outliers and missing values. It is important not to mix up fast and slow inputs and to use suitable units.

Because of noise, high frequency data contain spikes, which are removed in during despiking. The criterion by which high values are removed is comparing them to the standard deviation. The missing points can be filled in with running means or otherwise. Each EC application requires its own approach for despiking, as conditions differ site to site. Some unusually high values can be natural, such as nighttime storage release (Burba, 2013).

Calibration coefficient application is more important, requiring regularity, in closed-path gas analysers. In open-path and enclosed instruments with proper original calibration it can be done in their software.

Coordinate rotation is required to make sure that mean *w* (vertical wind speed) is zero, as this is one of the main assumptions for the use of the EC technique. This mean is not equal to zero for example when measuring above a sloping terrain, but mainly due to the impossibility of a perfectly leveled anemometer which results in the representation of other than vertical wind components in the measurements. An established method for this is to reach for zero mean *w* by rotating the coordinates. A more popular method useful for stations located at complex landscapes is the planar fit method (Wilczak *et al.*, 2001). It consists of introducing a hypothetical plane, calculated from long term measurements of the 3 wind components *u*,*v*, and *w*, with vertical flux being perpendicular to it. Time delay adjustments deal with the delay in obtaining signals from distinct measuring instruments. Although standards require precise clock synchronization between gas analyser, sonic anemometer and data acquisition devices (Rebmann *et al*., 2018), data measured at the same point of time may not be stored at the same point of time due to different signal acquisition time from the anemometer and gas analyser, caused by electronic, processing, and logging delays, instrument separation, gas analyser tube length and its contamination *etc*. This problem is more pronounced in closed-path devices. It can be partially corrected in the data logger software, but the magnitude can change over time, e.g.: with different wind velocities (Foken, 2008). In open-path devices most of the delay is caused by sensor separation and is very small. For enclosed gas analysers the causes of delay are balanced in magnitude and the delay is slightly greater, reaching 0.5s. The largest delay of multiple seconds occurs in closed-path instruments, due to the long intake tube. There are two approaches to the correction. The theoretical approach, which considers instrument specifics like tube diameter and flow rate is suited for open-path devices. The empirical way consists of performing a circular correlation and finding the maximum flux by shifting the delay. A combination of both concepts is recommended (Burba, 2013).

Detrending

Detrending consists of determining the mean value for a time interval from instantaneous values to calculate flux. The most popular way of detrending is block averaging.

The classic data averaging interval is 30 minutes or 1 hour.

Corrections

Frequency response corrections involve complex calculations and can be complicated, though they are commonly calculated by the processing program or are included in the specific instruments. These corrections compensate for flux loss at varying frequencies of turbulent transport, caused mainly by path averaging, tube attenuation, sensor separation and time response, filtering, *etc*. As stated, turbulent transport consists of eddies of different properties and is done at varying frequencies. Cospectrum mathematically represents how much of turbulent transport is done at every frequency and is a basis for these corrections. Ideal cospectrum for a certain height is routinely modelled according to (Kaimal *et al*., 1972). Sonic anemometer corrections are needed for obtaining actual air temperature. Applying

Webb-Pearman- Leuning terms (Webb, Pearman and Leuning, 1980) compensate for the effect of thermal expansion and water dilution on measured densities. After sufficient measurements and proper corrections, flux can be calculated (Burba, 2013).

Quality control

Group and networks use various protocols and methods for automatic quality control and removal of faulty data (Yver-Kwok *et al.*, 2021). Quality control is site specific, although they have in common establishing ranges of tolerance, focusing on precipitation periods, low-turbulence periods flagging, validating data with energy budget closure and cospectral models and missing data filling by models, regressions, or backup instruments. Nighttime needs approach for quality control, due to its atmospheric conditions, described in major assumptions and sources of errors (Aubinet *et al.*, 2012).

Gap-filling

After the removal of faulty data there is a need to fill in and complete datasets. There are multiple methods and strategies, although caution is needed due to the risk of bias. Some of the most used are look-up tables, marginal distribution sampling**,** nonlinear regression and artificial neural networks with the best results and the consistent mean diurnal variation method. Most techniques commonly used affect yearly NEE fluxes by an acceptable value within ±25 g C m^{-2} $year^{-1}$ (Moffat *et al.*, 2007). Various models are available for filling gaps of CO_2 fluxes, such as nighttime respiration modelling. Satisfying results were achieved by the unconstrained three parameter Lloyd and Taylor model along with the traditional Q_{10} model based on the effect of temperature on respiration, although only with the inclusion of seasonal variation in the sensitivity of respiration to temperature (Richardson *et al.*, 2006). There are two main approaches to gap-filling, called nighttime and daytime. The nighttime approach derives daytime ecosystem respiration sensitivity from the ecosystem respiration sensitivity during its respective nighttime. This is a more suitable approach than deriving the sensitivity from long-term (annual) data, which do not account for short-term temperature sensitivity and can overestimate ecosystem respiration up to 25 % or more on yearly scales (Reichstein *et al.*, 2005). The daytime approach uses nighttime NEP to infer the sensitivity of respiration to temperature at the site only at night and uses only the daytime data to derive the light and temperature driven models for daytime gross primary production and ecosystem respiration, respectively (Wohlfahrt and Galvagno, 2017).

2. Data and methodology

2.1. Sources of data

Ecosystem-atmosphere GHG flux data measured by the eddy covariance method along with auxiliary meteorological data analysed in this work were obtained from the CzeCOS network operated by CzechGlobe - Global Change Research Institute, CAS. This ecosystem station (ES) network aims to provide measurements and evaluations of GHG fluxes of ecosystems common in the Czech Republic, along with heat and water fluxes, meteorological and other associated measurements. Three distinct CzeCOS forest ecosystem stations were selected as data sources for this work, consisting of a floodplain forest in Lanžhot (LZ), an upland beech forest stand of Štítna (ST) and spruce upland forest in Rájec (RA). The LZ station is a part of ICOS and follows its standard of (Rebmann *et al.*, 2018). All stations are a part of the FLUXNET network. Each station represents one of the typical forest ecosystems of Czech Republic. Two measurements years were selected for analysis, the year 2016 having near average meteorological conditions and the year 2018 which was characterized by a summer drought that occured throughout the republic. Data from these stations thus provide valuable information about carbon balance (sink) of these ecosystems during different conditions.

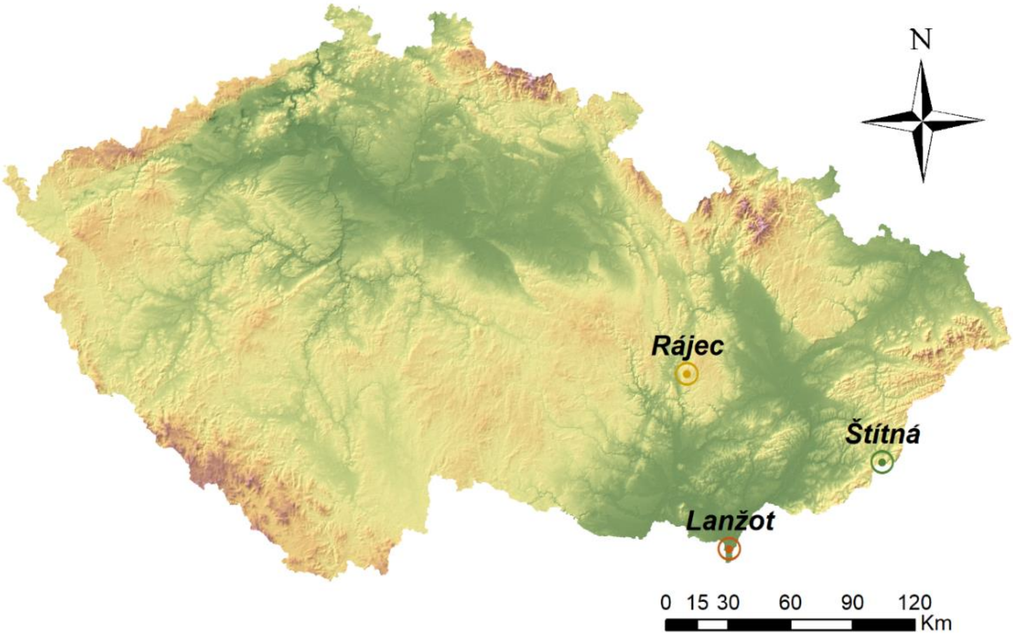


Figure 2.1 Map of the Czech Republic with the Štítná, Lanžhot and Rájec ecosystem stations

2.1.1. Štítná

The Štítná (ST) ecosystem station is located approximately 4 km south of the Štítná nad Vláří village in the White Carpathian Mountains (49°02′09.510“N 17°58′11.640“E) at an elevation of 540 meters above sea level on a slight slope of 10° with west to southwest exposure. At this locality, the climate is moderate with a mean daily temperature of 7.1 °C between the years 1990-2019 and long-term yearly precipitation of 864 mm. As for natural conditions, the ecosystem around the station is a 117 years old (as of 2018) deciduous broadleaf forest, with European beech (*Fagus sylvatica* L.) being the dominant tree species. In 2018, the mean tree height was 31 m, basal area was 34 m^2 ha^{-1} and the biomass totalled 389 tons per hectare. Soil type at this forest stand is Eutric Cambisol mesotrophic with a depth of 63 cm (McGloin *et al*., 2018).

CO_2 fluxes between the forest ecosystem and atmosphere at this ES were measured by the eddy covariance method. 20 Hz measurements of gas concentrations and three dimensional wind components necessary for this method were conducted at the height of 44 m by an enclosed infrared gas analyser LI-7200 (LI-COR Biosciences, Lincoln, USA) and Gill R3-100 (Gill Instruments Ltd, Lymington, UK), respectively.

Additional meteorological measurements required for the interpretation of CO_2 fluxes were conducted in the near proximity of EC instruments. For both air temperature and relative humidity, calibrated EMS 33 sensor (EMS, Brno, Czech Republic) was used at 42 m. 385C rain gauge (Met One Instruments, Grants Pass, USA) was employed for precipitation measurements. Another important meteorological variable of vapour pressure deficit was calculated from air temperature and relative humidity (Jocher *et al*., 2021).

2.1.2. Lanžhot

The ecosystem station of Lanžhot (LZ) is situated at a floodplain between the rivers March and Thaya, 6.5 km north of their confluence (48°40'53.574"N 16°56'46.794"E). It has a flat topography with an elevation of 150 m a.s.l. Mean long-term annual temperature and precipitation are 9.5 °C and 517 mm respectively, making the climate semi-dry warm-moderate. The ecosystem of interest, which is studied by the station, is a characteristic 118 years old (2018) floodplain forest consisting of mixed hardwood tree species, in this case mainly narrow-leaved ash (*Fraxinus angustifolia* Vahl), English oak (*Quercus robur* L.)

and hornbeam (*Carpinus betulus* L.). The complete basal area of all trees is 30 m^2 ha^{-1}. Although the mean tree height is 27 m, mean height of ash and oak in the canopy is 36 and 31 meters respectively, with hornbeam averaging at 23.5 m in the subcanopy. Soil types in this water affected area consist of Fluvisols with average groundwater level of -2.7 m. Due to anthropogenic hydrological management the water regime of this area has changed substantially with the last flood in 2013 only sparsely affecting the site in depressions. These regulations along with changes in climate render the site relatively dry for a floodplain (Kowalska *et al.*, 2020).

Since the same method of EC was used, instruments installed for measuring the CO2 fluxes of this ecosystem and additional variables are similar to those at Štítna. For EC, the anemometer model HS-50 (Gill Instruments Ltd, Lymington, UK) was employed along with the same gas analyser model as at Štítna at a height of 44 m until it was changed to 48m on the 8th of December 2018. Air temperature and relative humidity measurements were done at 35 m, by the EMS 33 model. Precipitation was measured by a Laser Precipitation monitor (Thies Clima, Göttingen, Germany).

2.1.3. Rájec

The Rájec (RA) ES stands on a 5° northeastern to eastern slope in the Drahanská vrchovina highlands at an elevation of 625 m, approximately 6 km northeast of the Rájec-Jestřebí town (49°26′37.405“N 16°41′47.445“E). With a yearly mean temperature of 6.9 °C and mean precipitation of 705 mm the moderate climate here is slightly warm and dry to slightly humid. The ecosystem around the station was a 115 years old (2018) evergreen coniferous forest stand of Norway spruce (*Picea abies* (L.) H. Karst.) with a mean tree height of 34 m and a basal area of 53 m^2 ha^{-1} until it was felled in 2021 because of its deteriorating health. Bark beetle infestation, which was the main reason Modal Cambisol oligotrophic makes up the 60 cm deep soil profile at this area (McGloin *et al.*, 2018).

EC measurements were performed at 41 m by the same instrument models as at ST station, *i.g.* Gill R3-100 sonic anemometer and LI-7200 enclosed gas analyser. With both intruments installed at 42 m, precipitation was determined by the Laser monitor from Thies CLIMA and an EMS33 sensor measured air temeprature and humidity (Jocher *et al.*, 2021).

2.2. Data processing

All flux calculations were calculated by the EddyPro EC software (Fratini and Mauder, 2014; LI-COR 2019). As stated in previous chapters, proper corrections are necessary to achieve high quality data results. The most important of these are coordinate rotation frequency loss corrections. Planar fit coordinate rotation (Wilczak *et al*., 2001) was applied and the high-frequency range flux losses were corrected according to Ibrom *et al*. (2007).

Biological flux sign convention was used in analysis. This convention considers fluxes directed from the surface (ecosystem) such as respiration as negative. Nevertheless, ecosystem respiration is presented as a positive value, to represent its rate for easier comparison. The CO_2 flux (hereinafter assumed to be equal to NEP) partitioning into gross primary production and ecosystem respiration, as well as flux gap-filling, were carried out in R (R Core Team 2017) package REddyProc (Wutzler *et al*. 2018). Regarding the flux partitioning, the “nighttime” approach was used as proposed by Reichstein *et al*. (2005).

Daily temperature and VPD means represent their daily arithmetic averages.

3. Results

Processed eddy covariance data of ecosystem-atmosphere CO_2 exchange during two years with different climatic conditions were evaluated and analysed for the three ecosystem stations The year 2016 was a normal to a slightly warmer year compared to the long-term average, while the year 2018 was distinguished by a prominent drought, negatively affecting forest ecosystems not only in the Czech Republic but also in other countries of Central Europe (Schuldt *et al*., 2020). To assess these negative impacts, ecosystem photosynthesis and respiration quantifications, along with the meteorological variables affecting these productivity rate measurements are presented separately for each ecosystem station down below.

3.1. Štítná

3.1.1. 2016 Data

At the beech forest stand in ST the complete yearly photosynthetic carbon gain (gross primary production (GPP)) in 2016 reached 1592 gC m^{-2} yr^{-1}. The growing season, during which most of the total CO2 was assimilated lasted *ca*. 6 months from the 1st of May to the 30th of September. GPP peaked at 16.3 gC m^{-2} d^{-1} on the 25th of July and it showed no significant prolonged decreases throughout the growing season, although short-term decreases in GPP were measured during periods of low photosynthetically active radiation intensity. Total ecosystem respiration (R_{eco}) was 1200 gC $m^{-2}yr^{-1}$, also peaking in July (**Figure 3.1**). Net ecosystem production (NEP), which is the balance between GPP and R_{eco} and represents the carbon sink of this ecosystem, thus equaled 392 gC m^{-2} yr^{-1} in 2016. Regarding climatic conditions during the year 2016, the mean daily temperature was *ca* 8.9 °C which is slightly warmer compared to the long-term average of 7.1 °C. Daily temperature was highest in late June reaching 26.2 °C, with another peak occurring in late July and interestingly also in early September. On growing season days with low measured PAR intensity, which were often accompanied by rainfall events, lower or even negative NEP values were measured. Vapour pressure deficit peaked at *ca* 13.1 hPa during the July temperature peak but did not stay as high for longer periods. Total precipitation was 670.3 mm out of which 417.5 mm of rainfall precipitated during the growing season, making this year drier than the long-term average of 864 mm. Rainfall events were, though, relatively evenly distributed across the growing season period. (**Figure 3.2**).

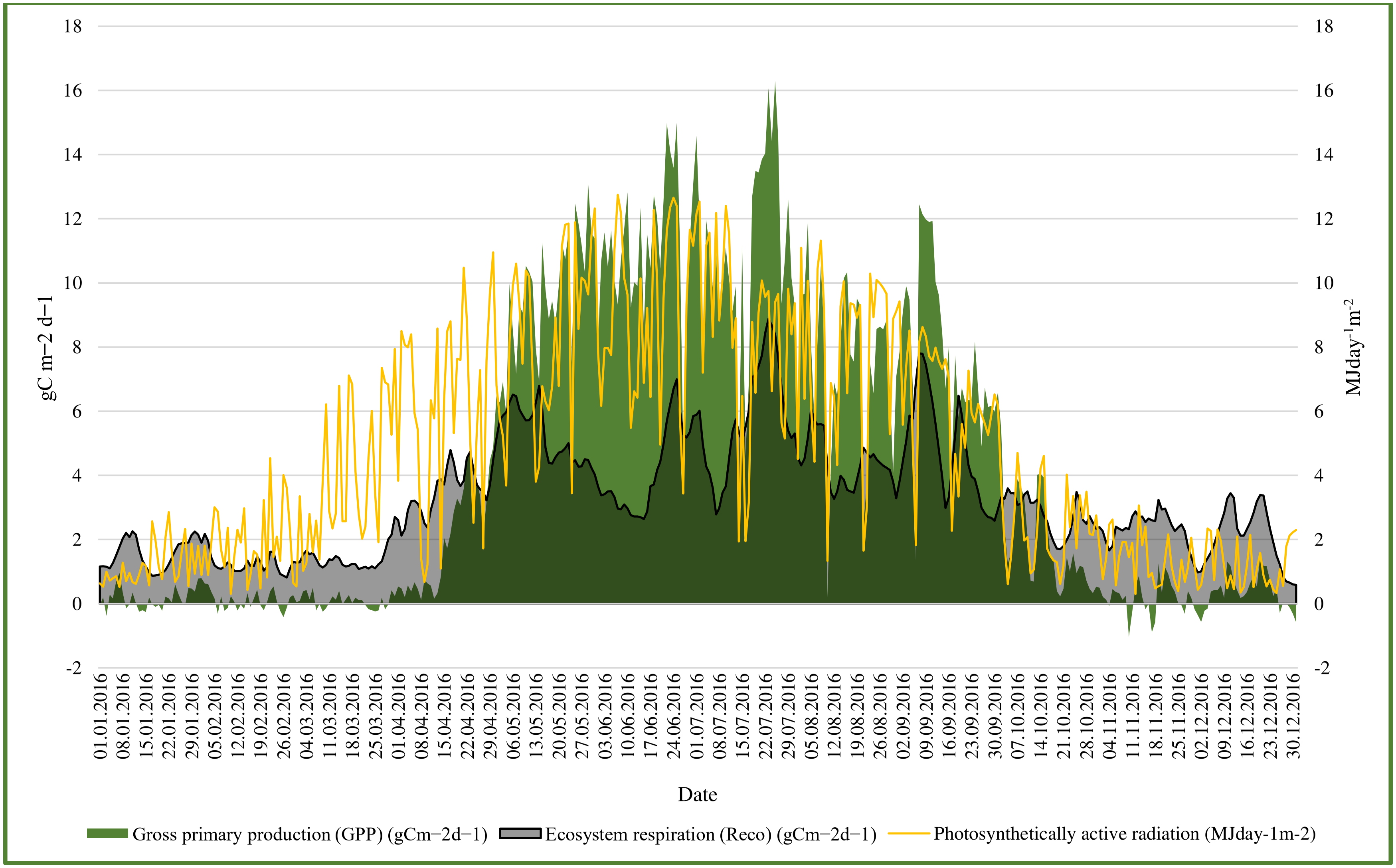


Figure 3.1 GPP and R_{eco} rates along with PAR intensity at Štítná in 2016, Respiration positive values represent its rates

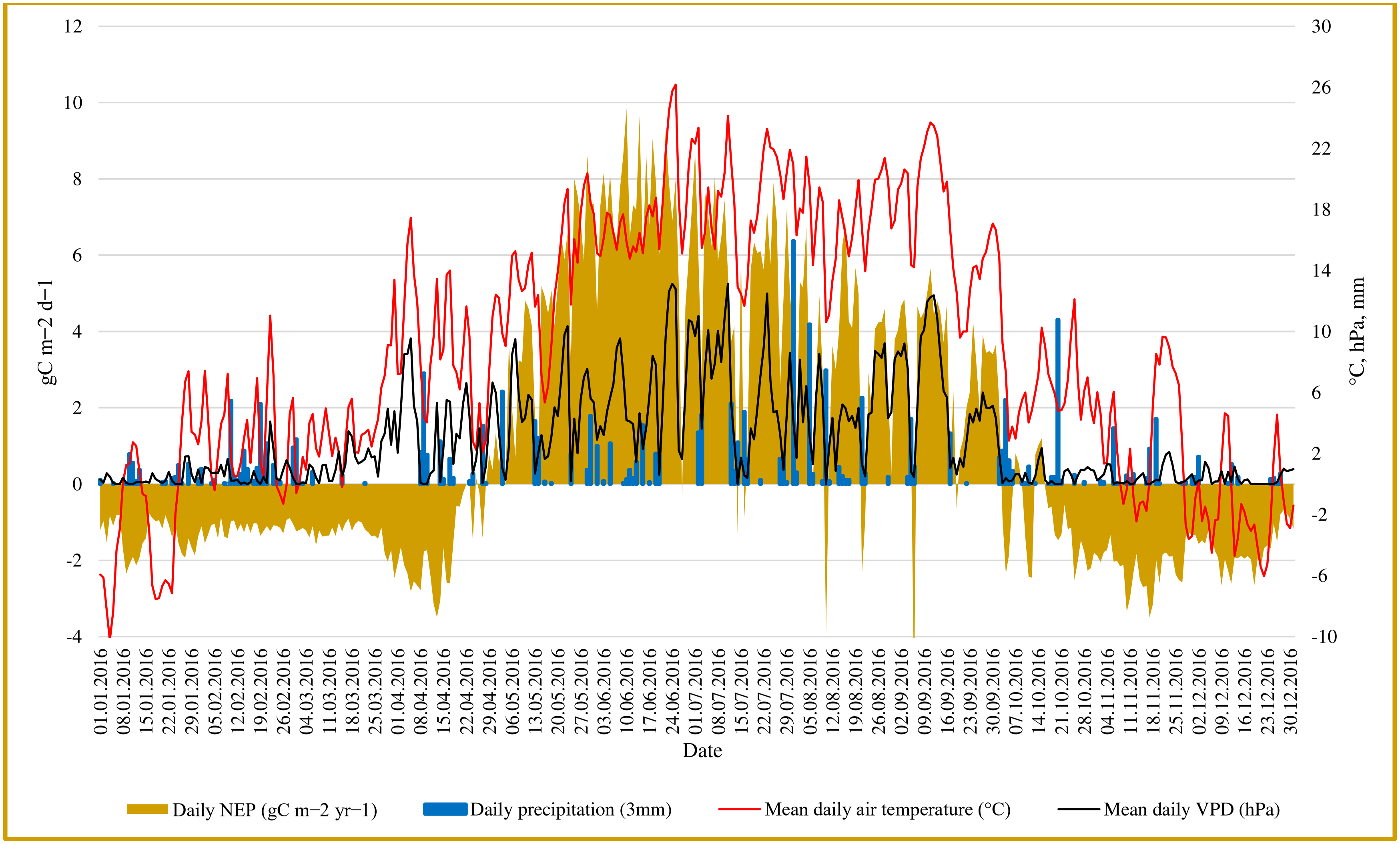


Figure 3.2 Daily NEP, precipitation, mean air temperature and mean VPD at Štítná throughout the year 2016

3.1.2. 2018 Data

During 2018 total carbon acquisition by the ecosystem at ST was 1610 gC m^{-2} yr^{-1}, GPP thus slightly increased. Nearly the whole bulk of GPP happened during the period from *ca* the 22nd of April to the 10th of October being longer by 14 days compared to 2016. GPP was highest in July peaking at *ca* 16 gC m^{-2} d^{-1} without significant decreases during growing season. Ecosystem respiration peaked at *ca* 12 gC m^{-2} d^{-1} in late June and overall amounted to 1107 gC m^{-2} yr^{-1}, rendering the 2018 net ecosystem production of 503 gC m^{-2} yr^{-1} higher by more than 25% compared to 2016 **(Figure 3.3).**

Daily temperature in 2018 at ST (10 °C) was on average 1.2 °C warmer than in 2016. Compared to the long-term average, the difference was almost 3 °C. Temperature peaked in August, which was the month during which the drought of 2018 was most prominent due to unfavourable climatic conditions. Although with alternations, it stayed relatively high in autumn up until the first half of November. VPD values peaked in August as well, reaching *ca* 17.6 hPa. Compared to the long-term average of 864 mm, the precipitation at ST was considerably lower in 2018, amounting only to 466.2 mm. Even if distributed regularly, mere 307.1 mm fell during the growing season (**Table 3.4**). Based on the EC data, this beech forest stand did not display carbon sink potential decrease in 2018.

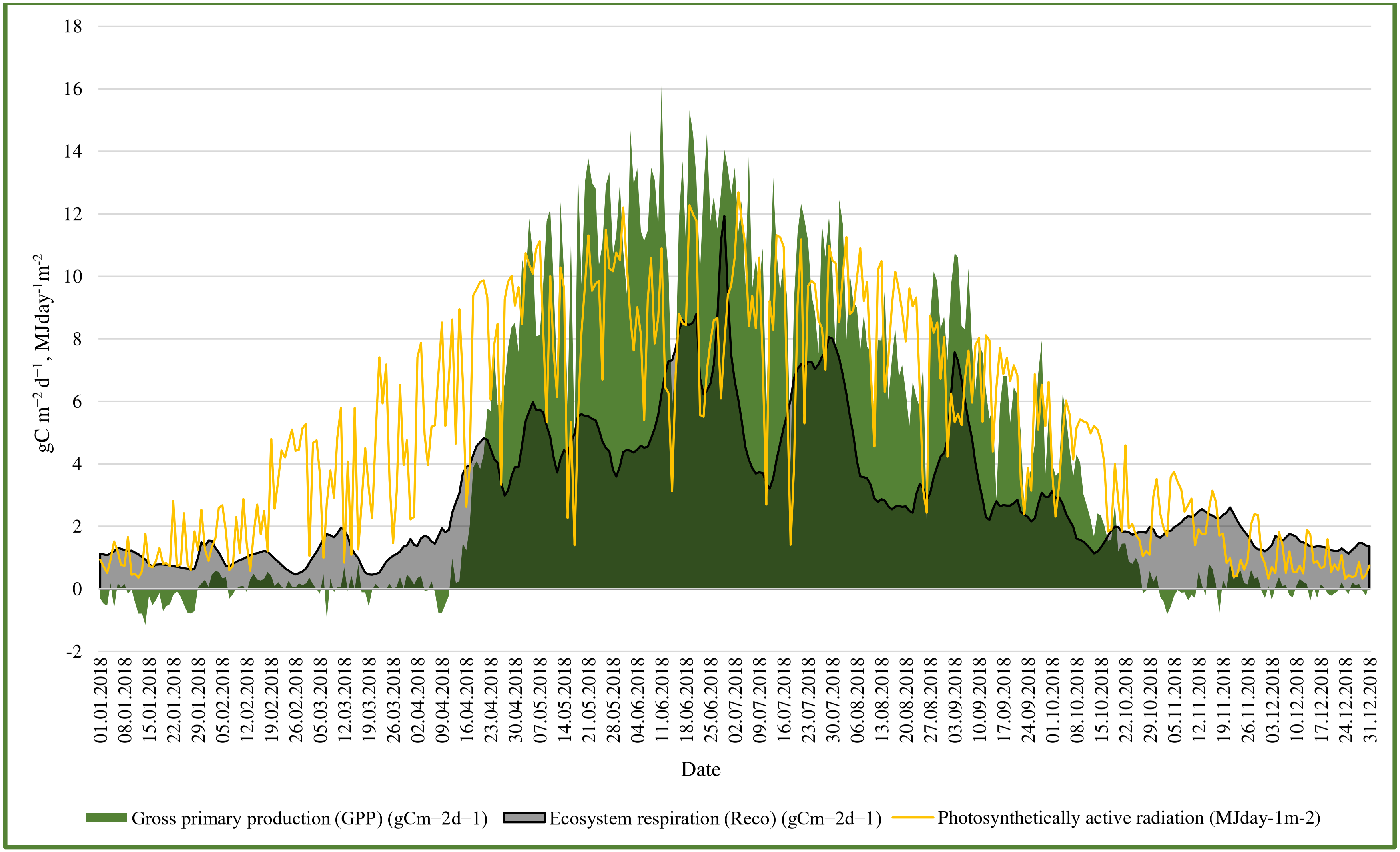


Figure 3.3 GPP and R_{eco} rates along with PAR intensity at Štítná in 2018, Respiration positive values represent its rates

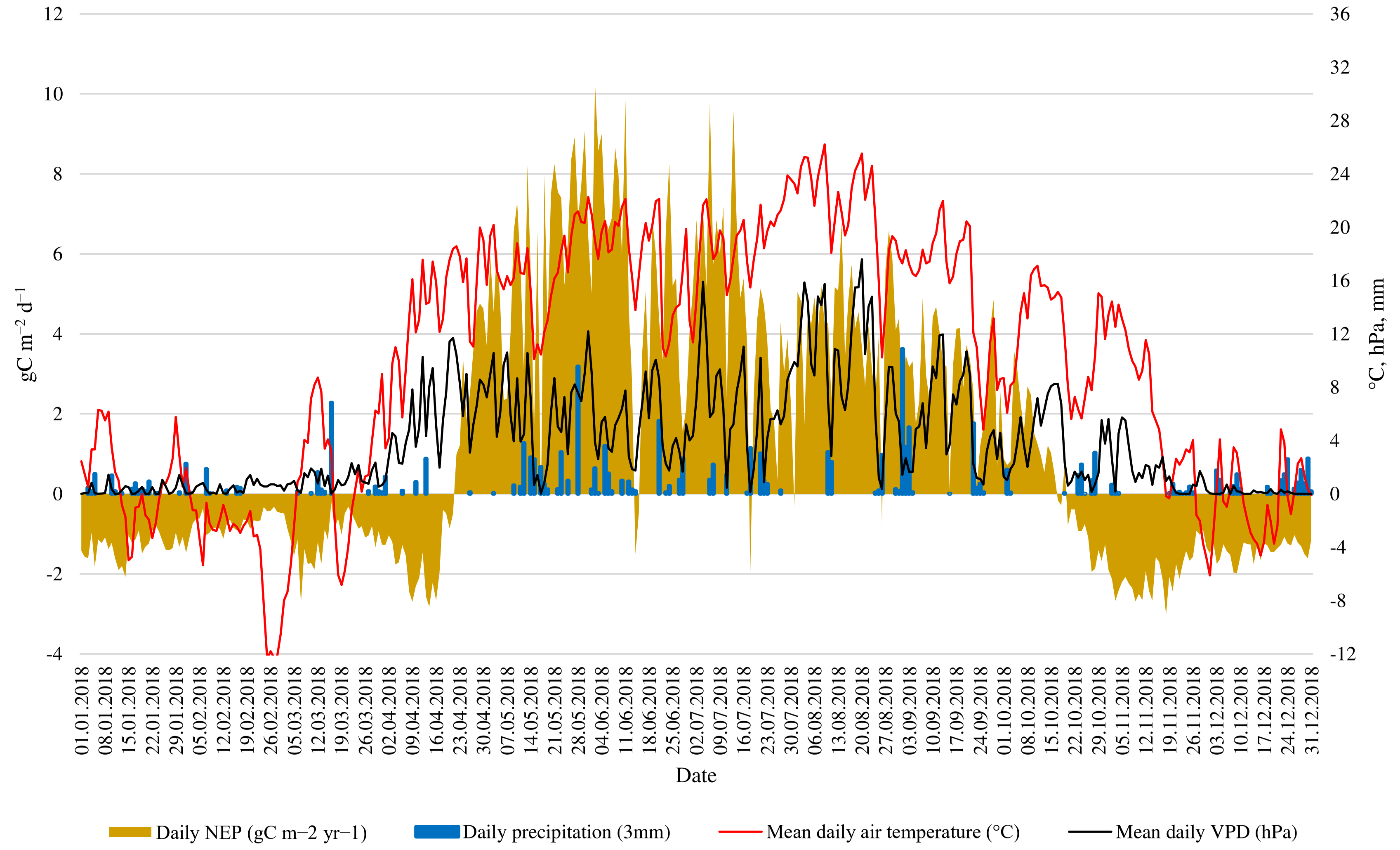


Table 3.4 Daily NEP, precipitation, mean air temperature and mean VPD at Štítná throughout the year 2018

3.2. Lanžhot

3.2.1. 2016 Data

Total GPP of the floodplain forest at LZ in 2016 was 1954 gC m^{-2} yr^{-1}. The period of highest carbon uptake rates lasted *ca* from half of April till the first week of October. This is prolongation in duration of almost 3 weeks compared to the beech stand at ST in 2016. Up until the middle of May most of the carbon captured by GPP was lost by respiration, NEP during this time was thus relatively low. The highest daily GPP value reached almost 20 gC m^{-2} d^{-1} on the last day of May (**Figure 3.5**). Yearly ecosystem respiration was 1501 gC m^{-2} yr^{-1}, resulting in the total NEP of 453 gC m^{-2} yr^{-1} stored by this forest in 2016. The year 2016 was warmer than usual at LZ, with an average yearly temperature of 12.9 °C compared to long-term average of 9.5 °C. High temperatures were measured in summer but also in September. With 504 mm of rainfall (317 mm during growing season) this year's precipitation was close to the site average of 517 mm. VPD was the highest during temperature maximums, reaching *ca* 12 hPa. There was no significant NEP decline observed during the growing season, except for the mentioned spring deficit (**Figure 3.6**).

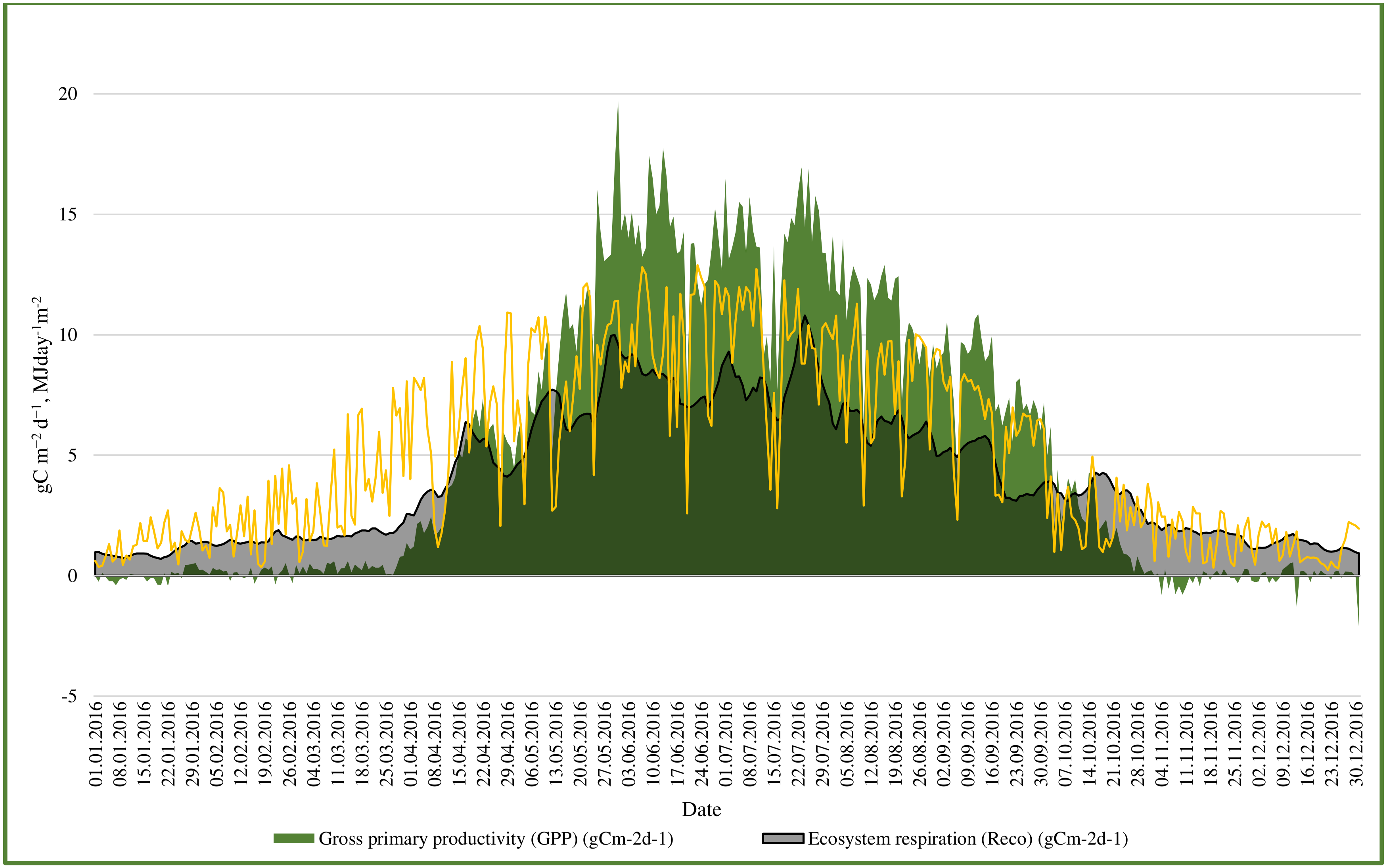


Figure 3.5 GPP and R_{eco} rates along with PAR intensity at Lanžhot in 2016, Respiration positive values represent its rates

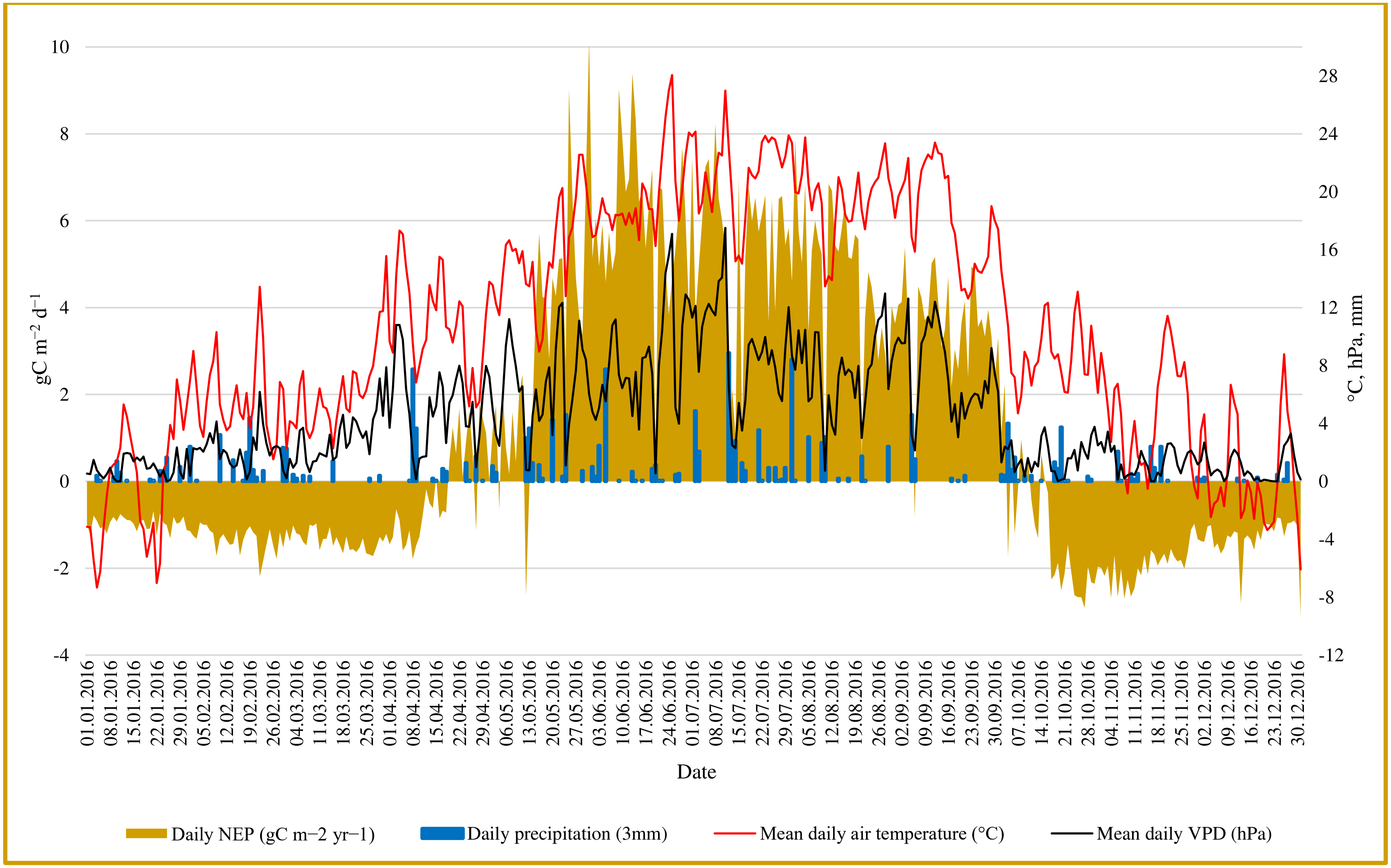


Figure 3.6 Daily NEP, precipitation, mean air temperature and mean VPD at Lanžhot throughout the year 2016

3.2.2. 2018 Data

Compared to 2016, the GPP at LZ in 2018 slightly increased to 2043 gC m^{-2} yr^{-1}. The time period of photosynthetic gain started in the last week of April and lasted into the beginning of October. GPP prevailed over respiration on the last week of April and the first half of May, resulting in higher NEP over this period compared to 2016 at this site. During the growing season prolongation into autumn, respiration prevailed GPP. Highest seasonal values of GPP were measured during late May and early June, reaching a maximum of 17.5 gC m^{-2} d^{-1}. R_{eco} over the year summed up to 1472 gC m^{-2} yr^{-1} (**Figure 3.7**). This leaves us with the 2018 net ecosystem production of 571 gC m^{-2} yr^{-1}, which is more than 25% higher in contrast to the floodplain forest NEP in 2016.

Mean 2018 LZ temperature of 12.1 °C was 1.6 °C higher than the long-term average, making this year slightly less warm than 2016 at LZ. Temperature values were nevertheless higher than average and stayed exceptionally high throughout August. During that month they were accompanied by high VPD values which rose above 20 hPa on multiple days. Yearly rainfall amount was below average at 435 mm compared to 517 mm, with no more than 282 mm during growing season. Only a small portion of this precipitation happened before the hot and dry month of August. (**Figure 3.8**).

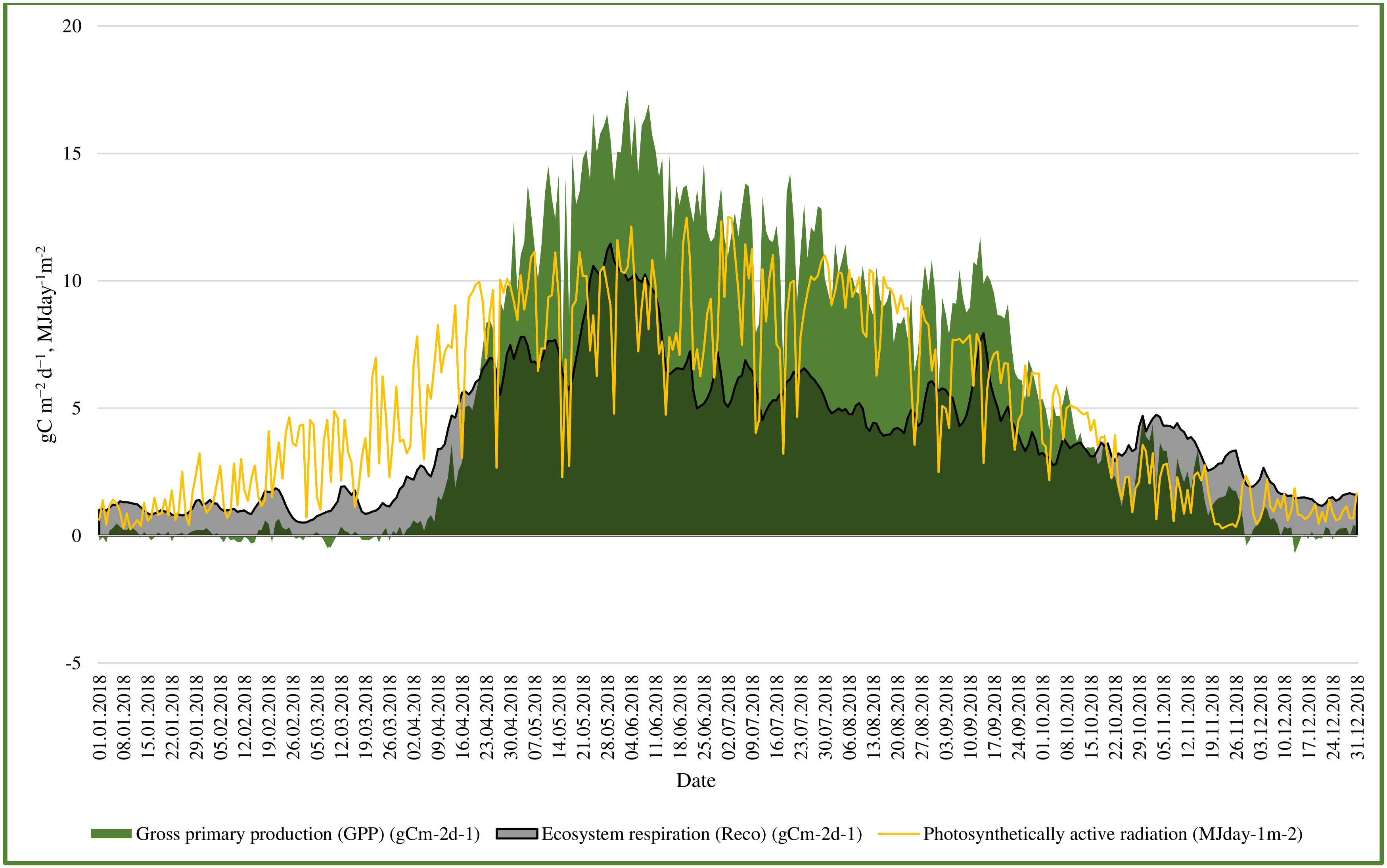


Figure 3.7 GPP and R_{eco} rates along with PAR intensity at Lanžhot in 2018, Respiration positive values represent its rates

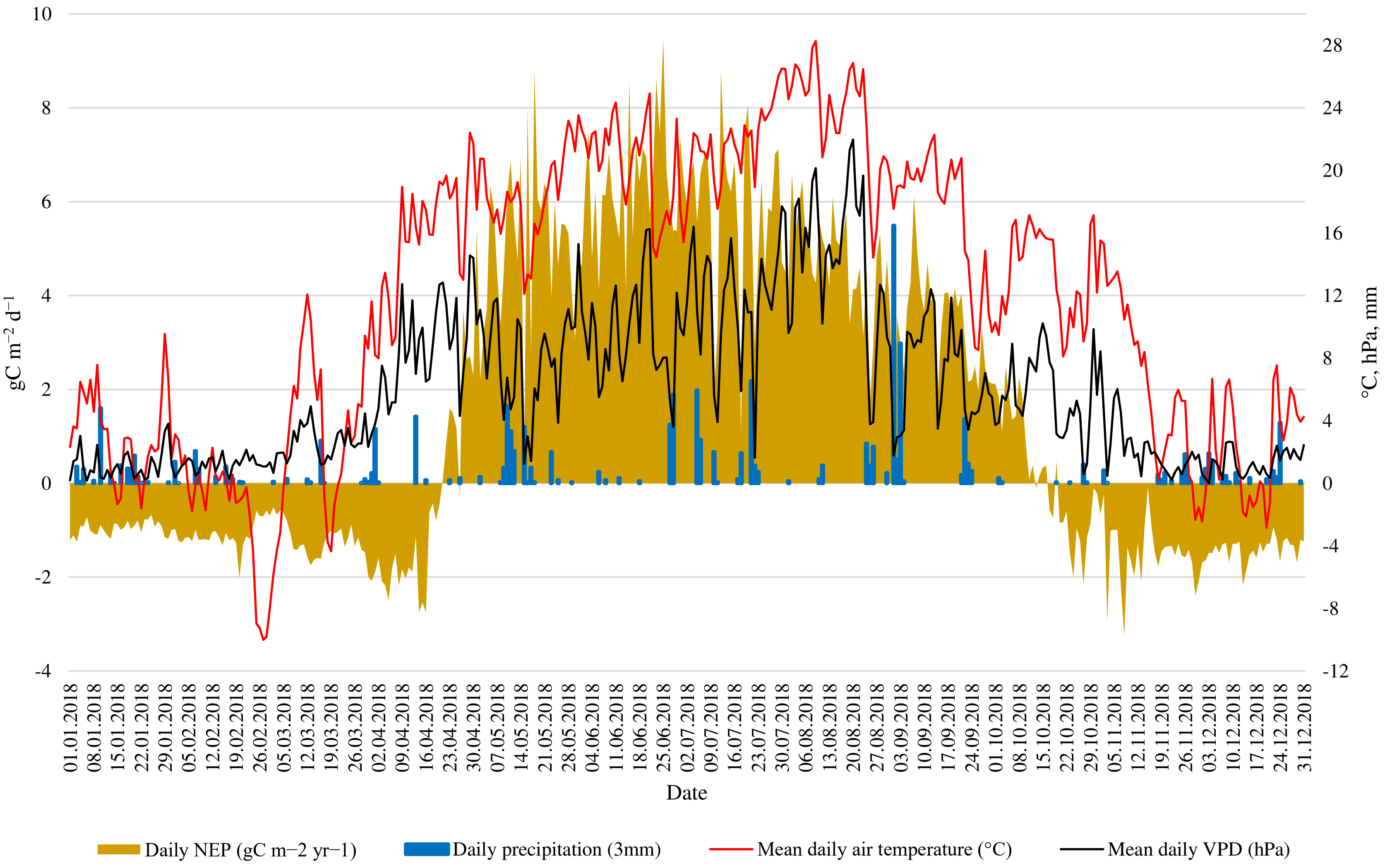


Figure 3.8 Daily NEP, precipitation, mean air temperature and mean VPD at Lanžhot throughout the year 2018

3.3. Rájec

3.3.1. 2016 Data

At the spruce forest stand of RA, gross primary production in 2016 was 1594 gC m^{-2} yr^{-1}. Based on EC measurement data, assimilation began in the middle of March and ceased after the end of October. During this period GPP gradually increased up until a maximum of 11.8 gC m^{-2} d^{-1} on 28th of June after which it started to, although with some periods of lower-than-expected values, steadily decline. Ecosystem respiration, which summed up to 885 gC m^{-2} yr^{-1}, was also the highest in summer (**Figure 3.9**) Consequently, the net ecosystem production at RA reached the value of 709 gC m^{-2} yr^{-1} and was the highest out of all three stations in 2016.

In 2016 the mean yearly temperature at RA (7.7 °C) was only 0.8 °C higher than the long-term average. Comparably to other stations, periods of the highest temperatures were measured in late June, late July and in September. These maximums were not particularly hot since 10-day temperature averages did not reach above more than 20.6 °C. VPD values peaked in September but were also high in summer. Yearly precipitation was 603 mm, making 2016 a slightly dry year. During growing season there was 401 mm of rainfall, out of which 77 mm fell on the 28th of May. There were three other notable (above 10 mm) rainfall events during the summer which together amounted to 75 mm. A slight decline in NEP during periods of higher temperatures, VPD and below average precipitation was measured during the last week of August and the first half of September (**Figure 3.10**).

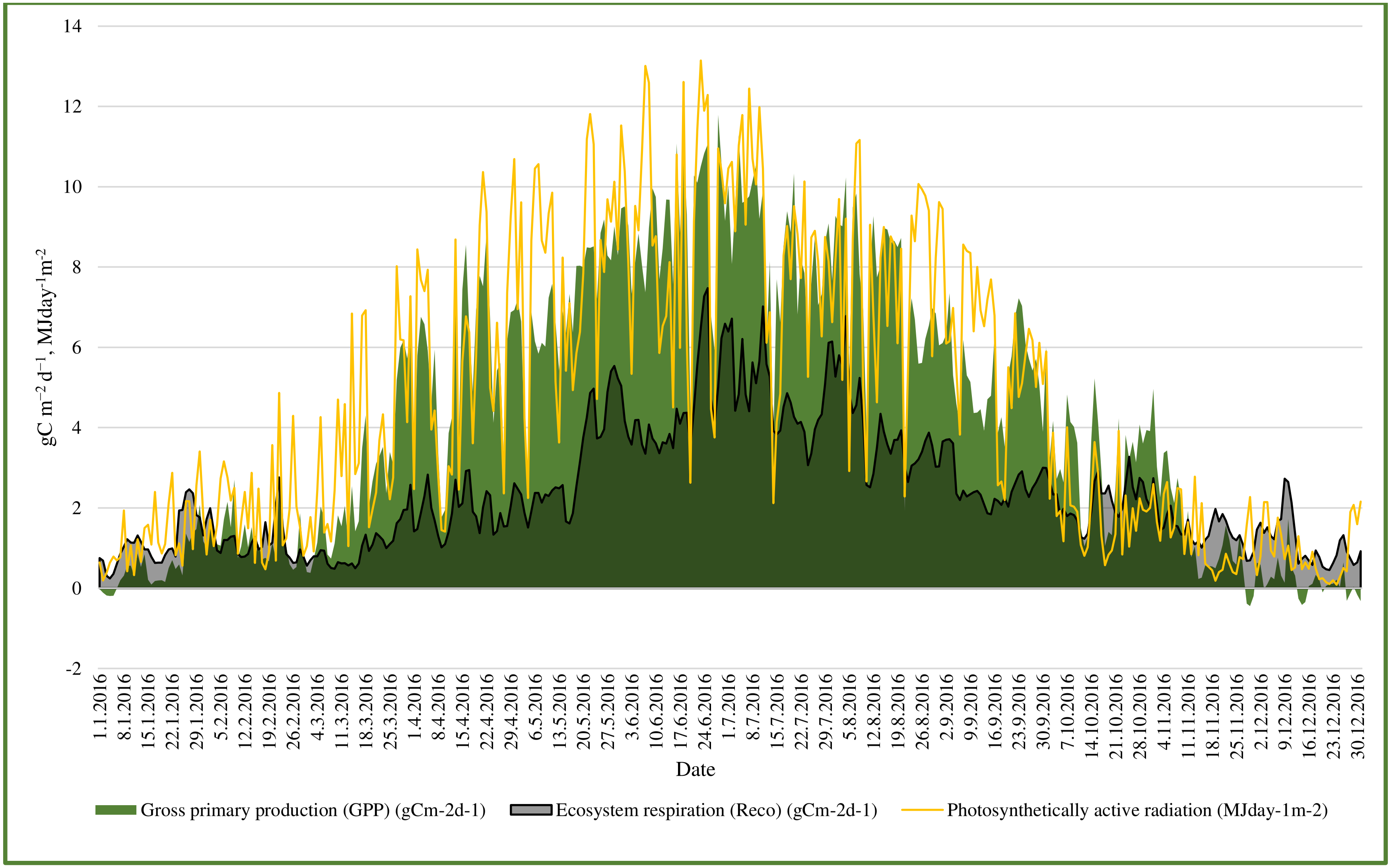


Figure 3.9 GPP and R_{eco} rates along with PAR intensity at Rájec in 2016, Respiration positive values represent its rates

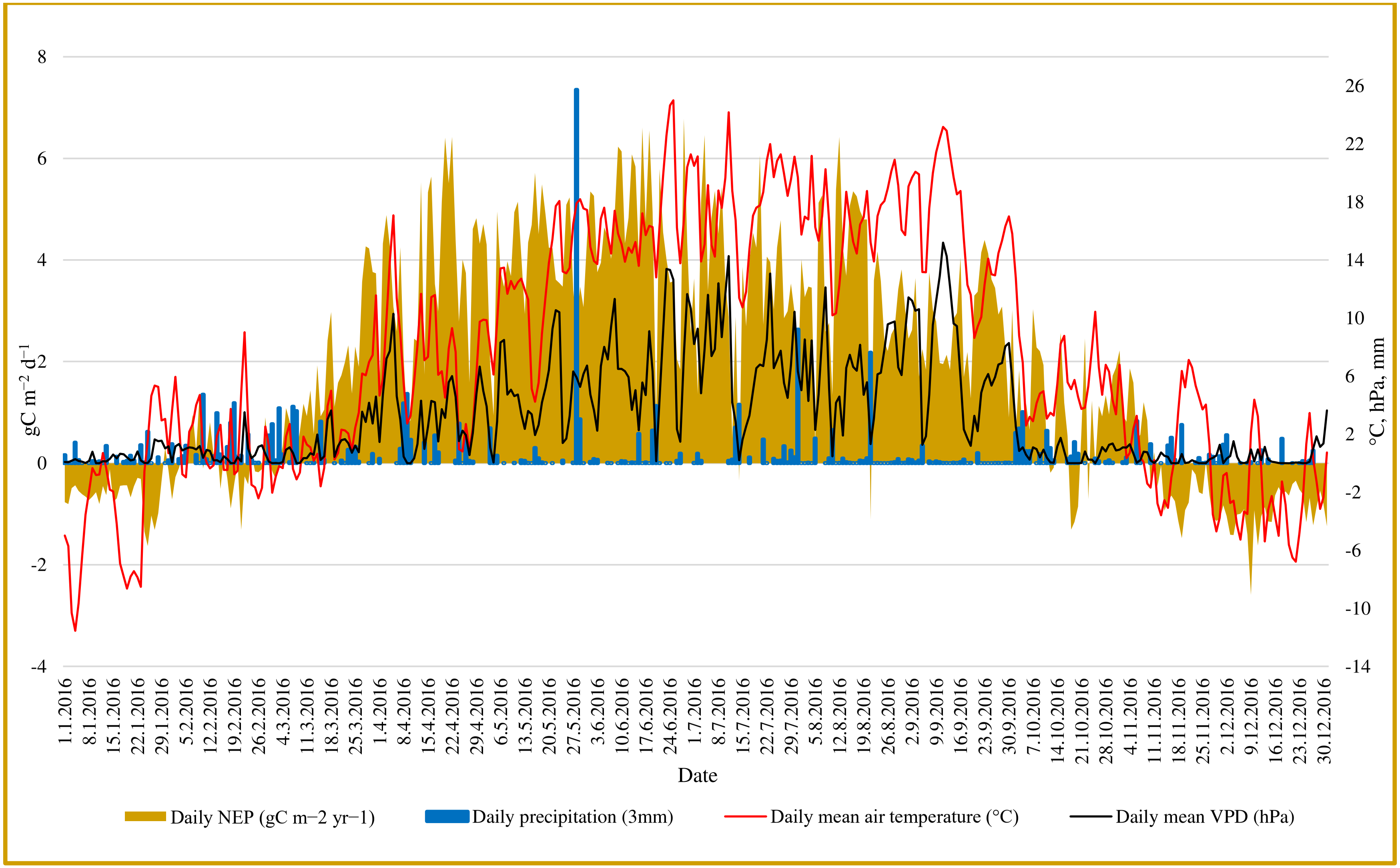


Figure 3.10 Daily NEP, precipitation, mean air temperature and mean VPD at Rájec throughout the year 2016

3.3.2. 2018 Data

In 2018 at RA, the growing season lasted from mid-March till mid-November, being *ca* a week longer than in 2016. Despite this fact, gross primary production of 2018 reached only 1133 gC m^{-2} yr^{-1}, declining by almost 29 % in comparison to the GPP two years ago. GPP rate was relatively low, with average daily rates seldom reaching more than 8 gC m^{-2} d^{-1}. There was a significant and prolonged reduction in GPP measured, which started on the last week of July, lasted the whole August, and ended over the first September week. Total ecosystem respiration of this year was 681 gC m^{-2} yr^{-1}. It peaked in late April and early July, but its rates were otherwise relatively stable, including during the low GPP period (**Figure 3.11**). These measurements combine to result in a net ecosystem production amount of *ca* 452 gC m^{-2} yr^{-1} in 2018.

Average daily temperature at RA during the dry year of 2018 was 8.88 °C, being 2 °C higher compared to the long-term average of 6.9 °C. Similarly to the other two ecosystem stations of ST and LZ, the highest average temperatures were measured during the last week of July and persisted throughout August. Temperatures also peaked this month, their 10-day averages staying above 22 °C for multiple days and reaching a maximum of 24 °C. Along with temperatures, VPD values stayed consistently high in this period, culminating at 18 hPa. Rainfall in 2018 was exceptionally low at RA. The precipitation of 474 mm, out of which only 322 mm fell during the growing season, marks this year as significantly dry in comparison to the average of 705 mm. In July and August combined, there was only 42.6 mm of rain. These prolonged extreme values of temperature, vapour pressure deficit and precipitation scarcity were measured along a severe decrease in NEP during these 5 summer weeks (**Figure 3.12**). As stated on the previous page, yearly NEP was significantly lower than in 2016. NEP of August added up to 20.6 gC m^{-2}, which is only 18.4 % of the NEP in August 2016. The RA spruce stand had a negative NEP on 8 whole days during this month of prominently lowered production, acting like a carbon source to the atmosphere.

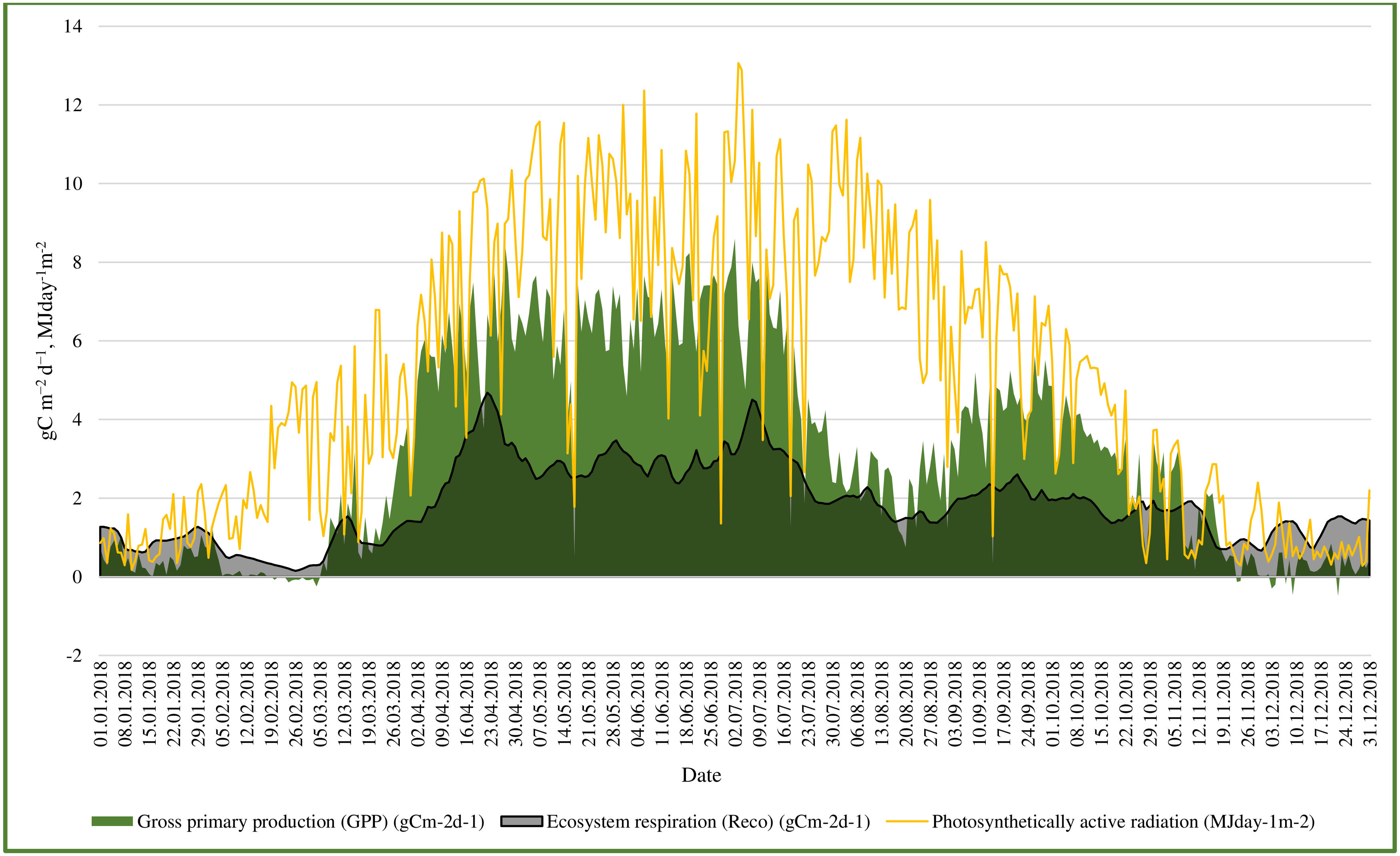


Figure 3.11 GPP and R$_{eco}$ rates along with PAR intensity at Rájec in 2018, Respiration positive values represent its rates

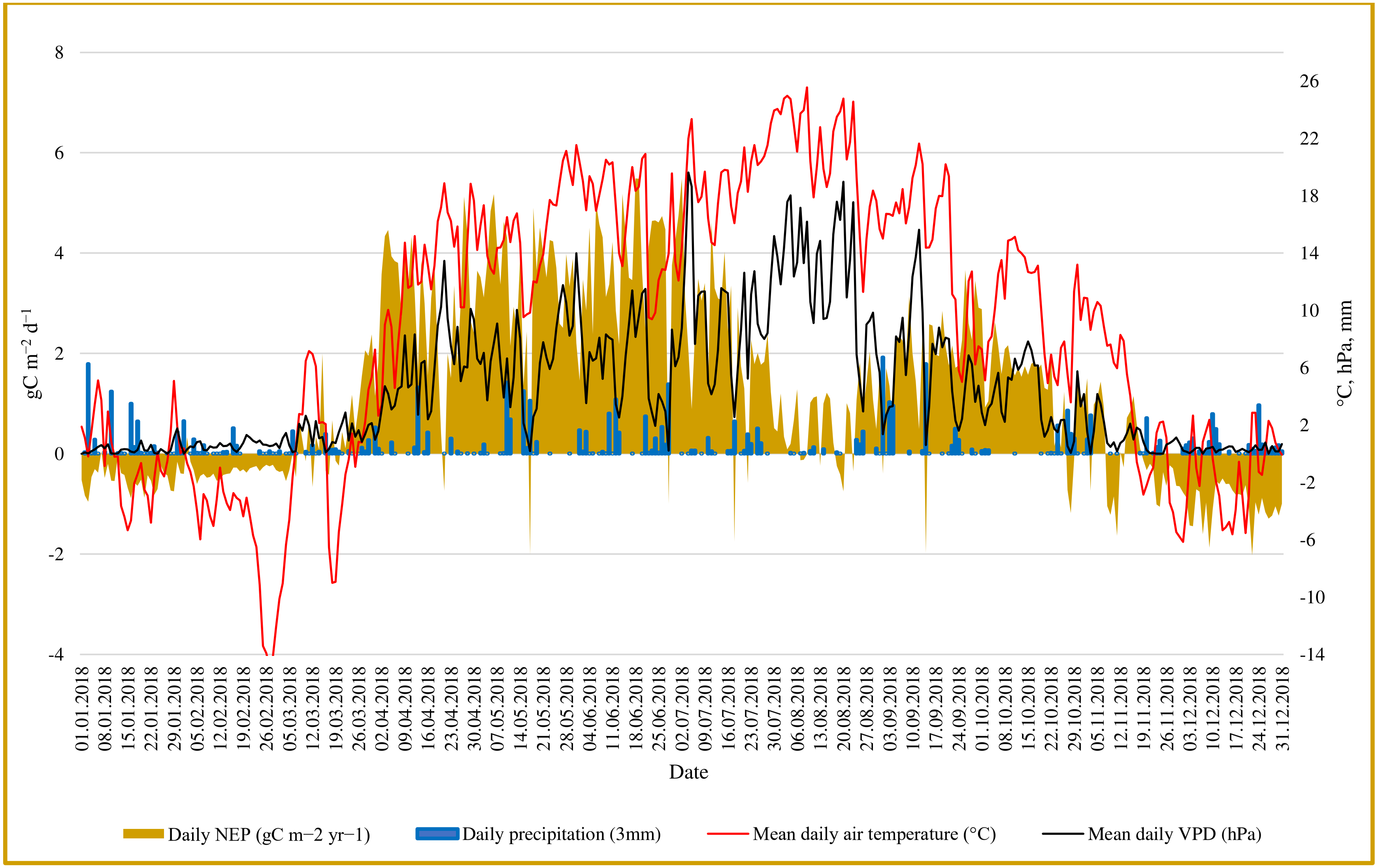


Figure 3.12 Daily NEP, precipitation, mean air temperature and mean VPD at Rájec throughout the year 2018

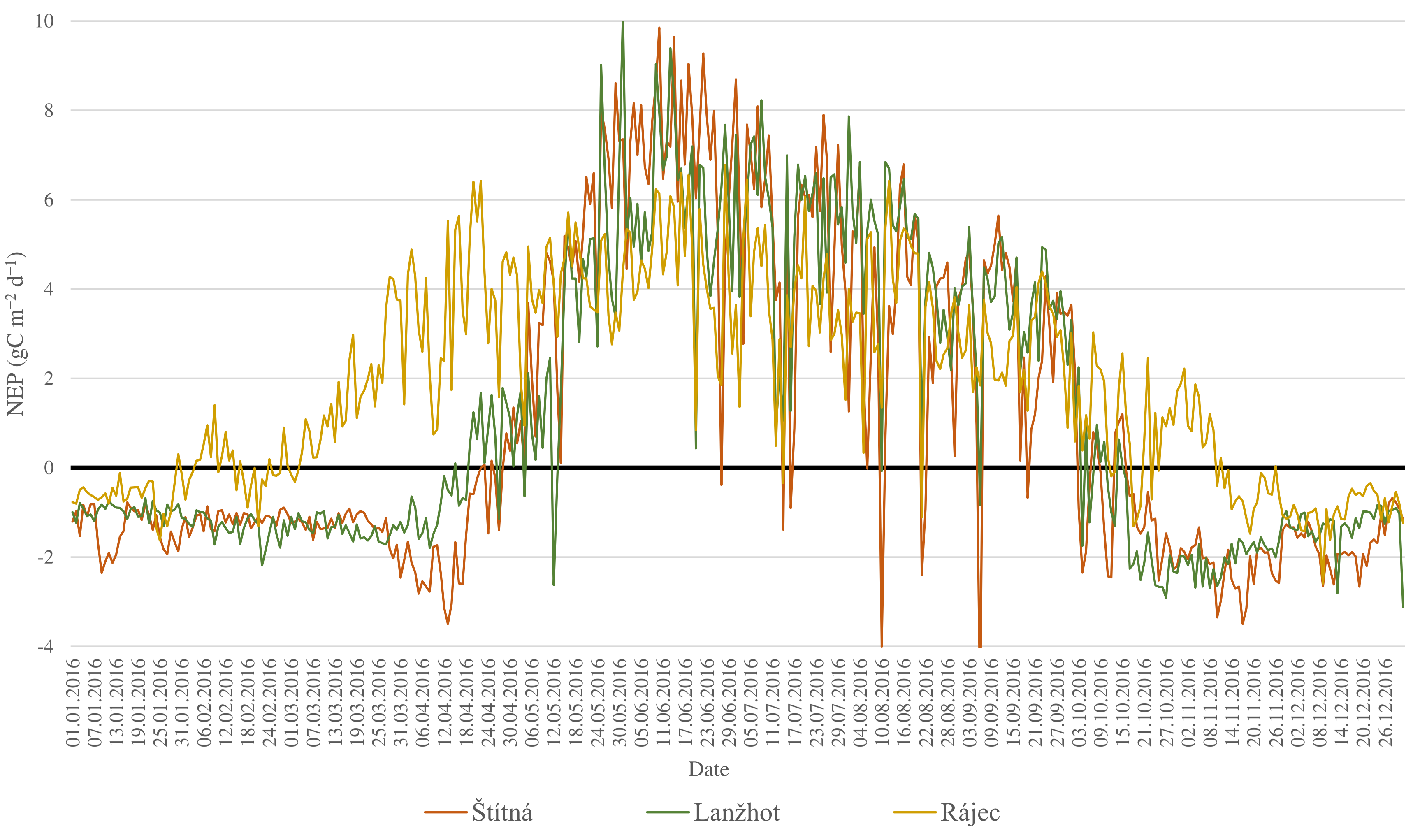


Figure 3.13 Comparison of NEP values at the three ecosystem stations of interest in 2016

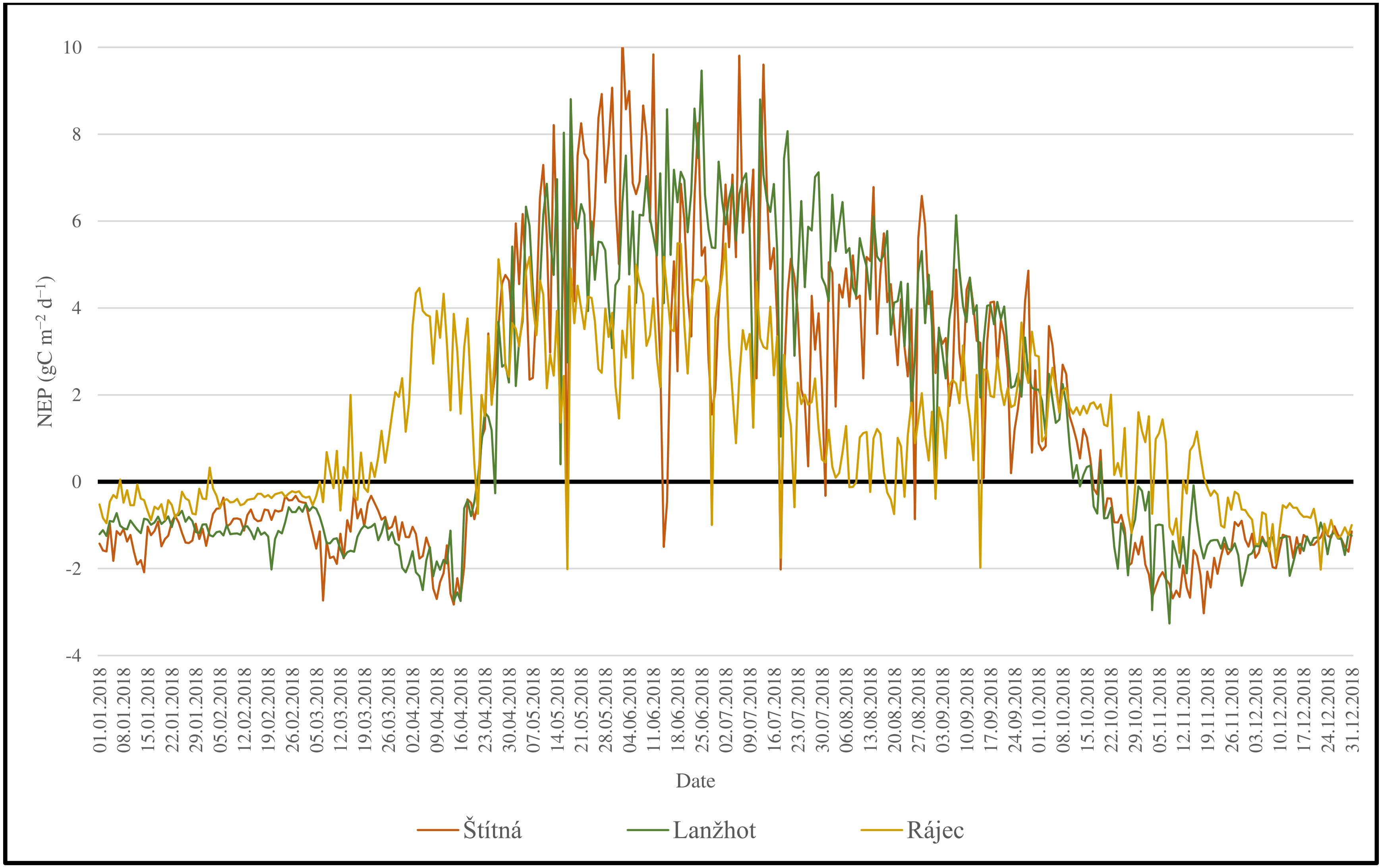


Figure 3.14 Comparison of NEP values at the three ecosystem stations of interest in 2018

4. Discussion

Meteorological variables like temperature, VPD, precipitation amount, incoming PAR intensity *etc*., are described in literature as the main driving factors of ecosystem production. They are also used in popular productivity models such as the 3-PG model (Landsberg and Waring, 1997). Eddy covariance measurements reflect the hourly to weekly effect of these variables on net ecosystem productivity in great accordance with available literature and were thus possible to use for an analysis. The net ecosystem production rates differed in time and magnitude throughout at the ecosystem stations in 2016. Spruce trees keep their photosynthetic organs throughout the whole year. Because of this, the evergreen coniferous forest at RA started to assimilate sooner by *ca* 2 months, as can be seen from the NEP data. The deciduous broadleaf forests of LZ and ST started their growing period by the budding of photosynthetic organs (leaves) later in spring. Bud break is characterized by a peak in growth respiration (Baldocchi and Valentini, 2004) The peak of respiration observed at ST, but not at LZ (**Figure 3.13**), can probably be attributed to the combination of mentioned growth respiration and the increasing soil respiration due to soil warming caused by solar radiation. At this stage of yearly plant leaf regrowth, when the sun height above the horizon is already high, radiation can reach the ground thanks to the insignificant area of the growing leaves not being an obstruction. Assimilation started sooner at LZ floodplain forest than at ST beech stand, but a sudden drop in temperature on the last week of April caused a stagnation of NEP rates until almost the middle of May. The beech forest stand at ST started to assimilate a little later than LZ due to lower temperatures at ST, not being affected by the harmful effects of the temperature drop as it proceeded to increase assimilation rates. Following winter, spring budding of late successional trees like beech and oak is dependent on temperature values after a certain photoperiod (day to night length ratio) is achieved. The budding of early successional species like hornbeam is, on the other hand, controlled by temperature only (Körner and Basler, 2010). Thus, the earlier assimilation onset of LZ compared to ST can be attributed to the higher spring temperature at this low altitude floodplain forest site, but probably also to a 34 % share of hornbeam trees growing at this stand. After budding, NEP rates of the deciduous forests at LZ and ST increased relatively rapidly during spring and the highest rates were measured during June at both stations, their daily rates reaching approximately 10 gC m^{-2} d^{-1}. At RA, the spruce forest did not reach such high NEP maximal rates as they did not exceed 7 gC m^{-2} d^{-1} **(Figure 3.13)**. These measured maximal daily NEP rates were higher compared to the averages of temperate broadleaved deciduous and temperate evergreen coniferous forests around the world (Baldocchi and Valentini, 2004) by *ca* 2 gC m^{-2} d^{-1} and almost 3 gC m^{-2} d^{-1}, respectively. Daily GPP rates during sufficient temperatures are mainly driven by PAR intensity (**Figure 3.1**). On days with heavy cloud cover, insufficient solar radiation decreases photosynthetic rates, causing short-term low or even negative NEP values (**Figure 3.2**). This is evident in the middle of July when multiple days of low radiation had caused a decline in GPP and subsequently NEP of all the studied ecosystems **(Figure 3.13)**. From approximately the 20th of August to the 20th of September 2018 a more prolonged strong decline in NEP rates was measured at RA. It was caused by a decline in GPP rates while R_{eco} rates remained relatively high. During this period, temperature and VPD reached relatively high values and precipitation rates were relatively low, which could have had caused insufficient water availability for the increased transpiration potential, resulting in stomatal closure and subsequent GPP decline. Before and after this period, when temperature and VPD were not as high, NEP rates displayed similar values like on the same days in 2016. The sensitivity of spruce at this site to these meteorological variables along with below average rainfall can thus be reaffirmed. In autumn, the leaves of deciduous trees are shed, causing an increase in ecosystem respiration thanks to the availability of fresh litter for the soil biota to decompose during the still relatively warm and moist conditions (Bréchet *et al.*, 2018; Baldocchi and Valentini, 2004). Spruce trees continued to assimilate during the warmer parts of late autumn. Although daily rates of assimilations were generally lower at RA, the longer growing season of spruce resulted in a higher carbon uptake at this station compared to LZ and ST, which is in accordance with the findings of Baldocchi (2008), who claims that longer assimilation period, not higher assimilation rates, result in greater production. NEP values were higher at the presented stations compared to most European forest stands (Valentini *et al.*, 2000). The ST beech stand had a greater NEP compared to the beech stands in France and Denmark studied by Grainer *et al.* (2002) by 89 % and 192%, respectively. Carbon sink at ST was approximately equal to a North

American deciduous forest, while the carbon sink of LZ was ca 12 % higher. As for conifers, the spruce stand at RA had a 40 % greater NEP than an American pine plantation (Novick *et al.*, 2015). Every ES had a greater NEP than is the FLUXNET average of 181 ± 269 gC $m^{-2}yr^{-1}$ (Baldocchi, 2008). In the year of 2018, there had been multiple changes and differences observed within the three ecosystem stations, regarding both the meteorological conditions and ecosystem carbon fluxes. The peak in respiration before bud break was present at both deciduous stands. ST and LZ started to assimilate CO_2 almost at the same time, increasing photosynthetic rates rapidly along with each other (**Figure 3.14**). Compared to 2016, there was no spring stagnation of NEP rates at LZ due to low temperatures. Later in spring, during the second half of May, temperatures and VPD values had continuously increased, reaching a high point on the last day of May (**Figure 3.4**). These conditions had caused two distinctly different changes in NEP rates at ST and LZ. The ratio of respiration to assimilation increased substantially at the floodplain forest of LZ, causing a decrease in net production. Simultaneously at the ST beech forest, this ratio had stayed the same or even decreased, resulting in the peak of NEP values at ST during this period. There were two short term severe declines in NEP at this station in summer which can be attributed to cloudy weather with insufficient incoming PAR (**Figure 3.3**). The decline in NEP at ST lasting from the 18th of July to the 5th of May was also initiated by a cloudy day but was prolonged by a period of increased respiration which was measured along with gradual temperature and VPD increase (Table 3.3). Baldocchi (2008) states that high temperatures increase ecosystem respiration in broadleaved temperate forests in summer. However, at LZ there was no respiration increase or NEP decrease measured during this summer period of maximal yearly temperatures and VPDs, demonstrating an opposite reaction of each broadleaved ecosystem to these values, which depends on the time of the year. Other factors which were not used in the analysis, like different soil temperature at each site might have affected these reactions. Nevertheless, during the warm and dry year of 2018 both of these ecosystems kept consistently acting like a carbon sink, the magnitude of which was even greater in 2018 than in 2016 by 28 % and 26 % at ST and LZ respectively.

The greatest difference in carbon sink magnitude between the year of 2016 and the dry year 2018 was observed at the spruce ecosystem of RA. Although the growing season there was still longer compared to the deciduous forest stands, net ecosystem production rates throughout year only reached 5.5 gC m^{-2} d^{-1} compared to 6.8 gC m^{-2} d^{-1} in 2016 (**Figure 3.11**). Decrease in NEP rates was caused by the sustained decrease in photosynthetic rates throughout the growing season. These rates only seldomly reached 8 gC m^{-2} d^{-1} (**Figure 3.12**) compared to 2016, during which they were continuously higher than that. (**Figure 3.10**). Besides the consistently lowered NEP rates, the exceptional climatic conditions of this year, namely strongly below average precipitation rates with the strongly above average temperature and VPD values of August, had combined to cause a prolonged severe decrease in NEP rates at the RA site during this month (**Figure 3.12**). This period had a significant impact on the net carbon balance of the spruce stand in 2018. Photosynthetic rates prominently declined and were even surpassed by respiration rates on 8 days of this month, resulting in negative NEP rates even with sufficient incoming PAR intensity, making this ecosystem a net carbon source during this period (**Figure 3.11**).

Reichstein *et al*. (2013) states drought as the most widespread factor which negatively affect the carbon balance of forest ecosystems globally. Dry and hot periods have negative effects by decreasing GPP rates, causing hydraulic system stress and its eventual failure and by leading to stomatal closure, which limits assimilation and transpiration rates. Limited cooling by transpiration causes the heat stress of the plant to further increase. Even a small change in the frequency and severity of such extreme climate periods can greatly reduce carbon sink potential of various ecosystems including forests, or even make it negative. Biomes of Central Europe are currently regarded as regions highly susceptible to drought and heat by this work. In my analysis of the carbon balance of tree distinct forest ecosystem, their different susceptibility to these conditions has been observed. At the beech stand of Štítná and the floodplain forest of Lanžhot, the relative insusceptibility to drought observed, along with the increase in forest carbon sink potential can be mainly explained by the tree species composition present at these sites and by site characteristics. In the White Carpathian Mountains, beech is naturally vastly dominant in the tree species composition. Leuschner (2020) claims that although beech is a rather anisohydric species, not capable of limiting its water expenditure, it has a high hydraulic safety and is not prone to cavitations during droughts. According to this study, beech also has a relatively high leaf area index. Nevertheless, even with its anisohydric behavior and high leaf area, beech is not a big water spender due to its relatively low leaf water vapour conductance and the fact that most of its leaves in the crown are shaded. While beech has a poor ability to reach deep moist soil layers with its roots, there has been some capability of this species to obtain water from deeper soil horizons by Brinkmann *et al*. (2019), who found that, in at least 70cm, it was able to divert root water absorption to these deeper soil part due to the drying out of topsoil. Annual transpiration of beech forest stand is estimated to be 324 mm yr^{-1} (Rötzer *et al*., 2017) or 289 mm yr^{-1} (Schipka *et al*., 2005), being substantially lower than the precipitation amounts at ST in 2016 and 2018. Nevertheless, in the changing climate beech may be at risk of suffering from droughts in the future.

The floodplain forest at Lanžhot also displayed an increase in NEP magnitude in 2018. Alike ST, negative NEP values only occurred during the dormant season and on days with low incoming PAR. Lanžhot site is characterized by relatively high temperatures, but also available groundwater levels. Tree species composition is suitable for this location (Neuhäuslová *et al*., 2001). Broadleaved trees like the ones growing at LZ are well adapted to the conditions at this site. One of their main advantages is their ability to extend roots deep into the soil horizon to reach groundwater levels, avoiding water scarcity during droughts. A study from Lewis and Burgy (1964) found that the English oak is capable of growing root more than 20 m deep into the ground in extreme cases. As for the increase in productivity, a study by Tumajer and Treml (2016) has determined that high temperatures during the growing period of oak trees in a floodplain forest result in increased wood ring growth. It also found out that these trees, mainly on the edges of the floodplain, are also susceptible to drought induced decrease in production. At this site, a study by Kowalska *et al*. (2020) was conducted to assess the impact of drought on this ecosystem productivity. Comparing the years 2016, 2017 and 2018, the highest values of seasonal GPP and evapotranspiration was observed during the last one (2018), probably thanks to sufficient soil moisture. Right porous species of the English oak and Narrow leaved ash were found out to be more drought resistant, with ash displaying the highest productivity and growth rates during these 3 years. Soil water content was nevertheless associated with the tree water deficit, showing the potential vulnerability of these species to droughts.

Regarding the spruce stand at RA, multiple authors state water availability as a key factor which limits the CO_2 assimilation and growth potential of the Norway spruce (Leuschner and Ellenberg, 2017; Krejza *et al*., 2020; Brázdil *et al*., 2015) with results also showing that water availability has become even more important and limiting for spruce in the last two decades (Čermák *et al*., 2019). Spruce is an isohydric species, being able to restrict its stomatal conductance. Low precipitation rates and subsequent low soil moisture availability, along with the exceptionally high daily temperature and VPD values had probably caused the stomata of spruce trees at RA to close and restrict assimilation rates during the dry period of 2018. Sullivan *et al*. (2017) reports that in isohydric species drought inducted health deterioration and eventual mortality consequently occurs due to long periods of unfavourable (warm and dry) conditions, which limit sufficient production during photosynthesis, rather than due to hydraulic failure which occurs in anisohydric species. Isohydric tree dieback is thus preceded by prolonged growth rate decline. Krejza *et al*. (2020) studied the stem radial growth of forest stands in the Czech Republic, finding that drought caused an early cease in its growth and subsequently lower productivity of spruce trees. The greatest desiccation was observed in trees at the altitude of *ca* 600 m a.s.l., comparable to the altitude of the RA station. In the publication from Brázdil *et al*. (2015) drought is stated as the main driver negatively affecting the growth of spruce in hilly areas and even low mountains during the last two decades, based on multiple dendrological studies throughout the Czech Republic but also in Poland and Slovakia. This publication also states that drought itself does not have to be the main stressor responsible for spruce tree health deterioration. Trees weakened by drought are susceptible to bark beetle infestation, which at the same time benefit from warm temperatures by being able to reproduce more rapidly during warm years. The spruce monoculture forest stand at RA, was planted at the site which even back then was not nearly entirely ecologically suitable for this species. The changes in climate, more frequent and severe climatic events of high temperatures and VPDs, along with insufficient precipitation amounts and eventual bark beetle infestation have caused a substantial decline in health, production rates and carbon sink potential at RA. These combined factors resulted in the eventual felling of this stand in 2021.

5. Conclusions

Eddy covariance measurement of ecosystem-atmosphere CO_2 exchange were used to precisely measure the net ecosystem production of three distinct forest ecosystems in the Czech Republic along with the meteorological factors responsible for changes in production rates. Results correspond to the relationship between different factors such as photosynthetically active radiation intensity, air temperature, vapour pressure deficit, precipitation amounts, and the photosynthesis and respiration rates described in literature and other studies. All three forest ecosystem displayed positive yearly net ecosystem production rates in both 2016 and 2018, removing CO2 from the atmosphere and acting like a carbon sink. The magnitude of their respective carbon sink potentials during both years was assessed. In 2016, all three forests acted like a strong carbon sink, with the spruce stand at the Rájec ecosystem station reaching the highest magnitudes compared to the beech forest at Štítná and the floodplain forest at Lanžhot (**Table 5.1**).

Table 5.1 The respective rates of net ecosystem production at the studied stations in 2016

Štítna	**392**	**Lanžhot**	**453**	**Rájec**	**709**	**gC m^{-2} yr^{-1}**

The effects of exceptionally warm and dry conditions during the year of 2018 on the studied forest ecosystems were assessed. At the two broadleaved forests of Štítná and Lanžhot yearly carbon sink potential increased compared to 2016, while spruce trees at Rájec were substantially negatively affected by the unfavourable dry and warm conditions resulting in a prominent yearly net ecosystem production decrease of 36 %, making the potential carbon sink of this forest lowest out of all stations in 2018 (**Tab. 5.2**).

Table 5.2 The respective rates of net ecosystem production at the studied stations in 2018

Štítna	**503**	**Lanžhot**	**571**	**Rájec**	**453**	**gC m^{-2} yr^{-1}**

All studied forest ecosystem emitted CO_2 into the atmosphere on some days during the growing period due to insufficient solar radiation causing restricted photosynthesis rates. However, prolonged decreases in assimilation were also observed during unfavourable meteorological conditions. The most severe decrease of such kind was observed at Rájec in August 2018 and resulted in the ecosystem emitting CO_2 during 8 days of this month.

The carbon sink of the studied spruce forest substantially decreased in the summer 2018 due to edaphic and atmospheric drought along with high temperatures. Based on the observed behaviour of the different studied forest ecosystems during changes in climatic conditions and after comparison with other studies, it is safe to say that spruce forest management in areas with unfavourable conditions such as Rájec is risky, while other two studied ecosystems seem to tolerate such condition, although with uncertainties for to upcoming future.

Summary

Tato práce využívá měření eddy kovariance ke kvantifikaci čisté ekosystémové produkce tří odlišných lesních ekosystémů, zahrnujících bukový les a smrkový les středních nadmořských výšek a nížinný lužní les během dvou let. Práce obsahuje podrobný popis řady nejdůležitějších fyziologických procesů rostlin a různých faktorů prostředí, které je ovlivňují. Byly popsány i dřeviny studovaných lesních ekosystémů s ohledem na jejich ekologické nároky.

V práci jsou prezentovány a popsány různé metody měření toku ekosystému a atmosféry spolu s jejich výhodami a nevýhodami. Dále je popsána použita metoda eddy kovariance s jejími matematickými a dalšími principy, výhodami a nevýhodami, spolu s popisem přístroje a posouzením všech nezbytností potřebných pro správné výsledky měření této metody.

Kromě eddy kovariančního měření byly měřeny i další meteorologické proměnné, aby bylo možné identifikovat a popsat vliv těchto proměnných na produkční rychlost a potenciál sinku uhlíku ve třech studovaných lesích během „normálního“ a „suchého“ roku.

Bylo zjištěno, že nepříznivé klimatické podmínky měly největší vliv na produkci smrkového lesa, který rostl v podmínkách prostředí značně odlišných od jeho ekologického optima, které byly dále umocněny změnami klimatu.

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