The University of South Bohemia in České Budějovice
Faculty of Science

The effect of cutting and fertilization under controlled conditions on photosynthesis and plant growth of two wet grassland species (*Carex canescens* and *Phalaris arundinacea*) representative of the competitive and conservative plant functional types

Bachelor's thesis

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Annotation

Wet grasslands play an important role in the preservation of biodiversity and food production, as they serve as habitat of many birds, insects and other plant species and provide food for farm animals. However, climate change is predicted to affect these wetlands significantly. Therefore, it is important to fully understand the mechanisms of such ecosystems.

In this thesis, the effect of fertilization and cutting of the plants on net photosynthesis rate, biomass production and chlorophyll fluorescens of plants of two different plant functional types (PFT) was investigated. The grasses *C. canescens*, a representative of conservative PFT and *P. arundinacea*, a competitive species, were used to gain a better understanding on how plants of these PFTs respond to changing environmental conditions and management regimes.

We will show that the photosynthesis capacity can differ within the same plant species under different management regimes (water and nutrition level). Additionally, we found that midday depression strongly and significantly influences chlorophyll fluorescens in a way that fertilization treatments can be neglected.

Declaration

I declare that I am the author of this qualification thesis and that in writing it I have used the sources and literature displayed in the list of used sources only.

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Hanna Angster

Acknowledgment

First and foremost, I want to thank Keith Edwards for supervising my thesis, giving me an insight in ecosystem research and also for his patience during my writing process. Next, my thanks go to Bernhard Glocker for his guidance during the experiment and for welcoming me with open arms.

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1. Introduction

1.1 Ecological Habitat and Niche

The term habitat (lat. *habitare* 'to live') describes a place in the natural ecosystem where a certain organism lives, takes up nutrients, and reproduces in. All nutrients that the organism needs to survive are provided by its habitat. An ecosystem can consist of several different habitats (Dianne, 2019).

In contrast to habitat, the term niche describes the interactions of species that take place within the habitat and how those interactions influence other organisms. So, in one habitat can be several niches (Peterson, 2011). Hutchinson (1957) defined the fundamental niche of a species as a *"hypervolume of environmental variables where every point of which corresponds to a state of the environment which would permit the species to exist indefinitely"* (Hutchinson, 1957 in Peterson, 2011). Based on that it can be said that the niche decreases from the niche optimum to the niche envelope where the growth rate is zero. This is defined as the niche shape. Everything out of that range is considered as negative growth rate (Tilman, 1980).

An application of the niche theory is habitat sustainability models (HSMs), which use environmental variables to predict the abundance, presence or absence of a species. (Hirzel & Le Lay, 2008)

The ecological niche can be modified by biotic factors like competition or facilitation, where it is important to understand PFT (plant functional type) and competition factors of different species (Díaz & Cabido, 2001).

1.2 Plant Functional Types (PFT)

A group of plants which show similar characteristics and purposes in ecosystem functions belong to the same Plant Functional Type (PFT) (Wullschleger et al., 2014). The PFT is derived from the traditional taxonomic grouping. However, it often happens that plants which are not taxonomically related show more similarities than related ones (Duckworth et al., 2000).

A link between allocation patterns and plant growth via plant traits leads to life history strategies which predict an exchange between the growth and survival and also the ability to tolerate different forms of stress (Metcalf et al., 2006).

The survival continuum describes the endpoints of the growth which are respectively conservative and competitive plant functional types.

1.2.1 Competitive Plants

Nutrient-richer habitats give ideal condition for the growth of competitive plant species. These species have greater photosynthesis and nutrient uptake rates which leads to faster growth of tissues. A higher nitrogen content in these tissues results in faster decomposition and nutrient turnover rates (Orwin et al., 2010).

Competitive plants distribute more of their biomass to the aboveground structures which results in a lower root-to-shoot (R:S) ratio. Additionally, more of the fixed carbon is invested in the root exudation (Baxendale et al., 2014; de Vries et al., 2012).

Generally, competition in plants refers to the negative influence a species has on its neighbours. Mostly competitive species reduce the availability of nutrients for the other plants. Basic elements like light, water, nitrogen and phosphorus are required by any plant, therefore competition is an important factor for the control of plant communities, resources, disturbance and mutualisms (Keddy & Cahill, 2012).

An example for a competition mechanism is the competition for light, which, at first sight, seems not very complex because the plant cannot control the light supply. Therefore, plants competing for light will grow taller as the light supply increases. This occurs as soon as the demand for carbon tops the supply of carbon from the environment. In contrast to competition for nutrients or water, competition for light leads to size-asymmetric dynamics because light availability is reduced exponentially from the top of the plant to the bottom (Craine & Dybzinski, 2013). Additionally, competitive plants are fast growing and therefore tend to be taller than conservative plants (Colesie et al., 2020).

1.2.2 Phalaris arundinacea

An example for a competitive species is *Phalaris arundinacea*, which is used in this thesis. *Phalaris arundinacea* is also known as reed canary grass (Kungnip, 2015). *Phalaris* means "canary grass" and *arundinacea* means "like a reed". Reed canary grass grows best in seasonally wet or continually moist areas, which are often adjacent to rivers or lakes. Fully grown stands can resist periods of flooding and short periods of drought (Kim et al., 2006).

However, Edwards et al (2020, not published) found out that under the condition of permanent flood, seedlings do not germinate or die right after germination.

P. arundinacea is highly competitive because of its rapid vegetation spread and stem elongation, its wide physiological tolerance, morphological plasticity and its early season growth (Lavergne & Molofsky, 2004). In this way, *P. arundinacea* can outcompete other species and form monospecific stands (Zedler & Kercher, 2005). *P. arundinacea* can outcompete the growth of other wet grassland plants which can decrease the biological diversity in an ecosystem. This is because *P. arundinacea* produce dense crowns and networks of underground rhizomes which allow an aggressive spread (Klimešová and Čížková, 1996). The stems can grow up to two meters (Kim, Ewing & Giblin, 2006). *P. arundinacea* are reproducing vegetatively or sexually (Kercher et al., 2007).

1.2.3 Conservative Plants

Conservative plants often grow in nutrient poor habitats and therefore have to cope with stressful conditions. These species allocate relatively more biomass to belowground structures (Wilschut & van Kleunen, 2021; Poorter et al., 2012).

Due to reduced nutrient uptake and the stressful conditions, litter of conservative species tend to decompose slower because of greater amount of persistent compounds. This delays nutrient release and is favourable for the slower growing species. Nutrient resorption efficiencies are also greater in conservative species (Aerts & Chapin, 1999; Wang et al., 2021).

Conservative species store nutrients longer in their aboveground tissue than competitive species, which is why their season is usually longer than the season of competitive plants (Aerts & Chapin, 1999).

1.2.4 Carex canescens

C. canescens is an example for conservative plants species. *C. canescens* is also known as Grey Sedge, which is because of the pale or silver-green colour of the stems and leaves. *C. canescens* is a perennial plant that has a circumpolar distribution. This means that it is widespread in the north of Europe, Asia, and America where sedge species preferably grow in relatively low level management ecosystems. (Schütz et al., 1997).

C. canescens is a member of the family Cyperaceae. These plants can grow well even in nutrient deficient, acidic wetlands. The stem is usually 20 to 40 cm long and triangular. (Schütz et al., 1997). The leaves assemble around the base.

C. canescens plants are a prominent indicator for environmental changes at the ecosystem level (Schütz, 2000) because their decay is an indication of increased nutrients or water saturation of soils which may be caused by the overuse of fertilizer in crop production (Toogood, 2005). In wetlands, sedges generally play an important role. For example, their heavy root system binds soil very well and therefore prevents soil erosion (Mishra et al., 2015). Additionally, the presence or absence of certain kinds of sedges can be an indicator of the overall health conditions of the whole wetland: Some sedges prefer high salinity or high pH to grow whereas other sedges are even calciphiles. Sedges are also very important for birds, invertebrates, crustaceans and insects (Mishra et al., 2015).

1.3 Photosynthesis, Photosynthesis Capacity, and LICOR 6400

1.3.1 Photosynthesis – Chemical Background

Photosynthesis is a biological process that converts electromagnetic energy into chemical energy in a set of reactions.

The process of photosynthesis is membrane-based and happens in the chloroplast of photosynthetic organisms. Inside the chloroplast are thylakoid membranes which can be organised in stacks forming granal thylakoids. Stroma is the non-membranous matrix inside the chloroplast. It contains enzymes, copies of the chloroplast genome, and starch granules (Blankenship, 2014). There are four stages of photosynthesis:

1. *The antenna complex absorbs light and transfers energy.*

Within the antenna system, the light harvesting complex (LHC) of the plant, the incoming light is absorbed by the pigments, which are associated with the photosynthetic apparatus. This absorption results in an excited state which then leads to a charge separation in the reaction centre (RC). There are no chemical reactions occurring in the antennas. They are responsible for the collection of light and the delivery of energy to the reaction centre (McConnell et al., 2010).

The transfer process of energy involves the migration of excited states from one molecule to another. The energy released is then needed by the antenna system where the pigments are attached to the protein (Blankenship, 2014).

The excitation energy cascades down from pigments with higher energy levels to ones with lower energy levels when being in the state of excitation; the energy moves towards the reaction centre. Photoactive pigments absorb more energy if aided by an antenna system. It is an advantage under conditions when light is available up to moderate intensity and intense light. Under these conditions more light energy might be absorbed than can be converted in a beneficial way by the system (Blankenship, 2014).

2. *Primary transport of electrons in the reaction centre*

The reaction centre is a multi-subunit pigment-protein complex which is attached to the photosynthetic membrane.

In the reaction centre a transformation from light energy to excited electrons takes place which leads to energy changes within the molecule. Quinones and iron-sulphur centres are bound to the hydrophobic polypeptide chains of chlorophylls and act as cofactors, which are essential.

for activating the enzymes involved in the process of photosynthesis. Besides the cofactors, dimeric chlorophylls act as primary electron donors. The transfer of energy to the dimer is the final step in the antenna system (Blankenship, 2014).

3. *Secondary reactions stabilize the process.*

As mentioned above an electron has to be transferred from an excited pigment to an acceptor molecule for the electron transfer chain which is critical for cellular respiration.

There are two different electron chains, one is for oxygenic and one for non-oxygenic photosynthesis. Non-oxygenic photosynthesis consists of a cyclic electron chain (Blankenship, 2014).

In PS I, which is the only photosystem involved, ATP and NAD(P)H are generated to assimilate atmospheric carbon. Because there are no reducing compounds formed, the ATP/NAD(P)H ratio is greater in the cyclic electron transfer chain than in the non-cyclic electron transfer chain (Nawrocki et al., 2019).

This results in a difference in pH, electric potential, or an electrochemical potential gradient. Those potential gradients are then responsible for driving the ATP synthesis which is called a protonmotive force (Blankenship, 2014).

Oxygenic photosynthetic organisms have two photochemical reaction centre complexes (PS I and PS II). PS I and PS II cooperate in a non-cyclic electron transfer chain. PS II removes electrons from water and oxidizes the water to molecular oxygen. Oxygen exceeding the current O_2 need of the plant will be exported out of the cell. A quinone and the cytochrome b_6f complex transport the extracted electrons from PS II to PS I. Before the electrons are transferred to PS I, the second light-driven electron transfer step happens to reduce $NADP^+$, which acts as an intermediate electron acceptor, to NADPH (Blankenship, 2014). The products of this process are NADPH, and ATP (Allen, 2013).

4. *Stable products are synthesized and exported.*

Stable high-energy molecules, which drive several cellular processes, are formed in a final step. The NADPH which was synthesized in the previous step is used together with the phosphate of ATP to reduce carbon dioxide to sugars in several steps. These sugars are transported out of the chloroplast and later used as a primary electron source and base material for cellulose, cell walls, starch and organic acids. Carbon assimilation and reduction reactions take place in the stroma. These reactions are enzyme catalysed (Blankenship, 2002).

1.3.2 Calvin Cycle (Dark Respiration) and Photorespiration

The final products of photosynthesis are sugars which are transported out of the chloroplast. This process, the Calvin cycle, takes place in the chloroplast membrane and is the only known pathway for carbon fixation in plants. With the help of ATP and NADPH CO_2 is reduced to carbohydrate (Martin et al., 2000 in Leegood et al., 2004). The Calvin Cycle can be described in three phases: In phase one **carbon fixation** is catalysed by Rubisco. One molecule of CO_2 binds to Ribulose-1,5-biphosphate (RuBP) which consists of five C-atoms. This leads to a molecule which is unstable and breaks into two molecules with higher stability called 3-phosphorglyceric acid (3-PGA). During the second phase, **reduction**, 3-PGA is reduced to glyceraldehyde-3-phosphate (G3P). This step requires the previously released ATP and NADPH. In the third phase, several molecules of G3P are needed produce glucose. The remaining ones are reused for the **regeneration** of RuBP acceptor molecule. One molecule of ATP is required in this step (Blankenship, 2014). To release one G3P, three CO_2 molecules have to come into the cycle and bring three fixed carbon atoms. Six molecules of G3P are produced, one leaves the membrane producing glucose, while the other five are needed to regenerate three molecules of RuBP acceptor (Martin et al., in Leegood et al., 2004).

An unwanted side reaction of the Calvin Cycle is photorespiration which happens when Rubisco reacts with oxygen instead of CO_2. Photorespiration is a very wasteful process producing PGA and 2-phosphoglycolate. 2-phosphoglycolate inhibits the Calvin Cycle because it has two carbons less than PGA (Blankenship, 2014; Douce &Heldt in Leegood et al., 2004). More than 15 enzymes, translocators and oxygenation steps are required for the recycling of 2-phosphoglycolate into PGA (Douce &Heldt in Leegood et al., 2004). Overall, five ATP and three NADPH are consumed for every oxygenation event. Photorespiration adds up about 50% of the amount of energy consumed in carboxylation (Blankenship, 2014).

1.3.3 Measurement of Photosynthesis Capacity with Infrared Gas Analyzer (IRGA)

The measurement of gas exchange is the most used technique to detect the total photosynthesis capacity of single leaves, the whole plant, or plant canopy. One method for the indirect measurement of the net photosynthetic rate, or carbon assimilation, is to use an infrared gas analyser (IRGA). In an infrared gas analysis, radiation is absorbed by gas molecules at specific infrared wavelengths (IR). There is a characteristic absorption spectrum profile for each gas. The reduction in transmission of IR is then measured by the IRGA. The presence of

CO_2 between a detector and the radiation source causes a reduction in the transmission rate of the used wavelength. Reduced transmission is understood as a decrease in CO_2 concentration. It is important to take the concentration of water vapor into account because its absorption maximum is close to the absorption maximum g of CO_2. This leads to an overlap with that of CO_2. The interference may be corrected by measuring the H_2O concentration additionally with another IGRA or by drying the air (Long et al., 1996).

The IRGA used for this thesis is an open path system, which means that the air from one single source can enter both the analysis and reference lines without any recirculation of airflow (Pandey et al., 2017).

The measurements of transpiration and photosynthesis are based on the differences between CO_2 and H_2O in the air stream that flows into the leaf cuvette in comparison to the air which flows out of the cuvette, after passing by the sample within the cuvette. For this method, it is not needed to remove the leave from the plant (Long et al., 1996).

CO_2 and H_2O IRGAs are in the sensor head of the LI-6400A (Li-COR, Nebraska), which was used for this thesis. The incoming air stream is conditioned for CO_2 concentration, humidity, and temperature, due to CO_2 and H_2O scrubbing chemicals and inlets for additional CO_2 from a gas bottle (Long et al., 1996).

1.4 Relative and Absolute Chlorophyll Content

Absolute chlorophyll contents show the mass of chlorophyll per leaf area. By measuring the chlorophyll content, the overall potential photosynthetic capacity and productivity of the plant can be determined. It is important to know the difference between the chlorophyll content and chlorophyll concentration (C_{CONC}). C_{CONC} describes the chlorophyll mass per unit mass of plant material, which indicates the physiological status of the plant and provides information on the nutrient level the plant experiences (C. L. Jones et al., 2007).

The relative chlorophyll content is measured under field conditions either by transmission and absorption ratios, or by detection of laser or sun-induced chlorophyll fluorescence. One way to measure relative chlorophyll content is with a MultispeQ V 2.0 (PhotosynQ, Michigan), which was used for this thesis.

There are several methods for detecting chlorophyll, for example, Special Products Analysis Division (SPAD) and chlorophyll fluorescence. SPAD, as used with the PhotosynQ, evaluates the relative chlorophyll content by measuring the relative transmission of red (650 nm) and infrared (940 nm) light. The relative chlorophyll content is calculated from a ratio of reflection versus absorption. This relative chlorophyll content is an indicator of beginning stress or disease and the plant's nitrogen status (Kuhlgert et al., 2016). Stresses of any kind result in a chance of chlorophyll a fluorescence which is then detected while measuring (Percival, 2005).

2. Study Aims and Hypothesis

The aim of the project was to investigate how changes in nutrient addition and cutting frequency influence photosynthesis capacity, biomass production and relative chlorophyll content of *Carex canescens* and *Phalaris arundinacea*, representative species of the conservative and competitive plant functional types (PFT), respectively.

Based on previously performed experiments by our team and on the literature, we hypothesized that:

1. Both species will show higher leaf photosynthesis rates and greater biomass after fertilization.
2. As *C. canescens* is a conservative species, the fertilization effect will be more noticeable.
3. After cutting new leaves will have increased chlorophyll content and higher photosynthesis rates compared to uncut plants.

3. Methods and Materials

3.1 Preparation of Mesocosm at JCU

A mesocosm was established to determine the effect of nutrient addition and cutting on the growth and functioning of representative species of the conservative and competitive plant functional types, *C. canescens* and *P. arundinacea*, respectively. The mesocosm consisted of 12 basins to which specific experimental treatment combinations were randomly assigned.

On 21 April 2021, *C. canescens* and *P. arundinacea* plants were transferred into pots filled with a 1:2 mixture of sand and peat in the mesocosm. Half of the *P. arundinacea* and the *C. canescens* plants were fertilized during the experiment, using a fertilizer containing 15v% Nitrogen (8.3v% from ammonia and 6.7v% from nitrate), 15v% Phosphate (P_2O_5) (8.5 from ammonium citrate) and 15v% Potassium (K_2O). The fertilizer was added in three equal doses during the growing season to mimic the normal procedure of local farmers.

The other plants were unfertilized. In total, 144 plants were planted in the 12 basins. Every basin contained only one treatment combination. The main factors were species (*P. arundinacea* or *C. canescens*); nutrient addition (fertilized or unfertilized) and cutting (cut or uncut). Cutting simulated how farmers would treat the plants if they were used for forage.

3.2 Stem number and plant height

Stem height and density (stem number) were determined at two-to-three-week intervals. In total, there were 7 counting days from May to August 2021. The counting days were:

Counting day **1**: May 20th, 2021
Counting day **2**: June 4th, 2021
Counting day **3**: June 16th, 2021
Counting day **4**: July 1st, 2021
Counting day **5**: July 15th, 2021
Counting day **6**: July 27th, 2021
Counting day **7**: August 8th, 2021

Only plants that were not harvested were considered in the statistics.

From these data, the average number of stems, average number of new shoots, and the average height were determined. Outliers were determined using the interquartile range rule (Schwertman et al., 2004).

The data were collected in an Excel (Microsoft Excel, Microsoft Corp., Washington) sheet where the average number of stems and new shoots, and the average height were determined. A Student's T-test was performed to find the standard deviation and confidence interval.

Then, a repeated measures ANOVA was applied to see significant differences between the treatment groups. The results are plotted in bar plots.

3.3 Harvest and determination of the plants' dry weight

The cutting treatment was administered on June 8th to half (72) of the plants, divided equally between *P. arundinacea* and *C. canescens* and the fertilization treatment. The plants were cut so that about 5 cm of the plant remained aboveground. This is similar to how those plants would be treated by a farmer if they were on the meadows and used in forage.

The dry weight of the cut-off leaves was determined after they were dried in a drying oven.

Half of the selected plants were harvested in early July following measuring of photosynthesis and root exudation collection.

A second harvest following the same procedure was conducted on August 16th.

Total dry weight and the root-to-shoot ratio (R:S) were determined from these data. Total dry weight is the sum of the aboveground dry weight (ADW) and the belowground dry weight (BDW). From this, the root-to-shoot ratio could be calculated using equation 1 (Crop Science Institute & Bláha, 2019):

$$\frac{Belowground\ dry\ weight\ (BDW)}{Aboveground\ dry\ weight\ (ADW)} = root - to - shoot\ ratio \qquad (1)$$

3.4 Photosynthesis Measurement

Starting in May 2021, the photosynthesis capacity of randomly selected plants was measured every month until August for all treatments using a LI-6400 A (LI-COR, Nebraska).

The following parameters were used:

Flow = 500
Mixer = on
Ambient temperature inside the measurement chamber = 24°C
Relative Humidity = 60%
CO_2 = 400 ppm

The desired leaf was placed in the measuring chamber and the leaf area was visually estimated.

Ideally, the leaf-covered half of the chamber. Photosynthesis rates were measured at different light levels, with photosynthetically active radiation (PAR) values ranging from 0 to 1500 nm, to produce a light curve. The collected data from the LICOR was used to generate fitted light curves, using the equation for a rectangular hyperbolic model (Equation 2; de Lobo et al., 2013; Rivera-Mendes and Romero 2017). Estimated values of maximum photosynthesis (P_{max}), the quantum yield (Φ), light compensation point (LCP) and dark respiration (R_d) were determined from the fitted line.

Using Microsoft Excel's (Microsoft Excel, Microsoft Corp., Washington) solver function equation 2 was applied and a fitted photosynthesis curve was determined for each measured plant following the procedure of Lobo et al (2013).

$$P_N = \frac{\phi_{I_0} * I + P_{gmax} - \sqrt{(\phi_{I_0} * I + P_{gmax})^2 - 4\theta * \phi_{I_0} * I * P_{gmax}}}{2\theta} - R_D \qquad (2)$$

Figure 1 shows an ideally fitted photosynthesis curve (Rivera-Mendes & Romero, 2017).

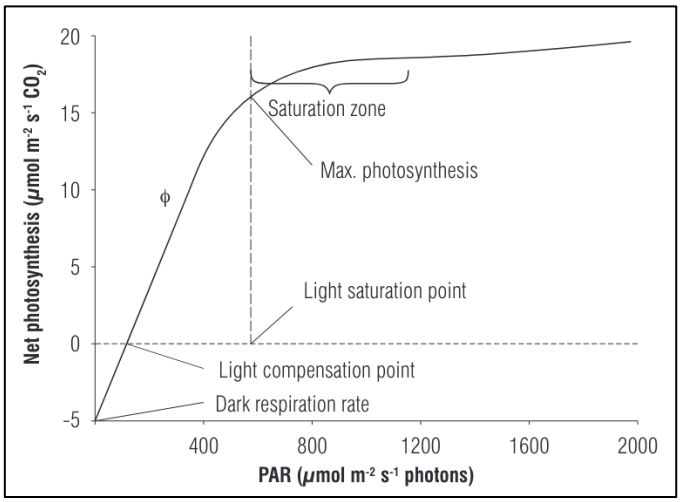

Figure 1: An ideally fitted photosynthesis curve should look like this one from Rivera-Mendes and Romero, 2017. All relevant points are marked and clearly visible. For this experiment the quantum yield, light compensation point, dark respiration rate and maximal photosynthesis were analysed.

For this thesis, the measurement from July 3rd, 2021, and August 4th, 2021, were analysed following the above procedure.

In July, a total number of eight *P. arundinacea*, four fertilized and four unfertilized, was analysed. Additionally, the photosynthesis rates of six *C. canescens*, 4 fertilized and 2 unfertilized, were measured.

In August a total number of six *C. canescens*, four fertilized and two unfertilized, was considered for the photosynthesis measurement. Further, ten P. *arundinacea*, half of them fertilized, were analysed.

The unequal number of measurements per treatment is a result of the randomness in which the plants were picked. Treatment was not considered when picking a plant, only its number was.

3.5 Chlorophyll Fluorescence

Chlorophyll fluorescence of all remaining *P. arundinacea* plants was determined in August before the last harvest. This was done using a PhotosynQ® MultispeQ device.

An ANOVA test was performed to prove that the Quantum yield of photosystem II (Phi2), the ratio of incoming light which goes towards photochemical quenching (NPQt), and the ratio of incoming light that is lost in non-regulated processes (PhiNO) are similar in all the

different treatments. The sum of these parameters gives the photosynthetic regulation which should be 1 (equation 3).

$$PhiNPQ + PhiNO + Phi2 = 1 \quad (3)$$

4. Results

4.1 Number of stems and plant height

Overall, *C. canescens* had significantly more stems than *P. arundinacea* regardless the treatment ($F = 36.13$; $p < 0.001$). Additionally, figure 2a shows, that fertilized plants of both species showed a steady increase of new stems whereas the shoot number of unfertilized plants remained relatively constant after the second measurement.

There was a significant fertilization effect in terms of new shoot production in both species (Figure 2b). On average, fertilized *P. arundinacea* grew 3 ± 0.4 new shoots in between the counting days while unfertilized ones only grew 1 ± 0.2 new shoots ($F = 41.96$; $p = 0.001$).

Fertilized *C. canescens* grew 9 ± 1 new shoots which is significantly higher ($F = 15.57$; $p = 0.01$) than the growth of unfertilized *C. canescens* (4 ± 0.8 new shoots). Fertilized *C. canescens* show the steadiest growth of new shoots over the measurement period, whereas unfertilized *C. canescens* show a relatively stable growth of new shoots. The most stable growth of new shoots is observed in unfertilized *P. arundinacea* (Figure 2a).

The species also differed significantly in their height ($F = 62.28$; $p < 0.001$). Regardless the treatment, *C. canescens* showed an average height of 28.23 ± 5.70 cm and *P. arundinacea* 49.78 ± 7.84 cm (Figure 2c).

Over the duration of the experiment, the height of both species kept increasing, and especially fertilized plants reached their maximum height in August. However, unfertilized *P. arundinacea* reached their maximum height on counting day 6 (June 16th) followed by a die-back in which the plant height remained stable until the end of the experiment. These differences resulted in a significant ($F = 18.63$; $p < 0.001$) time effect as well as a significant species-time interaction ($F = 7.68$; $p < 0.001$). Overall, there was no significant fertilization effect ($F = 0.20$; $p = 0.657$) but this is because of very similar heights of the fertilized and unfertilized *P. arundinacea* plants. However, fertilized, and unfertilized *C. canescens* showed

a significant difference in plant height (F = 5.208; p = 0.030), with unfertilized plants being smaller than fertilized ones (Figure 2c).

Figure 2d shows the mean total number of shoots, which is significantly higher in *C. canescens* than in *P. arundinacea* regardless of the treatment. Both species show a positive fertilization effect, which is greater in *C. canescens* than in *P. arundinacea*. All plants showed a major decrease of shoots in count 3, which may be the result of a heavy hailstorm. Fertilized *C. canescens* had the most drastic decrease but they also recovered best. In count 3, they have an average loss of 18 stems and in count 4 they grew 17 stems back on average. Unfertilized *C. canescens* showed a similar behaviour but with less stems. Fertilized *P. arundinacea* also lost stems but not as much as *C. canescens.* They also were able to grow more stems back than the ones that were lost.

Unfertilized *P. arundinacea* showed a low but steady growth, being unbothered by the storm.

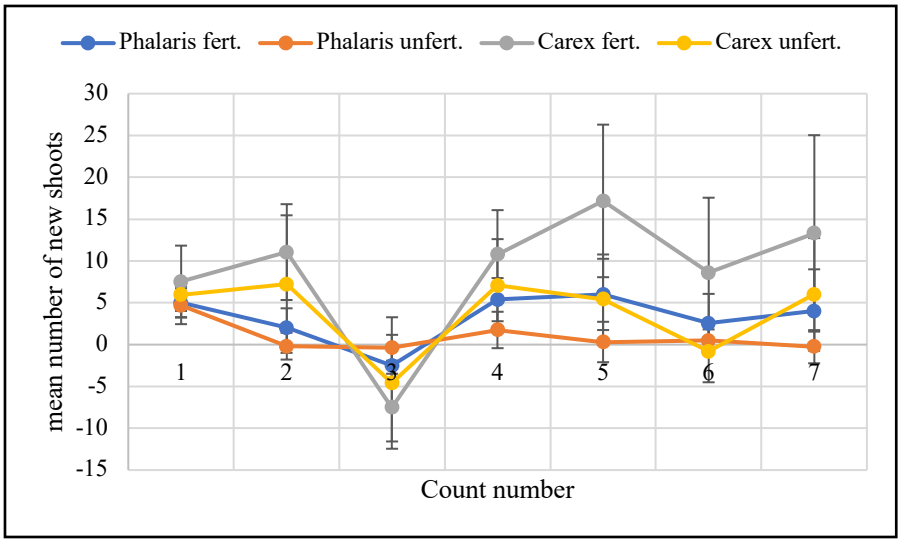

Figure 2a: The average number of new shoots of all treatments over time (mean ± 1 SD); Acronyms: unfert = unfertilized; fert = fertilized (300 kg NPK * ha^{-1})

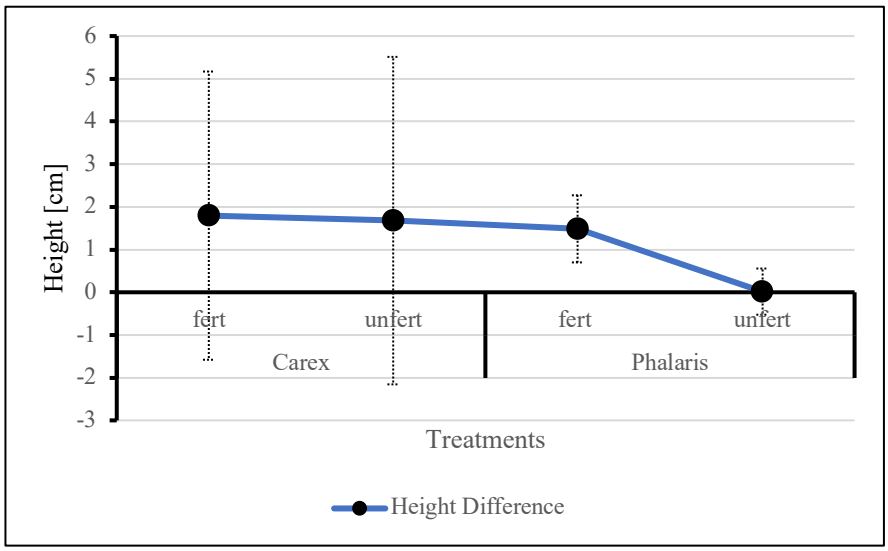

Figure 2b: The average height of all treatment groups is summarized here as mean ± 1SD, both species show a positive fertilization effect. Acronyms: unfert = unfertilized; fert = fertilized (300 kg NPK * ha^{-1});.

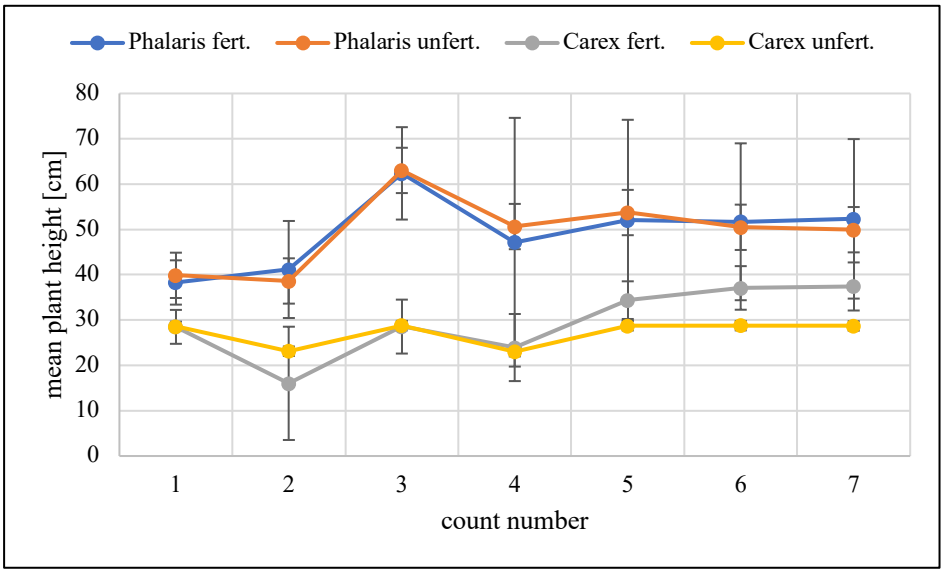

Figure 2c: Change of plant height over time (mean ± 1 SD); Acronyms: unfert = unfertilized; fert = fertilized (300 kg NPK * ha^{-1}).

4.2 Dry weight and Root–to–Shoot ratio

Fertilization significantly impacted both aboveground and belowground dry weight (DW) ($p < 0.001$) in both months (Figure 3a, b). Fertilized *P. arundinacea* plants had the highest above and belowground DWs, while unfertilized *C. canescens* had the lowest. However, a significant relationship between species and fertilization could not be found ($F = 1.80$; $p > 0.05$), because of the similar DWs in fertilized *C. canescens* and unfertilized *P. arundinacea*. The highest aboveground DW is observed in fertilized *P. arundinacea* plants. This differed significantly ($F = 13.35$; $p > 0.001$) from the DW of unfertilized *P. arundinacea* plants. A significant ($F = 21.86$; $p < 0.001$) fertilization effect was also seen in *C. canescens*. Fertilized *C. canescens* plants have a higher aboveground DW than unfertilized ones.

A similar fertilization effect was observed for total plant mass (Figure 3c). This effect was also seen in both species, with there being a significant difference in total DW between fertilized and unfertilized plants in both months (July: $F = 11.36$; $p = 0.002$; August: $F = 9.31$; $p = 0.004$). *P. arundinacea* had an overall total dry weight of 2.69 ± 1.74 g and *C. canescens* had 1.46 ± 0.76 g in July, while the August overall mean DWs were 4.0 ± 2.0 g and 2.69 ± 1.36 g for *P. arundinacea* and *C. canescens*, respectively (Figure 3c).

The root-to-shoot ratio (R:S) was calculated for all species and treatments. In July, a positive fertilization effect could be found in *C. canescens* ($F = 13.07$; $p > 0.01$), But *P. arundinacea* did not show the same relationship. In August, there was no significant difference between fertilized and unfertilized plants nor between the species (Figure 3d).

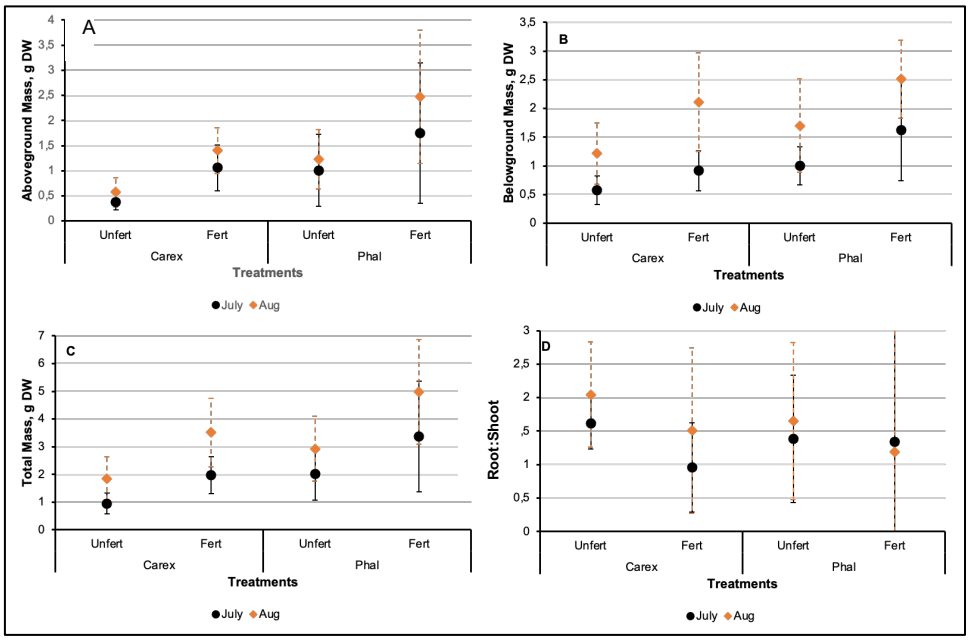

Figure 3: A: Aboveground biomass of both species and treatments in July and August. **B:** Belowground biomass of both species and treatments in July and August. **C:** Total mass of biomass of both species and treatments in July and August. **D:** Root:Shoot of both species and treatments in July and August. All values are represented as mean ± 1 SD.

4.3 Photosynthesis Capacity

In July, the photosynthesis rates for both species differed between treatments. The highest P_{max} values were found in both species for the cut and fertilized treatment, whereas the lowest values were found in unfertilized plants, uncut for *C. canescens* and cut for *P. arundinacea* (Figures 4 a, b). These differences are all significant ($p < 0.001$)

The main factor affecting P_{max} in *P. arundinacea* was nutrient addition (Figure 4b), with fertilized *P. arundinacea* having a significantly higher ($F = 11.12$; $p = 0.0123$) P_{max} than unfertilized ones. There is no significant difference between the cut and the uncut fertilized and unfertilized plants ($p > 0.05$).

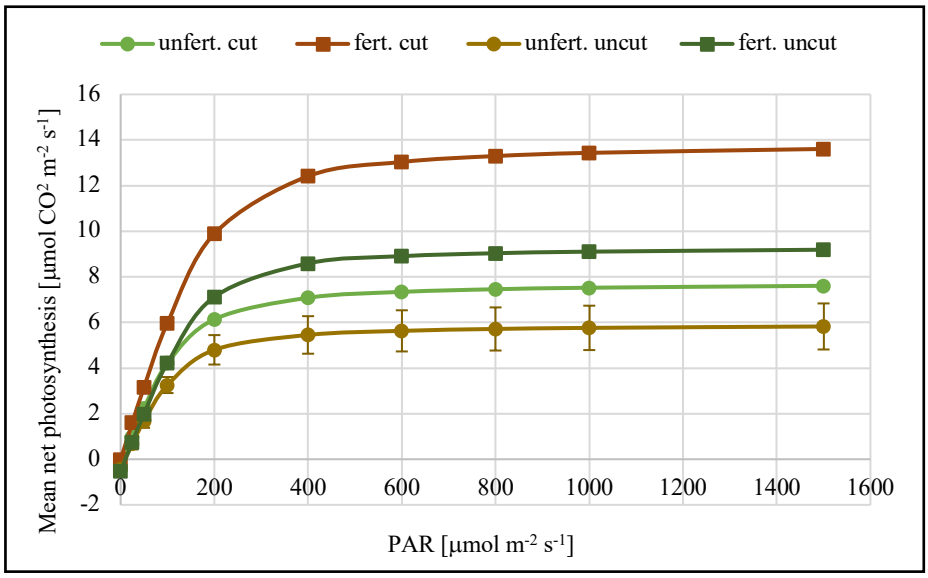

Figure 4a: Light curves for ***C. canescens*** in July (mean ± 1 SD for unfert uncut, for the other treatments only one sample each was measured). The fertilized show higher photosynthesis curves than the unfertilized plants do. Acronyms: PAR = photosynthetically active radiation; unfert = unfertilized; fert = fertilized (300 kg NPK * ha^{-1}).

In August, P_{max} for *C. canescens* was the highest in the fertilized uncut treatment (8.5 µmol CO^2 m^{-2} s^{-1}) and the lowest in the unfertilized cut plants ($P_{max} < 4$; Figure 5a). The opposite situation occurred with *P. arundinacea*, with the unfertilized cut plants having the highest P_{max} (5.5) while P_{max} (3.5) was similar for plants of this species subjected to the other three treatments (Figure 5b).

Neither fertilization nor cutting had any effect on the light compensation point (LCP), dark respiration or quantum yield for both species ($p > 0.05$). This was the same in August, with the exception that fertilized *P. arundinacea* had significantly higher LCP than unfertilized plants ($p = 0.028$; Figure 5b).

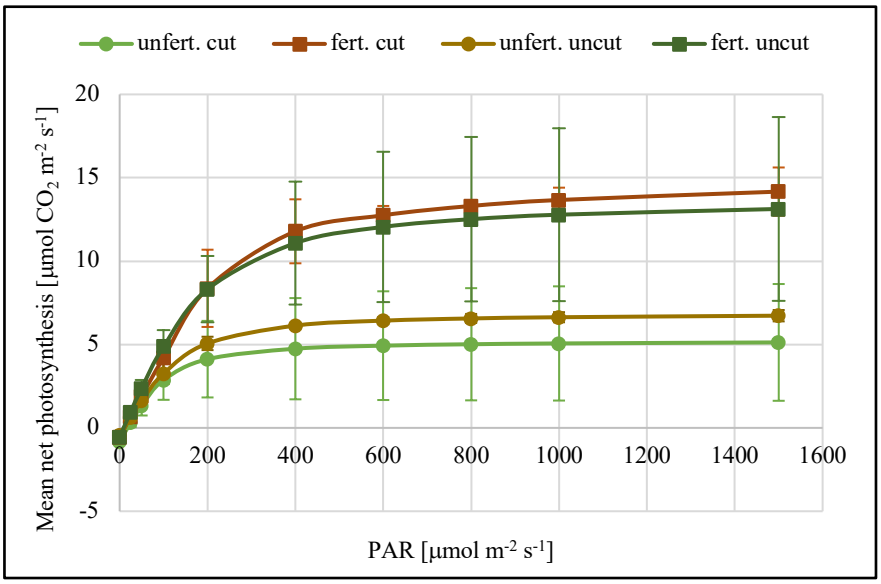

Figure 4b: Estimated photosynthesis curves of ***P. arundinacea*** (mean ± 1SD) for July. PAR = photosynthetically active radiation; unfert = unfertilized; fert = fertilized (300 kg NPK * ha^{-1}).

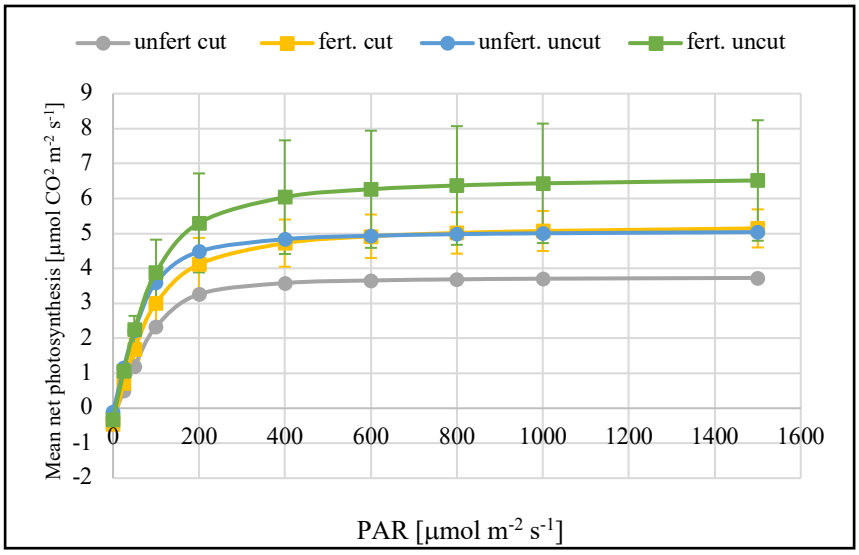

Figure 5a: The mean estimated photosynthesis curves of ***C. canescens*** in August are shown here ± 1 SD; for the unfert uncut and the unfert cut treatment only one measurement was taken. PAR = photosynthetically active radiation; unfert = unfertilized; fert = fertilized (300 kg NPK * ha^{-1}).

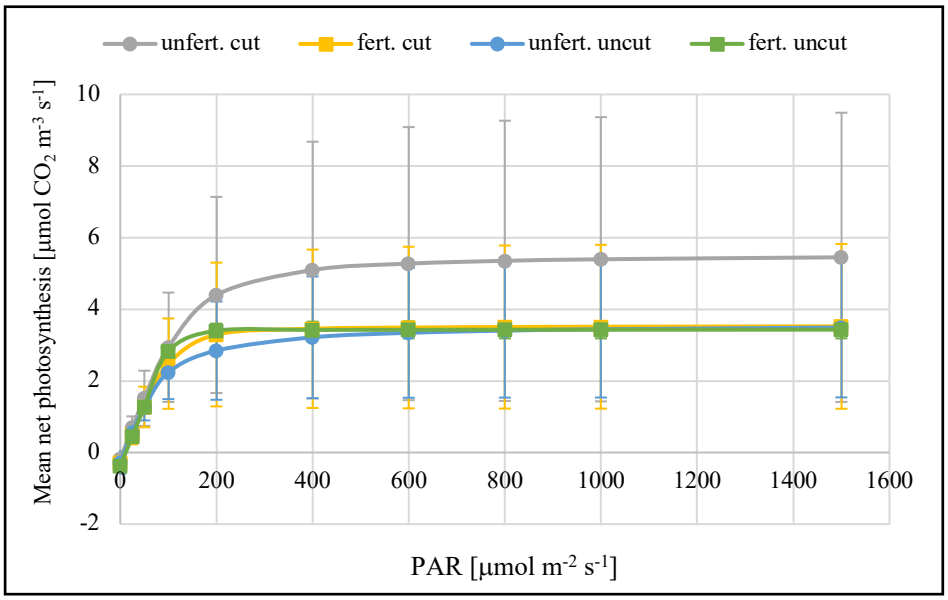

Figure 5b: Mean estimated photosynthesis curves of ***P. arundinacea*** in August ± 1 SD. PAR = photosynthetically active radiation; unfert = unfertilized; fert = fertilized (300 kg NPK * ha^{-1}).

Both species had significantly greater photosynthesis rates, measured as P_{max}, in July compared to August ($p < 0.001$). However, only *C. canescens* showed a positive fertilization effect. Between species no significant difference could be found.

4.4 Chlorophyll Fluorescence

The average quantum yield of PSII (Phi2), PhiNO, which tells the ratio of incoming light that is lost in non-regulated processes and PhiNPQ, the ratio of incoming light that goes towards non-photochemical quenching, all significantly differed between fertilized and unfertilized *P. arundinacea* ($p < 0.001$; Figure 6a).

Besides nutrition, cutting also influenced Phi2. Cut fertilized plants showed a significantly higher Phi2 of 70% than uncut fertilized plants, which had a Phi2 of 62% ($p < 0.001$). Unfertilized *P. arundinacea* did not show a significant difference between cut and uncut.

Cutting also significantly influenced PhiNPQ, especially between fertilized cut and uncut plants ($p = 0.006$). PhiNPQ was the highest (43%) for uncut unfertilized plants (Figure 6a).

Equation 3 was applied and is true for all treatments except the uncut and unfertilized treatment. This discrepancy may be partly caused by rounding errors.

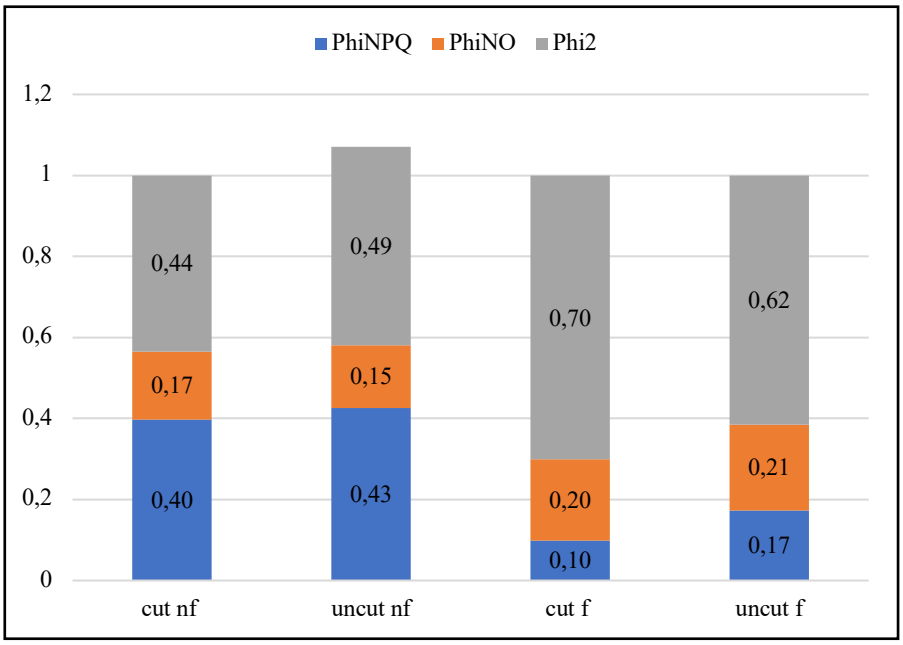

Figure 6a: The sum of PhiNPQ, PhiNO and Phi2 of all treatments is visualized here. Equation 3 applies to all treatments except uncut and unfertilized *P. arundinacea*. nf = unfertilized, f = fertilized (300 kgNPK * ha^{-1}).

When plotting Phi2 against the time of day it can be observed that Phi2 is higher when measured later in the day (Figure 6b). Therefore, the cut and fertilized *P. arundinacea* show the highest (0.71 PAR) and cut unfertilized *P. arundinacea* show the lowest (0.23 PAR) values of Phi2.

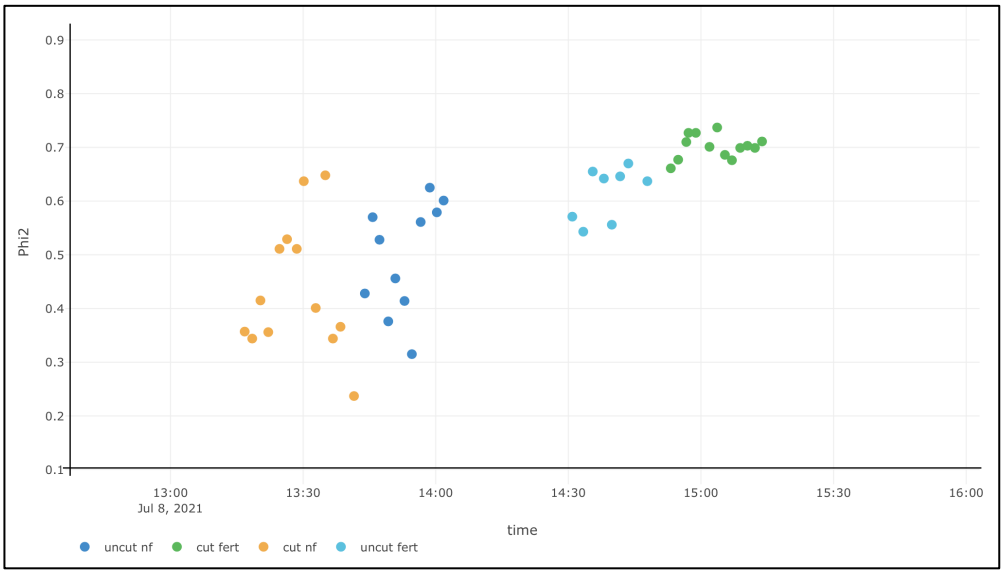

Figure 6b: The correlation between time and Phi2 are shown here. This figure indicates that the plants undergo midday depression because the ones that were measured sooner show smaller values in Phi2 than the ones which were measured later in the afternoon. Treatments: nf = unfertilized; fert = fertilized (300 kgNPK * ha^{-1}).

The temperature at the time of measuring was higher at the beginning of the measurement period when cut unfertilized and uncut unfertilized plants were measured. At 2:30 pm the temperature started decreasing, which resulted in increased values of Phi2 (Figure 6b, c).

A nested ANOVA was performed in R which proved that the only factor affecting Phi2 was the time of measurement ($p > 0.001$).

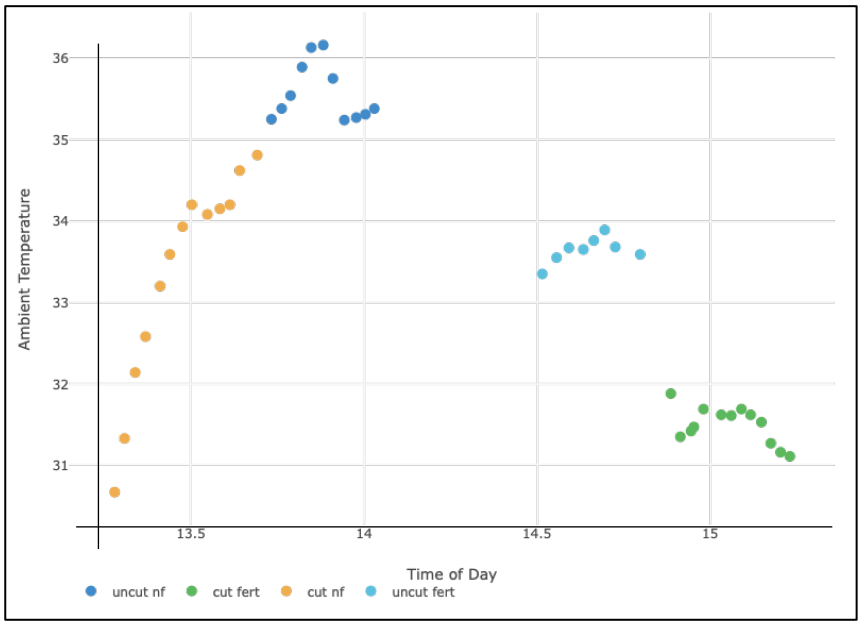

Figure 6c: The change of temperature over the measurement period. The temperature was lower for the plants which were measured later in the afternoon. Treatments: nf = unfertilized; fert = fertilized (300 kgNPK * ha^{-1}).

Phi2 and PhiNPQ were negatively correlated (Figure 6d), which would be expected based on equation 3. However, the different treatment groups, except cut and fertilized, are distributed all over the graph, which indicates that the treatments may not have the expected impact on chlorophyll fluorescence.

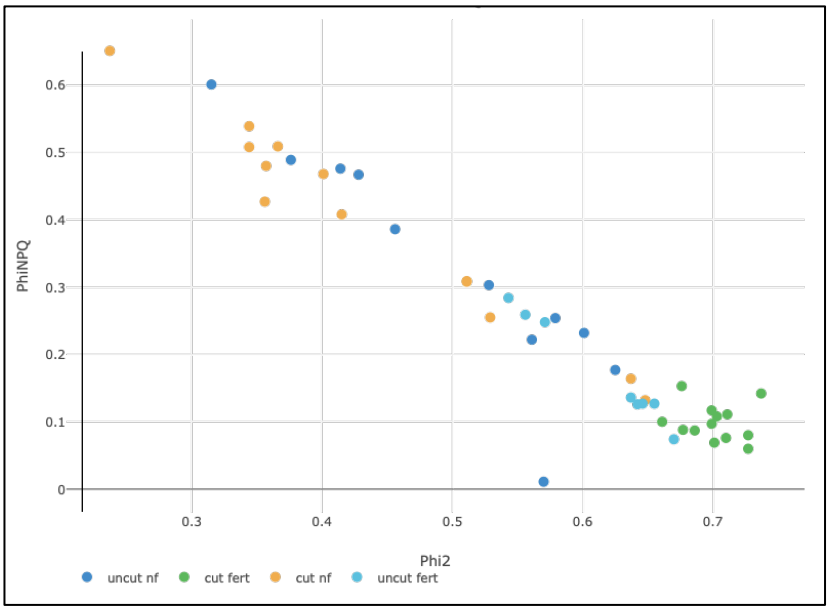

Figure 6d: The correlation between Phi2 and PhiNPQ shows a negative linear relationship. Treatments: nf = unfertilized; fert = fertilized (300 kgNPK * ha^{-1}).

5. Discussion

The effect of two different nutrient and cutting conditions were investigated on *C. canescens* and *P. arundinacea* plants.

When comparing the height and the stem number of both species, *C. canescens* kept their height almost constant while producing new shoots continuously, whereas *P. arundinacea* showed the opposite trend. The height of *P. arundinacea* plants increased steadily while the number of new shoots decreased over time.

All plants experienced a major die-back in count number 3. This may have been the result of heavy hailstorms over the Czech Republic during summer 2021. However, fertilized *C. canescens* managed to recover best because they showed the highest difference of new shoots between count 3 and 4 whereas *P. arundinacea* showed a significantly lower difference. This is not in agreement with (Stiles et al., 2008) who found that *P. arundinacea* has the ability to grow back rapidly after disturbance like thunder or hailstorms. In natural wetlands, such an event would give other species a perfect opportunity to sprout and even replace *P. arundinacea* (Kaplova 2011).

A steady increase of new shoots regardless of the fertilization treatment, and a constant height, indicates that *C. canescens* expands horizontally and *P. arundinacea* vertically, which is in

accordance with their PFT. A prominent competition mechanism of *P. arundinacea* is the growth of high stems to outcompete other species and gain more sunlight (Zedler & Kercher, 2005). Additionally, conservative plants such as *C. canescens* can tolerate stress better than competitive ones and accommodate well to changes in nutrient availability (Colesie et al., 2020). When Edwards and Čížková (2020) performed a similar experiment with one competitive species (*G. maxima*) and one conservative species (*C. acuta*) they found similar results as in our experiment: They expected the growth of the conservative species to be favoured under nutrient poor conditions whereas the addition of nutrients would lead to an increase in growth of the competitive species. However, this hypothesis was only partially confirmed. In our experiment, fertilized *C. canescens* showed a significantly higher total shoot number than unfertilized ones, which is in agreement with our hypothesis two.

Considering only the fertilization treatments and not the cutting, fertilized plants generally show higher photosynthetic rates, which supports hypothesis one. This is in agreement with Evans (1989) who states that photosynthesis is related to nitrogen content because the majority of leaf nitrogen is represented by proteins of the Calvin cycle and thylakoids. Additionally, there are strong linear relationships between both RuBP carboxylase and chlorophyll and nitrogen content (Field and Mooney, 1986).

When comparing the light response curves of all treatment groups of both species in both months, fertilized and cut *P. arundinacea* had the highest value for P_{max} and the greatest light response curve followed by fertilized and uncut *P. arundinacea* plants. Also fertilized and cut *C. canescens* showed a higher net photosynthesis rate than fertilized uncut *C. canescens* plants. This indicates that cutting had a positive influence on the net photosynthesis rate in July, but in August the plants did not follow the same pattern. Thus, this only partially supports hypothesis three. Looking at figure 5b, one can see that the light response curves do not follow the expected Michaelis-Menten - like plot but show something completely different. This may be a result of *P. arundinacea* being already at the end of their growing period which means that nutrients have already been transported to the belowground storage tissue (Aerts et al., 1991). This is also in agreement with the belowground DW of all *P. arundinacea* groups in August. It is significantly greater than the belowground DW of *P. arundinacea* in July. Alternatively, the decrease at higher light levels in *P. arundinacea* could indicate that the plants undergo photoinhibition (see appendix figure 23-32; Huang et al., 2015).

Figure 6a shows the photosynthetic regulation which, according to equation 1, should be 1. However, this was not the case for unfertilized uncut *P. arundinacea*. An explanation for this could be rounding errors or the loss of data during the import from the smartphone app to the website. As this does not seem to be an issue caused by the plants itself, it will not be further discussed.

During the chlorophyll fluorescence measurement, the time of the day was not considered, which may be of importance now because figure 6b shows an increase of Phi2 as the afternoon progresses. The measurement was started at around 1:30 pm where the values for Phi2 were relatively low and constant for both uncut unfertilized and cut unfertilized plants. It seems that neither the fertilization nor the cutting treatment had an influence on Phi2. This indicates that the plants undergo midday depression. According to Xu (2005 in Pessarakli, 2005) the photosynthesis rate and therefore Phi2 increase after midday in the early afternoon which applies to our results. Fu et al. (2011) found similar results when comparing the net photosynthetic rate of *P. arundinacea* with the time of measurement. Around 1 p.m. the net photosynthetic rate decreased significantly. To improve further experiments, a more precise planning of the measurements would be necessary. Either randomizing the order in which the measurements are taken or measuring more plants at the same time with more MulitspeQ-apparatuses would produce more accurate results. Another way of improving the next experiment could also be starting way earlier in the day than we did so the measurements are finished before any midday depression could interfere with the results.

A long-term study would be necessary to sufficiently prove this theory and for understanding plant dynamics (Green and Galatowitsch, 2002).

6. Conclusion

The results of our study showed the following:

1. In agreement with the first hypothesis, fertilization had a significant effect on both photosynthesis and biomass production. In July, fertilized plants of both species showed significantly higher net photosynthesis rates as well as a higher number of new shoots and plant height.
2. Both species showed a positive fertilization effect, however, the effect was more noticeable in *C. canescens*, the conservative species. This agrees with hypothesis two.
3. Our results only partially confirm hypothesis three, because a positive cutting effect on the net photosynthesis could only be observed in July for both species. In August *P. arundinacea* showed parabolic net photosynthesis curves, which are an indicator of photoinhibition at higher light levels. Additionally, we did not consider midday depression during our chlorophyll measurements, so we could neither confirm nor reject the hypothesis, that cutting may increase the chlorophyll content in newly grown leaves.

For future experiments like this, one has to consider randomization of samples even more than we did. Figure 6b shows clearly that the measurements were taken for each treatment at a time, which makes it very difficult to see if there was a treatment or a time effect. However, the time of the measurement and resulting consequences such as midday depression were not considered.

To fully understand the mechanisms and to conceal small mistakes that were made, a long-term study would be necessary.

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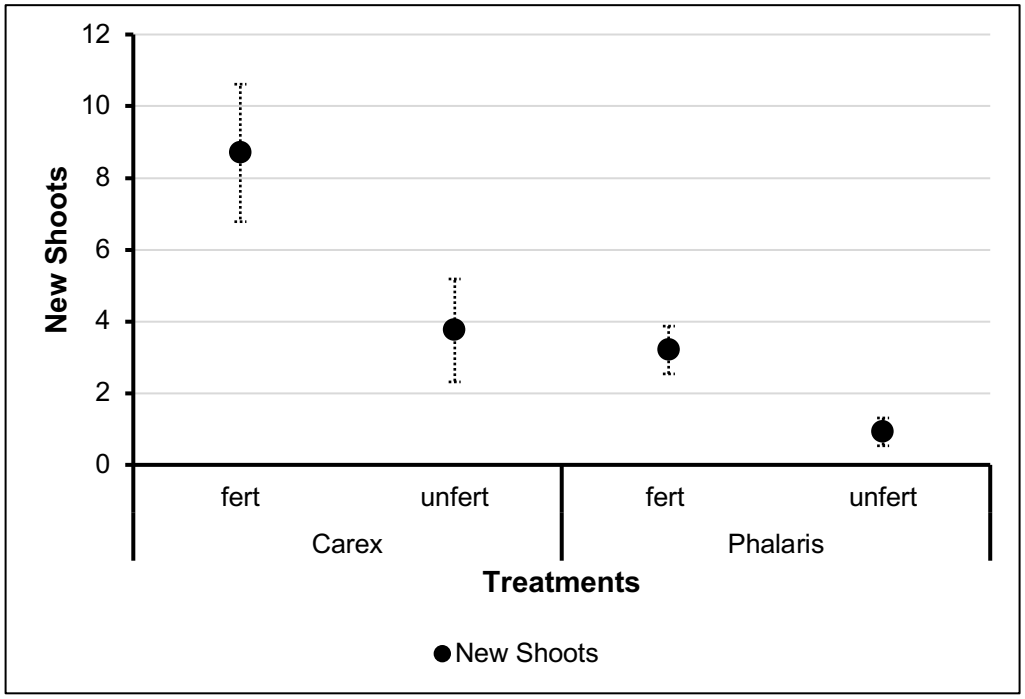
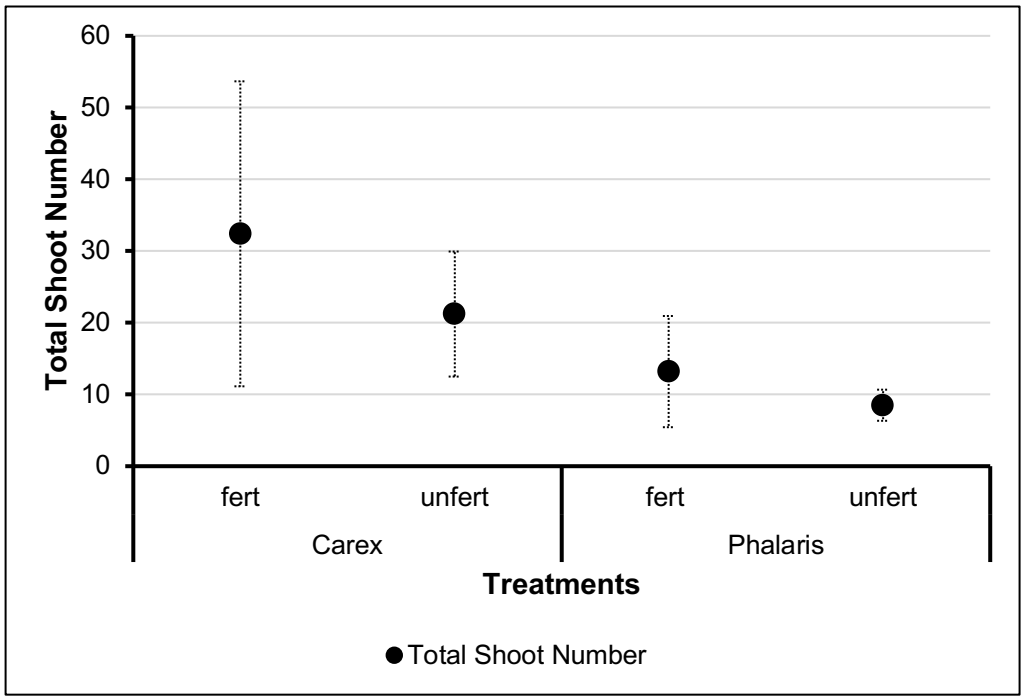
4. Appendix

a. Number of stems and plant height



Appendix 1: Change of number of new shoots over time (mean ± 1 SD).

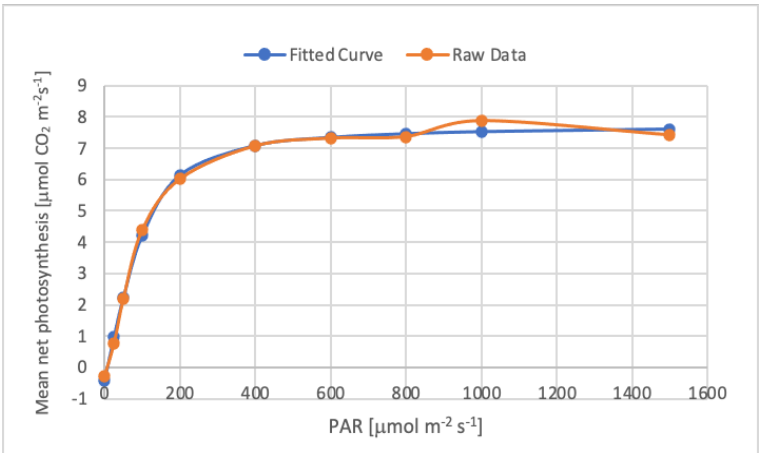


Appendix 2: The mean total shoot number of all species and treatments is represented ± 1 SD.

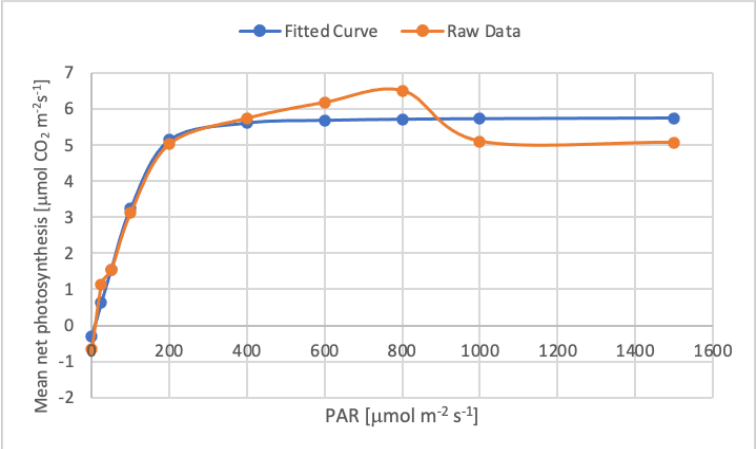
b. Photosynthesis Capacity

The following figures (Appendix 3 – 32) represent the individual fitted photosynthesis curves, which was made using Excel's solver function and the raw data, which comes directly from the LI-COR apparatus. For unfertilized plants the blue line represents the fitted curve and the orange line the raw data. Fertilized plants have an orange coloured fitted curve and the raw data is presented in yellow.

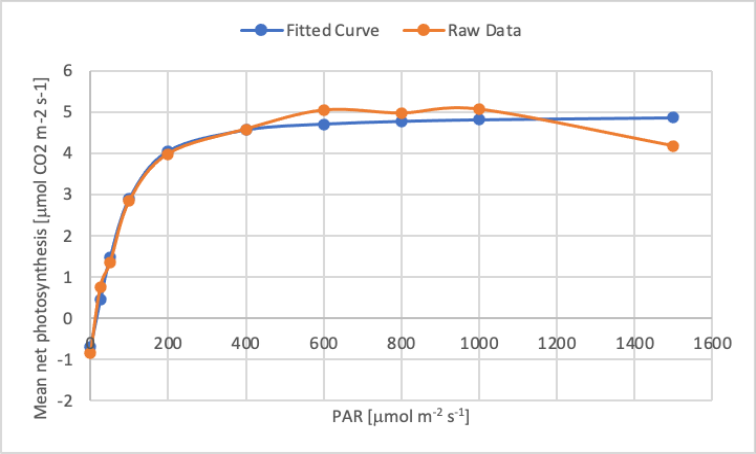
i. Photosynthesis Measurements in July



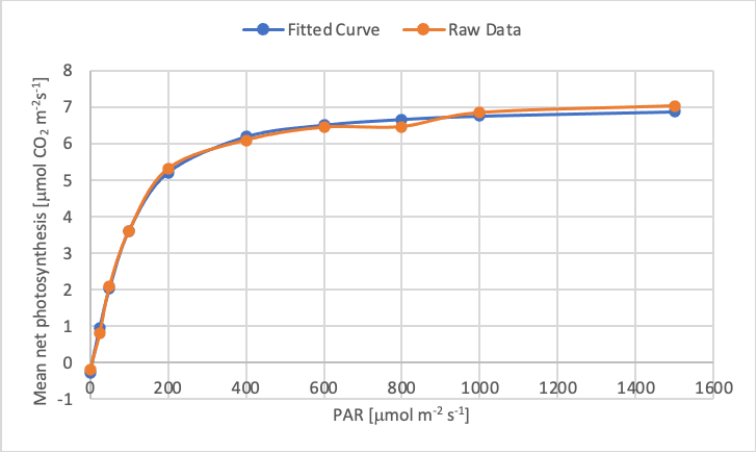
Appendix 3: *C. Canescens* No. 20: cut, unfert.



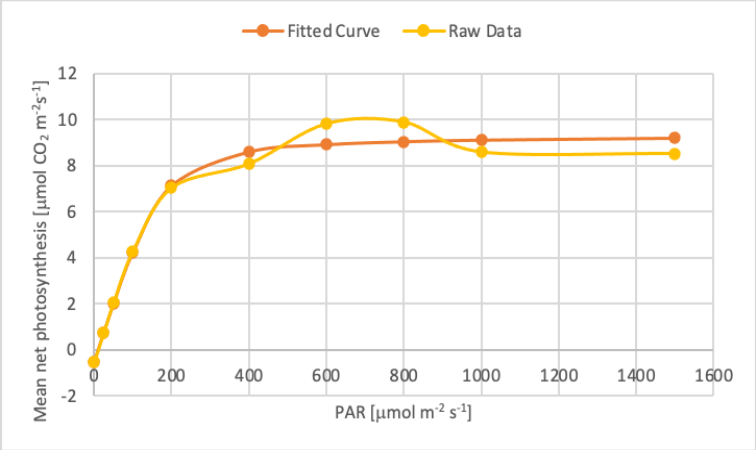
Appendix 4: *C. Canescens* No. 7: cut, unfert.



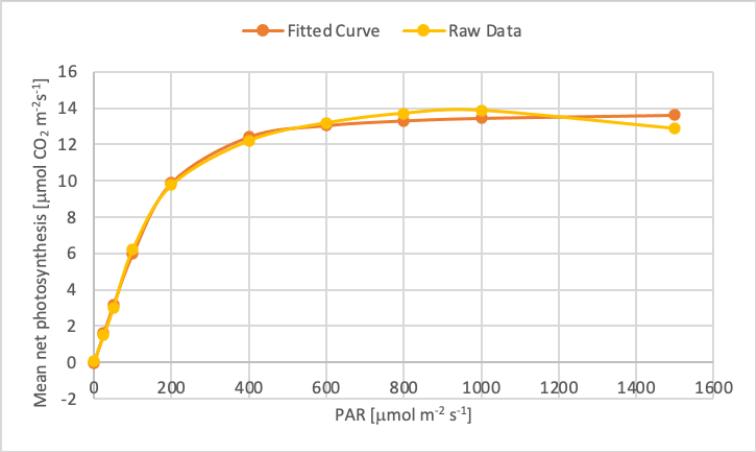
Appendix 5: *C. canescens* No. 11: cut unfert.



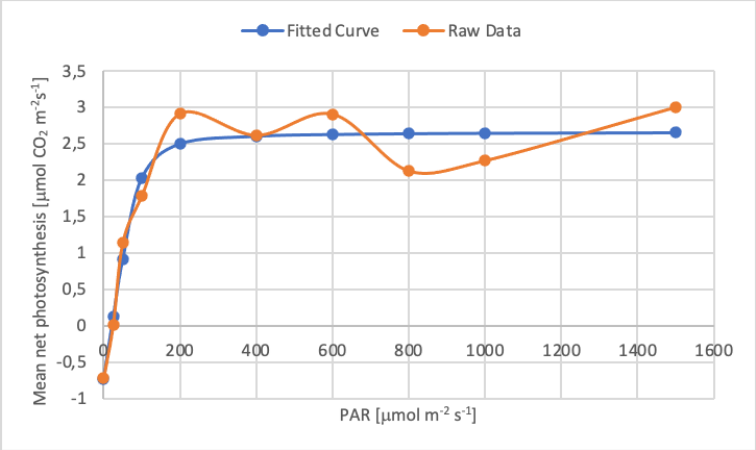
Appendix 6: *C. canescens* No. 18: cut, unfert.



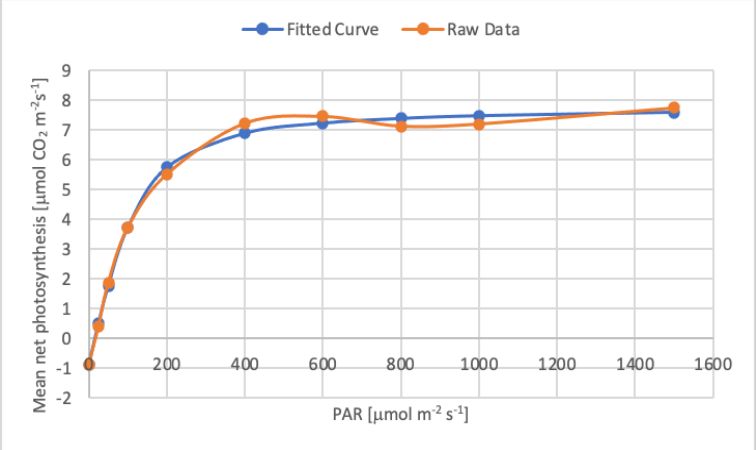
Appendix 7: *C. canescens* No. 82: uncut, unfert.



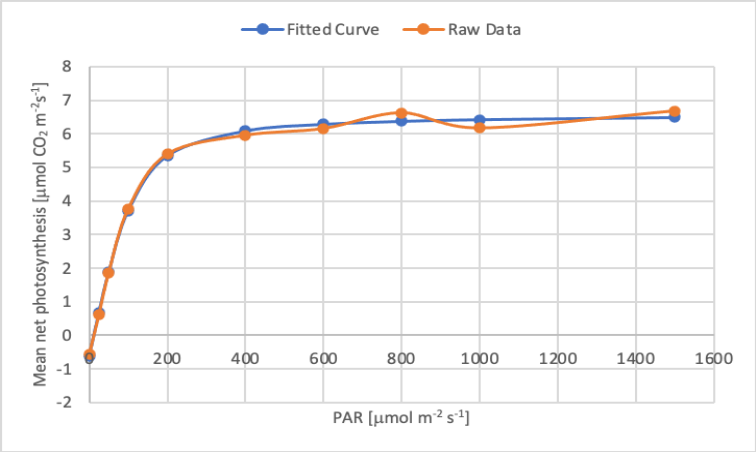
Appendix 8: *C. canescens* No. 87: cut, unfert.



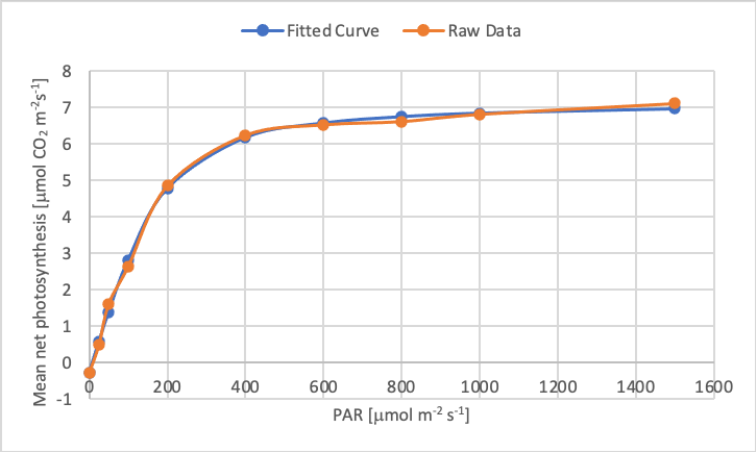
Appendix 9: *P. arundinacea* No. 47: cut, unfert.



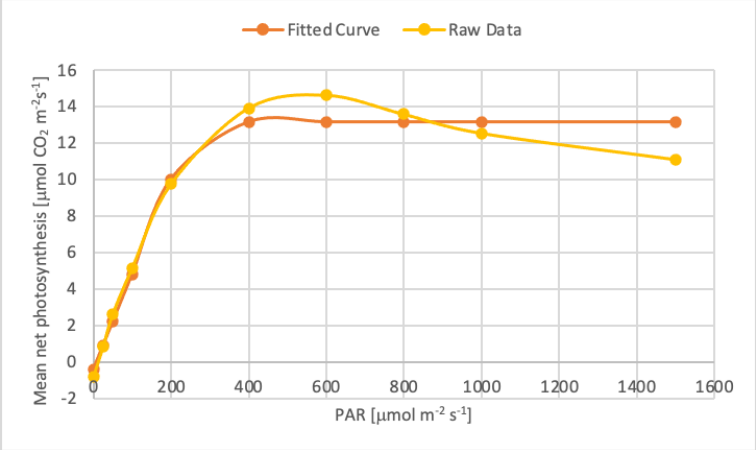
Appendix 10: *P. arundinacea* No. 59: cut, unfert.



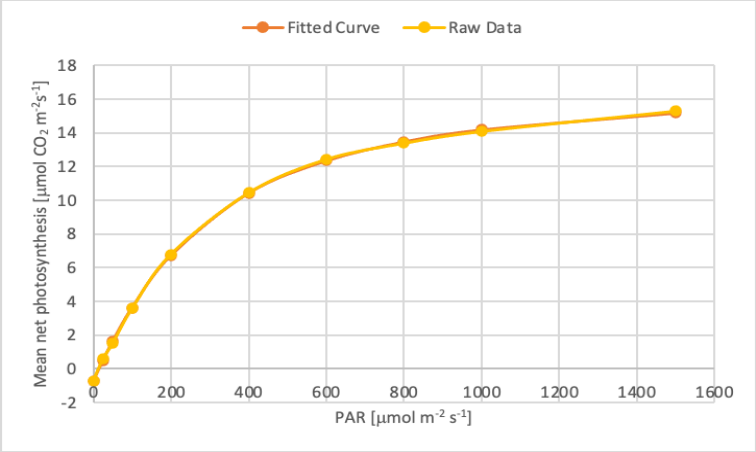
Appendix 11: *P. arundinacea* No. 47: uncut, unfert.



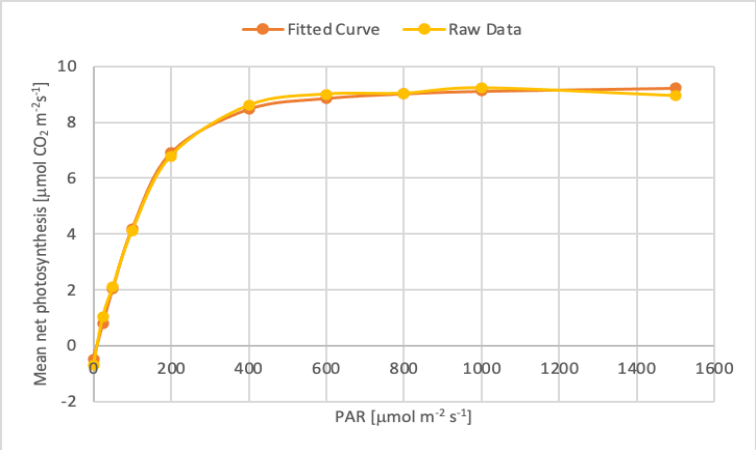
Appendix 12: *P. arundinacea* No. 50: uncut, unfert.



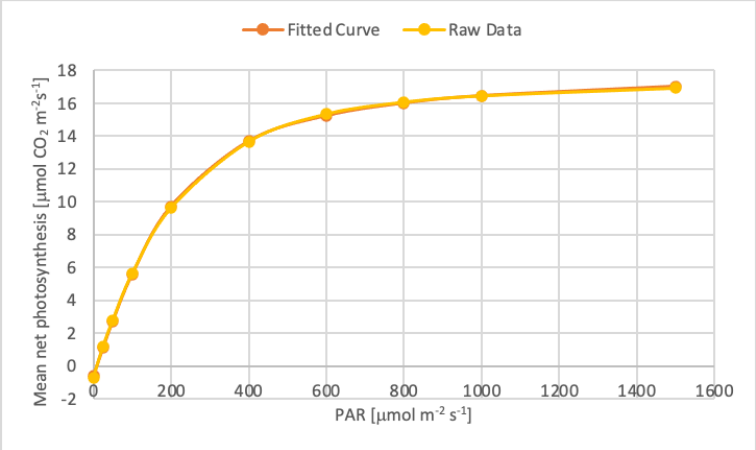
Appendix 13: *P. arundinacea* No. 113: cut, fert.



Appendix 14: *P. arundinacea* No. 132: cut, fert.

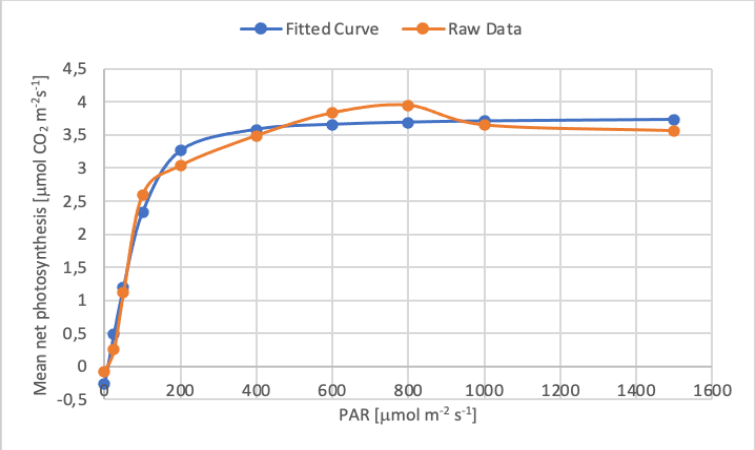


Appendix 15: *P. arundinacea* No. 120: uncut, fert.

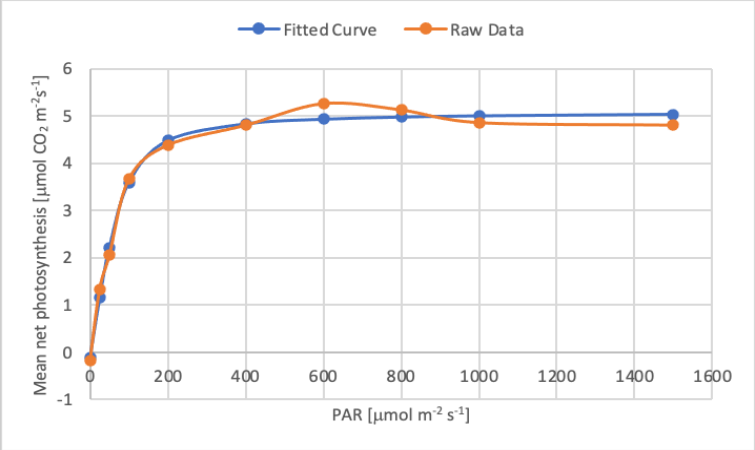


Appendix 16: *P. arundinacea* No. 128: uncut, fert.

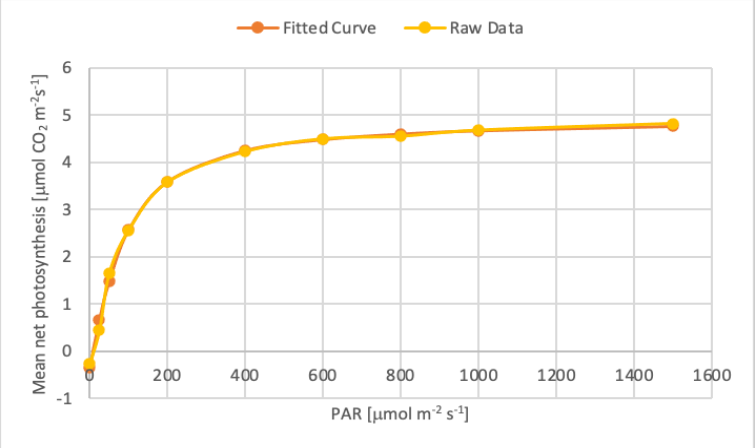
ii. Photosynthesis in August



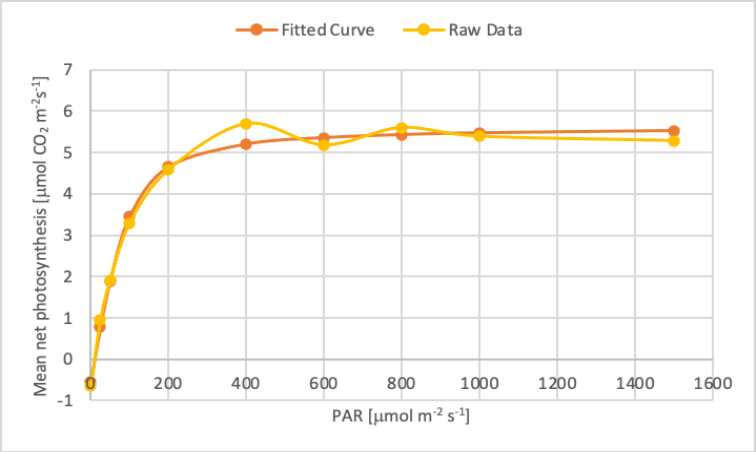
Appendix 17: *C. canescens* No. 23: cut, unfert.



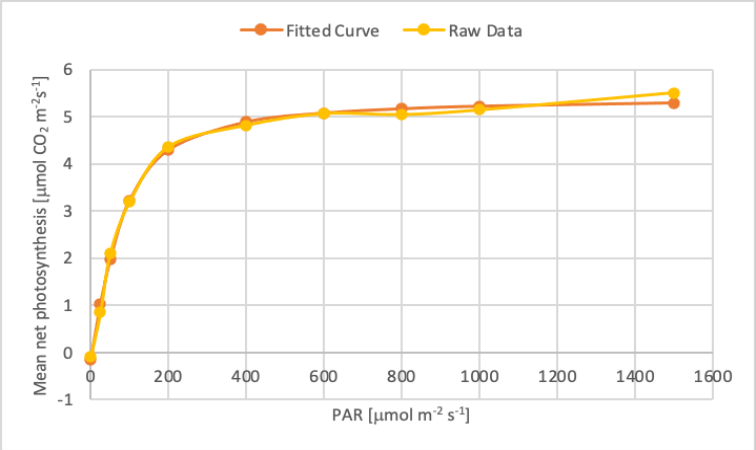
Appendix 18: *C. canescens* No. 19: uncut, unfert.



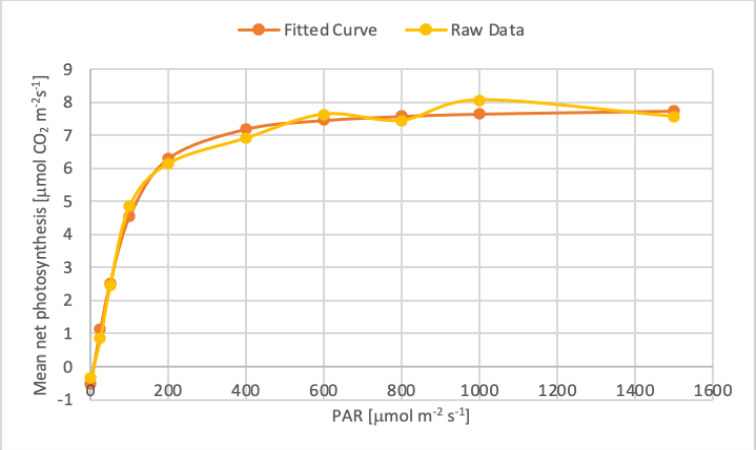
Appendix 19: *C. canescens* No. 86: cut, fert.



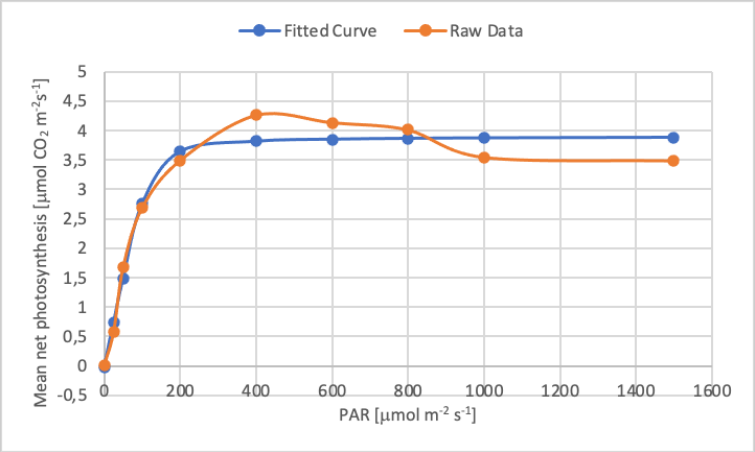
Appendix 20: *C. canescens* No. 91: cut, fert.



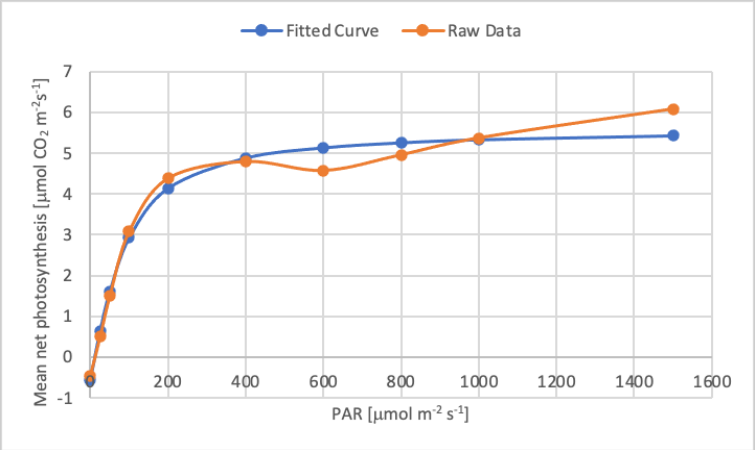
Appendix 21: *C. canescens* No. 92: uncut, unfert.



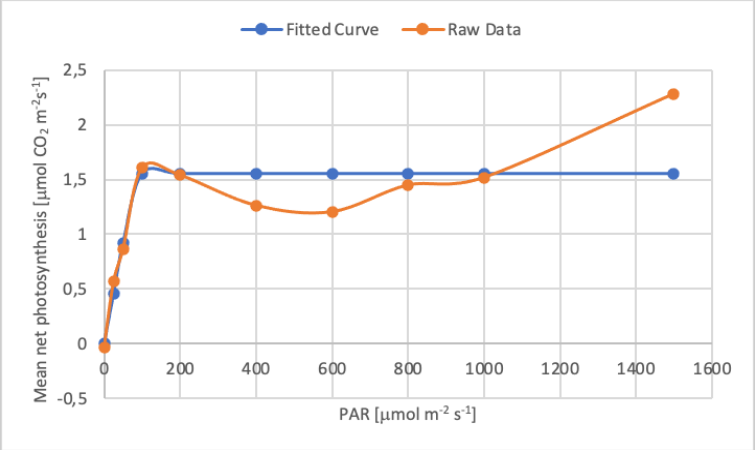
Appendix 22: *C. canescens* No. 79: uncut, fert.



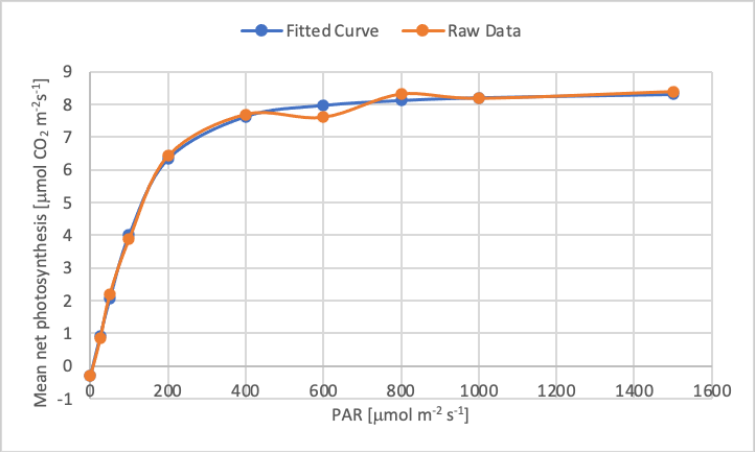
Appendix 23: *P. arundinacea* No. 45: uncut, unfert.



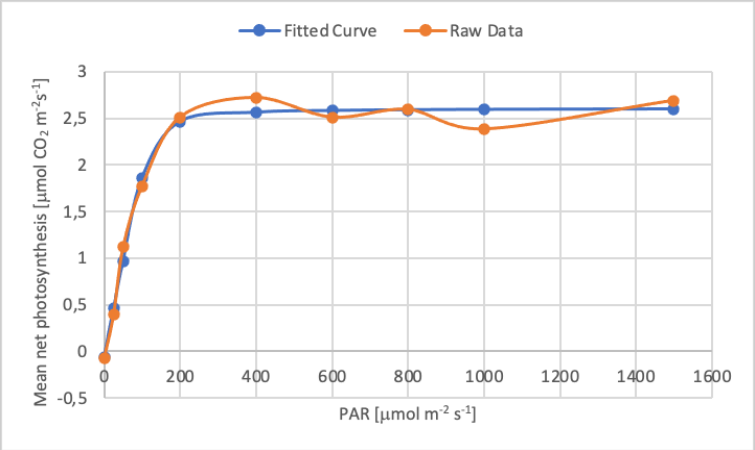
Appendix 24: *P. arundinacea* No. 49: uncut, unfert.



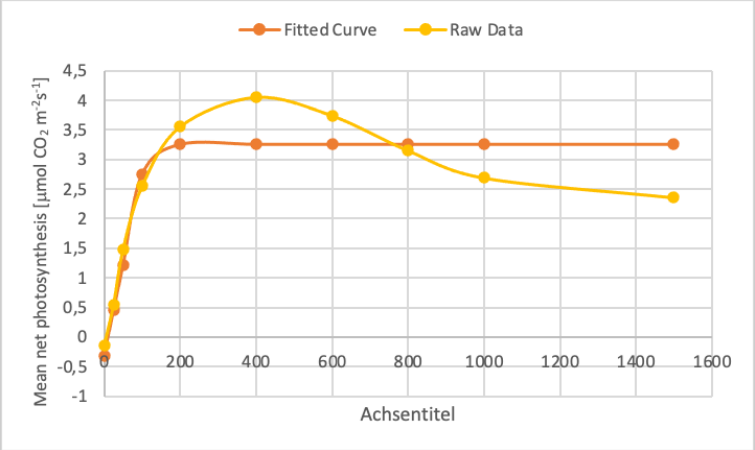
Appendix 25: *P. arundinacea* No. 51: uncut, unfert.



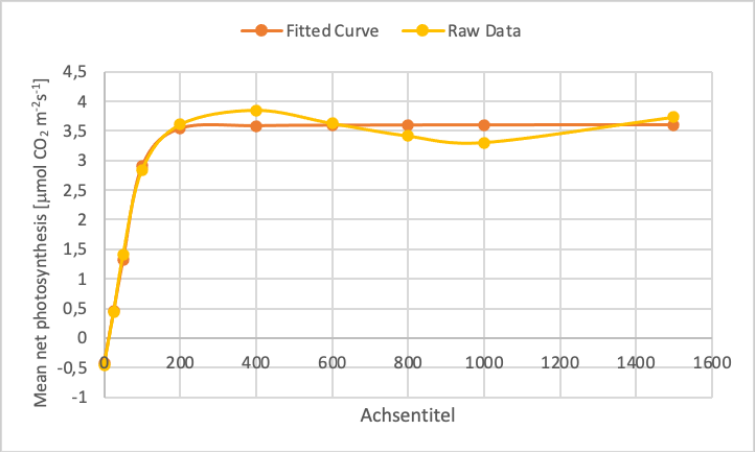
Appendix 26: *P. arundinacea* No. 45: cut, unfert.



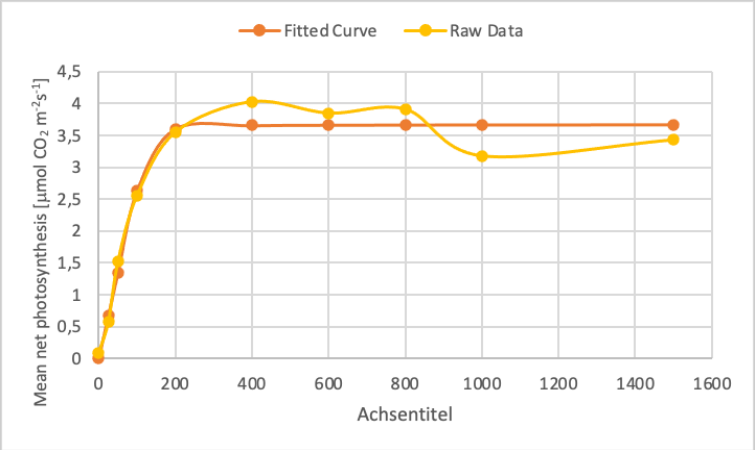
Appendix 27: *P. arundinacea* No. 47: cut, unfert.



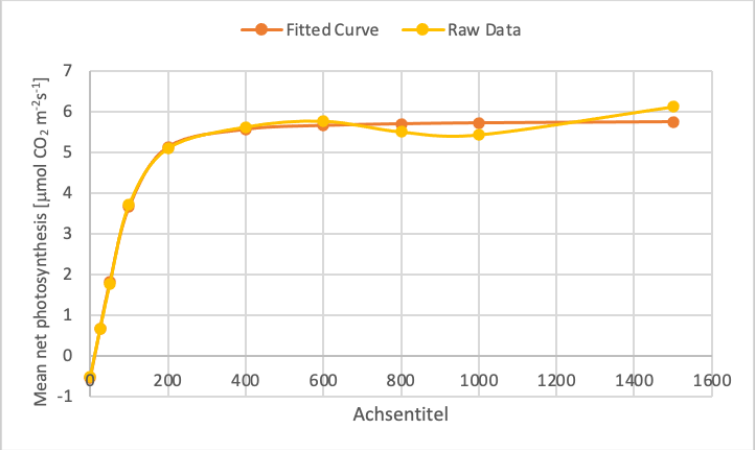
Appendix 28: *P. arundinacea* No. 124: uncut, fert.



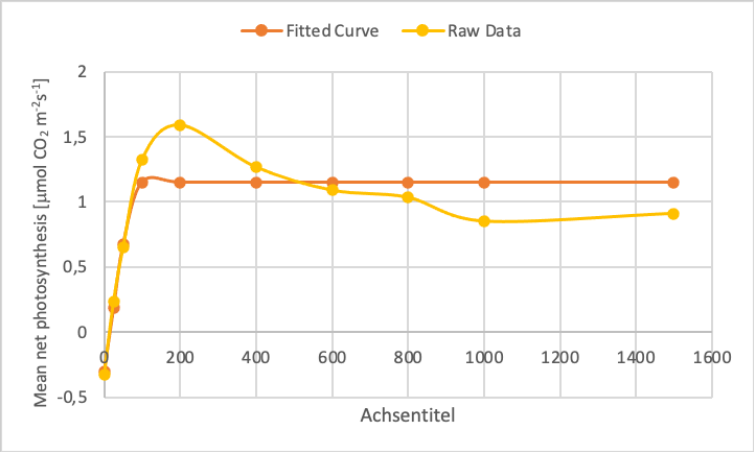
Appendix 29: *P. arundinacea* No. 140: uncut, fert.



Appendix 30: *P. arundinacea* No. 127: cut, fert.



Appendix 31: *P. arundinacea* No. 136: cut, fert.



Appendix 32: *P. arundinacea* No. 137: cut, fert.