**Dissertationes Forestales 162**

# Seasonal response of biomass growth and allocation of a boreal bioenergy crop (*Phalaris arundinacea* L.) to climate change

Chao Zhang

School of Forest Sciences
Faculty of Science and Forestry
University of Eastern Finland

## Academic dissertation

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*Author*: Chao Zhang

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*Thesis supervisors:*
Professor Seppo Kellomäki (main supervisor)
School of Forest Sciences, University of Eastern Finland, Finland
Professor Kaiyun Wang (co-supervisor)
School of Forest Sciences, University of Eastern Finland, Finland

*Pre-examiners:*
Prof. Ülo Mander
Institute of Ecology and Earth Sciences, University of Tartu, Estonia
Prof. Katrin Heinsoo
Institute of Agricultural and Environmental Sciences, Estonian University of Life Sciences, Estonia

*Opponent:*
Prof. Bjarni Diðrik Sigurðsson
Faculty of Environment, Agricultural University of Iceland, Iceland

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# ABSTRACT

The aim of this work was to analyse how the seasonal biomass growth and allocation in a boreal bioenergy crop (*Phalaris arundinacea* L., hereafter RCG) were affected by elevated temperature and $CO_2$ under different levels of groundwater. For this purpose, plants in peat monoliths representing young and old cultivations were grown in auto-controlled environmental chambers over two growing seasons (April-September, 2009 and 2010) under elevated temperature (ambient + 3.5°C) and $CO_2$ (700 µmol mol$^{-1}$) (CON: ambient conditions, EC: elevated $CO_2$, ET: elevated temperature, ETC: elevated temperature and $CO_2$). Three levels of groundwater, ranging from high (HW, 0 cm below the soil surface), to normal (NW, 20 cm below the soil surface) and low (LW, 40 cm below the soil surface), were used.

Compared to growth under CON, ET enhanced leaf development and photosynthesis in the RCG plant. Consequently, ET enhanced biomass growth during early growing periods. It also reduced photosynthesis and caused earlier leaf senescence during later growing periods. ET therefore reduced total biomass growth across the entire growing season. EC significantly increased biomass growth throughout the growing period primarily because of increased leaf area and photosynthesis. LW decreased the growth of RCG, mainly because of lower leaf area and photosynthesis. Furthermore, LW accelerated the cessation of growth, thus making the growing season shorter compared with the effects of higher groundwater levels. The LW-induced reductions in biomass growth were exacerbated by ET and partially mitigated by EC. The ETC slightly increased final plant growth. The age of cultivation did not affect the biomass growth among the three major organs (leaf, stem and root) and thus did not affect total biomass growth.

Biomass growth was mainly allocated to leaves (LMF) and stems (SMF) in the early growing season, to stems in the middle of the growing season and to roots (RMF) later in the growing season. Compared to CON, ET and ETC increased LMF and SMF, and decreased RMF over the whole growing season under NW and HW. Under LW, ET and ETC decreased LMF and increased RMF throughout the growing season, and increased SMF in early periods and then decreased later in the growing season. EC decreased the LMF and SMF and increased the RMF over the growing season but did not significantly affect the seasonal biomass allocation pattern between plant organs. The LMF was higher and the RMF was lower throughout the growing season in response to the higher groundwater level, while the effect of groundwater level on the SMF depended on the developmental phase of the plants. Our results show that climatic treatments affected biomass growth and biomass allocation to each of the three plant organs, while the direction and extent of climate-related changes in biomass growth and allocation depended on the availability of groundwater. The influence of groundwater level appeared to be crucial for the carbon gain regarding the production of RCG biomass for energy purposes and the concurrent sequestration of carbon in soils under changing climates in the mire sites used to cultivate RCG.

**Keywords:** $CO_2$, temperature, water regimes, age of cultivation, biomass growth, biomass allocation, *Phalaris arundinacea* L.

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Joensuu, March 2013

Chao Zhang

# LIST OF ORIGINAL ARTICLES

The thesis is a summary of the following papers referred to in the text with Roman numbers. Papers I, III and IV are reprinted with the kind permission of the publishers, while Paper II is the author's version of a submitted manuscript.

I Ge, Z.M., Zhou, X., Kellomäki, S., Zhang, C., Peltola, H. & Wang, K.Y. 2012. Acclimation of photosynthesis in a boreal grass (*Phalaris arundinacea* L.) under different temperature, $CO_2$, and soil water regimes. Photosynthetic, 50(1): 141-151. doi: 10.1007/s11099-012-0014-x

II Zhang, C., Kellomäki, S., Wang, K.Y., Gong, J.N., Qiao, Y.Z. & Zhou, X. 2013. Seasonal biomass allocation in a boreal bioenergy crop (*Phalaris arundinacea* L.) under elevated temperature and $CO_2$ with varying groundwater levels- a model approach. Manuscript.

III Zhang, C., Ge, Z.M., Kellomäki, S., Wang, K.Y., Gong, J.N. & Zhou, X. 2013. Effects of elevated $CO_2$ and temperature on biomass growth and allocation in a boreal bioenergy crop (*Phalaris arundinacea* L.) from young and old cultivations. BioEnergy Research, 6(2): 651-662. doi: 10.1007/s12155-012-9283-2

IV Zhang, C., Kellomäki, S., Gong, J.N., Wang, K.Y., Ge, Z.M., Zhou, X. & Strandman, H. 2013. Impacts of elevated temperature and $CO_2$ with varying groundwater levels on seasonality of height and biomass growth of a boreal bioenergy crop (*Phalaris arundinacea*) - a modeling study. Botany, 91(4): 260-272. doi: 10.1139/cjb-2012-0188

Chao Zhang was primarily responsible for the work performed in Papers II, III and IV. The co-authors participated in the experiment design, chamber experiments and manuscript comments. In Paper I, Chao Zhang made a large contribution to the chamber measurements and commentary for the manuscript.

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# ABBREVIATIONS

| **Symbol** | **Unit** | **Description** |
|---|---|---|
| CON | / | Ambient temperature and $CO_2$ |
| ET | / | Elevated temperature |
| EC | / | Elevated $CO_2$ |
| ETC | / | Elevated temperature and $CO_2$ |
| HW | cm | High groundwater level |
| NW or MW | cm | Normal or Medium groundwater level |
| LW | cm | Low groundwater level |
| (Period) I–VII | / | Seven development periods over the growing season for photosynthesis and biomass growth measurements |
| GP-I, GP-II | / | Two periods for photosynthetic parameters measurements |
| $C_a$ | $\mu$mol mol$^{-1}$ | $CO_2$ concentration |
| $C_i$ | $\mu$mol mol$^{-1}$ | Intercellular $CO_2$ concentration |
| $C_c$ | $\mu$mol mol$^{-1}$ | Chloroplast $CO_2$ concentration |
| $g_s$ | mol mol$^{-1}$ | Stomatal conductance |
| $g_m$ | mol mol$^{-1}$ | Mesophyll conductance |
| $g_{sat}$ | mol mol$^{-1}$ | Light-saturated stomatal conductance |
| $\Delta H_a$ | kJ mol$^{-1}$ | Activation energy |
| $\Delta H_d$ | kJ mol$^{-1}$ | Deactivation energy |
| J | $\mu$mol m$^{-2}$ s$^{-1}$ | Rate of electron transport |
| $J_{max}$ | $\mu$mol m$^{-2}$ s$^{-1}$ | Maximum rate of electron transport |
| $K_c$ | $\mu$mol mol$^{-1}$ | Rubisco Michaelis constants for $CO_2$ |
| $K_o$ | mmol mol$^{-1}$ | Rubisco Michaelis constants for $O_2$ |
| $N_L$ | g.m$^{-2}$ | Nitrogen content based on leaf area |
| O | mmol mol$^{-1}$ | $O_2$ concentration |
| $P_n$ | $\mu$mol m$^{-2}$ s$^{-1}$ | Net photosynthetic rate |
| $P_c$ | $\mu$mol m$^{-2}$ s$^{-1}$ | Rubisco-limited rate of photosynthesis |
| $P_j$ | $\mu$mol m$^{-2}$ s$^{-1}$ | RuBP-regeneration-limited rate of photosynthesis |
| $P_{sat}$ | $\mu$mol m$^{-2}$ s$^{-1}$ | Light-saturated net photosynthetic rate |
| PPFD | $\mu$mol m$^{-2}$ s$^{-1}$ | Photosynthetic photon flux densities |
| R | J mol$^{-1}$ K$^{-1}$ | Molar gas constant |
| RCG | / | Reed canary grass |
| $R_d$ | $\mu$mol m$^{-2}$ s$^{-1}$ | Mitochondrial respiration in light |
| $\Delta S$ | J K$^{-1}$ mol$^{-1}$ | Entropy of the desaturation equilibrium |
| $T_{opt}$ | $^{O}$C | Optimal temperature |
| $V_{cmax}$ | $\mu$mol m$^{-2}$ s$^{-1}$ | Maximum rate of carboxylation by Rubisco |
| $\alpha$ | $\mu$mol m$^{-2}$ s$^{-1}$ | Quantum efficiency |
| I* | $\mu$mol mol$^{-1}$ | $CO_2$ compensation point (absence of dark respiration) |
| $\theta$ | / | Curvature of the light response curve |
| WUE | $\mu$mol mmol$^{-1}$ | Light-saturated water use efficiency |
| VPD | kPa | Vapour pressure deficit |
| H | cm | Stem height |
| D | cm | Stem basal diameter |
| LAI | m$^{2}$ m$^{-2}$ | Leaf area index |

| | | |
|---|---|---|
| $Bio_L$ | $g\ m^{-2}$ | Leaf biomass |
| $Bio_S$ | $g\ m^{-2}$ | Stem biomass |
| $Bio_R$ | $g\ m^{-2}$ | Belowground or root biomass |
| $Bio_{Sh}$ | $g\ m^{-2}$ | Shoot biomass |
| $Bio_T$ | $g\ m^{-2}$ | Total biomass |
| $GR_L$ | $g\ m^{-2}\ d.d^{-1}$ | Growth rate of leaf biomass |
| $GR_s$ | $g\ m^{-2}\ d.d^{-1}$ | Growth rate of stem biomass |
| $GR_R$ | $g\ m^{-2}\ d.d^{-1}$ | Growth rate of root biomass |
| $GR_{sh}$ | $g\ m^{-2}\ d.d^{-1}$ | Growth rate of shoot biomass |
| $GR_t$ | $g\ m^{-2}\ d.d^{-1}$ | Growth rate of total biomass |
| SLA | $m^2\ kg^{-1}$ | Specific leaf area |
| NAR | $g\ kg^{-1} day^{-1}$ | Net assimilation rate |
| LMF | $g\ g^{-1}$ | Leaf biomass fraction |
| SMF | $g\ g^{-1}$ | Stem biomass fraction |
| RMF | $g\ g^{-1}$ | Root biomass fraction |
| RSR | $g\ g^{-1}$ | Root to shoot ratio |

# 1 INTRODUCTION

## 1.1 Background

The sequestration of carbon (C) in boreal peatlands plays an important role in the global carbon cycle (Gorham 1991, Roulet et al. 2007), whereas land use (i.e., peat extraction) for social and economic purposes eliminates the carbon sink function of such ecosystems (Waddington et al. 2001). After peat extraction, peatland may become a large and persistent source of C (Waddington et al. 2002a and b). In Finland, native strains of the perennial reed canary grass (RCG hereafter, *Phalaris arundinacea* L.) have been cultivated on peat mining sites for eco-restoration (Shurpali et al. 2009, 2013). This grass thrives in boreal conditions, and it is fairly productive and suitable for the production of energy biomass (Pahkala et al. 2008, Shurpali et al. 2009). Furthermore, this grass has the potential to sequestrate carbon on organic soils, especially in young cultivations, due to its high C transfer to belowground C pools (Xiong and Kätterer 2010). In cultivating RCG on peat mining sites, the key question is how to optimise the biomass production of RCG and to balance carbon uptake and emissions in extracted peatlands.

Until now, the studies on the success of RCG in the boreal zone have had the focus mainly on the seasonal growth and development pattern (Sahramaa 2004, Reinhardt and Galatowitsch 2005) and variations in biomass production under different biotic and abiotic factors, including cultivars (Sahramaa and Ihamäki 2003a, Heinsoo et al. 2011), age of cultivations (Xiong and Kätterer 2010), soils (Xiong and Kätterer 2010, Heinsoo et al. 2011), geographical locations (Sahramaa 2004) and varying management regimes, i.e., fertilisation (Kätterer and Andrén 1999), irrigation (Kätterer et al. 1998, Kätterer and Andrén 1999) and harvest (Landström et al. 1996, Xiong et al. 2009, Heinsoo et al. 2011). These studies have provided basic information about the optimisation of energy biomass, but they do not address uncertainties about the concurrent sequestration of C in the environment. In addition, the subjects mentioned above should be understood in the context of projected climate change (Ge et al. 2011, Zhou 2011). To date, little is known about how the biomass growth and allocation of RCG will respond to the changing growing environment (i.e., climate change).

Northern Europe is among the most vulnerable regions to climate change. Under these conditions, an increase of up to 6 °C in the annual mean temperature may occur by 2100 due to the doubling of atmospheric $CO_2$ (IPCC 2007). These increases may be accompanied by a change in the seasonal precipitation pattern, and an increase in annual precipitation may be expected in these areas. Summer drought conditions may be aggravated in some areas, however, due to enhanced evaporation (Kellomäki et al. 2005). Ge et al. (2011 and 2012a) and Zhou (2011) found that warming climate and elevated $CO_2$, alone or in combination with varying soil water regimes, modified the physiological characteristics of RCG. How seasonal biomass growth and allocation of RCG will respond to climate change alone or in combination with changing groundwater levels is still poorly understood, however. Furthermore, soil moisture is the key factor affecting the growth and development of RCG, which is adapted to high soil moisture. Consequently, effective methods of field management and groundwater level regulation for sustainable biomass production and the maintenance of a positive carbon balance are a primary focus for the future.

## 1.2 Physiological acclimation

Numerous studies have been conducted to understand the acclimated photosynthetic response of $C_3$ plants to rising temperature and $CO_2$ levels (Long et al. 2004) and water stress (Flexas et al. 2004, Hu et al. 2010). This information is needed to understand how the photosynthetic parameters of a plant respond to various growth conditions and predict carbon uptake over the growing season. The maximum rate of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) activity ($V_{\mathrm{cmax}}$) and the potential rate of electron transport ($J_{\mathrm{max}}$) are two core parameters indicating the levels of Rubisco-limited photosynthesis and RuBP-regeneration-limited photosynthesis, respectively (Sharkey et al. 2007).

The widely used biochemical photosynthesis model developed by Farquhar et al. (1980) and Farquhar and von Caemmerer (1982) allows studying the photosynthetic response of $C_3$ plants and its acclimation to elevated temperature and atmospheric $CO_2$ (Bernacchi et al. 2001). *First*, the biochemical reactions of photosynthesis may be limited by the capacity of Rubisco to consume *RuBP* called Rubisco-limited photosynthesis occurring under low supply of $CO_2$. This implies that the initial slope of the net photosynthesis response to intercellular $CO_2$ is determined by the Rubisco capacity ($V_{\mathrm{cmax}}$) (Zhou 2011). *Second*, the biochemical reactions are limited by *RuBP* regeneration rate, which was controlled by electron transport capacity ($J_{\mathrm{max}}$). Its value is estimated using the response of net photosynthesis rate to the photosynthetic photon flux density *(PFFD*) under saturating $CO_2$ (Zhou 2011). *Third*, chloroplasts can produce more triose phosphate than the leaf can consume, this is called triose phosphate use (*TPU*) limitation, but it seldom affects photosynthesis under natural conditions (von Caemmerer and Quick 2000, Sharkey et al. 2007).

Elevated $CO_2$ favours carboxylation, which leads to carbon fixation through the photosynthetic carbon reduction cycle (Morison and Lawlor 1999, Long et al. 2004). Elevated temperature shifts the specificity of Rubisco for $O_2$ relative to $CO_2$, which increases the proportion of respiration in photosynthesis (Jordan and Ogren 1984). It is generally believed that the stimulation of photosynthesis by rising $CO_2$ will increase with temperature (Long 1991). However, highly elevated temperature may inhibit carbon uptake due to the deactivation of photosynthetic enzymes (Ziska 2001, Qaderi et al. 2006), whereas this negative effect can be mitigated by elevated $CO_2$ (Cheng et al. 2009). The inhibitory effects of water shortage on photosynthesis may be associated with low $CO_2$ availability caused by limits on diffusion through the stomata and the mesophyll for photosynthesis (Flexas et al. 2004). Meanwhile water shortage shifts the optimum temperature for photosynthesis to lower temperatures, most likely as a result of biochemical impairments (Flexas et al. 2004). Nonetheless, the direction and extent of acclimation (both regulation and changes in capacity) to the elevation of temperature and $CO_2$, either alone or in combination with varying groundwater levels, has received limited attention.

## 1.3 Biomass growth responses

The individual and combined effects of elevated temperature and $CO_2$ on biomass growth have been widely studied in environmentally controlled experiments (Poorter 1993, Lee et al. 2010, Wang et al. 2012). Elevated temperature may have either a positive or negative effect on biomass growth, depending on the species, growth conditions and developmental stage (Morison and Lawlor 1999). Species with conservative growth strategies may have a limited ability to respond to a changing climate. At high latitudes and altitudes, plant species are adapted to low temperatures, but their growth is still temperature-limited. Thus, climatic warming may enhance their growth under climatic change- the opposite of warm-adapted species (Josep et al. 2007, Way and Oren 2010). Regarding herbaceous $C_3$ crops, their growth and development are often related to thermal time (Ritchie and NeSmith 1991). Rising temperature causes organ initiation to occur earlier and shortens the duration of the growing period, with an earlier cessation of growth and reduced biomass production over the whole growing season (Morison and Lawlor 1999).

In general, $CO_2$ enrichment increases biomass growth in the short term (Long et al. 2004, Wand et al. 1999, Wang et al. 2012). In the review by Poorter (1993), the growth stimulation of 156 plant species was found to be 37 % under $CO_2$ enrichment on average. Long et al. (2004) found that above-ground biomass increased 20% on average for 29 $C_3$ species grown in six different free air $CO_2$ enrichment (FACE) experiments. In studies of perennial grasses such as *ryegrass* (van Ginkel and Gorissen 1998, Casella and Soussana 1997) and *Holcus lanatus* (Jongen and Jones 1998), a doubling of the ambient $CO_2$ concentration resulted in a 28 to 36% stimulation of plant growth. However, the long-term response of plant biomass growth exposed to elevated $CO_2$ has been found to vary among species (Makino and Tadahiko 1999). Prolonged exposure to $CO_2$ enrichment reduced the initial stimulation of photosynthesis in many species and frequently suppressed photosynthesis (Makino and Tadahiko 1999). Mohan et al. (2006) found, in a study performed in Duke FACE, that $CO_2$ enrichment did not increase rates of sample biomass accumulation over 6 years for most species. Liberloo et al. (2007), however, found that photosynthetic stimulation caused by elevated $CO_2$ after 6 years of exposure in a closed-canopy poplar coppice might be sustained in the long term.

A number of papers and reviews emphasised the lack of a $CO_2$ effect on growth at low temperature. Warmer temperatures showed a larger $CO_2$ stimulation (Long 1991). Hakala and Mela (1996) reported that there was little or no yield response for swards at normal temperatures. However, when temperatures were increased by 3 °C, there was a 10 to 29% increase in sward yield under increased $CO_2$. On the other hand, high temperature had a negative effect on biomass growth, and this negative effect could be alleviated by increased $CO_2$ levels. Many studies on crop species such as RCG (Ge et al. 2011 and 2012a), rice (Cheng et al. 2009) and beans (Jifon and Wolfe 2005) have shown that temperature-induced stresses during crop growth could be partially mitigated by elevated $CO_2$.

Water shortage generally reduces biomass or yield (Çakir 2004), whereas growth patterns differ among species and their developmental phases (McMaster and Wilhelm 2003, Çakir 2004). In wheat, for example, early developmental stages showed little response to soil water availability, while such a response was clear later in the growing season (McMaster and Wilhelm 2003). In contrast, Jamieson et al. (1995) found that final biomass in barley was more sensitive to the maximum potential soil moisture deficit for early rather than late drought treatments. However, Ge et al. (2011 and 2012a) reported that water shortages clearly reduced photosynthesis and biomass accumulation in RCG over the whole growing season. Furthermore, Coops et al. (1996) found that the biomass of *Phalaris arundinacea* L. was reduced when the water depth dropped below 30 cm, while *Phragmites australis (Cav.*) Trin. Ex Steudel and *Scirpus maritimus* L. showed reduced biomass at 80 cm water depth, and *Scirpus lacustris* L. showed no biomass reduction even at 80 cm water depth. In comparison, high soil water availability favoured the biomass growth of RCG in an abandoned peatland (Shurpali et al. 2009). Busch et al. (2004) also reported that flooded conditions resulted in large increases in aboveground, root, rhizome, and total biomass in *Eleocharis cellulosa*. There are very few studies, however, concerning the interaction between climatic factors and soil water availability on biomass growth under the conditions of climate change (Ge et al. 2012a).

## 1.4 Biomass allocation responses

The biomass allocation of plants plays an important role in plant growth and is considered to be a stronger driver of the capacity of plants to take up C, water and nutrients for future use (Evans, 1972). Biomass allocation between different organs depends on the net carbon balance, ontogenetic development (i.e., the ordered initiation of meristems and determination of their vegetative or reproductive characteristics) and the expansion of meristems into organs (morphogenesis) (Morison and Lawlor 1999).

Low temperature will affect soil water status and availability (Lambers et al. 2003). Furthermore, several plant functions are impaired, including photosynthesis, nutrient uptake, and growth, and more biomass may be allocated to roots for water and nutrient uptake (Poorter et al. 2012), as is found in boreal trees (Kellomäki and Wang 2001, Vogel et al. 2008). In these conditions, warming climate may enhance the availability of soil water and nutrients (Lambers et al. 2003, Fan et al. 2009) and create favourable conditions for shoot building (i.e., leaves and stems) (Ge et al. 2012b). However, highly temperature levels have been shown to directly inhibit leaf photosynthesis and shoot growth (Ziska 2001, Xu and Zhou 2005) and to enhance the biomass allocated to roots (Lamber et al. 2003).

Most plants respond to elevated $CO_2$ by increasing photosynthesis and biomass growth, at least in short term (Long et al. 2004). Increased biomass growth is accompanied by an increased requirement for nutrients and water (Poorter and Nagel 2000, Poorter et al. 2012). In contrast, $CO_2$ enrichment generally reduces leaf nitrogen levels. Thus, it is possible that plants allocate more biomass to roots for the uptake of nutrients to sustain the increased biomass growth, which had been widely observed in grasslands and crops (see reviews by Andrews et al. 2001, Poorter and Nagel 2000, Poorter et al. 2012).

Numerous studies have examined changes in biomass allocation in relation to the availability of soil water (e.g. Coops et al. 1996, Blanch et al. 1999, Vretare et al. 2001, Edwards et al. 2003, Busch et al. 2004, Smith and Brock 2007). Under water shortage, biomass allocation may change in such a way that the proportion of water-absorbing biomass increases, while the proportion of water-loosing biomass decreases, as widely observed in grasslands and crops (Huang and Fu 2000, Poorter and Nagel 2000, Xu and Zhou 2005). Plants adapted to high soil moisture generally respond to increased water levels by increasing biomass allocation to above-ground parts while decreasing allocation to roots or below-ground parts (Coops et al. 1996, Vretare et al. 2001, Smith and Brock

2007). In addition, higher-root mortality and turnover have generally been observed (Bai et al. 2010, Poorter et al. 2012).

## 1.5 Phenological responses

Shifting plant phenology is an adaptive response of natural ecosystems to environmental changes (Cleland et al. 2006). The initiation and expansion of leaves, shoots, tillers, branches, roots, and reproductive organs are strongly driven by temperature (Morison and Lawlor 1999). Rising temperatures in recent decades are associated with acceleration in the phenological cycle (i.e., the onset, flowering and greening of the canopy) for many plant species (Parmesan and Yohe 2003, Root et al. 2003). However, this pattern is not universal; a number of species have also displayed delayed phenology in recent decades (Fitter and Fitter 2002). These phenological delays may come from sites where the environmental cues for delay are stronger than the cues for accelerated phenology or from plant species that are more sensitive to the environmental cues that lead to phenological delays (Cleland 2006).

The effects of elevated $CO_2$ on shifts in plant phenology are generally considerably smaller than the effects of warming temperature (Morison and Lawlor 1999). For example, small or no effects on vegetative and reproductive development rates have been reported for wheat (Mitchell et al. 1993, Batts et al. 1997). Regarding the effects of elevated $CO_2$ on grassland communities, flowering has been found to occur earlier in forbs and yet was delayed in grasses (Cleland et al. 2006). Furthermore, flowering in some crops was delayed by elevated $CO_2$ (Cleland et al. 2006). Similarly, the patterns of soybean flowering in response to elevated $CO_2$ were found to be highly variable with advancing and retarding both being observed (Ellis et al. 1995, Morison and Lawlor 1999). Most studies, however, show no significant effects of elevated $CO_2$ on phenology (Asshoff et al. 2006, Cleland et al. 2007). Crop species seem to respond more strongly to elevated $CO_2$ than do wild species (Jablonski et al. 2002, Asshoff et al. 2006). This is most likely because their growth is not limited by the availability of other resources such as nutrients, water and light (Cleland et al. 2007). On the other hand, plants generally respond to increased water levels by growing more slowly and producing fewer longer shoots (Richards et al. 2011). In comparison, water shortage generally reduces the crop growth rate and accelerates both reproduction and senescence (Desclaux and Roumet 1996, McMaster et al. 2011).

## 1.6 Aims of the study

The general aim of this work was to analyse how the seasonal biomass growth and allocation in a boreal bioenergy crop (*Phalaris arundinacea* L., hereafter RCG) were affected by elevated temperature and $CO_2$ under different groundwater levels. In this context, the main hypotheses to be tested were: (i) elevated temperature and $CO_2$ alone or combined will modify the biomass growth of RCG in boreal conditions compared to ambient conditions, and these modifications were related to the physiological acclimation and regulation in seasonality; (ii) plant phenology controlled the seasonal course of biomass allocation in RCG, and the below-ground biomass growth will contribute more to the total biomass growth under elevated $CO_2$ compared to the above-ground biomass, opposite to what is observed under elevated temperature; and (iii) the extent of climate-induced modification of biomass growth and allocation in RCG will depend on the levels of groundwater and age of cultivation. Consequently, the specific objectives of the study were:

I. To analyse the acclimation of RCG photosynthesis to elevated temperature and $CO_2$ climate change under varying groundwater levels **(Paper I)**.

II. To analyse the response of biomass growth and allocation in RCG to elevated temperature and $CO_2$ under varying groundwater levels **(Paper II)**.

III. To identify how the biomass growth and allocation in RCG is affected by the age (young vs. old) of cultivation under elevated temperature and $CO_2$ **(Paper III)**.

IV. To determine the seasonality of biomass growth in RCG under elevated temperature and $CO_2$ under varying groundwater levels **(Paper IV)**.

For this purpose, RCG plants in peat monoliths representing young and old cultivations were grown in an auto-controlled environment chambers over two growing seasons (April-September, 2009 and 2010) under elevated temperature (ambient + 3.5°C) and $CO_2$ (700 µmol $mol^{-1}$). Three levels of groundwater, ranging from high (0 cm below soil surface), to normal (20 cm below soil surface) and low (40 cm below soil surface) were tested. Young and old cultivations were grown with the normal groundwater level.

# 2 MATERIALS AND METHODS

## 2.1 Outlines of the work

Figure 1 shows an outline of this thesis. In Paper I, the seasonal acclimation of photosynthesis of RCG under elevated temperature and $CO_2$ and different levels of soil water moisture was studied. More specifically, the light-saturated net photosynthetic rate ($P_{sat}$), light-saturated stomatal conductance ($g_{sat}$), maximum rate of ribulose-1,5-bisphosphate carboxylase/oxygenase activity ($V_{cmax}$) and potential rate of electron transport ($J_{max}$) were studied at two different periods (early: heading, late: florescence completed) during the growing season. In Paper II, the objective was to analyse and model how biomass was allocated to each plant organ (leaf, stem and root) of RCG under elevated temperature, $CO_2$ enrichment and varying groundwater levels over the course of the growing season. In Paper III, the seasonal morphology development, biomass growth and allocation were studied from young and old cultivations of RCG under the conditions of a warming climate and $CO_2$ enrichment. In Paper IV, the seasonality of height and the concurrent accumulation of aboveground biomass of RCG under elevated temperature, $CO_2$ enrichment and varying groundwater levels were studied. More specifically, the onset and timing of peak growth rate and the cessation and duration of growth of RCG in thermal time and growing days were analysed. The outline of measurement work and calculations are also shown in Figure 1.

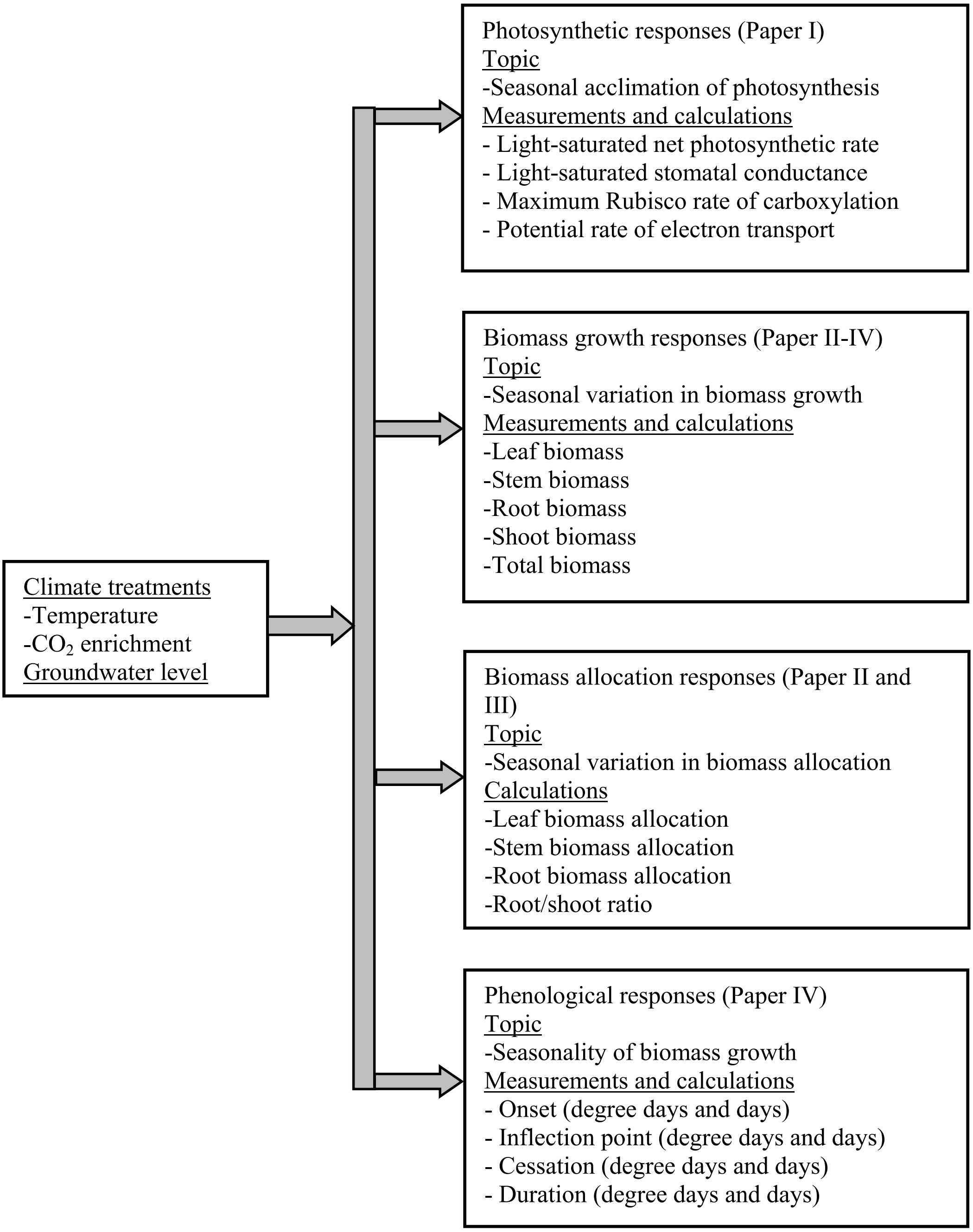

**Figure 1.** Outline of the measurement work and calculations in papers I-IV.

## 2.2 Experimental design and treatments

The experiments for this study were performed in the auto-controlled environmental chambers at the Mekrijärvi Research Station of the University of Eastern Finland (62°47′ N, 30°58′ E, 145 m asl) in the eastern part of Finland. In mid-April 2009, a total of 80 frozen peat monoliths containing intact RCG vegetation were dug up close to the research station, representing three RCG cultivations established 3, 7 and 10 years ago (local cultivar "Palaton") by the company *Vapo BioEnergy* Ltd. Before treatments were initiated, the dead aboveground mass of the previous-year crop was removed and fertiliser was applied according to established field management practices (Fig. 2 and 3).

The 16 chamber units working independently from each other were divided into four climate treatments, and each treatment was replicated four times. The treatments were as follows: ambient conditions (CON), elevated $CO_2$ (EC), elevated temperature (ET) and a combination of elevated temperature and $CO_2$ (ETC). The ambient chambers were set to follow the external free air $CO_2$ concentration and temperature. In the EC and ETC chambers, the $CO_2$ level was maintained at 700 $\mu$mol mol$^{-1}$. In the ET and ETC chambers, the temperature was elevated to 3.5 °C above the ambient temperature. The technical details, seasonal climate at the experimental site and performance of the chamber system were described in detail by Zhou et al. (2012).

Five containers in each chamber represented three different groundwater levels, including a high groundwater level (HW, 0 cm below the soil surface), to normal groundwater level (NW, 20 cm below the soil surface, roughly the same as field peatland fields) and low groundwater level (LW, 40 cm below the soil surface) (Fig. 2 and 3). The groundwater level was monitored, and water was added daily if necessary to maintain the specified groundwater level for each container.

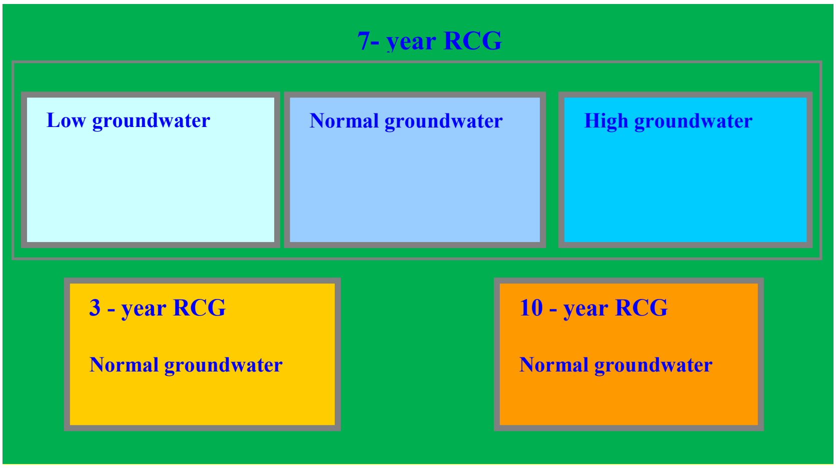

**Figure 2.** Layout of containers in each chamber.

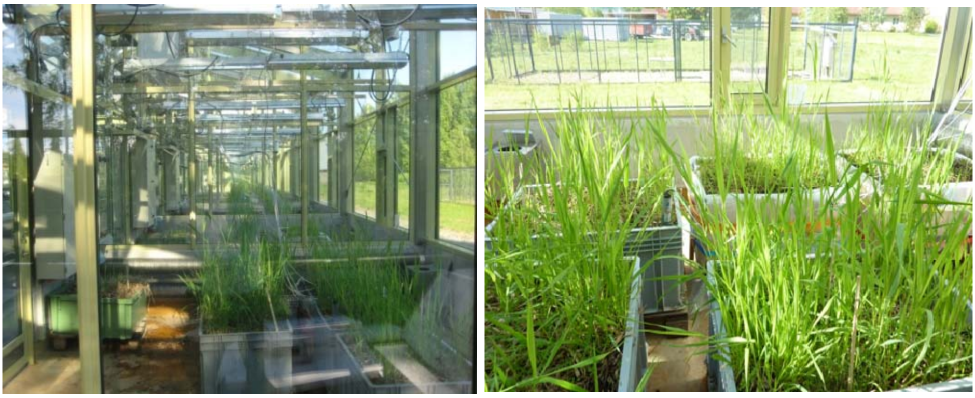

**Figure 3.** Climate chamber system used for RCG cultivation.

## 2.3 Measurements and calculations

### *2.3.1 Response of photosynthesis*

The study of the response of photosynthesis to elevated temperature and $CO_2$ under varying groundwater level was performed using a portable steady-state photosynthesis system (*Li-6400, Li-cor Inc.*, Nebraska, USA) in two phases. *First*, the measurement of the temperature response of the light-saturated net photosynthetic rate ($P_{sat}$) and light-saturated stomatal conductance ($g_{sat}$) were performed at 5 °C intervals from 5 to 30 °C for leaf temperature, under a photosynthetic photo flux density (PPFD) of 1500 μmol $m^{-2}s^{-1}$. *Second,* the carboxylation efficiency ($V_{cmax}$) and electron transport capacity ($J_{max}$) were estimated based on two sets of $P_n$ measurements, including the responses of photosynthesis to the $CO_2$ concentration in the intercellular spaces ($P_n$-$C_i$) and the photosynthetic photon flux density ($P_n$-*PPFD*). The $P_n$-$C_i$ curves were produced under a saturating *PPFD* of 1500 *μ*mol $m^{-2}$ $s^{-1}$. Similarly, the $P_n$-*PPFD* curves were produced under 1400 μmol $mol^{-1}$ $CO_2$ concentration by the stepwise reduction of the value of the *PPFD* from 1500 to 20 μmol $m^{-2}$ $s^{-1}$. All measurements were performed at 5 °C intervals from 5 to 30 °C for leaf temperature. The $P_n$-$C_i$ and $P_n$-*PPFD* response curves were used to estimate $V_{cmax}$ and $J_{max}$, applying the biochemical photosynthetic model of Farquhar et al. (1980) (see also Farquhar and von Caemmerer 1982). Details of measurements and calculation are given in Paper I.

### *2.3.2 Response of growth*

Samplings were performed seven times over the growing season, following the phenological development of RCG (Sahramaa and Jauhiainen 2003b): I, 5th May-31st May (from sprouting to flag leaf emergence); II, 1st June-15th June (visible inflorescence); III, 16th June-30th June (emerged inflorescences); IV, 1st July-15th July (beginning of anthesis); V, 16th July-30th July (anthesis completed); and IV, 1st August-31th August (seed development and ripening). The shoot number in the sample area was recorded. Plant morphology (height, diameter and leaf area (*Li-3100, Li-cor Inc*., Nebraska, USA)) was measured. All of the harvested shoots were further divided into leaves and stems, and the root biomass was obtained from the soil core samples. The root biomass was separated from the peat using water and a sieve. Details of the sampling methods and measurements are provided in Paper II- IV.

The logistic function used by Sahramaa and Jauhiainen (2003b) was applied to relate the biomass values to time (days from the onset of growth) or to the accumulated temperature sum from the beginning of the climatic treatments (Paper IV). Regarding biomass allocation, the seasonal momentary allocation of photosynthesis under elevated temperature and $CO_2$ along with varying groundwater levels was analysed in Paper II. Furthermore, the share of each biomass component in the total biomass was calculated in Paper III to identify the differences in biomass allocation from young and old cultivations under elevated temperature and $CO_2$.

### 2.4 Statistical analysis

The effects of climatic treatments and groundwater level on the photosynthetic and growth responses were analysed using three-way ANOVA. The groundwater level and the climatic treatments were fixed factors, whereas the parameters of photosynthetic and phenological performance, biomass growth and allocation, and the parameters of the logistic model for biomass growth were dependent factors. The mean differences in all parameters among the four climatic treatments (CON, EC, ET and ETC) at the three different groundwater levels at each growing period were tested using Tukey's HSD test. Differences in the parameter values were considered to be statistically significant at $p < 0.05$. Statistical analyses were carried out using the SPSS software package (Version 17, Chicago, IL, USA).

## 3 RESULTS

### 3.1 Seasonal response of photosynthesis to temperature, $CO_2$ and varying water regimes (Paper I)

Light-saturated net photosynthetic rate ($P_{sat}$) was significantly lower during late growing season than during early growing season (Paper I, Fig. 1, Table 1), regardless of climatic treatment and water regime. For two growing periods, soil water availability affected the variation in photosynthesis and biochemical parameters much more than climatic treatment did (Paper I, Fig. 1 and 2, Table 1 and 3).

During early growing season, a greater temperature-induced enhancement of $P_{\text{sat}}$ (11.8%) was detected at higher measurement temperatures, which disappeared during late growing season (Paper I, Fig. 1, Table 1). Over two growing periods, EC significantly increased $P_{\text{sat}}$ regardless of water regime (Table 1, also Paper I, Fig. 1, Table 1). $P_{\text{sat}}$ was on, average, 31% lower in LW compared to HW and NW (Table 1, also Paper I, Fig. 1, Table 1). During the late growing period, $P_{\text{sat}}$ showed the lowest values when LW and ET were combined (Paper I, Fig. 1, Table 1).

$V_{\text{cmax}}$ and $J_{\text{max}}$ were significantly lower during late growing season relative to early growing season (Paper I, Fig. 2, Table 1). $V_{\text{cmax}}$ and $J_{\text{max}}$ at lower measurement temperatures (5-15°C) under ET were lower than those under ambient temperature during early period. When the measurements were performed at 20-30°C, the situation was opposite (Paper I, Fig. 2, Table 1). During late growing period, $V_{\text{cmax}}$ and $J_{\text{max}}$ under ET were lower compared to CON, across measurement temperatures regardless of water regime (Paper I, Fig. 2). However, EC treatment slightly decreased $V_{\text{cmax}}$ and $J_{\text{max}}$ across measurement temperatures regardless of water regime (Paper I, Fig. 2). $V_{\text{cmax}}$ and $J_{\text{max}}$ were lower in LW compared to NW and HW, regardless of climate treatments and growing periods (Table 1, also Paper I, Fig. 2, Table 1).

ET shifted the optimum temperature of photosynthesis to higher temperatures in early periods regardless of water regime, whereas the optimum temperature for photosynthesis was not significantly changed under ET treatment later in the growing season (Paper I, Fig. 3). The effect of $CO_2$ enrichment on the optimum temperature for photosynthesis was not significant, regardless of growth temperature, water regime and developmental phases (Paper I, Fig. 3). Under low groundwater level, the optimum temperature for photosynthesis shifted to lower temperatures regardless of climatic treatment (Paper I, Fig. 3).

### 3.2 Seasonal biomass growth under elevated temperature and $CO_2$ along with different groundwater levels (Paper II- IV)

Relative to CON, the values of final leaf biomass ($Bio_L$), stem biomass ($Bio_S$), root biomass ($Bio_R$), shoot biomass ($Bio_{Sh}$) and total biomass ($Bio_T$) were lower under ET treatments, which is opposite to that observed under EC and ETC treatments (Table 1, also Paper II-IV). Compared to the growth observed under CON, EC enhanced biomass growth of RCG ($Bio_L$, $Bio_S$, $Bio_R$, $Bio_{Sh}$ and $Bio_T$) over the whole growing season (Table 1, also Paper II-IV). At the same time, ET increased RCG biomass growth in early periods (Period II-III), but decreased growth in late stages, regardless of groundwater level (Paper II and IV) and age of cultivation (Paper III). Biomass growth was higher under ETC in early periods than in other climatic treatments (Paper III, Fig. 3). However, the negative effect of ET later in the growing season was partially mitigated by EC treatment; i.e., the biomass at the final harvest was not significantly enhanced by ETC (6% higher compared to ambient conditions on average) (Table 1, Paper III and IV).

The values of $Bio_L$, $Bio_S$, $Bio_{Sh}$ and $Bio_T$ were significantly lower in LW than in NW and HW (Table 1, also Paper II and IV, Fig. 1 and Table 1), whereas highest values of $Bio_R$ were observed under NW compared to LW and HW (Paper II and IV, Fig. 1 and Table 1). The effect of groundwater on biomass growth was stronger than the effect of climatic treatments (Paper IV, Table 1 and 2). The older the cultivation was, the higher the values of $Bio_L$, $Bio_S$, $Bio_{Sh}$, $Bio_R$ and $Bio_T$ were (Paper III, Fig. 3). There was no difference in biomass growth among the plant organs (leaf, stem and root) and the total biomass between plants representing young and old cultivations throughout the growing season (Paper III, Fig. 5).

The higher the groundwater was, the greater were the climate-related changes of biomass growth under EC and ETC (Paper IV, Table 1 and 4). This was opposite to that observed under ET (Paper IV, Table 1 and 4). Regarding the age of cultivation, the climate-related changes in biomass growth were smaller in the plants from the older cultivation compared to those from the younger cultivation (Paper III, Table 2). The level of biomass growth was lowest when ET and LW were combined (Paper II and IV, Fig. 1, Table 1). The temperature- and drought-induced stresses were partially mitigated by EC treatment (Paper II- IV, Table 1 and 2).

### 3.3 Seasonal biomass allocation under elevated temperature and $CO_2$ along with different groundwater levels (Paper II- III)

Biomass was mainly allocated to leaves (LMF) and stems (SMF) in early growing season, to stems in middle of the growing season, and to roots (RMF) later in the growing season (Paper II, Fig. 3). Compared to growth under ambient conditions, ET increased LMF and SMF, and decreased RMF over the whole growing season under NW and HW (Table 1, also Paper II and III, Fig. 3 and 4). Under LW, ET decreased LMF and increased RMF throughout the growing season, increased SMF in early periods and then decreased it later in the growing season (Paper II, Fig. 3). EC treatment increased RMF and decreased LMF and SMF over the growing season regardless of groundwater levels (Paper II and III, Fig. 3 and 4), whereas EC treatment did not significantly alter the biomass allocation pattern between plant organs (Table 1, also Paper II and III, Fig. 3 and 4). The response of the biomass allocation pattern to ETC was similar to the responses to ET alone (Paper II and III, Fig. 3 and 4).

The higher the groundwater level was, the higher LMF and the lower RMF were throughout the growing season, whereas the effect of the groundwater level on SMF depended on the plant developmental phase (Table 1, Paper II, Fig. 3). The effect of the groundwater level on the biomass allocation was stronger than the effect of climatic treatments (Paper II, Fig. 3), and the variations among groundwater levels could be enhanced by ET treatment, opposite to what was observed under EC treatment (Paper II, Fig. 3). The older the cultivation was, the lower the values of *LMF* and *SMF* were. The opposite results were detected for the *RMF* and root: shoot ratio (*RSR)* (Paper III, Fig. 4).

### 3.4. Seasonality of the height and above-ground biomass growth to temperature, $CO_2$ and varying water regimes (Paper IV)

Elevated temperature strongly controlled the seasonal course of height development and biomass accumulation. Soil water levels further accelerated or delayed these processes (Paper IV, Table 2 and 5).

Temperature and $CO_2$ did not significantly affect the onset timing (days), whereas groundwater and the interaction between groundwater and temperature significantly affected the growth onset date (Paper IV, Table 2 and 3). The inflection point of growth was achieved substantially earlier under ET treatments than in CON or EC (Table 1, also Paper IV, Table 1). Additionally, the growth inflection took place earlier under LW compared to NW and HW (Table 1, also Paper IV, Table 1). When LW and ET were combined, growth inflection was the earliest (Paper IV, Table 1). The total length of the period with any growth was shorter in ET and ETC than that in CON and EC (Table 1, also Paper IV, Table 2). Regardless of the climatic treatment, the total length of growing season was clearly shorter under LW than under NW and HW (Table 1, also Paper IV, Table 2). The timing of growth cessation occurred significantly earlier in ET and ETC than under CON and EC (Table 1, also Paper IV, Table 2). Regardless of the climatic treatment, growth was completed earlier under LW than under NW and HW (Table 1, also Paper IV, Table 2).

The effects of temperature and groundwater were both statistically significant regarding the onset of growth (d.d.) (Paper IV, Table 6). Compared to CON and EC, ET and ETC seemed to delay the onset of growth (Table 1, also Table 5 and 6). High groundwater also delayed the onset of growth (Table 1, also Paper IV, Table 5 and 6). The growth inflection was similar for each climatic treatment. Lower values for the inflection point were associated with a low groundwater level, whereas higher values represented the NW and HW (Table 1, also Paper IV, Table 4). The effects of temperature and groundwater were both statistically significant regarding cessation (Table 1, also Paper IV, Table 6); i.e., the cessation of growth occurred at a higher temperature sum in ET and ETC than in CON or in EC (Table 1, also Paper IV, Table 5). However, higher values of cessation were associated with a high groundwater level, whereas lower values represented the LW (Table 1, also Paper IV, Table 5). The total temperature sum over the whole growth cycle was fairly similar for each climatic treatment (Paper IV, Table 5); i.e., groundwater alone affected the duration of growth in relation to the temperature sum (Table 1, Paper IV, Table 6).

**Table 1** Summary table for photosynthetic and growth parameters of RCG (Papers I- IV) regarding the statistical results from the ANOVA analysis on the effects of elevated temperature (T), $CO_2$ enrichment (C) and groundwater level (W) based on measurements during the years 2009 and 2010. Significant differences ($P < 0.05$) are indicated by *, and non-significant differences are shown as ns. Significant effect in terms of the increase or decrease of parameter values due to elevated temperature compared to ambient temperature, or elevated $CO_2$ compared to ambient $CO_2$, and high soil moisture compared to low soil moisture are shown by ↑ and ↓ in parentheses.

| **Parameters and dimensions** | | T | C | W | T × C | T × W | C × W | T × C × W |
|---|---|---|---|---|---|---|---|---|
| **Gas exchange** | **$P_{sat}$ (μmol m$^{-2}$ s$^{-1}$)** | ns | *(↑) | *(↑) | ns | ns | ns | ns |
| | **$g_{sat}$ (mol m$^{-2}$ s$^{-1}$)** | ns | *(↓) | *(↑) | ns | ns | ns | ns |
| **Biochemical parameters** | **$V_{cmax}$ (μmol m$^{-2}$ s$^{-1}$)** | ns | ns | *(↑) | ns | ns | ns | ns |
| | **$J_{max}$ (μmol m$^{-2}$ s$^{-1}$)** | ns | ns | *(↑) | ns | ns | ns | ns |
| **Phenology** | **Onset (days)** | ns | ns | *(↑) | ns | *(↑) | ns | ns |
| | **Cessation (days)** | *(↓) | ns | *(↑) | ns | ns | ns | ns |
| | **Inflection (days)** | *(↓) | ns | *(↑) | ns | ns | ns | ns |
| | **Duration (days)** | *(↓) | ns | *(↑) | ns | ns | ns | ns |
| | **Onset (d.d.)** | *(↑) | ns | *(↑) | ns | *(↑) | ns | ns |
| | **Cessation (d.d.)** | *(↑) | ns | *(↑) | ns | ns | ns | ns |
| | **Inflection (d.d.)** | *(↑) | ns | *(↑) | ns | ns | ns | ns |
| | **Duration (d.d.)** | ns | ns | *(↑) | ns | ns | ns | ns |
| **Morphology** | **Height (cm)** | *(↓) | *(↑) | *(↑) | ns | ns | *(↑) | ns |
| | **Diameter (cm)** | *(↑) | *(↑) | *(↑) | *(↑) | *(↑) | *(↑) | ns |
| | **Leaf area ( m$^{-2}$ m$^{-2}$)** | ns | *(↑) | *(↑) | ns | ns | *(↑) | ns |
| **Biomass growth** | **Leaf biomass (g m$^{-2}$)** | *(↓) | *(↑) | *(↑) | ns | ns | ns | ns |
| | **Stem biomass (g m$^{-2}$)** | *(↓) | *(↑) | *(↑) | ns | ns | ns | ns |
| | **Root biomass (g m$^{-2}$)** | *(↓) | *(↑) | *(↑) | ns | ns | ns | ns |
| | **Shoot biomass (g m$^{-2}$)** | *(↓) | *(↑) | *(↑) | ns | ns | ns | ns |
| | **Total biomass (g m$^{-2}$)** | *(↓) | *(↑) | *(↑) | ns | ns | ns | ns |
| **Biomass allocation** | **LMF (g g$^{-1}$)** | *(↑) | ns | *(↑) | ns | ns | ns | ns |
| | **SMF (g g$^{-1}$)** | *(↑) | ns | *(↑) | ns | ns | ns | ns |
| | **RMF (g g$^{-1}$)** | *(↓) | ns | *(↓) | ns | ns | ns | ns |
| | **RSR (g g$^{-1}$)** | *(↓) | ns | *(↓) | ns | ns | ns | ns |

# 4 DISCUSSION

## 4.1 Effect of elevated temperature and $CO_2$ on biomass growth

The aim of this thesis was to analyse how seasonal photosynthesis, and biomass growth and allocation in a boreal crop plant (reed canary grass (RCG), *Phalaris arundinacea*) is affected by elevated temperature and $CO_2$ and varying groundwater levels. For this purpose, RCG plants in peat monoliths, representing young and old cultivations, were grown in an auto-controlled environment chambers over two growing seasons under elevated temperature (ambient + 3.5°C) and $CO_2$ (700 μmol $mol^{-1}$). In both respects, the chamber system was successful, as demonstrated by Zhou et al. (2012). They demonstrated that target temperature was well achieved in the ET and ECT chambers, where the average temperatures were both approximately 3 °C higher than under ambient conditions. Regarding the $CO_2$ elevation, the performance of chambers was also successful; i.e., the mean concentration of $CO_2$ in the EC and ETC chambers was 704 μmol $mol^{-1}$ and 703 μmol $mol^{-1}$, respectively. For further details of the chamber systems and its performance, see Zhou et al. (2012).

The growth and development of herbaceous $C_3$ crops are strong functions of temperature, and the relationships are often conveniently summarised in terms of thermal time (i.e., the accumulation of the effective temperature sum) (Ritchie and NeSmith 1991). Consequently, even a small increase in temperature could have considerable cumulative effects on plant early growth and development (Morison and Lawlor 1999). Compared to ambient conditions, ET accelerated leaf initiation and expansion with larger leaf areas for RCG accompanied by increased leaf photosynthesis (Paper I). Consequently, biomass growth in early periods was enhanced with taller and thicker stems and larger leaf area compared to ambient temperature (Paper III). Increased leaf area mainly contributed to the increased leaf area per leaf and tiller number; i.e., no significant effects of temperature on leaf number were found. However, leaf photosynthesis declined earlier under ET treatment (from the mid-growing period), as was observed in Zhou et al. (2011) and Ge et al. (2012b). Additionally, leaf area also decreased under ET treatment later in the growing season. The net assimilate rate (NAR) and specific leaf area (SLA) were significantly lower in the later growing season compared to the early growing season (Paper III). On the other hand, ET did not accelerate the onset of RCG but made leaf senescence occur earlier (by approximately 10 days), resulting from the faster accumulation of thermal time (Table 1, also Paper IV). This resulted in less time for carbon fixation and biomass accumulation before seed set (Morison and Lawlor 1999, Ge et al. 2012b). A lower biomass was observed at the final harvest under ET relative to CON (Table 1, also Paper II-IV).

EC did not significantly increase the biomass growth at the beginning of the growing season (Paper III), possibly because of the low temperatures during the early growing seasons. This low temperature inhibited the initiation, expansion and size of leaves, with the consequence that photosynthesis remained low even under EC treatment (Morison and Lawlor 1999). Later, EC significantly increased biomass accumulation throughout the growing period relative to ambient conditions. This can generally be explained by the increased leaf photosynthesis, as found by Zhou (2011) and Ge et al. (2012b). Additionally, measurements showed that the leaf area, height and diameter of RCG plants were significantly enhanced by EC treatment (Table 1, also Paper III). Consequently, stimulated carbon uptake and increased leaf area enhanced the biomass growth of the plants (e.g., Long et al. 2004, Cheng et al. 2009). Increased leaf area was mainly related to the increased leaf area per leaf, but no significant effect of $CO_2$ on shoot density or leaf number was detected.

Higher biomass growth was also observed under ETC in early periods compared to other climatic treatments (Paper III). Moreover, leaf area, height and diameter were higher compared to other climatic treatments (Paper III). Increased leaf area under ETC was not only because of leaf initiation and expansion with a large leaf area per leaf but also because of an increased number of tillers. However, the lower biomass growth observed in late periods in ETC compared to EC may have been due to the decreased leaf area (Paper III), leaf photosynthesis (Paper I) and accelerated leaf senescence of plants (Paper IV) because of elevated temperature, which is likely to shorten the time for $CO_2$ assimilation and biomass accumulation (Paper IV). Furthermore, high temperatures are also likely to increase autotrophic respiration from RCG carbon pools (Zhou 2011).

## 4.2. Effect of elevated temperature and $CO_2$ on biomass allocation

The optimal partitioning theory suggests that plants will respond to environmental changes by shifting their biomass partitioning patterns to obtain the most limiting resource (Bloom et al. 1985, Hilbert 1990). The optimum temperature for RCG photosynthesis is approximately 20-25 °C throughout the growing season (Paper I). In 2009, current air temperatures may have represented a limiting factor (Paper III). Compared to biomass allocation in CON, the expected higher LMF and SMF values under the ET and ETC treatments were observed under NW and HW, which corresponds to the optimal partitioning theory. In comparison, ET and ETC treatments decreased LMF and increased RMF throughout the growing season under LW (Table 1, also Paper II). This likely prevented water loss and maximised water absorption (Poorter and Nagel 2000). Zhou (2011) and Ge et al. (2012b) both reported that LW inhibited the biomass growth of RCG. This negative effect could be exacerbated by elevated temperature; i.e., ET treatment could not only increase evaporation from soil (Kellomäki et al. 2005) but also decrease water use efficiency (Ge et al. 2012b).

EC increased RMF and RSR but reduced LMF and SMF, regardless of groundwater level (Paper II and III). This result is in line with the findings of Ge et al. (2012b), who reported that EC caused higher $^{13}C$ assimilation in RCG roots compared to shoots. On the other hand, EC reduced leaf nitrogen content, resulting in a greater biomass allocation to the root biomass likely to ensure the supply of nutrients (Farrar and Williams 1991, Suter et al. 2002). Additionally, to alleviate the pressure of carbohydrate accumulation in the leaves and shoots under EC treatment, the plants may transport more carbohydrate to the roots (Farrar and Williams 1991, Xu et al. 2006). Because of high nitrogen availability, biomass allocation was not significantly altered under EC treatment (Ge et al. 2012b).

### 4.3 Effects of water regimes on biomass growth and allocation

LW significantly reduced biomass accumulation compared to NW and HW (Table 1, also Paper II and IV); i.e., LW inhibited leaf expansion, with lower leaf area and higher specific leaf weight (SLW) (Zhou et al. 2011). A significant decline in the stomatal conductance $g_{sat}$ was found in LW compared to NW and HW (Table 1, also Zhou et al. 2011). Restrained stomatal behaviour and increased SLW conserved water under drought conditions (Zhou et al. 2011, Ge et al. 2012b). However, they limited $CO_2$ diffusion to the intercellular space with a reduction in carbon uptake (Flexas and Medrano 2002). Thus, photosynthesis was inhibited under LW compared to NW and HW (Zhou 2011, Ge et al. 2012b). This decreases the $CO_2$:$O_2$ ratio and thus increases photorespiration, which decreases net photosynthesis. Additionally, LW significantly decreased the number of tillers compared to NW and HW. Furthermore, the inflection point, cessation and duration of growth related to time (days) and thermal time (d.d.) were lower under LW compared to the values under NW and HW (Table 1, also Paper IV). Thus, there was less time for carbon fixation and biomass accumulation (Paper IV, Table 2 and 5). In comparison, a higher groundwater level increased RCG growth compared to low groundwater level, mainly because of higher leaf photosynthesis (Paper I), a delay in the timing of the peak growth rate and the cessation and duration of the growing season (Table 1, also Paper IV).

Under water shortage, biomass allocation may change in such a way that the proportion of water-absorbing biomass increased, while the proportion of water-loosing biomass decreased, as has been widely observed in grassland and crop plants (Huang and Fu 2000, Poorter and Nagel 2000, Xu and Zhou 2005). As expected, a higher RMF was detected under LW treatments relative to NW and HW treatments (Table 1, also Paper II). As a crop adapted to high soil moisture, Zhou et al. (2011) and Ge et al. (2012b) both reported that higher soil water enhanced RCG leaf expansion (i.e., leaf area) and leaf biomass growth, as was observed in this thesis. Higher SMF was observed under LW during the early growing season. This was most likely an investment made by the plant to enhance the transportation of water, which had been reported in other crop species (Poorter and Nagel 2000). On the other hand, a decreased RMF under NW and HW relative to LW was possible because of the increased mortality of root tissues. This had been observed for plants growing in waterlogged or submerged conditions (Poorter et al. 2012).

### 4.4. Interactive effects of climatic treatments, water regimes and the age of cultivation

ETC did not enhance the total biomass growth relative to CON as measured at the end of growing season. This was in agreement with Cheng et al. (2009), who demonstrated that high temperature reduced the stimulatory effect of elevated $CO_2$ on the production of rice, if both continue to increase. EC increased water use efficiency (WUE) and prevented excessive water loss by the plants in LW, thus drought-induced stress could be mitigated by EC treatment (Paper II and IV). In comparison, ET may decrease water use efficiency in these conditions, which were characterised by enhanced evaporation (Kellomäki et al. 2005). Drought-induced stress could be exacerbated by ET treatment. Consequently, the lowest growth values were observed when ET and LW were combined, and the highest values were found with the high groundwater level under elevated temperature and $CO_2$, alone or combined (Paper II and IV). The variations in biomass allocation among groundwater levels could be enhanced by ET treatment and reduced by EC treatment (Paper II). Furthermore, a higher belowground biomass was detected in RCG plants from old cultivation, where more carbohydrates and other resources for growth were likely available in the following years than in young cultivation (Asaeda and Karunaratne 2000). Van der Toorn and Mook (1982) found that rhizome biomass and the mean diameter of emerging shoots in the following spring were closely correlated in *Phragmites australis* (Paper III). Additionally, differences in LMF, SMF, RMF and RSR were mainly observed between young and old RCG because of the significant differences in the belowground biomass relative to the aboveground biomass (Paper III).

# 5 CONCLUSIONS

Compared to growth under ambient conditions, ET increased RCG biomass growth in early periods but decreased growth in late periods. EC significantly increased biomass growth over the whole growing season. ETC slightly increases the final biomass growth of plant. Higher groundwater levels favoured RCG biomass growth. Temperature-and drought-induced stresses were partially mitigated by elevated $CO_2$. Changes in biomass growth due to climatic change were smaller in plants from the older cultivation than in plants from the younger cultivation. There was no difference in biomass growth among the plant organs (leaf, stem and root) and the total biomass between plants from young and old cultivations.

Biomass allocation was clearly controlled by plant phenology. Compared to growth under ambient conditions, ET increased LMF and SMF and decreased RMF over the whole growing season under well-watered conditions. Under LW, ET decreased LMF and increased RMF throughout the growing season and increased SMF in early periods, and then decreased it later in the growing season. EC decreased LMF and SMF and increased RMF but did not significantly affect the seasonal biomass allocation pattern between plant organs. The response of the biomass allocation pattern to ETC treatment was similar to the responses to ET treatment alone. The higher groundwater level was, the higher the LMF and the lower the RMF values were throughout the growing season, whereas the effect of the groundwater level on SMF depended on the plant developmental phase.

In conclusion, climatic treatments affected biomass growth and biomass allocation to each of the three plant organs, while the direction and extent of climate-related changes in biomass growth and allocation depended on the availability of groundwater. The effect of the ground water level on variations in biomass growth and allocation was stronger than that of the climatic treatment. These results suggest that the management of soil water and the maintenance of high groundwater levels are the key questions to address in the production of RCG biomass for energy purposes in response to climate change. Furthermore, the maintenance of high groundwater levels until the completion of anthesis is recommended to favour shoot building. A moderate groundwater level is recommended thereafter to optimize the growth of root biomass later in growing season, considering both the production of energy biomass and the concurrent sequestration of carbon in soil in the mire sites used to cultivate RCG.

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