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# Expression patterns of C- and N-metabolism related genes in wheat are changed during senescence under elevated CO<sub>2</sub> in dry-land agriculture

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#### ABSTRACT

Projected climatic impacts on crop yield and quality, and increased demands for production, require targeted research to optimise nutrition of crop plants. For wheat, post-anthesis carbon and nitrogen remobilisation from vegetative plant parts and translocation to grains directly affects grain carbon (C), nitrogen (N) and protein levels. We analysed the influence of increased atmospheric CO<sub>2</sub> on the expression of genes involved in senescence, leaf carbohydrate and nitrogen metabolism and assimilate transport in wheat under field conditions (Australian Grains Free Air CO<sub>2</sub> Enrichment; AGFACE) over a time course from anthesis to maturity, the key period for grain filling. Wheat grown under CO<sub>2</sub> enrichment had lower N concentrations and a tendency towards greater C/N ratios. A general acceleration of the senescence process by elevated CO<sub>2</sub> was not confirmed. The expression patterns of genes involved in carbohydrate reduction and metabolite transport differed between CO<sub>2</sub> treatments, and this CO<sub>2</sub> effect was different between pre-senescence and during senescence. The results suggest up-regulation of N remobilisation and down-regulation of C remobilisation during senescence under elevated CO<sub>2</sub>, which is consistent with greater grain N-sink strength of developing grains.

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#### 1. Introduction

Within-plant translocations of nutrients and assimilates during senescence processes are important determinants of grain yield, nutrient use efficiency and grain quality in cereals and other annual crops [1]. Grain N and protein concentrations are important components of the nutritional value and functional properties of cereal grains [2,3]. In wheat, when grown under water-limited conditions,

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grain N and protein concentrations are largely dependent on N that is remobilised from vegetative plant parts and translocated to the developing grain during grain filling and leaf senescence [4,5]. For example, it was reported [4] that 69% of the N measured in the spike was remobilised from vegetative parts under low rainfall conditions in Western Australia. Hence, senescence processes are investigated in crop improvement programs with the aim to increase yields and nutrient use efficiency [1,6]. Manipulation of senescence processes has good potential as a target for crop improvement: For example, delayed senescence in 'stay green' varieties can prolong the period of active photosynthesis and enhance yield and nutrient use efficiency [1]. However, the synchronisation of senescence with environmental factors is important, and delayed senescence can be unfavourable in water-limited environments that are characterised by rapid soil drying during the grain filling phase [5].

In crop improvement, lead times of 10–20 years from identification of target traits to the release of new cultivars are not uncommon. Hence, target traits must take into account future

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*Abbreviations:* C, carbon; N, nitrogen; NPF, nitrate transporter 1/peptide transporter family; e[CO<sub>2</sub>], elevated CO<sub>2</sub>; a[CO<sub>2</sub>], ambient CO<sub>2</sub>; NRE, normalised relative expression; dpa, days post-anthesis.

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environmental conditions including the change in global atmospheric CO<sub>2</sub> concentration [CO<sub>2</sub>], which is likely to increase from ~400  $\mu$ mol mol<sup>-1</sup> in 2014 to ~550  $\mu$ mol mol<sup>-1</sup> by 2050 [7]. This >35% increase in [CO<sub>2</sub>] will affect all plants in fundamental ways: While biomass production and yield of C3 crops generally increase under elevated [CO2], tissue concentrations of nutrients, such as N, as well as proteins are typically decreased [8-10] influencing the nutritional quality significantly [11,12]. A number of hypotheses have been proposed to explain the decreases in nutrient concentrations under elevated [CO<sub>2</sub>], among them dilution by increased biomass. For example, [13] suggested that dilution caused by the accumulation of total non-structural carbohydrates (TNC) from stimulated photosynthesis under high [CO<sub>2</sub>] significantly contributes to decreasing nutrient concentrations under CO<sub>2</sub> enrichment. However, [13] also found that nutrients expressed on a TNC-free biomass basis remained significantly reduced suggesting it is unlikely that dilution is solely responsible for the observed decreases in nutrient concentrations under CO<sub>2</sub> enrichment. Also, decreases in nutrient concentration under elevated [CO<sub>2</sub>] can vary greatly between individual nutrients (between 0.7% and 19.5%) [3,14–17]. Therefore other potential contributors to decreased nutrient concentrations under elevated CO<sub>2</sub> are suggested, including decreased mass flow based on decreased transpiration rates or changes in root architecture and function [18]. Recent results indicated that elevated [CO<sub>2</sub>] reduces nitrate assimilation in wheat leading to decreased nitrate reduction and/or changes in nutrient allocation and remobilisation [19].

In particular in grains, where protein concentration is an important component of the nutritional value and functional properties, such decreases are undesirable and may counteract efforts to increase grain quality [2,3,20,21]. As carbon assimilation increases and N concentration decreases under elevated [CO<sub>2</sub>], tissues can have greater C/N ratios, and altered metabolite concentrations [22–24]. Elevated [CO<sub>2</sub>] may also change leaf senescence: In cereals such as wheat and barley, changes in leaf functioning under elevated [CO<sub>2</sub>] were ascribed to accelerated senescence processes, marked as faster chlorophyll decline [25]. Several studies linked accelerated senescence under elevated [CO<sub>2</sub>] to changes in relative C and N demand of maturing grains [19,26].

Transcription analysis of relevant genes can help revealing the processes underpinning grain yield, nutrient use efficiency and grain quality, and inform new steps for crop improvement [27–29]. The influence of elevated  $[CO_2]$  on the transcriptome is well characterised in trees such as Populus and Betula species [30-33]. In Populus, expression in leaves of up to 50 genes was changed by elevated [CO<sub>2</sub>], depending on the developmental age of the leaves [30]. Long term (12 years) exposure of *Populus* to elevated [CO<sub>2</sub>] led to increased radial growth with enhanced expression of genes related to Calvin cycle activity and linked pathways in leaves, and the pathways involved in cell growth, cell division, hormone metabolism, and secondary cell wall formation were altered in the vascular cambium of the stem [32]. Pot experiments on Arabidopsis and sugarcane showed an influence of elevated [CO<sub>2</sub>] on different metabolic pathways, mainly in relation to C- and N-metabolism and photosynthesis [34,35]. Few gene expression studies have investigated crops under elevated [CO<sub>2</sub>] in realistic field conditions [22,36,37]. Results from these studies suggest that during active growth (in pre-senescent leaves) expression of genes relating to the photosynthetic apparatus commonly decreases [22,37] while many respiratory and carbohydrate metabolism related genes are expressed at higher levels under elevated [CO<sub>2</sub>] [36,37]. Similar observations on Arabidopsis grown under elevated [CO2] were interpreted as increased starch breakdown to meet sink strength resulting from the rapid growth demand [35]. Also, changes in gene expression under elevated [CO<sub>2</sub>] show complex interactions with developmental stages, especially during leaf ageing [22]. Leaf-age related changes under elevated [CO<sub>2</sub>] were reported for *Populus*: Pathways for secondary metabolism and glycolysis were significantly up-regulated by elevated [CO<sub>2</sub>] during senescence, in particular, those related to anthocyanin biosynthesis [38].

Despite considerable interest in expression patterns of key genes in N- and C-metabolism and metabolite transport in postanthesis metabolite remobilisation during leaf senescence in cereals, so far no such studies assessed the influence of elevated  $[CO_2]$  on these processes. For ambient  $[CO_2]$ , transcriptome analysis in the flag leaf of wheat illustrated a senescence related change of key genes involved in degradative, biosynthetic, transport and regulatory processes in complex and coordinated patterns [39]. Also, for senescence and metabolite remobilisation in wheat leaves, several studies identified a high C/N ratio as well as concentrations of metabolites such as sugars as possible triggers [40–43].

Rubisco is not only the key enzyme of photosynthetic CO<sub>2</sub>fixation, but also the major N pool in leaves; consequently its degradation is critical for an efficient N remobilisation [44]. Changes in the expression of Rubisco-related genes are therefore considered good markers for the switch from active photosynthesis to senescence-related remobilisation. C1A-cysteine protease genes are thought to be involved in protein degradation, and one gene of this family is a well characterised senescence marker (senescence associated gene) in *Arabidopsis*, where it is most likely involved in protein degradation during leaf senescence [45]. Glutamine synthetases and glutamate dehydrogenases also seem to play important roles during N-remobilisation in wheat [46–48], while nitrate reduction is a good marker for the proportion of N absorbed relative to N remobilised [49].

Starch and soluble sugar metabolism are also affected by senescence related changes in post-anthesis carbohydrate assimilation and degradation processes. Genes involved in synthesis and turnover of sucrose, fructans (the major soluble carbohydrate pool in wheat) and starch are all good candidates to mark such changes in C metabolism. For example, senescence related increase of  $\alpha$ -amylase as well as sucrose synthase 1 expression indicated the importance of starch degradation and sucrose synthesis for carbon remobilisation in wheat [39].

Metabolite remobilisation from leaves to grains also requires coordinated regulation of subcellular and cell to cell/tissue to tissue metabolite transport. The sucrose transporter TaSUT localised in leaf phloem sieve elements is a good candidate to mark sucrose translocation from senescing leaves to the grain [50]. Several amino acid transporters show increased expression during senescence [39]. Recent analyses of low affinity nitrate transporters (NFP) have identified senescence correlated gene expressions [51].

To date it remains unclear whether elevated [CO<sub>2</sub>] simply accelerates a senescence program (perhaps triggered by increased C/N ratios), or whether changes are specific to particular processes, such as metabolism, recycling or translocation of C and N compounds during senescence. To address this question we investigated the progress of senescence as affected by elevated [CO<sub>2</sub>]. Expression patterns of selected genes covering important steps in N and C metabolism and translocation as well as genes recognised as general leaf senescence markers were assessed. We followed gene expression patterns at anthesis (pre-senescence) and during leaf senescence in wheat leaves grown either under ambient or an elevated  $[CO_2]$  concentration of ~550 ppm (expected for 2050). Plant material was field-grown within the Australian Grains Free Air CO<sub>2</sub> Enrichment (AGFACE) facility, a semi-arid low-rainfall cropping system representing the water limited environments relevant for a significant proportion of the global wheat production. The following hypotheses were tested: (1) Pre-senescent leaves grown under elevated [CO<sub>2</sub>] show changes in gene expression consistent with increased carbohydrate metabolism; (2) Associated with higher C/N ratios, CO<sub>2</sub> enrichment will accelerate senescence in Download English Version:

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