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MARSCHNER REVIEW

Preserving the nutritional quality of crop plants under a changing climate: importance and strategies

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Abstract
Background Global climate is changing more rapidly than ever, threatening plant growth and productivity while exerting considerable direct and indirect effects on the quality and quantity of plant nutrients.
Scope This review focuses on the global impact of climate change on the nutritional value of plant foods. It showcases the existing evidence linking the effects of climate change factors on crop nutrition and the concentration of nutrients in edible plant parts. It focuses on the effect of elevated CO_2 (eCO_2), elevated temperature (eT), salinity, waterlogging and drought stresses, and what is known regarding their direct and indirect influence on nutrient availability. Furthermore, it provides possible strategies to preserve the nutritional composition of plant foods under changing climates.
Conclusions Climate change has an impact on the accumulation of minerals and protein in crop plants, with eCO_2 being the underlying factor of most of the reported changes. The effects are clearly dependent on the type, intensity and duration of the imposed stress, plant genotype and developmental stage. Strong interactions (both positive and negative) can be found between individual climatic factors and soil availability of nitrogen (N), potassium (K), iron (Fe) and phosphorous (P). The development of future interventions to ensure that the world's population has access to plentiful, safe and nutritious food may need to rely on breeding for nutrients under the context of climate change, including legumes in cropping systems, better farm management practices and utilization of microbial inoculants that enhance nutrient availability.

Key words Climate change · Environmental factors · Elevated carbon dioxide · Minerals · Nutrient concentration

Introduction

Although the total global cultivated land area available for farmers has not changed significantly in the last 25

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years (O'Mara 2012), in many regions of the world crop yields have considerably increased. This has been due mostly to agricultural intensification practices and to targeted efforts in plant breeding aiming to increase yield. Nonetheless, human population is growing at a fast pace, with a 33% increase expected to happen in the next 30 years, reaching 9.6 billion by 2050 (Godfray et al. 2010; Manners and van Etten 2018; Ziervogel and Ericksen 2010). Consequently, global demands for food will continue to rise throughout this century. Crop yields and nutritional security are extremely dependent on the climatic conditions projected for the future, and consequently, most of the food produced for human consumption is under its menace (Burritt 2019). Despite efforts to increase global food availability, a key requirement for food and nutrition security, the global burden of malnutrition and micronutrient deficiencies remains alarming and closely linked to climate changes, particularly in low income communities (FAO 2017). Furthermore, climate changes are also responsible for changing the relationships between crops, pests, pathogens and weeds. It can also aggravate several trends, including decreasing pollinator insects, increasing water scarcity and ozone concentrations at ground level and reducing fishery levels. Therefore, it is imperative to know in more detail the impacts of climate change on food security and undernourishment and its potential implications for nutritional outcomes, reviewed by Myers et al. (2017) and Fanzo et al. (2018).

Climate change is a multifactorial stress (Gray and Brady 2016), and in the last decades, plants have experienced significant environmental fluctuations, which resulted in the global warming of the planet and in perturbations of the hydrological cycles. These environmental changes are likely to worsen, and their frequency of occurrence is likely to increase in the upcoming decades. Without mitigation and adaptation strategies, these changes will have a cumulative effect as time progresses (Fanzo et al. 2018). Therefore, in the coming decades climate change will present a major challenge to agriculture, natural ecosystems, and global economies, for producing enough and nutritious food, which has been reflected in a sustainable intensification of agricultural systems (Pretty et al. 2018).

Climate change has varying effects on plants responses at the level of molecular function, developmental processes, morphological traits, and basic physiological responses. It has been well documented that eCO_2 increases plant growth and yield by enhancing photosynthesis, while oftentimes improving crop water-use efficiency (Dietterich et al. 2015; Grover et al. 2015; Guo et al. 2015; Han et al. 2015; Li et al. 2018b). However, improved plant growth at eCO_2 contrasts with reducing grain quality responses, which are being recognized across a range of plant species (Dong et al. 2018b; Myers et al. 2014). This suggests that eCO_2 changes the equilibrium among plant carbon metabolism and mineral uptake, and nutrient-use efficiency (Nakandalage and Seneweera 2018). Micronutrient deficiencies are a substantial public health problem, presenting serious health and nutritional consequences (Anandan et al. 2011). A great deal of emphasis has been given in recent decades to zinc (Zn) and iron (Fe) nutritional deficiencies, particularly in developing countries where a considerable proportion of people depend on grains and legumes as main food sources of these elements (Myers et al. 2014). Micronutrient limitation has also an impact on the susceptibility of plants to biotic and abiotic stresses. However, the response largely depends on plant genotype and each mineral element has complex interactions with several changing climate variables (Nakandalage and Seneweera 2018).

Elevated CO_2 is closely related to increased demands for nutrients and water, resulting from increased plant growth. (Briat et al. 2015). Extending this knowledge to micronutrients, is also of particular importance because of their role in key biochemical pathways. In order to manipulate the most effective pathways for nutrient provision, it is important to propose predictive models that explain the future response mechanisms of plants to approaching worldwide environmental changes.

Herein we have focused on the current understanding of how climatic changes, with emphasis to eCO_2, impact the nutritional quality of crop plants and their associated molecular and physiological response mechanisms. In addition, analysis of the interaction between CO_2 enrichment and low soil nutrient availability will also be addressed. The final part of the review will be dedicated to report some of the strategies that can be used to preserve nutrient concentrations in future climates.

An overview of climate changes as a global problem

The climatic conditions in which our food-producing systems depend on have been shifting quickly and are projected to continue their current pathways unless significant interventions are made. The main cause of climate change is the release of anthropogenic greenhouse gases to the atmosphere, which have intensely increased since the pre-industrial era, determined largely by economic and population growth, and are now higher than ever. Constant release of greenhouse gases has led to atmospheric concentrations of CO_2 at an unprecedented level and will cause further warming and exacerbate changes of the climate system, increasing the likelihood of severe and permanent impacts for people and ecosystems (Myers et al. 2017). These impacts, together with those of other anthropogenic drivers, have been the dominant cause of the observed global warming during the last decades. Thus, significant reductions in greenhouse gas emissions are required and here governmental authorities have a major role to play (Fanzo et al. 2018; IPCC 2014; Myers et al. 2017). Overall, 1.0 °C increase in global warming since the pre-industrial era has been observed, and is expected to reach 1.5 °C by 2050 if increases at the current rate are maintained (IPCC 2018). Moreover, it is expected that almost two billion people will be affected by almost complete water deficiency over the course of this century, and that close to 65% of the human population will be affected by circumstances of partial water insufficiency (Nezhadahmadi et al. 2013). Oscillations in the occurrence and intensity of normal precipitation patterns are also increasingly becoming a major global problem for agriculture, with a direct effect on the bioavailability of plant nutrients in the soil. The consequences may be a change in soil moisture that is a key factor in nutrient acquisition, as soil water provides the medium in which plants absorb and transport nutrients from, and that can affect nutrient allocation (Fischer et al. 2019).

Even if there will be yield improvements in some crops in different regions of the world, the global impact of climate change on agricultural products is expected to be negative, threatening global food security. Developing countries, which are already vulnerable to food shortage, are likely to be most seriously affected (Nelson et al. 2009). Consequently, our ability to ensure the required amounts of food and nutritional quality in the face of rapidly changing environmental conditions will be an important task for the near coming future.

The importance of micronutrients in humans and in plants

Micronutrients play a decisive role in maintaining health, because they have an essential role in cognitive growth and development, in reproductive functions and cell metabolism, and also in immune system responses of humans (Nakandalage and Seneweera 2018). Dietary deficiencies of micronutrients (i.e. hidden hunger) are considered as a global public health problem and it is already estimated to affect around two billion people worldwide (Haddad et al. 2015).

Accordingly, Fe limitation adversely disturbs growth, immune function and is the most common and widespread nutritional disorder in the world causing anemia (Murgia et al. 2012). Millions of people in developing countries are anemic comprising 50 and 40% of pregnant women and preschool children, respectively (Bouis and Saltzman 2017). Current studies show that Fe-deficit in the first year of life is responsible for permanent effects on brain development, structure and function (Beard 2008). Furthermore, 0,2% of deaths in children under 5 years of age can be attributed to Fe deficiency (Murgia et al. 2012).

Various biological functions have been atributed to Zn, since it cooperates with many enzymes and other proteins and performs critical structural, functional and regulatory roles in the body (Krężel and Maret 2016). A large consumption of cereal-based foods is considered the main driver to Zn deficiency, since cereals have low concentration and bioavailability of Zn and cannot meet the human demand for Zn (Cakmak and Kutman 2018). Nowadays, wheat, rice and corn account for about 60% of the world's daily energy consumption, and bread wheat alone is the staple food for about 35% of the world's population (Poursarebani et al. 2014). In Asian countries with a high incidence of Zn and Fe-deficiencies, rice and wheat deliver over 70% of the daily calorie intake in rural areas (Cakmak et al. 2010; Cakmak and Kutman 2018).

The goal of biofortification is to solve some of these problems by increasing the concentration of micronutrients in the edible parts of crops and improving their bioavailability and absorption in the human body after digestion (Carvalho and Vasconcelos 2013; Ramzani et al. 2016; Vasconcelos et al. 2017). More than 20 million people in developing countries are consuming biofortified crop products. These include beans and pearl millet fortified with Fe, maize, cassava and sweet potato fortified with provitamin A, and rice and wheat fortified with Zn (Bouis and Saltzman 2017). Vitamin A enriched rice (golden rice) produced by transgenic approaches has been made available since the beginning of this century (Wesseler and Zilberman 2014). However, this rice has not been introduced in any country, largely due to the lack of regulatory approval processes. These varieties have enormous nutritional potential and can be an effective economic solution reducing health costs.

Plants require 14 mineral nutrients to achieve for optimal development and growth (Marschner 2012). These elements are structural components of numerous macromolecules including nucleic acids, phospholipids, certain amino acids, and several coenzymes and play a central role in plant cellular metabolism (Grusak 2001). In addition, they are beneficial in chlorophyll biosynthesis, redox reactions, plasma membrane integrity and contribute to the osmotic potential of cells (Nakandalage and Seneweera 2018).

Micronutrient insufficiencies impact plant growth and yield by limiting the biosynthesis or expression of important mechanisms of energy capture and/or metabolism (Grusak 2001). Therefore, an increase in the vulnerability to abiotic stresses is usually encountered in plants that experienced micronutrient deficiency (Bencke-Malato et al. 2019; Hajiboland 2012; Jin et al. 2009). A comprehensive understanding of how these abiotic factors affect the regulatory mechanisms of micronutrients in plants is essential, in order to mitigate their negative effects on the nutritional quality of crop plants when grown under a changing climate.

The influence of eCO_2 on mineral accumulation

The atmospheric CO_2 levels have been progressing from the 280 ppm preindustrial reference levels (Ainsworth and Long 2005; Myers et al. 2017) to current global levels which are now above 400 ppm (IPCC 2018). Although the increasing concentration of atmospheric CO_2 is the main driver of harmful anthropogenic climate changes, it can also improve crop performance by increasing rates of photosynthesis and water-use efficiency, particularly in C3 plants. The putative positive effect in agriculture is in fact denoted to as the "CO_2 fertilization effect" (Ainsworth and Long 2005; Bowes 1993; Bunce 2015; Dietterich et al. 2015; Högy and Fangmeier 2008; Loladze 2014; Long et al. 2004; Myers et al. 2017; Ziska and Bunce 2007). This effect has already been observed in crop plants and vegetables, including wheat (Dong et al. 2018c; Fernando et al. 2012a; Han et al. 2015; Högy and Fangmeier 2008), maize (Zong and Shangguan 2014), rice (Guo et al. 2015; Pang et al. 2006; Yang et al. 2007), barley (Haase et al. 2008; Mitterbauer et al. 2017), bean (Bunce 2008; Ma et al. 2017), soybean (Bunce 2015; Kumagai et al. 2015), cowpea (Dey et al. 2017), potato (Kumari and Agrawal 2014), lettuce, carrot, parsley (Dong et al. 2018b; Long et al. 2004; Mortensen 1994) and tomato (Jin et al. 2009) among others. However, longer treatments with eCO_2 might lead to photosynthetic acclimation, due to increased soluble sugars leading to an imbalanced C:N ratio, accelerated leaf senescence and/or limited growth rate (Ainsworth and Long 2005; Ainsworth et al. 2004; Kaplan et al. 2012; Ludewig and Sonnewald 2000).

Future models of climate change for the period of 2000-2100 predicted an overall decrease of the growing season length and crop transpiration, and increase in water-use efficiency, biomass production, and yields, but with considerable variation among crop models (Ahmed et al. 2017; Bassu et al. 2014).

Despite all the compelling evidence, there is still insufficient knowledge on the role of eCO_2 in shifting the nutritional composition of crops and on the direct consequences to humans (Dong et al. 2018b; Duval et al. 2012; Fernando et al. 2012a; Guo et al. 2015; Högy and Fangmeier 2008; Jablonski et al. 2002; Li et al. 2018b; Loladze 2002; Myers et al. 2014). Therefore, Figure 1 gives an overview of the influence of climatic changes, particularly eCO_2, on grain mineral concentrations and the mechanisms proposed as responsible for changing the plant mineral content.

Using a meta-analysis of FACE and non-FACE studies, Loladze (2014) described a significant reduction in overall mineral concentration (~8%) in C3 plants, including foliar and edible tissues. Precisely, CO_2 enrichment lowered Fe, Zn, and Cu by 6.5–10%, with Mn showing no significant changes. Through a detailed analysis of various plant groups, eCO_2 reduced the mineral concentrations in crops (-7.2%), wild (-9.7%), herbaceous (-7.5%), and woody (-9.6%) plants combining data from foliar and edible tissues. Regarding different tissues, eCO_2 decreased mineral concentrations in foliar (-9.2%) and edible (-6.4%) tissues, including grains (-7.2%). The cereal specific decreases in grains were -7.6, -7.2 and -6.9% for wheat, rice and barley, respectively (Loladze 2014).

Similar findings were obtained by Myers et al. (2014) in the edible portions of C3 grasses and legumes grown under field conditions at eCO_2. A significant reduction in protein concentration in C3 grasses (-6.3% in wheat grains and -7.8% in rice grains), and no significant effects in soybeans or C4 crops were detected at eCO_2. Authors also evaluated phytate concentration that affects mineral bioavailability. The phytate concentration declined significantly at eCO_2 in wheat, which might partly counterbalance the nutritional impact of lower Fe and Zn concentrations in this crop caused by eCO_2, and thus increasing their bioavailability (Myers et al. 2014). Decreases in the concentration of these important micronutrients in such significant food crops will put at risk the populations of the developing world. Iron concentration was also significantly reduced in soybean seeds at fresh edible stage (R6), while Zn and Mn concentrations varied among cultivars (Li et al. 2018b). It was also found that eCO_2 decreased N, Mg, Fe, and Zn concentrations, and not affected P, K, S, Cu, and Mn concentrations in the edible part of vegetables (Dong et al. 2018b).

Nowadays, there is strong evidence that Zn deficiency is a significant global health problem affecting 17% of the world's population, and that increasing CO_2 levels lower the concentration of Zn in significant food crops (Myers et al. 2017; Myers et al. 2015; Myers et al. 2014). In a meta-analysis with previously published data from FACE and growth chamber experiments, Myers et al. (2014) found a significant reduction in Zn concentration in wheat (-9.1%), rice (-3.1%), barley (-13.6%), field peas (-6.8%), and soybean (-5.0%) grown at eCO_2. Similarly, eCO_2 decreased by 9.4% the Zn concentration in vegetables as described by Dong et al. (2018b). Thus, due to increased concentrations of atmospheric CO_2 it was anticipated that 138 million of people will be placed at new risk of Zn deficiency by 2050, and the most affected populations live in Africa and South Asia, with a particular incidence in India with 48 million people at risk (Myers et al. 2015).

The mechanisms responsible for the overall decline of plant mineral concentrations are not completely deciphered. Despite the “carbohydrate dilution” being a likely cause, it cannot elucidate all the mineral reductions because of the heterogenous response of each mineral tested for a given crop or for different species (Loladze 2002; Poorter et al. 1997). Moreover, decreases in transpiration rates reduces mass flow of nutrients, and shifting nutrient allocation driven by altered biochemical processes between tissues can both change nutrient uptake (McGrath and Lobell 2013). In addition, root architecture modification and down-regulation of photosynthesis, reviewed in Taub and Wang (2008), and also inhibition of nitrate assimilation by decreased photorespiration (Bloom et al. 2002) have been proposed to elucidate the variations in mineral concentrations.

The CO_2 concentration has also a direct effect on the bioavailability of nutrients in soils, and consequently affecting the number and diversity of existing microorganisms. A positive effect on soil nutrient bioavailability was described under CO_2 enrichment conditions (Jablonski et al. 2002; Kimball et al. 2002). However, the increase in plant growth with eCO_2 may have a disadvantage in terms of competition for micronutrient acquisition with microorganisms prevailing in the soil (Guo et al. 2015). Abbas et al. (2009) showed that eCO_2 promoted increases in P, K, Fe, Mn and Zn in the soil. Possibly, eCO_2 -induced changes in soil pH improves some exudation processes which affects the availability of nutrients in the soil. Similarly, it was described that eCO_2 responses averaged across two N treatments increased the concentrations of Ca, Mg, Fe, Zn and Mn at the soil surface by 15.6, 9.5, 23.4, 138.2 and 16.9%, respectively (Guo et al. 2015). In another study, Jin et al. (2019) described the interaction of long-term CO_2 conditions with different soil types (chromosol, vertosol, and calcarosol) on grain nutrient concentrations of wheat, field pea, and canola. At eCO_2, the concentrations of N, P, and Zn decreased by 6, 5, and 10%, respectively, regardless of soil, crop and year. In addition, the concentrations of K, Fe, Mn and Cu were not affected by CO_2 enrichment in any crop grown in the soils tested.

Data concerning the impact of CO_2 on other micronutrients, including selenium (Se), chromium (Cr), and iodine (I), in food crops is still very limited. To our knowledge only two studies specified CO_2 responses to Se and Cr accumulation (not significantly lowered by eCO_2) in wheat (Högy et al. 2013, 2009), and none report data pertinent on I. Given that a billion people are I-deficient and I is the primary reason of preventable brain damage, cretinism, and lower IQ in children (Loladze 2014), so studies focusing on the impact of climate change on I content in food crops would be important.

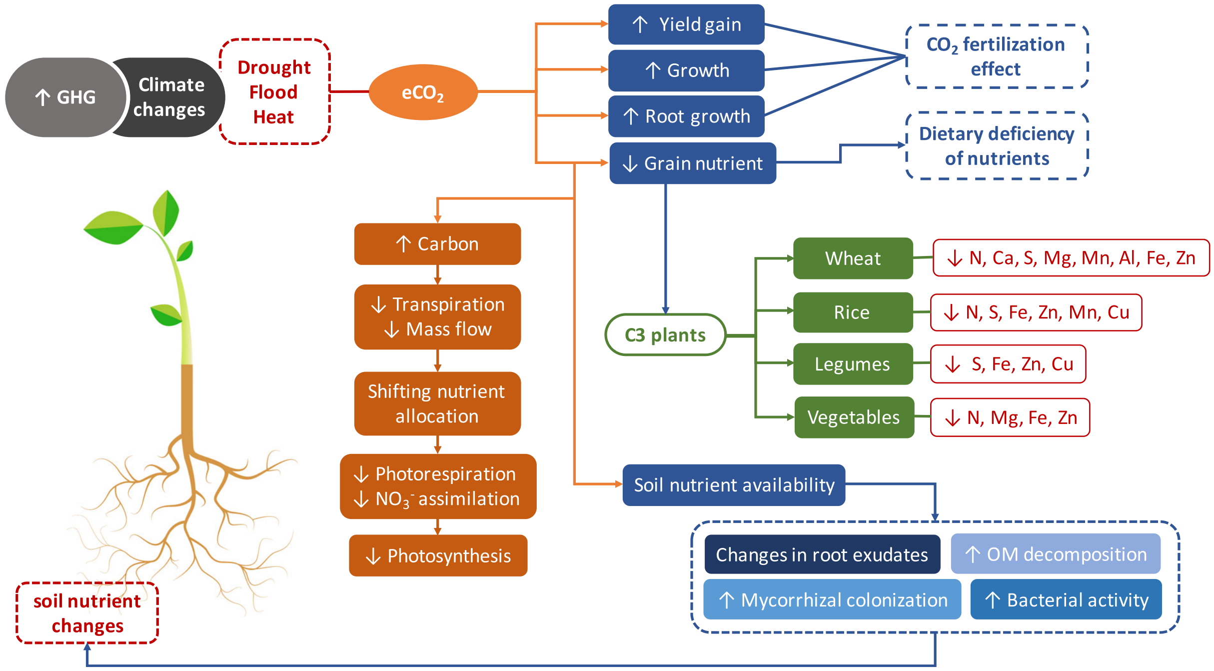


Fig. 1 Schematic illustration of the influence of climatic changes, driven by increased greenhouse gas (GHG) emissions, on grain mineral concentrations and their bioavailability in soil. The effects of CO_2 on nutrient concentrations in edible tissues of C3 plants are reflected in FACE and non-FACE studies. The mechanisms proposed as responsible for changing the plant mineral concentration are: "carbohydrate dilution" in which there is an increase in carbon (C) assimilation relative to the mineral concentration, decrease in transpiration rates that reduces mass flow of nutrients, and shifting nutrient allocation by altered biochemical processes between tissues can affect nutrient uptake. In addition, down-regulation of photosynthesis and increased photorespiration have been also expected to elucidate the variations in mineral concentrations. The CO_2 concentration has also a direct effect on the bioavailability of nutrients in soils and, consequently, affecting the quantity of existing microorganisms. Possibly, due to changes in soil pH, eCO_2 improves the exudation processes affecting nutrient availability. Furthermore, the role of eCO_2 increasing mycorrhizal colonization and organic matter (OM) decomposition in the soil, facilitating the availability of several nutrients

Furthermore, eCO_2 may increase mycorrhizal colonization and protect plants against some stresses, having led to improved P nutrition, particularly on legumes (Jakobsen et al. 2016) and increased soil organic carbon decomposition (Cheng et al. 2012) facilitating the availability of some nutrients. In sum, a clear understanding of the nutrient-related processes that are impacted by climate change will increase our ability to predict responses for diverse crops and could benefit farmers in agronomic management to adapt crops to higher CO_2.

One important final consideration under eCO_2 is the overall effect of lower mineral concentrations while in promoting higher yields. For some situations it has been suggested that regardless of the decrease in grain nutrient concentrations at eCO_2, overall availability of Fe, Zn, Mn, B, Cu, Ca, N, and other macronutrients on a land area basis would actually be enhanced, due to grain yield increase at eCO_2 conditions (Asif et al. 2017a; Fernando et al. 2012b). However, a trade-off effect must be considered because per serving size, the actual amount of minerals provided will still be lower, albeit the higher overall grain yields, which may not be sustainable in the long run due to CO_2 acclimatization effects and faster depletion of mineral nutrients from the soil.

The influence of eCO_2 on protein accumulation

Elevated CO_2 has generally been shown to decrease the concentration of protein in grains of many crops species (Dong et al. 2018b; Högy and Fangmeier 2008; Medek et al. 2017; Myers et al. 2017, 2014), directly affecting human nutrition (Toreti et al. 2019). Consequently, millions of people may face protein deficiency since a great part of worldwide population depends on plant proteins (Medek et al. 2017).

Medek et al. (2017) confirmed that when grown under eCO_2 conditions expected by the middle of this century (500-700 ppm), a lower protein concentration was found in C3 grains (wheat, rice and barley with -7.8, -7.6, and -14.1%, respectively), potato (-6.4%), vegetables (-17.3%), and fruit (-23.0%). The eCO_2 was also responsible for a slight decrease in protein in legume species (-3.5%), and no significant effects were found in oil crops and C4 plants. Accordingly, they anticipated a decrease in protein intake under eCO_2 conditions by >5% in 18 countries predominantly throughout Middle East and India. Moreover, it was highlighted that almost 12% of the world's population is currently at risk of protein deficiency. In the case of constant atmospheric CO_2, they predict that globally, 15% (1.4 billion people) of world population would be at risk of protein deficiency by 2050 due mainly to demographic changes. However, with projections of CO_2 levels above 500 ppm by 2050, it was expected that an additional 148.4 million people will be at risk of protein deficiency compared to the 2050 aCO_2 scenarios.

The effects of other climate change factors on nutrient accumulation

A permanent state of equilibrium in nutrient concentration is a decisive regulatory factor in maintaining nutritional quality and determining the ability of plants to withstand the impact of climate changes (Nakandalage and Seneweera 2018). Several studies have shown that several climatic changes may disturb the nutrient accumulation in major crops as demonstrated in Table 1. Therefore it is important to look at those studies dealing with the nutritional impact of eCO_2 (Bunce 2015; Dietterich et al. 2015; Jin et al. 2015; Kumagai et al. 2015; Myers et al. 2014) or combined with water scarcity (Wu et al. 2004), soil mineral deficiency (Asif et al. 2018; Haase et al. 2008; Jin et al. 2009, 2014, 2015), elevated temperature (eT) (Bellaloui et al. 2016; Chaturvedi et al. 2017; Fernando et al. 2014), or salt stress (Chrysargyris et al. 2019; Petretto et al. 2019; Petropoulos et al. 2017; Scagel et al. 2019).

The effect of drought on nutrient accumulation was studied by Fischer et al. (2019) comparing food crops in two different regions of East Africa. Severe drought caused a decrease in nutrients, whereas mild drought actually caused an increase in nutrient concentrations. This shows that that the effects on nutrient accumulation are very depended not only on the type of climatic change but also on it intensity level. Water stress also resulted in significant changes in mineral concentrations of legumes (Hummel et al. 2018; Wijewardana et al. 2019) and vegetables (Sarker and Oba 2018). Contrastingly, limiting irrigation of grapevine in a glasshouse experiment did not result in significant differences in leaf micronutrient concentrations. However, when drought was accompanied by Zn deficiency, authors found that Zn pulverization was effective in increasing Zn, Fe and Mn in leaf blades (Sabir and Sari 2019). Da Ge et al. (2010) reported a field study in order to assess the nutritional quality in maize grains at different soil moisture levels. Severe drought increased N, Ca, Mg, Cu and Zn accumulation by 12%, 28%, 11%, 18%, and 33%, respectively, when compared to control. However, significant decreases in P and K concentration by 17% in both minerals were observed at severe drought. This suggests that the effects of drought on mineral concentration are nutrient specific.

The effects of combined water and heat stresses were studied by Velu et al. (2016) in 54 field-grown wheat varieties. Grain Zn concentration was higher under heat and drought stress conditions, whereas a lower increase of grain Fe was observed in water stress environments.

The interaction of drought stress with eCO_2 on wheat was reported by Wu et al. (2004), and the authors found that CO_2 enrichment alleviated the negative effects of drought stress, increasing water-use efficiency. However, grain quality was lower under eCO_2 as reflected by consistent decreases in mineral nutrients (N, P, K and Zn). Parvin et al. (2019) observed a reduction in Fe, Zn, P, and S concentrations in faba bean and lentil facing drought and eCO_2 conditions. Asif et al. (2017a) reported interaction of eCO_2, drought and soil Zn availability in wheat. It was found that eCO_2 combined with low water and/or Zn availability resulted in reduced grain Zn and protein values. In addition, Asif et al. (2018) found that eCO_2 partially improved the detrimental effect of soil K deficiency on wheat grain yield.

Climate changes are also characterized by soil-related waterlogging complications due to natural factors or by human activities such as excessive irrigation and low drainage (Smethurst et al. 2005). Waterlogging leads to a decreased O_2 availability in the soil with possible accumulation of phytotoxins, leaf chlorosis, stomatal closure (Wei et al. 2018) and restricted crop performance by decreasing soil mineral nutrient accessibility (Ashraf 2012). When *Medicago sativa* was exposed to flooding stress, a marked reduction in leaf and root nutrient accumulation (B, Cu and Zn) was

Table 1 Effects of climate changes on crop nutritional quality

Treatments	Crops	Experimental method	Micronutrients	Protein	Macronutrients	References
D	Maize	Field trial	↑ Cu, Zn		↑ N, Ca, Mg; and ↓ P, K	Da Ge et al. (2010)
D	Maize,	Field trial	= Cu, Mn; and ↑ Fe, Zn		↓ S; = K; and ↑ Ca, Mg, P	Fischer et al. (2019)
	Cassava	Field trial	↓ Mn; = Fe, Cu; and ↑ Zn		= K; and ↑ Mg, P, S, Ca	
	Maize	Field trial	↓ Fe, Mn, Cu; and = Zn		= Mg, P, K, S, Ca	
	Musa acuminata	Field trial	↓ Fe, Mn; = Cu; and ↑ Zn		↓ Mg, P, K, S, Ca	
D	Gravepine	Glasshouse	= Fe, Zn, Mn, Cu, B (leaves)		= P, K, Ca, Mg (leaves)	Sabir and Sari (2019)
D	Common bean	Field trial	↓ Fe; and ↑ Zn	↑		Hummel et al. (2018)
D	Soybean	GC	↑ Fe, Zn, Cu, B		↓N, P, K, Ca; and ↑Mg	Wijewardana et al. (2019)
D	*Amaranthus tricolor*	Field trial	↑ Mn, Cu, Mo, B; and ↓ Fe, Zn (leaves)		↑ Ca, S, Mg, K Na; and ↓ P (leaves)	Sarker and Oba (2018)
eCO$_2$	Wheat, field peas, and canola	FACE	↓ Zn = Mn, Fe, and Cu	↓	↓ P = K, and Mg	Jin et al. (2019)
eCO$_2$	Wheat	Meta-analysis	↓ Cd, Cu, Fe, Mn, Zn; and = B	↓	↓ Ca, Mg, P, S; = Na; and ↑ K	Broberg et al. (2017)
eCO$_2$	Cucumber	OTC	↓ Fe, Zn (low N); and = Cu, Fe, Mn, Zn (moderate and high N)		↑ Ca, K, P, Mg (low N); and = Ca, K, P, Mg (moderate and high N)	Dong et al. (2018a)
eCO$_2$	C3 plants	Meta-analysis	↓ Fe, Zn, Mn, and Cu = Mn	↓	↓ K, P, Ca, and Mg	Loladze (2014)
eCO$_2$	Wheat	Meta-analysis	↓ Fe, Zn	↓		Myers et al. (2014)
	Rice		↓ Fe, Zn, Mn, Cu; = Mn; and ↑ B	↓	↓ S; and = Ca, K, P	
	Peas		↓ Zn, Fe, Mn, Cu, S; and =B	↓	↓ P; = Mg, Ca; and ↑ K	
	Soybean		↓ Fe, Zn, Cu, B; and = Mn	=	↓ Mg, Ca, S; and = K, P	
	Maize		↓ Fe		↓ Mg, K, P	
			= Zn, Mn, Cu, B	=	= Ca, S	
	Sorghum		= Fe, Zn, Mn, Cu, B	=	= Mg, Ca, S, K, P	
eCO$_2$	Soybean	OTC	↓ Fe, Zn, Mn; and = Cu		↑ Mg, Ca, S; and = P	Li et al. (2018b)
eCO$_2$	Vegetables	Meta-analysis	↓ Fe, Zn; and = Cu, Mn	↓	↓ Mg; = P, K, S; and ↑ Ca	Dong et al. (2018b)
eCO$_2$	Wheat	FACE	↓ Fe, Cd; = Zn, Se, Cu, Mn, Cr, Ni, Mo, Si; and ↑ Pb	↓	↑ K; and = Na, Ca, P, S, Mg	Högy et al. (2009)
eCO$_2$	Chickpea	OTC	↓ Zn; and = B, Cu, Fe, Mn	↓	↓ K, Ca; and = P, Mg	Saha et al. (2015)
S	*Amaranthus tricolor*	Pot experiment	↑ Fe, Mn, Cu, Zn (leaves)		↑ Ca, Mg, Na; and ↓ K (leaves)	Sarker et al. (2018)
S	Basil	GH	↓ B, Cu, S; and = Fe, Mn, Zn (leaves)		↓ P; ↑Na, K; and = Ca (leaves)	Scagel et al. (2019)
S	Lettuce	GH	↑Mn, Zn, Cu, Fe (leaves)		↓ K, Ca; and = N, P, Mg (leaves)	

Table 1 (continued)

Treatments	Crops	Experimental method	Micronutrients	Protein	Macronutrients	References
						Neocleous et al. (2014)
S	Rocket	GH			↓ Ca, K, Mg (leaves)	Petretto et al. (2019)
S	Spearmint	GH	↓ Zn; and = Cu (shoot and leaves) ↑Cu, Zn (roots)		↑Na, P; ↓ N, Mg, K (shoot and leaves) ↑Na; ↓ P, Mg, K; and =N (roots)	Chrysargyris et al. (2019)
S	*Cichorium spinosum*	GH	↑Fe, Mn, Zn (leaves)		↓ K; and↑Na, Ca, Mg (leaves)	Petropoulos et al. (2017)
T	Lettuce	GH	↓ Mn, Mo; and = Fe, B, Zn (leaves)		↓ Mg, K, Ca (leaves)	Sublett et al. (2018)
W	*Medicago sativa*	GH	↓ Zn, B, Cu in leaf and root; and ↑ Fe in root		↓N, P, K, Ca in leaf and root; and ↑ Na in leaf	Smethurst et al. (2005)
W	Barley and wheat	Pot experiment	↓ Zn, Cu, Mn; and = Fe in shoots		↓ N, P, K, Mg; and = Ca in shoots	Steffens et al. (2005)
W	Tomato	Pot experiment		↓	↓K; ↑ Na; and = Ca (fruit)	Rasheed et al. (2018)
W	Wheat	GH	↓ Zn, Cu		↓ P, K	Tarekegne et al. (2000)
D or T	Wheat	Field trial	↑ Zn; and = Fe	↑		Velu et al. (2016)
D and S	Maize	GH	= most ions at D and S (leaves)		= most ions at D and S (leaves)	Hu et al. (2007)
eCO_2 x D	Wheat	GC	↓ Zn		↓ N, P, and K	Wu et al. (2004)
eCO_2 x D	Faba bean and lentil	FACE	↓ Fe, Zn		↓ P, S	Parvin et al. (2019)
eCO_2 x D x Zn	Wheat	GC	↓ Zn	↓		Asif et al. (2017a)
eCO_2 x S	Green leaf lettuce Red leaf lettuce	GC	↓ Fe; = Zn; and ↑ Cu, B, Mn ↑ Zn; and = Fe, Cu, B, Mn		↓ N, Na, K, Ca, Mg, P ↓ Na; and = N, K, Ca, Mg, P	Pérez-López et al. (2015)
eCO_2 x T x AM	Wheat	GH			↑ N, K, Ca, Mg, Na (shoot)	Zhu et al. (2018b)
eCO_2 x T	Wheat	FACE	↑ Fe, Zn	↓	↑ Ca, S	Fernando et al. (2012a)
eCO_2 x T	Soybean	T-FACE	↑ Fe, Zn			Köhler et al. (2018)
eCO_2 x T	Wheat	FACE	↓ Fe, Zn, Cu	↓	↓ P, Ca, Mg, S; and = K	Fernando et al. (2014)
eCO_2 x T	Rice	OTC	↓ Fe, Zn, Mn, Cu	↓	↓ Ca, Mg	Chaturvedi et al. (2017)
eCO_2 x T	Soybean	GH, and GC	↓ Fe, Zn, B, Cu, Mn	↓	↓ N, P, K; Mg	Bellaloui et al. (2016)
eCO_2 x T	Soybean	OTC	↓ Mn; ↑ Fe; and = Zn	=	↑ P, K; and = Ca	Qiao et al. (2019)

observed. Similar findings were obtained in barley and wheat shoots indicating that Cu, Zn, and Mn concentrations decreased significantly. The concentration of Fe was not affected (Steffens et al. 2005). Tarekegne et al. (2000) demonstrated that waterlogging-sensitive wheat genotypes appeared to accumulate less Cu and Zn. Conversely, there were higher concentrations of Fe in waterlogged roots of stressed plants (Smethurst et al. 2005).To the best of our knowledge, there are no studies yet that have looked at the combined effect of waterlogging and eCO_2 and their influence on plant nutritional quality, two conditions that are likely to interact in the future.

Sublett et al. (2018) studied the consequence of eT (+8°C) on lettuce in a greenhouse experiment, and found a decrease in leaf Mg, K, Ca Mn and Mo concentrations. When looking at temperature and eCO_2, it was shown that the combination of both factors may restore soybean (Köhler et al. 2018) and wheat (Asif et al. 2019) seed Fe and Zn concentrations to levels obtained under ambient CO_2 (aCO_2). However, since there is a strong species and cultivar dependency on these responses, care must be taken to look at these aspects in detail. In a field study, Fernando et al. (2014) observed a cultivar-based response of wheat to eCO_2 with high temperature. In addition, a decreasing trend in phytate concentration was also detected. Perceived genetic variability in terms of grain minerals could be easily combined into future wheat breeding programs to enable adaptation to climate changes.

In a FACE experiment, Fernando et al. (2012a) grew wheat at aCO_2 and eCO_2 in combination with two different sowing dates to mimic high temperature during grain filling. Grain mineral (Ca, S, Fe and Zn) concentrations were lower under eCO_2 conditions. Most of the grain mineral concentrations were significantly increased at late sowing date, suggesting that at eT may counterbalance some of the negative effects of eCO_2 on grain mineral concentration. Contrasting findings were obtained in rice (Chaturvedi et al. 2017) and soybean (Bellaloui et al. 2016). Qiao et al. (2019) also investigated the effects of eT in combination with eCO_2 on grain quality of soybean and maize grown in open-top chambers in a Mollisol during five growing seasons. Elevated temperature with eCO_2 increased K, and Fe, whereas Ca and Zn concentrations were not statistically affected in both species. In addition, P and Mn concentrations were species dependent. The metabolic responses to eT (+10°C) under eCO_2 were studied in tall

Table 1 (continued)

Treatments	Crops	Experimental method	Micronutrients	Protein	Macronutrients	References
	Maize		↑ Fe, Mn; and = Zn	=	↑ K; and = P, Ca	

↑ increase, = no significant change, ↓ decrease; D, drought; T, temperature; S, salinity, W, waterlogging; OTC, Open top chamber, GH, Green house, GC, Growth chamber; AM, arbuscular mycorrhizal fungi inoculated in wheat plants. The trend of the concentration of nutrients regards to the seeds, otherwise it will be mentioned in the table.

fescue, a cool-season grass species. Plants showed a significant increase in the quantity of several organic acids, amino acids, and carbohydrates involved in photosynthesis, respiration, and protein metabolism. Consequently, it was determined that eCO_2 could play a role in mitigation of heat stress damage (Yu et al. 2012). In rice, eCO_2 at ambient temperature increased plant growth and led to increased seed yield. However, increasing temperature to 35°C or higher, exceeded the beneficial effects of eCO_2 (Madan et al. 2012). The combination of eCO2 with eT has a variable effect on growth and photosynthesis, and is dependent on the range of temperature increase, but in general eCO_2 reduced the negative impact of eT (Köhler et al. 2018; Qiao et al. 2019; Yu et al. 2012). This was confirmed in soybean and maize over five-year growing seasons in open top chambers (Qiao et al. 2019).

Soil salinity is a global problem for agricultural production, since almost 20% percent of the total arable land is deteriorated due to high salinity (Neocleous et al. 2014; Scagel et al. 2019). There are several studies assessing the effects of salinity on mineral concentration and nutritional quality on crops plants. These studies have been conducted mainly in vegetables (Chrysargyris et al. 2019; Neocleous et al. 2014; Petretto et al. 2019; Petropoulos et al. 2017; Scagel et al. 2019), with contrasting responses among different species (Table 1). Pérez-López et al. (2015) studied the effect of salt stress combined with eCO_2 on the nutritional quality of two differently pigmented lettuce cultivars. The red cultivar was the best adapted to eCO_2 because it better adjusted mineral uptake. They concluded that eCO_2 alone or in combination with short environmental salt stress allows increasing the concentration of some minerals. Hu et al. (2007) induced short-term events of drought and salinity stress in maize and found that both stresses frequently originate lower nutrient accessibility in soil and low nutrient translocation in plants. However, reduction in the micronutrient concentrations in the grain was not detected.

It is now clear that one of the main nutrient groups being impacted by climate change are minerals, and one of the biggest challenges of today's agricultural sector is to increase crop productivity and maintain nutritional quality of grains in a sustainable way, despite the influences of climate change.

Plant molecular and physiological responses to climate change factors

Plant responses underlying nutritional losses due to climate change involve complex biological processes that include several physiological and metabolic mechanisms. How plants respond to these changes has been the subject of several studies (Ahuja et al. 2010; Dong et al. 2018b; Feng et al. 2014; Hashiguchi et al. 2010; Hatfield and Walthall 2014; Hummel et al. 2018; Nakandalage and Seneweera 2018; Nakashima et al. 2009; Newton et al. 2011; Saeed et al. 2012). In this section, we will discuss the current understanding of how plants respond to environmental stresses at the molecular and physiological level.

Vicente et al. (2018) reported the impacts of eCO_2, temperature and N supply on the regulation of C and N metabolism in durum wheat. They found a coordination between C and N metabolisms at biochemical and transcriptional levels. Genes from N uptake and assimilation were co-expressed with genes belonging to the respiratory pathway, highlighting the coordination between the synthesis of organic N compounds and C metabolism. Moreover, included in this coordination were Rubisco and nitrate reductase activities. The combination of eT with eCO_2 in soybean seed composition and transcript levels was also studied. The impact of temperature on seed composition and transcripts level was pronounced, particularly on Gm8, similar to ADR12, and on Gm19, similar to β-glucosidase, but there was no effect of CO_2 concentration (Thomas et al. 2003). Additionally, a network analysis of relationships between biochemical parameters of soybean grains showed that interaction of eCO_2 with eT significantly affect carbohydrate and lipid metabolisms (Palacios et al. 2019). However, as previously shown, in some cases, a positive interaction of eCO_2 and eT may also occur (Pérez-Jiménez et al. 2019; Vu and Allen 2009) particularly in biomass accumulation. Parameters such as leaf area, leaf dry weight and stem dry weight of sugarcane was increased under eCO_2 or eT (4.5°C). Such changes were even greater under the combined treatment of eCO_2 and eT (Vu and Allen 2009).

As previously mentioned, the effects of CO_2 enrichment on plants depend on soil water availability, and plants can greatly benefit from eCO_2 in terms of biomass accumulation when enough water is provided (Wu et al. 2004; Zhao et al. 2006). Most studies confirm that CO_2 enrichment tends to mitigate drought negative effects (Asif et al. 2017a; Bencke-Malato et al. 2019; Li et al. 2018a; Sicher and Barnaby 2012; Wang et al. 2018a; Yuhui et al. 2017) by improving plant water relations, reducing stomatal opening and transpiration, increasing photosynthesis, shortening crop growth period and increasing the antioxidant activity (Kumar et al. 2019). In rice, both treatments have no interactive effects on maximal quantum yield of PSII photochemistry, intrinsic efficiency of PSII and non-photochemical quenching. However, in soybean eCO_2 reduced the negative effects of drought on effective quantum yield of PSII photochemistry and photochemical quenching coefficient (Wang et al. 2018a), showing that these responses are very species specific.

Drought and temperature induce oxidative damage in legumes and grasses. These effects may be mitigated by eCO_2, more extensively in legumes, due to lowered photorespiration and reduction of NADPH oxidase activity. The increased antioxidant activity (flavonoids and tocopherols) possibly also contributes to the stress mitigation effect of CO_2 enrichment (Abdelgawad et al. 2015). In another study looking at drought and eCO_2, in maize, transcript levels of 14 genes encoding stress responsive proteins were monitored. All the transcripts were induced by drought except for *rbcS1*, but this response was delayed by CO_2 enrichment. Accordingly, eCO_2 had a larger impact on maize responses to drought at the beginning rather than at the end stages of water stress (Sicher and Barnaby 2012), showing that the importance of the developmental stage on understanding these responses.

Li et al. (2018a) used a metabolomics approach to search for metabolites that were affected by eCO_2 under drought stress in cucumber leaves. The results showed that under severe drought, eCO_2 changed several metabolic pathways related to the metabolism of several amino acids and carbohydrate synthesis. In eCO_2 plants accumulated more amino acids and carbohydrates, 1,2,3-trihydroxybenzene, pyrocatechol, glutamate, and $_L$-gulonolactone, for better tolerating drought stress. The improved root growth and mitigation of drought stress under eCO_2 was also described by Burgess and Huang (2014). This could be associated with alteration in proteins involving nitrogen metabolism (glutamine synthetase), energy metabolism involving respiration (glyceraldehyde-3-phosphate dehydrogenase), and stress defense by increasing antioxidant metabolism (ascorbate peroxidase, superoxide dismutase, and catalase) and chaperone protection (HSP81-1).

Elevated CO_2 and salinity, individually, seem to affect plant growth in opposite directions (Shahbaz and Ashraf 2013; Zaghdoud et al. 2016). Salt stress, in contrast to eCO_2, is generally considered a negative driver for growth of crop plants, especially in arid and semi-arid zones (Zaghdoud et al. 2016). This was confirmed by Kazemi et al. (2018) in rice who described a significant cultivar-dependent response to eCO_2 under different salinity concentrations. Both treatments, besides influencing secondary metabolism, can disturb the oxidative system while acting in different directions, with salinity provoking, and eCO_2 alleviating, oxidative stress (Sgherri et al. 2017). Similarly, Kanani et al. (2010) investigated the effects of eCO_2 with salinity on the transcriptional and metabolic responses of *Arabidopsis thaliana*. The observed metabolic differences suggest that eCO_2 mitigates the metabolic effect of the salinity stress. However, a strong similarity was observed between the transcriptional responses to salt stress and combination of eCO_2 with salt stress (Kanani et al. 2010). In lettuce, both treatments originated a higher concentration of phenolic compounds, in particular luteolin, and increased plant growth and nutritional quality comparing to salinity alone (Pérez-López et al. 2015). Broccoli treated with 90 mM NaCl and eCO_2, had higher photosynthetic rate and water-use efficiency. These factors led to greater leaf area and biomass as well as to increased abundance of aquaporins in roots and leaves at eCO_2, in comparison with aCO_2 (Zaghdoud et al. 2013). In Bermuda grass, salinity stress induced a reduction in leaf water content, leaf photosynthetic rate, transpiration rate, stomatal conductance, and cellular membrane stability. Elevated CO_2 mitigated the depression of those physiological parameters and promoted osmotic adjustment by accumulation of soluble sugars, proline, and glycine betaine under salinity stress (Yu et al. 2015).

Recently, a transcriptome combined with proteome study discovered key factors involved in alfalfa waterlogging-based responses. The authors identified genes-related to beta-amylase, ethylene response factor, calcineurin B-like interacting protein kinases, glutathione peroxidase, and glutathione-S-transferase with key roles in conferring alfalfa tolerance to waterlogging (Zeng et al. 2019). Elevated CO_2 is also capable of reducing the negative effects of waterlogging as demonstrated in several species (Arenque et al. 2014; Lenssen et al. 1995; Pérez-Jiménez et al. 2017a, b; Shimono et al. 2012). Hence, waterlogging affected sweet cherry cultivars severely by reducing photosynthesis, stomatal conductance, transpiration, chlorophyll fluorescence and plant growth (Pérez-Jiménez et al. 2017a). Proline accumulation, to cope with oxidative damage, was also observed. Nevertheless, increasing CO_2 concentration not only mitigated all these effects but also induced the production of soluble sugars and starch in the leaf (Pérez-Jiménez et al. 2017b). In woody plants, Lawson et al. (2017) found species-specific effects of CO_2 concentration and waterlogging on plant growth, gas exchange, and functional traits, and no evidence for an overall effect of eCO_2 in mediating plant responses to flooding. In pea and soybean, an association among tolerance to hypoxia (induced by flooding), the rate of reactive oxygen species production, and antioxidant enzyme activities was recognized. The environment with the higher CO_2 concentration induced higher changes in the processes of reactive oxygen species accumulation and activities of lipoxygenase and antioxidant enzymes (Ershova et al. 2011).

In fact, the observed nutritional impacts due to climate change may also be linked to alterations in below ground interactions between plants and microorganisms. In flooded soils, rice plants responded more positively to the CO_2 enrichment than the non-flooded soil. The results advocate that in tropical rice soils, eCO_2 amplified C accumulation in the soil, which possibly stimulates growth of N fixing bacteria and thereby higher available N (Das et al. 2011). In wheat, a mutualistic symbiosis with arbuscular mycorrhizal increased carbohydrate and nutrient accumulation in plants exposed to eCO_2 and salinity (Zhu et al. 2018b). Thus, looking at the impact of climate change on below ground traits and linking these with processes of nutrient absorption and accumulation seems like a promising line of research for future studies. However, care must be taken at factoring in issues of low nutrient availability in the soil.

Effects of eCO_2 under low soil nutrient availability

The availability of nutrients in the soil has a significant influence on the effects of eCO_2 on plant nutritional quality. Usually, a low nutrient availability limits the eCO_2 effect on plant photosynthetic rates, possibly resulting in less carbon available for producing secondary compounds (Dong et al. 2018b).

Under different levels of N supply, rice grain quality was not significantly affected by eCO_2 in a FACE experiment (Yang et al. 2007). In addition, soil mineral bioavailability was enhanced by eCO_2 in rice, both under high and low N supply. It was also demonstrated that eCO_2 can favor the translocation of Ca, Mg, Fe, Zn and Mn from the soil to the stem, leaf and panicle but decreased in grains (Guo et al. 2015). However, Haase et al. (2007) observed symptoms of N deficiency in common bean plants grown under eCO_2 conditions. The authors suggest that this is possibly due to improved root exudation and a related stimulation of soil microbial growth causing enhanced plant-microbial N competition. Asif et al. (2019) studied the interactive effects of predicted climate (eCO_2 and +3°C) and N and Zn supply on growth and yield of wheat plants. In both predicted climate and environment conditions, low supply of N, significantly decreased straw and grain yield by affecting the number of spikes per plant and number of grains per spike.

The bioavailability of soil P to plants is often restricted due to their strong bonding in insoluble forms. However, plants generally develop potential adaptive mechanisms that enhance P uptake in plants under P starvation (Wissuwa et al. 2005). The photosynthetic inhibition caused by low P supply could be overcome by eCO_2. Furthermore, photosynthetic down-regulation at eCO_2 could be reversed by increasing P supply. This might be due to the availability of sufficient P to support increased protein degradation and metabolic rates at eCO_2, enhancement in Rubisco activation, ribulose-1,5 bisphosphate regeneration and global energy demands (Pandey et al. 2015). In addition, in cotton plants grown under P stress, an apparent limitation of CO_2 diffusion across stomata and mesophyll was observed (Singh et al. 2013; Singh and Reddy 2014). Under limited P supply, eCO_2 increased acid phosphatase activity, responsible for hydrolyzing insoluble P in the soil (Barrett et al. 1998; Niu et al. 2012). However, there are some studies reporting no increase in root phosphatase activity in response to P shortage caused by eCO_2 (Norisada et al. 2006; Wasaki et al. 2003). Elevated CO_2 with low P supply also results in increased root dry matter. Changes in the processes at the soil level including root morphology, exudation and mycorrhizal association are also influenced by eCO_2 and P bioavailability (Pandey et al. 2015; Pang et al. 2018; Watts-Williams et al. 2019).

Potassium is an important plant nutrient with a significant role in key physiological processes as described by Cakmak (2005). Yilmaz et al. (2017a) determined growth performance and antioxidant response in wheat plants grown at different K levels under different CO_2 conditions. In low and deficient K plants, biomass was either not affected or even decreased by eCO_2. Additionally, limitation of K induced oxidative stress, and eCO_2 had no significant impact on the antioxidant system. Similarly, K deficiency clearly limited the effects of eCO_2 induced biomass enhancement in both well-watered and drought stressed plants (Asif et al. 2017b). Under severe K limitation, several photosynthesis-related parameters were down regulated in common bean. However, eCO_2 also stimulated carbon assimilation and K utilization efficiency when K deficiency was not severe (Singh and Reddy 2018).

Magnesium has a determinant role in biosynthesis of proteins, nucleic acids, ATP and chlorophyll by activating several enzymatic reactions involving carboxylases, polymerases, kinases, and phosphatases (Cakmak and Kirkby 2008). To our knowledge, there is only one published study dealing with interaction of eCO_2 with low and adequate Mg treatments on durum wheat growth and nutrient composition. Low Mg plants responded to eCO_2 by decreasing biomass, particularly in roots and eCO_2 increased photosynthesis in adequate-Mg plants, but not in low Mg plants. Leaf carbohydrate concentration was increased 2-fold by low Mg at aCO_2 and 3-fold at eCO_2, (Yilmaz et al. 2017b) suggesting that low Mg and eCO_2 decreased carbohydrate transport from source to sink tissues.

In plants, Zn is associated with the activity of several enzymes, it has a structural role in cell metabolism and is implicated in DNA replication and transcription as an intrinsic component of Zn metalloproteins. Zinc deficiency is related with the suspension of photosynthetic activity since this mineral is required for the activity of carbonic anhydrase and because the availability of substrate for carboxylation is limited under Zn limitation (Broadley et al. 2012). Asif et al. (2017a) noticed that eCO_2 increased wheat grain yield, number of spikes per plant and straw yield under sufficient and low Zn conditions. Furthermore, Zn efficiency (yielding ability under low Zn supply) was positively affected by eCO_2 which also reduced grain Zn concentration.

Iron metabolism in crop plants as well as its influence on productivity are already well referenced in the literature (Briat et al. 2015; İncensu et al. 2015; Kobayashi and Nishizawa 2012; Li et al. 2008; López-Millán et al. 2009; Zocchi et al. 2007). Therefore, similar to eCO_2 it is very likely that restricted Fe availability will impact on nutritional quality of foods, which we will consume in the future (Vasconcelos et al. 2014; Vasconcelos et al. 2017). So far, researchers have been assessing these issues independently and studies linking these two important aspects are scarce.

Expanding this knowledge to Fe is of particular interest because of its major role in the photosynthetic process and because its bioavailability to plants is often limited, particularly in calcareous soils, which represent 30% of cultivated soils (Briat et al. 2015; Robin et al. 2008). Several papers described organic acid concentration increases, mainly citrate and malate, in xylem sap, leaf apoplastic fluid and whole leaves of plants with Fe deficiency (Abadía et al. 2002; Larbi et al. 2010; López-Millán et al. 2009; López-Millán et al. 2000). Further changes include shifts in the redox state of the cytoplasm, increases in the activity of phosphoenolpyruvate carboxylase and in several enzymes of the Krebs cycle and of the glycolytic pathway. For a detailed description of the metabolic changes induced in Fe-stressed plants, see Zocchi (2006) and Zocchi et al. (2007). Transcriptomic (Thimm et al. 2001), proteomic and metabolomic studies (Brumbarova et al. 2008; Li et al. 2008; Rellán-Álvarez et al. 2010; Rodríguez-Celma et al. 2016) in Fe-deficient plants have also reported increases in root transcript and protein abundances, respectively, of enzymes-related to the glycolysis, Krebs cycle, anaerobic respiration, stress-related and metabolism-related proteins, among others. In barley, CO_2 enrichment increased biomass production in Fe-deficient and Fe-sufficient plants, both in hydroponics and soil experiments. Higher Fe accumulation in shoots (+52%) of barley grown in soil without Fe supply under eCO_2 conditions were achieved, demonstrating an improved Fe-use efficiency (Haase et al. 2008). Similar findings were obtained in tomato (Jin et al. 2009). Plant biomass and root-to-shoot ratio were greater under eCO_2 conditions than plants grown in aCO_2. Root and shoot Fe concentration significantly increased in Fe-deficient plants under eCO_2 attenuating the symptoms of chlorosis, and were not changed in the Fe-sufficient plants. Authors also suggested some involvement of nitric oxide in enhancing Fe deficiency responses (increased ferric chelate reductase activity, and expression of FRO1, IRT1, and FER genes in roots) when Fe limitation and eCO_2 occured together. The nutrient supply and, accordingly, the nutrient status of plants should be a critical issue defining growth responses to the eCO_2. It was observed that eCO_2 treatments significantly increased the Fe concentrations in tomato leaves and alleviated the Fe deficiency induced chlorosis when grown in Fe-limited medium (Jin et al. 2009).

The data concerning the interaction of eCO_2 and Fe deficiency are very scarce in the literature despite the importance of this micronutrient in plant metabolism. Thus, a better understanding of the interaction of these two factors and how they affect metabolic pathways in plants is required.

Strategies to preserve the nutritional content in future climates

As described in the previous sections, the combination of different climate change factors will impact precipitation patterns, plant physiology and the functioning of the ecosystem, ultimately resulting in environmental constraints which limit nutrient uptake and accumulation. Several practices are under way to mitigate and/or adapt to climate change consequences (Fig. 2), but the high variability in research regarding their real environmental impact impair the definition of a strategy to be successfully implemented in supply chains (Parajuli et al. 2018).

The practices associated to agricultural production are a main target for climate change mitigation. Agricultural planning and farmers' sensitization might contribute not only for climate change mitigation, but also to climate change adaptation. For example, one strategy frequently mentioned in adaptation frameworks is the relocation and protection of farms, namely by moving crop production to promote food security from extreme weather events (Prior et al. 2018).

With climate change, soil quality declines, mostly because soil microbial communities are deeply affected, negatively impacting the degradation of organic pollutants (Ai et al. 2018) and soil organic matter (Chen et al. 2016) or nitrogen fixation (Lobo et al. 2018). In order to prevent nutritional losses of crops farmers must work towards yield optimization and smart fertilization decisions. Currently, fertilization decision support systems can be accessed via online platforms. These are based on algorithms that include experimental data on soil nutrition and crop nutritional requirements and provide farmers fertilizer recommendations and professional fertilization information specific to their farming conditions (Elia and Conversa 2015; He et al. 2011). This allows utilizing a controlled amount of fertilizer, achieving optimum yields and increasing nutrient-use efficiency. Nowadays, the development of technologies for non-invasive nutritional estimation in plants is growing. With these, crop monitoring and diagnosis are improved and targeted, once again facilitating the optimum fertilizer application for desirable production outcomes (Zheng et al. 2018). Examples of these techniques include hyperspectral imaging, successfully utilized in discriminating N nutritional levels in tea plants (Wang et al. 2018b), as well as N, P, K, S, Cu, Zn, Fe and Mn levels in maize and soybean plants (Pandey et al. 2017); unmanned aerial vehicle based multispectral imagery applied in the estimation of plant nitrogen concentration and management of N fertilizer application in rice (Zheng et al. 2018) and in wheat (Zhu et al. 2018a); and reflectance spectroscopy through which authors were able to characterize Fe deficiency symptoms in grapevine and prospect the possibility of detecting in field Fe deficiency conditions (Rustioni et al. 2017).

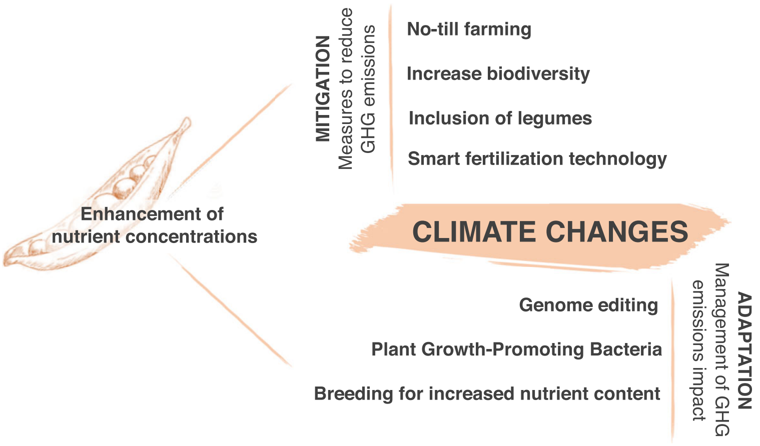
Additionally, sustainable alternatives to synthetic fertilizers which may sustain plant nutrition in a changing climate include plant growth-promoting bacteria (PGPB) inoculants, which can be used as biological fertilizers (Olanrewaju et al. 2017). These are associated with many mechanisms that improve not only plants' health, but also soil conditions, such as, phosphate solubilisation, nitrogen fixation, siderophore and phytohormone production, ethylene regulation and biological control (Lobo et al. 2018). For example, the inoculation of *Pseudomonas fluorescens* in a grass species was able to aid in the decomposition of the increased plant C inputs associated with eCO_2, while promoting plant productivity (Nie et al. 2015). In another study, the best performing PGPB under drought stress conditions was selected from field-grown sorghum (Silva et al. 2018). Also, under drought stress conditions, the application of N fixing bacteria reduced the requirement of chemical fertilizer and enhanced macro and micronutrient concentrations in *Medicago scutellata* (Shabani et al. 2015). Even in poor soil strata, a mixture of five PGPB was found to have a significant impact on nutrient availability, alongside with the capacity to rehabilitate the soil (Radhapriya et al. 2018). With this strategy, it is possible to perform a pre-selection of the PGPB to optimize plant growth for each specific field condition (Silva et al. 2018). This might be optimal for small farming conditions, but in a wider scale, challenges still reside regarding stability and economic feasibility (Lobo et al. 2018).

Another efficient strategy for climate change mitigation is the inclusion of legumes in farming systems, since it allows to naturally reduce the amount of inorganic N fertilizer, reduce CO_2 emissions, amend soil physical properties, maintain soil fertility and decrease pest susceptibility, as recently reviewed by Karkanis et al. (2018). A predictive model that included climate data from the last 80 years demonstrated that the inclusion of a legume in a crop rotation system would decrease 25% of the greenhouse gas emission (Ma et al. 2018). Besides decreasing denitrification, the inclusion of legumes in intercropping systems has also contributed to improve P-fertilizer-use efficiency and led to increased plant availability of P, Fe and Zn (Xue et al. 2016). Although the use of legumes or legume-residues as cover crops (green manure) might be associated with some disadvantages, such as, lack of persistence or excess N supply in high vigor crops, they have much lower environmental impact than non-leguminous crops, lower energy demand per unit area and lower global warming potential (Tani et al. 2017). This strategy is key in the modern paradigm of 'sustainable intensification' (Mungai et al. 2016; Pretty et al. 2018), where we find it urgent to shift agriculture practices to be more sustainable and efficient, while also meeting rising human needs.

Amongst the most common promising sustainable agricultural practices, reduced or no-till farming decreases decomposition rates of organic matter and enhances recycling of nutrients, soil structure and water infiltration (Barão et al. 2019). Although this technique was used in ancient agriculture, during Europe's agricultural revolution, tilling was largely adopted, which in the long run, resulted in soils which are eroded, nutritionally poor and deprived of microbial activity (Gomiero 2016; Lal et al. 2007). Lately, the benefits of no-till farming have been discussed in the context of sustainable agriculture, however, due to its fall into disuse, information on the implementation and economics of this strategy is still scarce in certain agricultural areas, which prevents its successful and widespread implementation (Bavorova et al. 2018). Nowadays, technologies for no-till farming are more effective and require less efforts from the farmers (Rafiq et al. 2017). Evidence has shown that these practices also reduce methane emission (Zhao et al. 2016), contribute to the reduction in dissolved-P loss when combined with other land management strategies (Daryanto et al. 2017) and influence the distribution of pesticides between the soil solution and the solid phase (Elias et al. 2018).

While limited research focus has been put on understanding the regulatory mechanisms of differential gene expression under climate change conditions, newest genetic technologies will most certainly impulse sustainable practices in agriculture. However, the limiting conditions to transfer strategies from the research field to crop improvement impair further advances (Kromdijk and Long 2016). Historically, the major focus of plant breeders has been on yield and resistance, but as plants' nutrient content decrease is progressively evident, reversing this problem should also be a priority. Hence, some approaches are under development and are based, for example, on the identification of QTLs for nutrient efficiency under eCO_2 and warmer temperatures

Fig. 2 Strategies for mitigation and adaptation to climate changes



(Pilbeam 2015) or on the study of differentially expressed genes in response to eCO_2 (Zhang et al. 2018). With this information, predictive models can be designed and selection for increased food quality can be made (Dwivedi et al. 2018). This can be achieved with the application of gene editing tools (Haque et al. 2018) such as the CRISPR/Cas9 system, which has been successful in developing rice lines with improved seed longevity, high amylase content and resistant starch (Mishra et al. 2018).

Concluding remarks

Several studies have been conducted in recent decades on the effects of climate change on plant productivity and yield parameters. However, there is a lack of knowledge dedicated to the nutritional dynamics, particularly, on micronutrient-use efficiency under climate changes, which impacts crop nutrient uptake, transport, and remobilization. Rising CO_2 has been shown to affect the nutritional value of not only cereals and legume crops, but also fruits and leafy vegetables, but few studies point out that this is not a generalizable phenomenon.

Nowadays, we are facing a compromise between the necessities for higher yields and the prevention of food quality loss. Knowing that nutrient deficiencies are one of the major causes of quality and production losses around the world, understanding the interaction of these stresses with eCO_2 is of paramount importance. It seems clear that we can no longer underestimate the effect of eCO_2 on food mineral composition and that the likelihood of growing less nutritious food in the future is a real threat both to agriculture and human health.

In this way, a better understanding of the genetic mechanisms, and of the physiological and molecular processes determining mineral nutrient absorption is essential and will help to improve the nutritional performance of grains subject to climate change. In addition, germplasm screening to identify varieties that have a better use of nutrients will provide the tools for biofortification strategies.

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