Climate Change Impacts on Sunflower Plants

Subjects: Area Studies
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Elevated concentrations of atmospheric carbon dioxide (CO2) and increased temperatures, carbon and nitrogen metabolism will affect the plant's oxidative state in sunflower (Helianthus annus L.) plants

carbon metabolism growth

1. Effects of Elevated CO_2 and Elevated Temperatures on Sunflower Plants Growth

In general, elevated CO_2 levels, directly and indirectly affect plant growth and development, modifying numerous physiological processes. Elevated concentrations of CO_2 tend to increase plant growth and produce large quantities of biomass, especially C3 plants, since they provide additional C (fertilization effect) [1]. Plant growth is determined by cell division and expansion. These processes are coordinated and controlled during organogenesis though a series of factors, including vegetable hormones, and they respond to environmental signals [2][3][4]. An elevated atmospheric CO_2 concentration level may positively influence cell division and expansion [5][6]. Increased cell expansion is associated with greater extensibility of the cell wall and increased activity of the enzymes that fluidify the wall, such as xyloglucan endotransglucosylase (XET) [7]. It has been found that in soy leaves and *Betula papyrifera,* which are grown in a CO_2-enriched environment, certain genes participating in the cell cycle (coding histones) or fluidifying the cell wall (coding expansins and XET) increase their expression [8][9]. It has been verified that a major supplement of carbon at elevated CO_2 concentrations may contribute to accelerating cell division and expansion in meristematic tissues and improves early plant growth and development [10]. Sunflowers grown at elevated CO_2 concentrations were shown to reveal improved growth, reflected in an increased specific leaf mass (SLM), which refers to the dry weight of young leaves (16 days) [11]. It is unclear whether or not this increased cell cycle activity resulting from the increased CO_2 is due to the fact that the plant has more photoassimilates for growth or whether it is because of the divergence produced in gene expression in response to the increased sugar levels [12]. However, in sunflower plants grown at elevated temperatures, a reduced growth has been observed, as reflected when determining the SLM and area of the leaf as well as the soluble protein content [13]. Elevated temperatures negatively affect cell division as well as cell expansion since temperature is one of the main stresses stimulating protein degradation and causing tissue senescence or death [14][15]. Elevated CO_2 stimulates the root and shoot growth of wheat, but this stimulation was found to reduce when plants were grown in combined elevated temperature and elevated CO_2 [16].

2. Elevated CO_2 Levels and Elevated Temperatures on Carbon Metabolism in Sunflower Plants

Elevated levels of CO_2 increase the photosynthetic rate; therefore, crop growth and productivity are increased [17]. It has been observed that an elevated concentration of CO_2 stimulates the photosynthetic fixation of CO_2, as well as stoma transpiration and conductance in young sunflower plant leaves [11]. Elevated levels of CO_2 concentration increase the photosynthesis rate in C3 plants, since the Ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) enzyme involved in the fixation process of CO_2 and photorespiration, is not saturated in the environmental CO_2 concentration [18]. Therefore, an increase in atmospheric CO_2 would increase the leaf's level of internal CO_2, as well as the CO_2/O_2 ratio, affecting the Rubisco and thereby favoring the carboxylation reaction as compared with the oxygenation process. Elevated CO_2 concentrations may reduce the photorespiration process in C3 plants and, therefore, the production of cellular hydrogen peroxide (H_2O_2) derived from the metabolism of glycolate [19][20]. On the other hand, it has been shown that the efficiency of photosystem I and II (PSI and PSII) increases at elevated levels of CO_2, producing more adenosine triphosphate (ATP) and reduced nicotinamide adenine dinucleotide phosphate (NADPH) [21][22]. In addition, increased efficiency in the use of light is observed as a result of the increased flow of electrons between the PSII and PSI under circumstances of high CO_2 [23]. Vicente et al. [24] revealed an increased gene and protein expression related to light reactions of photosynthesis.

This stimulating effect of photosynthesis caused by elevated levels of CO_2 may be temporary, given the acclimation of photosynthesis to elevated concentrations of CO_2, which initially stimulates the fixation of C but is followed by a slow decrease in the C fixation process [25]. Various studies have indicated that the acclimation of photosynthesis is due to factors such as reduced content of Rubisco [26], the inhibition of the assimilation of C due to the accumulation of non-structural carbohydrates that suppress the expression of genes related to photosynthesis [26][27], and a reduction in the concentration of nutrients, especially N in plant tissues, due to the inhibition of photoassimilates of NO_3^- [28][29][30]. In *Populus tremuloides* and *B. papyrifera* in the presence of elevated CO_2, net photosynthesis increased by 43–73% and the hexose ratio increased when compared with that of sucrose [31]. This was also observed in sunflower leaves [11]. When cucumber plants were grown at high concentrations of CO_2, an increase in the content of starch and soluble sugars was also observed in the leaf, as well as a decrease in the content of nitrogen [32][33]. However, the effect of the elevated CO_2 on the accumulation of hexose varied between species [34][35], as did the sensitivity of the distinct plant tissues [36].

The plant growth and yield depend upon the species specific temperature optimum [37]. An elevated temperature conditions the rate of enzymatic reactions and modifies the structure and activity of macromolecules [38]. In addition, it is known that elevated temperatures modify the composition and structure of cell membranes, increasing the fluidity of membrane lipids and decreasing electrostatic interactions between polar groups of the proteins within the aqueous phase of the membrane and producing a loss of ions [39]. Therefore, photosynthesis at elevated temperatures is modified, since the thylakoid membrane is altered along with the thylakoid shape and arrangement [40]. On the other hand, high temperatures also cause photoinhibition of the PSII through the effect on the oxygen emitter complex, which is destroyed by heat [41][42][43]. The decreased photosynthetic rate may also be due to the fact that elevated temperatures cause stomatal closure to prevent water loss, resulting in a decreased exchange of gases between the leaf and the atmosphere [44]. De la Mata et al. [13], attributed the lower net photosynthesis to elevated temperatures in primary sunflower leaves, compared with a control group, causing a reduction in photosynthetic pigments and partial stomatal closure. Greer and Weedon [45] observed that the average rates of photosynthesis of *Vitis vinifera* leaves decreased by 60% when temperatures increased from 25 to 45 ºC. This reduction in photosynthesis was attributed to 15–30% stomatal closure. The photosynthetic rate is also determined by the capacity of carboxylation of Rubisco, which is highly dependent on temperature. Elevated temperatures decrease the state of activation of Rubisco due to the inactivation of the Rubisco activase enzyme, thereby affecting the carbamylation process of the Rubisco [46][47][48][49]. When Rubisco acts as carboxylase, products are frequently formed that prevent its activation, and these should be eliminated from the active site by the Rubisco activase [50][51]. Rubisco activase is relatively labile to heat [48][52]; therefore, its capacity to maintain the Rubisco's state of activation is expected to decrease with elevated temperatures. Plants expressing a more thermotolerant Rubisco activase have higher net photosynthesis at elevated temperatures [53][54]. On the other hand, as the temperature increases, the rate of photosynthesis decreases, with the rate of photorespiration increasing more rapidly [55]. There are two reasons for this. First, as temperatures increase, Rubisco's affinity for CO_2 decreases compared with that of the O_2. Thus, the oxygenation reaction of the Rubisco is more frequent [56][57]. Second, as the temperature increases, the O_2 solubility decreases more slowly than the CO_2 solubility [58]. Therefore, in warm environments, there is relatively more O_2 available to react with the Rubisco.

3. Elevated CO_2 Levels and Elevated Temperatures on Nitrogen Metabolism in Sunflower Plants

Nitrogen is the mineral with the greatest impact in terms of limiting the primary growth and productivity of plants in natural systems and in agriculture. In most soils, nitrogen tends to appear in the form of nitrate (NO_3^-), since ammonium (NH_4^+), including that which is added to the soil as fertilizer, is rapidly oxidized to NO_3^- by nitrifying bacteria. In plants, nitric nitrogen converts into ammonium nitrogen, a process known as assimilatory reduction in NO_3. The assimilation of NO_3^- is regulated by endogenous and/or exogenous factors, such as NO_3^-, carbon compounds, and light. NH_4^+ produced from the assimilatory reduction in NO_3^-, combined with that resulting from other metabolic reactions, is added to the carbon compounds to synthesize nitrogenated compounds that the plant uses for its growth [59].

Stitt and Krapp [60] initially assumed that some plant species required a higher rate of NO_3^- assimilation to permit increased plant growth under conditions of elevated CO_2 concentrations. However, it was found that CO_2 enrichment inhibits the assimilation of NO_3^- in sunflowers [61] as well as in wheat plants, *Arabidopsis* [62], and field-grown wheat [28]. The assimilation of NO_3^- requires the reduced form of nicotinamide adenine dinucleotide (NADH) in order for the nitrate reductase (NR) to catalyze the formation of NO_2^- based on NO_3^-. Photorespiration stimulates the release of malate from the chloroplasts and increases the availability of NADH in the cytosol, thereby increasing the NR activity [63], which permits the first step in NO_3^- assimilation [64]. Elevated CO_2 concentrations reduce photorespiration and thus, decrease the quantity of NADH available for the reduction in NO_3^-. This may explain the decreased levels of NR activity observed in sunflower plants under conditions of elevated CO_2 [61]. However, six transporters from the Nar1 family are involved in the translocation of NO_2^- from the cytosol to the chloroplast in *Chlamydomonas* some of these transport both NO_2^- as well as HCO_3^- [65]. Bloom et al. [66] revealed that HCO_3^- inhibits the entry of NO_2^- in isolated chloroplasts of wheat and peas, indicating that an analogous system is operating in higher plants. Therefore, a decrease in the affluence of NO_2^- to the chloroplast may result from higher CO_2 levels, which may also explain the reduced glutamine synthetase (GS) activity observed in sunflower plants grown under enriched CO_2 conditions [61].

In sunflower plants grown at elevated CO_2 levels (800 µL L) and elevated nitrate availability (25 mM), the primary leaves reveal an increased growth, photosynthetic capacity, assimilation of nitrogen, and antioxidant defenses compared with plants grown at elevated CO_2 levels and limited nitrogen. This results in a delay in the leaf's senescence process, demonstrating that the induction of the senescence process is directly related to the C/N ratio of the leaf [67]. This C/N ratio should be balanced in order for the plant to be more productive. An elevated CO_2 increases this ratio in plants due to the decrease in nitrogen content in the leaf [61]. Sunflower plants that are biofertilized via inoculation with mycorrhizal fungi (*Rhizophagus irregularis*) and are grown in environments of elevated CO_2, and reveal a decrease in the C/N ratio compared with plants grown at elevated CO_2 levels and without biofertilizers.

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