



Review

Photosynthesis, N₂ fixation and taproot reserves during the cutting regrowth cycle of alfalfa under elevated CO₂ and temperature

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ARTICLE INFO

Article history:

Received 15 July 2011

Accepted 29 July 2011

Keywords:

Alfalfa

Biological nitrogen fixation

Photosynthesis down-regulation

Regrowth

Isotopes

ABSTRACT

Future climatic conditions, including rising atmospheric CO₂ and temperature may increase photosynthesis and, consequently, plant production. A larger knowledge of legume performance under the predicted growth conditions will be crucial for safeguarding crop management and extending the area under cultivation with these plants in the near future. N₂ fixation is a key process conditioning plant responsiveness to varying growth conditions. Moreover, it is likely to increase under future environments, due to the higher photosynthate availability, as a consequence of the higher growth rate under elevated CO₂. However, as described in the literature, photosynthesis performance is frequently down-regulated (acclimated) under long-term exposure to CO₂, especially when affected by stressful temperature and water availability conditions. As growth responses to elevated CO₂ are dependent on sink-source status, it is generally accepted that down-regulation occurs in situations with insufficient plant C sink capacity. Alfalfa management involves the cutting of shoots, which alters the source-sink relationship and thus the photosynthetic behaviour. As the growth rate decreases at the end of the pre-cut vegetative growth period, nodulated alfalfa plants show photosynthetic down-regulation, but during regrowth following defoliation, acclimation to elevated CO₂ disappears. The shoot harvest also leads to a drop in mineral N uptake and C translocation to the roots, resulting in a reduction in N₂ fixation due to the dependence on photosynthate supply to support nodule function. Therefore, the production of new shoots during the first days following cutting requires the utilization of reduced C and N compounds that have been stored previously in reserve organs. The stored reserves are mediated by phytohormones such as methyl jasmonate and abscisic acid and in situations where water stress reduces shoot production this potentially enables the enhancement of taproot protein levels in nodulated alfalfa, which may lead to these plants being in better condition in the following cut/regrowth cycle. Furthering our knowledge of legume performance under predicted climate change conditions will be crucial for the development of varieties with better adaptation that will achieve greater and more efficient production values. Furthermore, for this purpose it will be necessary to improve existing methodologies and create new ones for phenotype characterization. Such knowledge will provide key information for future plant breeding programs.

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Introduction

Since the beginning of the industrial revolution in the 18th century, the amount of CO₂ emitted by man has been the consequence of economic development and a population that has quadrupled to 6.4 billion during the last one hundred years (Krausmann et al., 2009). In 1750, the atmospheric concentration of CO₂ was around 280 ppm, whereas it has now reached 389 ppm and currently increases at 1.9 ppm per year on average (Intergovernmental Panel on Climate Change; IPCC, 2007). According to the predictions of the IPCC, at the end of the present century this concentration may be around 700 ppm.

The primary effect of increasing CO₂ is photosynthetic enhancement in C₃ plants, and consequently increased plant productivity (Daepf et al., 2000). So in the absence of other growth limiting factors such as mineral nutrition or water availability, photosynthesis may be enhanced under elevated CO₂ conditions (Campbell et al., 1988; Chaves and Pereira, 1992). Increasing CO₂ will favour carboxylation over photorespiration of ribulose-1,5-bisphosphate (RuBP) (Andrews and Lorimer, 1987). Moreover, the reduction in stomatal conductance by elevated CO₂ will lead to a lower leaf transpiration, and consequently, to a higher water use efficiency (WUE) (Drake et al., 1997).

Due to the greenhouse effect, elevated CO₂ also has indirect effects related to the increase in temperature. By the end of the present century, global warming may lead to a temperature increase of 4 °C (IPCC, 2007). As highlighted by previous studies (Long, 1991; Morison and Lawlor, 1999; Aranjuelo et al., 2005, 2008), plant performance under elevated CO₂ is affected by ambient temperature. These studies showed that a temperature enhancement increased photosynthetic performance of plants exposed to 700 ppm due to the kinetic properties of rubisco (Long, 1991) and partly due to better utilization of the end products of photosynthesis through increased sink metabolism at elevated temperatures. Enhanced C sink strength of plants exposed to 700 ppm avoided leaf carbohydrate build up with a consequent avoidance of photosynthetic down-regulation and an increase in plant biomass. Another point of major concern in elevated CO₂ and temperature studies is the effect of the temperature increase on plant population dynamics (Bélanger et al., 2002, 2005). In mid- and high-latitudes, characterized by seasonal periods of dormancy (winter) and active growth (summer), plant phenology is mainly driven by temperature (Chmielewski et al., 2004). Thus, an indirect effect of increasing air temperatures means the prolongation of the growing season (Menzel and Fabian, 1999; Chmielewski and Rötzer, 2001).

Most climate scenarios are predicted to be affected by climate change, and in the case of the Mediterranean area (IPCC, 2007), an increasing aridity is expected with subsequent water stress for crops. Water deficit is the most important environmental factor limiting photosynthesis, plant growth and production in the Mediterranean climate (Chaves et al., 2002). Moreover, several experiments have revealed that the plant production response to elevated CO₂ can be affected significantly by soil water availability (Owensby et al., 1999; Körner, 2000; Volk et al., 2000).

The interaction between CO₂ concentration and the climate parameters (temperature, precipitation, relative humidity, etc.) makes studies combining different growth conditions fundamental to evaluation of the possible effects of future climatic conditions.

The objective of this review is to summarize the current knowledge concerning the alfalfa response to elevated CO₂, temperature and drought conditions in order to identify the target processes that condition photosynthesis behaviour, biological N₂ fixation and consequently plant growth under predicted climate change conditions. This information might help define different factors conditioning plant adaptation to varying growth conditions and assist with designing new strategies and assigning priorities within future breeding programs through the establishment of novel selection criteria.

Biological nitrogen fixation is stimulated by increasing CO₂

The increase in crop productivity under elevated CO₂ as a consequence of the higher photosynthetic rates is dependent on other essential elements, and low productivity resulting from nutrient limitations is not usually remedied by growth in higher atmospheric CO₂ (Pritchard and Amthor, 2005). In several cases, N availability is a critical factor, limiting plant growth or increasing the response to elevated CO₂. Although the influence of CO₂ on plant growth and photosynthetic activity has been studied extensively (Long et al., 2004; Nowak et al., 2004; Ainsworth and Long, 2005; Erice et al., 2006b; Aranjuelo et al., 2005, 2008, 2009a; Sanz-Sáez et al., 2010), less attention has been given to the role of nodule activity in plant performance under elevated CO₂. Nodule activity depends on photosynthates supplied by the plant, which are used by the nitrogenase enzyme as a source of energy and reducing power to fix N₂ (Larrainzar et al., 2009; Aranjuelo et al., 2011). This cycle coupling causes nitrogenase activity in plants to be regulated by photosynthesis (carbon supply), N availability (N source strength) and N demand (N sink strength) (Aranjuelo et al., 2011). Similarly, the products of N₂ fixation are exported throughout the plant via the xylem to other organs where N is required; for example, protein and osmoregulant synthesis (Ladrera et al., 2007; Aranjuelo et al., 2011). This coupling results in the regulation of nitrogenase activity in plants by photosynthesis (carbon supply), nitrogen availability (N source strength), and N demand (N sink strength). This growth enhancement associated with exposure to elevated CO₂ may lead to a higher N demand, so it is expected that the plant response to CO₂ may be limited by N availability (Hartwig, 1998; West et al., 2005). In this context, legumes are particularly interesting due to their symbiotic relationship with N₂-fixing bacteria, which provides them with N autonomy. That is why, under the N limitation situations that usually occur in nature, growth under elevated CO₂ is more stimulated in legumes than in non-legumes so long as the phosphate availability is high enough (Hebeisen et al., 1997; Ainsworth and Rogers, 2007). Many studies have confirmed that most N₂-fixing legumes increase their level of N₂ fixation per plant under elevated CO₂ conditions (Hartwig, 1998; Rogers et al., 2006). This phenomenon is possible because of the higher growth rate under elevated CO₂. Furthermore, if current photosynthesis determines nitrogenase activity, then an increase or decrease in the atmospheric CO₂ concentration would also cause an immediate increase or decrease in nitrogenase activity (Hartwig, 1998). Most authors agree on the fact that exposure of N₂ fixing plants to elevated CO₂ will stimulate symbiotic fixation through a greater supply of carbohydrates to the nodules.

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