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Cenchrus ciliaris Responds to CO_2 Enrichment under Defoliation Stress

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Abstract

The combined impact of CO_2 enrichment and defoliation stress needs further investigation in order to assess growth responses of plants. Unfortunately, few studies investigated the impact of C4 plant species under arid environment. Additionally, a smaller number of these studies dealt with C4 non-crop species. Three CO_2 enrichment treatments were tested: ambient (ACO_2) enriched (ECO_2) and alternating ($ALCO_2$). Consequently, in this study the aim was to find out how can a C4 grass like *Cenchrus ciliaris* responds to defoliation stress under enriched atmospheric CO_2, and whether the CO_2 elevation can alter growth allocation to the different vegetative and reproductive parts. *C. ciliaris* that were grown under elevated CO_2 and were defoliated had larger leaf area than non-defoliated grasses under the same concentration of CO_2. It is believed that elevated CO_2 reduced the effect of defoliation stress by increasing blades area. Plants usually adapt to defoliation stress by increasing tiller numbers and decreasing tillers weight and size. Plants under $ALCO_2$ may have considered the alternating supply of CO_2 as an additional stress, which led to a different response by *C. ciliaris*.

Keywords: Defoliation stress; CO_2; Enrichment; *C. ciliaris*

Introduction

Grazing-induced defoliation has caused serious challenges to natural and semi- natural grasslands worldwide. Especially with the anticipated increase in green-house gases such as carbon dioxide and the global impact on species growth. Simply because plants respond differently when subjected to environmental stresses. Unfortunately, attention had been given to the change in the atmospheric CO_2 concentration and most of the published studies on plant response to elevated CO_2 focus on response under environmental stresses such as drought, high soil salinity, nutrient limitations and high and low temperatures. Very few studies [1], however, assessed plant responses under defoliation conditions coupled with CO_2 enrichment. Additionally, a smaller number of these studies dealt with C4 non-crop species. Defoliation, defined as the removal of photosynthetic organs of the plant [2] could be caused by many factors such as insect attack, wind or hail damage, or feeding by livestock, is to be studies in combination with the impact of CO_2 increase. The direct effect of elevated CO_2 on plants is mainly increasing its biomass [3] by increasing photosynthesis. The concern about defoliated plants' response to elevated CO_2 comes from the fact that defoliated plants have reduced photo- synthetic organs. Defoliation stress caused an improvement in tree blade quality [4], and decrease in blade size and weight [5]. During defoliation stages, plants require remobilization of the stored and accumulated N and C in plant organs [3]. Defoliation stress gradually reduces N uptake and photosynthesis. This leads to plant growth being highly affected by the extra CO_2 supply and plant storage status [2]. Elevated CO_2 have the ability to improve mineralization and plant uptake of N [4]. In addition, elevated CO_2 increased the carbon content in the soil [1]. Soil carbon content may lead to increased concentration of the non structural carbohydrate in crown and roots [2]. Photosynthetic processes are therefore affected [6] which may impact the plant's regrowth after defoliation events. The combination of stresses such as defoliation with atmospheric CO_2 enrichment wills very likely lead to different growth responses as compared to one of the factors alone. This difference in responses may also be dependent on the photosynthetic pathway (i.e. C3 vs. C4 species). Elevated CO_2 by itself stimulated the regrowth of C3 plants but inhibited that of C4 plants after defoliation [2]. Consequently, in this study the aim was to find out how can a C4 grass like *Cenchrus ciliaris* responds to defoliation stress under enriched atmospheric CO_2, and whether the CO_2 elevation can alter growth allocation to the different vegetative and reproductive parts.

Materials and Methods

This trial was conducted between December 2009 and May 2010 in the United Arab Emirates (UAE) University greenhouse in Al-Ain (N 24. 2, E 55. 6). Two plastic chambers (336×244×22 cm) were used, with one chamber left at the greenhouse CO_2 level of about 500 ppm (ACO_2). The second chamber had enriched CO_2 concentration of about 1000 ppm (ECO_2). Input of CO_2 was from 20 kg canisters. Monitoring was done using a CO_2 monitor and controller (TONGDY Ltd.). All other conditions (temperature, humidity and light) were kept constant in both chambers. Three groups of *C. ciliaris* plants were grown in plastic pots.

ECO_2 plants were exposed continually to enriched atmospheric CO_2 during the whole trial between 7:00 to 18:00. A third group of alternating CO_2 conditions ($ALCO_2$) included plants grown within each of the two chambers every two weeks. Plants under defoliation stress were clipped at about 10 cm above ground level to mimic defoliation stress. Clipping was performed early in the growing stage (3 and 7 weeks from seed emergence).

Shoot length, number of blades (green/dry), blade area and inflorescence production were measured every week throughout the trial period. Percent allocation to various morphological parts (green blades, dry blades, inflorescence, and sheath and root production) was also assessed within each CO_2 enrichment treatment.

Pigment concentration was measured as an indicator of the chlorophyll content [7]. The chlorophyll content (mg/ml) was calculated using the formula: Chlorophyll content=A/Ed, where A is

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the observed absorbance, E is the extinction coefficient (=5 mg/ml), and d is the distance of the light path (=1 cm).

SPSS [8] was used to perform ANOVA analysis to compare the main effects (ambient, alternating and enriched CO_2) for each of the variables under study within each collection date.

Results and Discussion

Eco-physiological growth

Shoot length of defoliated plants for all three treatments (ECO_2, ACO_2, and $ALCO_2$) fluctuated with similar patterns (Figure 1). There was no significant difference between plants under the three CO_2 concentrations (P>0.05) until the 29th of April 2010, when $ALCO_2$ plants had lower shoot length than ACO_2 and ECO_2 (P=0.061). By the end of the trial plants under the three treatments had similar shoot length averages. For union-defoliated plants, ECO_2 was higher than the other two treatments only during two dates (25 and 31 March) at P=0.05.

Defoliated plants for the three CO_2 treatments had similar average blade areas (Figure 2) at P>0.05. Plants under ECO_2 had the largest blade area of all, where it reached the peak on the 25th of March 2010 with more than 100 cm2 of area. For non-defoliated plants, however, the blade area was significantly lower for $ALCO_2$ than the other two treatments, starting 31st March until the end of the trial ($P \leq 0.05$).

The number of green blades for the defoliated plants was highest for ECO_2 (when compared to the other two treatments on 8 March at $P \leq 0.05$ (Figure 3). It is important to remember that the clipping was done on 31 March. After 31st of March, the average number of green blades of all plants sharply increased. Toward the end of the trial plants under ACO_2 had a higher average number of green blades (50 blades per plant), followed by $ALCO_2$ (45 blades per plant) and then ECO_2 plants with an average number of green blades of around 40 blades per plant. Non defoliated plant under ECO_2 treatment had significantly higher green blades on 7 and on 14 April ($P \leq 0.05$).

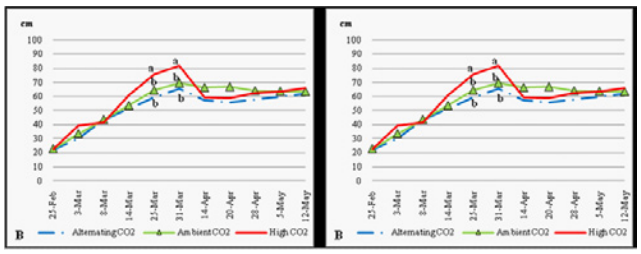

Figure 1: Variations in shoot length of *C. ciliaris* subjected to defoliation stress under various levels of atmospheric CO_2; ambient (500 ppm); enriched (1000 ppm) and alternating between ambient and enriched levels a) subjected to defoliation, b) under non stressed condition.

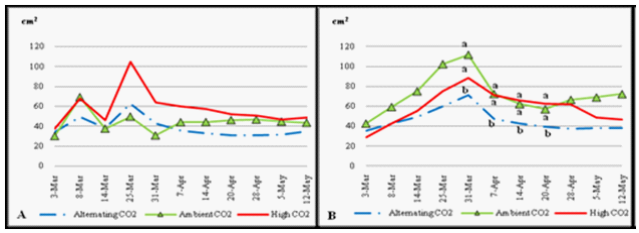

Figure 2: Variations in blade area of *C. ciliaris* subjected to defoliation stress under various levels of atmospheric CO_2; ambient (500 ppm); enriched (1000 ppm) and alternating between ambient and enriched levels a) subjected to defoliation, b) under non stressed condition.

The average number of dry blades under defoliation was highest for ACO_2 before the clipping treatment was applied ($P \leq 0.05$). No significant differences were observed after the clipping was performed at P>0.05 (Figure 4). There was an increasing trend in the number of dry blades similarly for the three treatments (P>0.05). Defoliation, however, seemed to boost the overall average of dry blades for all three treatments. The average number of dry blades did exceed 15 blades for defoliated plants, while the highest average did not exceed 15 dry blades for non-defoliated plants.

Although defoliated plants in the three treatments started with the similar number of stomata, ACO_2 plants had the highest average at the end of the trial at P=0.05 (Figure 5). This was not the case for non-defoliated plants.

For defoliated plants, the amount of chlorophyll/a varied between 2.9 and 5.1 mg/ml but was not significantly different among the three treatments (Figure 6; P>0.05). The average chlorophyll/a for non-defoliated plants was highest, however, for $ALCO_2$ on 16 May (P=0.05). A declining trend was observed for both defoliated and on-defoliated plants under the three treatments.

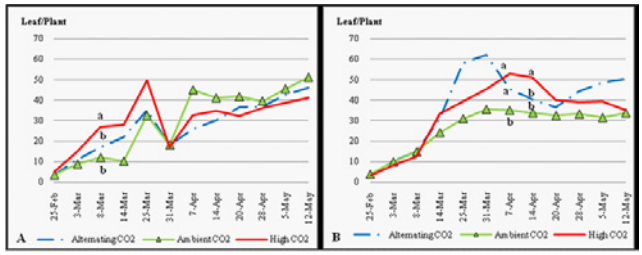

Figure 3: Variations in green blade average number of *C. ciliaris* subjected to defoliation stress under various levels of atmospheric CO_2; ambient (500 ppm); enriched (1000 ppm) and alternating between ambient and enriched levels a) subjected to defoliation, b) under non stressed condition.

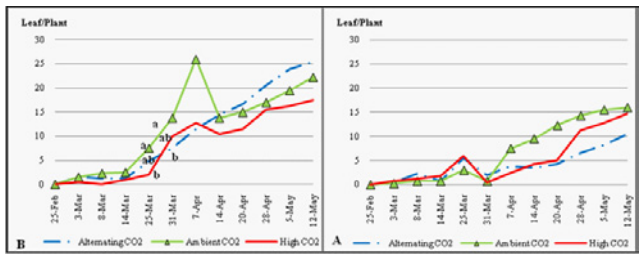

Figure 4: Variations in dry blade average number of *C. ciliaris* subjected to defoliation stress under various levels of atmospheric CO_2; ambient (500 ppm); enriched (1000 ppm) and alternating between ambient and enriched levels a) subjected to defoliation, b) under non stressed condition.

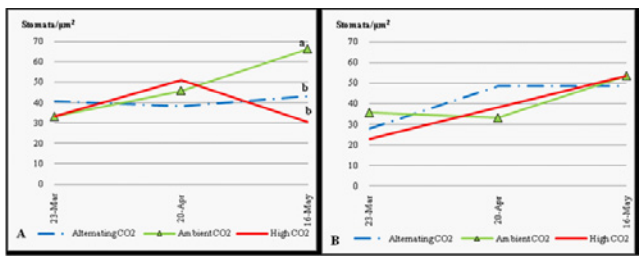

Figure 5: Variations in stomata average number of *C. ciliaris* stress under various levels of atmospheric CO_2; ambient (500 ppm); enriched (1000 ppm) and alternating between ambient and enriched levels a) subjected to defoliation, b) under non stressed condition.

All defoliated plants had similar chlorophyll/b pigment during the whole trial at P>0.05 (Figure 7). A Non-defoliated plant under ACO_2, however, was lowest on 23 March and highest on 16 May ($P \leq 0.05$).

Growth partitioning

In this section, the effect of nutrient stress was looked at by comparing the biomass growth partitioning of *C. ciliaris*-in percent of total biomass-comparing defoliated and non-defoliated plants within each CO_2 treatment (Figure 8).

Under ECO_2, green blade allocation was higher for defoliated plants than non-defoliated plants (17.2% vs. 8.6%; respectively). Inflorescence allocation was 14.26% and 9.48% and root allocation was 10.09% and 3.75%, for defoliated and non-defoliated plants; respectively. Sheath allocation, however, was higher for non-defoliated plants (55.61% vs. 76.13%; respectively).

Plants grown under ACO_2 condition showed more pronounced differences in growth allocation between defoliated and non-defoliated plants for green blades (21.26% vs. 39.48%), for inflorescence (9.87% vs. 28.32%), dry blades (2.7% vs. 9.12%) and sheath growth (53.52% vs. 11.54%); respectively.

$ALCO_2$ plants had similar growth allocation differences. Growth allocation to sheath production was 55.74% vs. 11.06% for defoliated and non-defoliated plants; respectively. Green blades, inflorescence, root, and dry blades percent allocation were lower under defoliation (13.51% vs. 32.65%; 21.81% vs. 36.34%; 7.13% vs. 11.06% and (1.82% vs. 8.87%).

Soil characteristics

Soil moisture, salinity and carbon content were not affected by the defoliation under the three CO_2 treatments (P>0.05). Soil pH, however, was highest for both defoliated and non-defoliated plants under ECO_2 at $P \leq 0.05$. Only soils pH data is shown (Figure 9).

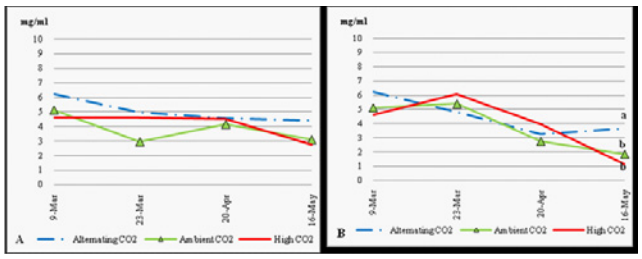

Figure 6: Variations in Chlorophyll/a pigment of *C. ciliaris* subjected to defoliation stress under various levels of atmospheric CO_2; ambient (500 ppm); enriched (1000 ppm) and alternating between ambient and enriched levels a) subjected to defoliation, b) under non stressed condition.

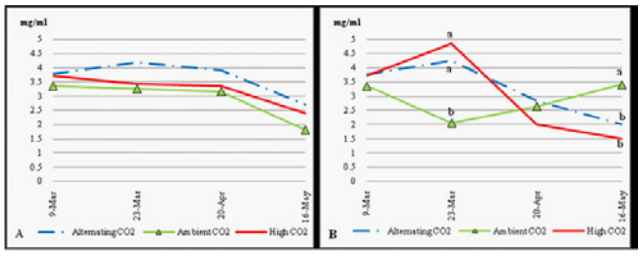

Figure 7: Variations in Chlorophyll/b pigment of *C. ciliaris* subjected to defoliation stress under various levels of atmospheric CO_2; ambient (500 ppm); enriched (1000 ppm) and alternating between ambient and enriched levels a) subjected to defoliation, b) under non stressed condition.

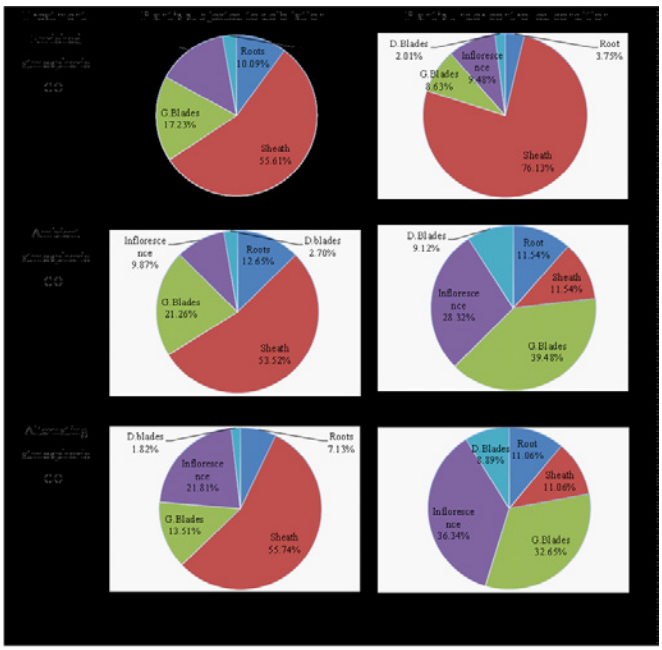

Figure 8: Percentage of growth partitioning of all green parts of *C. ciliaris* for plants subjected to defoliation stressed and plants that were not subjected to defoliation stress under various levels of atmospheric CO_2; ambient (500 ppm); enriched (1000 ppm) and alternating between ambient and enriched levels.

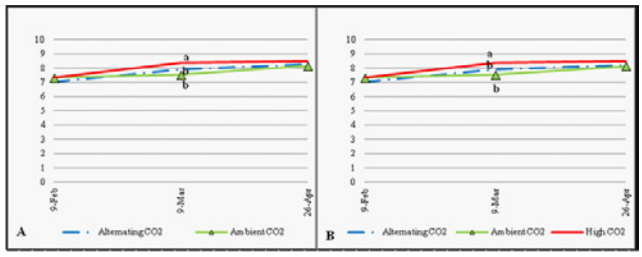

Figure 9: The change in the pH level of plants pots soil, under various levels of atmospheric CO_2; ambient (500 ppm); enriched (1000 ppm) and alternating between ambient and enriched levels: a) subjected to defoliation, b) under non stressed condition.

Discussion

Plants usually show a negative response to defoliation in many parameters such as, shoot length and biomass [9]. Increasing CO_2, however, has a fertilization effect that improves plants' net primary productivity [10]. Rhodes grass, for example, benefited from CO_2 enrichment in the UAE environment [11]. In the present trial, the results showed that *C. ciliaris* was able to regrow after defoliation and reach the normal non-defoliated growth similar to non-defoliated levels, especially under ECO_2 concentration. Defoliating in the early stages of the plants life cycle seems to benefit the plant growth: longer shoot, more green blades, less dry blades, and larger blade area. Within a short period of time, under ECO_2 concentration, plants recovered from defoliation and grew the same level of plant biomass as it was before defoliation. Plants under elevated CO_2 doubled their biomass within the same period of time [12]. *C. ciliaris* that were grown under elevated CO_2 and had been defoliated had larger leaf area than non defoliated grasses under the same concentration of CO_2. It is believed that elevated CO_2 reduced the effect of defoliation stress by increasing blades area. Plants usually adapt to defoliation stress by increasing

tiller numbers and decreasing tillers weight and size [5]. Published data concluded that atmospheric CO_2 elevation can speed up plant growth and development by affecting plant cells division and elongation [13]. The difference in response between young and mature blades comes from the difference in sugar content and hormone concentration, which reduces the stomata conductance under ECO_2 [13]. Chlorophyll/a and chlorophyll/b increased under $ALCO_2$ condition. It is believed that the plants under $ALCO_2$ may have considered the alternating supply of CO_2 as an additional stress, which led to a different response by *C. ciliaris*. Defoliation stress seems to prevent the long term decline in plant pigment specially chlorophyll/a. Even with lower chlorophyll content, some plants had higher photosynthetic activities [14]. As expected, defoliation stress decreased the weight of all *C. ciliaris* sheath even under elevated CO_2. Frequently defoliated plants under elevated CO_2 changed their growth partitioning. Under defoliation stress, plants adapted by altering the carbon allocation to non harvestable yield [5]. The inhibition for vegetative growth did not lead to the reduction of photosynthesis, but it is a consequence to the rapid conversion of photosynthetic to structural dry matter [2]. Most of the non-structural carbohydrates that are re-mobilized are used for root respiration after defoliation [2]. The results of the present study showed that defoliation stress seems to benefit *C. ciliaris* by increasing the root system. Since plants lose their photosynthetic organs by defoliation, the regrowth after defoliation depends on the remobilization of nitrogen and non-structured minerals from the roots and crowns to the growing shoot [2]. Percent growth allocation was more pronounced under ACO_2 than under the other two treatments. But for both defoliated and non-defoliated plants, most measured variables were affected under all three treatments. Allocation to root growth, for instance, could have a benefit to the plant as roots are the main respiration organ that supports the remaining plant parts after the loss of the main respiration organs by defoliation stress [3]. The results of this study suggest that the elevation of CO_2 benefited some parts of *C. ciliaris* after defoliation. Enrichment of atmospheric CO_2 did encourage a fast growth of green blades, especially biomass after defoliation. This could be explained by the fast reallocation and compensation of C and N in the plant derived by the root meristematic activity [15]. ECO_2 increased the concentration of the non-soluble carbohydrates and carbohydrate remobilization in the plant [2], which is needed for plant regrowth. Soil moisture, salinity and carbon content were not affected by the defoliation under the three CO_2 treatments ($P>0.05$). Soil pH, however, was highest for both defoliated and non-defoliated plants under ECO_2 at $P=0.05$. pH was not affected by CO_2 concentration in oak dominated soils [16]. Over all, when comparing defoliated and non-defoliated plants, under the same conditions of CO_2 concentration, we found that the effect of CO_2 enrichment was more pronounced on the non-defoliated plants. Controlled condition of stress positively improved the response in of plants biomass [9]. Defoliated plants under elevated CO_2 had a positive effect on the regrowth of *C. ciliaris* after defoliation [2]. There is a need for more studies to explore the effect of defoliation stress on plants' interactions under natural conditions.

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