



Interactive effect of elevated CO₂, drought and weed competition on carbon isotope discrimination ($\Delta^{13}\text{C}$) in wheat (*Triticum aestivum*) leaves

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ABSTRACT

An experiment was conducted in open top chambers (OTCs) during 2006–07 to study the carbon isotope discrimination ($\Delta^{13}\text{C}$) in wheat (*Triticum aestivum* L. emend Fiori & Paol.) leaves in response to elevated CO₂, drought and competition by weeds (*Phalaris minor*, *Chenopodium album* and *Avena fatua*). It was observed that drought and weed competition had decreased the Δ whereas, elevated CO₂ had increased the Δ and partially ameliorated the negative effects of drought and weeds on Δ . However, the Δ in wheat was not much influenced by stress but, by elevated CO₂ when it was in association with *P. minor* suggesting the variability in Δ due to variation in competition by different weeds.

Key words: Carbon isotope discrimination, Drought, Elevated CO₂, Weeds

There are two naturally occurring stable isotopes of carbon, ¹²C and ¹³C. Most of the carbon is ¹²C (98.9%) with 1.1% being ¹³C. Plants discriminate against ¹³C when fix carbon dioxide through photosynthesis (O'Leary 1988). Plants contain smaller ratio of ¹³C to ¹²C than does the CO₂ of the air that feeds them. Apparently, C₃ species had larger (more negative) discrimination effects than C₄ species.

When soil moisture levels are decreased, a common response is simultaneous decreases in photosynthesis, transpiration and leaf conductance (Kondo *et al.* 2004, Xu *et al.* 2007). In response to changes in leaf water status, a number of species show dramatic shifts in carbon isotope composition (up to 10–15%) associated with photosynthetic metabolism. Physical resistance to root penetration, such as might occur in dry soils, induces a reduction of Δ , as observed with reduced soil moisture levels (Philippe *et al.* 2006). Competition from neighboring plants whether other crop plants or weeds, create stress on crop plants. Competition by weeds induces stress on crop by reducing the plants ability to absorb nutrients and water and reduce the ability to photosynthesize. Since the stable isotopes are incorporated in the leaves during the whole plant life, the isotopic ratios reflect a long-term integration of the environmental impacts responsible for variations in the carbon-water relationships. Therefore, the stable isotope analysis is used to assess the

integrated effect of elevated CO₂, drought and weed competition on Δ .

MATERIALS AND METHODS

The experiment was conducted during 2007–08 at Directorate of weed science Research, Jabalpur. Plants of wheat and weeds (*Phalaris minor*, *Chenopodium album* and *Avena fatua*) were grown in pots inside open top chambers under ambient (370±20ppm) and elevated CO₂ (550±30) conditions. The crop and weed seeds were sown individually and in 1:1 mixture of crop and weed in 30 cm diameter pots and six plants each of the crop and weed in each pot were maintained. The drought was induced at 50 DAS and the irrigation was withheld for 10 days and subsequently irrigation was reinstated so that the soil water content recovered. The moisture level of soil under irrigated (control) condition was maintained at around 24%, whereas, under drought condition it ranged between 10 and 12%. After 60 DAS the leaf (penultimate leaves) samples were collected for isotope analysis. For measuring the carbon isotope discrimination (Δ) leaves were taken because, it enables metabolic changes to be detected within few days of drought imposition or after restoring irrigation. The leaf samples were immersed in liquid nitrogen, freeze-dried, and then ground to a fine powder. Around 1 mg of dried leaf sample was combusted in the Flash Elemental Analyzer interfaced to an Isotope Ratio Mass Spectrometer via a continuous flow device (Conflo-III) at Department of Crop Physiology, University of Agricultural Sciences, Bangalore. The stable carbon isotope composition ($\delta^{13}\text{C}$) was expressed relative to the Pee Dee

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Table 1 Interactive effect of drought, elevated CO₂ and weed competition on biomass production in wheat

	Ambient CO ₂			Elevated CO ₂		
	Control	Drought	Mean	Control	Drought	Mean
Wheat	4.79	2.77	3.78	5.88	3.73	4.8
Wheat (+ <i>P. minor</i>)	2.89	2.34	2.62	4.39	2.70	3.5
Wheat (+ <i>C. album</i>)	2.43	2.37	2.40	4.61	3.75	4.2
Wheat (+ <i>A. fatua</i>)	3.04	2.56	2.8	4.55	3.00	3.78
Mean (drought)	3.29	2.51		4.86	3.29	
Mean (CO ₂)		2.9			4.07	
CD (<i>P</i> <0.05)	Weed competition : 0.226					
	CO ₂ : 1.6					
	Drought : 1.6					
	Interaction : 0.32					

belemnite standard. The carbon isotopic composition of plant samples ($\delta^{13}\text{C}_p$) was determined with an analytical precision of less than 0.1‰. Carbon isotope discrimination ($\Delta^{13}\text{C}$) was calculated as given below according to Farquhar (1983, 1989), assuming the isotopic composition of atmospheric air ($\delta^{13}\text{C}_a$) to be -8‰ (Francey *et al.* 1995, Keeling *et al.* 1995).

$$\Delta^{13}\text{C} (\text{‰}) = [\delta^{13}\text{C}_a - \delta^{13}\text{C}_p] / [1 + \delta^{13}\text{C}_p / 1000].$$

The carbon isotope analysis was done only for the wheat leaf samples as the aim was to find out the effect on wheat.

RESULTS AND DISCUSSION

The results show that drought can be very detrimental to biomass accumulation in wheat (Table.1). The negative effect of drought on the biomass production was partially ameliorated by the elevated CO₂. The association of weeds with wheat had caused significant reduction in biomass and drought had further added to the effect of weeds on the biomass reduction. Association of wheat too had similar effect on the biomass of weeds but, it was variable with different weeds (Fig 1). From the data (Table 1) it was observed that due to CO₂ enrichment the wheat plant could gain biomass against the weeds. But, under drought the CO₂ effect on wheat was reduced when it was in association with *Phalaris minor*, i e the latter had advantage due to CO₂ enrichment under stress (Fig 1). The biomass data was presented because the variation in ¹³C discrimination (Δ) observed in leaf tissues is representative of Δ in the plant biomass.

The carbon isotope discrimination (Δ) inversely represents the incorporation of the heavier fraction of the stable carbon isotope, i e ¹³C in the plant biomass and the accumulation of ¹³C fraction of the carbon was influenced by several factors and particularly the CO₂ enrichment, drought and weed competition in this experiment. The computation of Δ in wheat leaves suggest the response of wheat to the interaction effect of elevated CO₂, drought and weed competition. The drought treatment had a prominent effect on plant biomass and Δ . The elevated CO₂ significantly

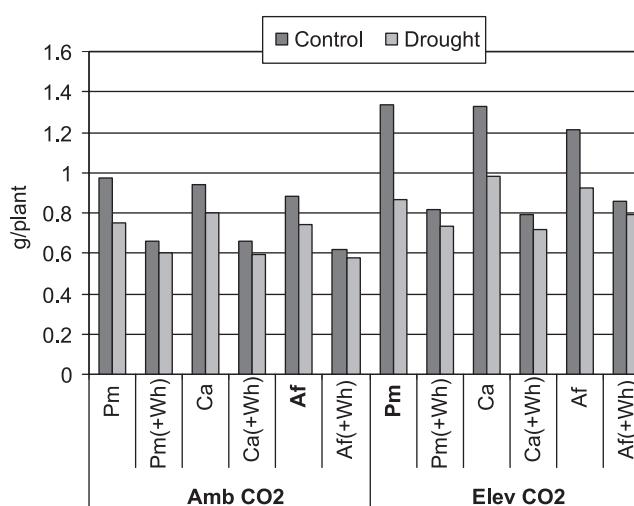


Fig 1 Interactive effect of drought, elevated CO₂ and association with wheat on biomass production in weeds (*Phalaris minor*, *Chenopodium album* and *Avena fatua*)

affected the Δ in both the control and drought-stressed plants. However, the response of Δ to the CO₂ treatment had depended on water supply. Under higher water availability (drought free) wheat leaves had higher Δ under elevated CO₂ compared to ambient CO₂. Fig 2 shows that Δ in wheat was affected by CO₂, drought and association of weeds. Under ambient CO₂ conditions there was considerable reduction in the Δ due to drought; and the CO₂ enrichment increased the Δ under control and stress conditions. This might be due to enhanced photosynthesis under elevated CO₂ coupled with reduced stomatal conductance (Ainsworth and Rogers 2007). High values of $\Delta^{13}\text{C}$ would be associated with an enhanced ability to exploit water resources from drying soil with higher survival and reflect a better adaptation to the environment (Pita *et al.* 2001). The interaction of stress and weed association (Fig 3) on the Δ shows that the stress had decreased the Δ and at the same time the increase of Δ in wheat, when it was in association with *P. minor*, under stress conditions

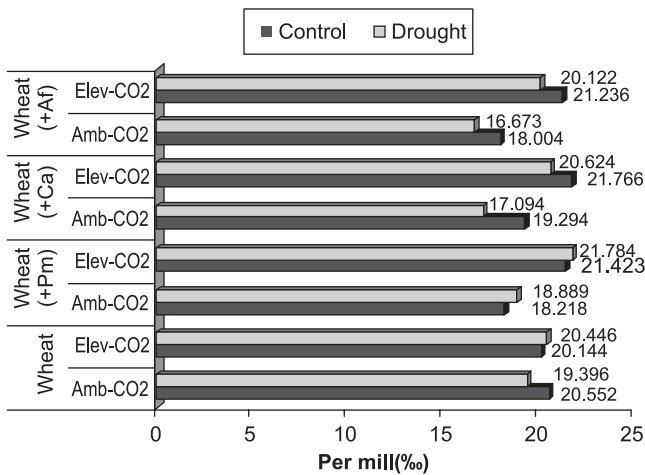


Fig 2 Interactive effect of drought, elevated CO₂ and weed competition on carbon isotope discrimination ($\Delta^{13}C$) in wheat leaves

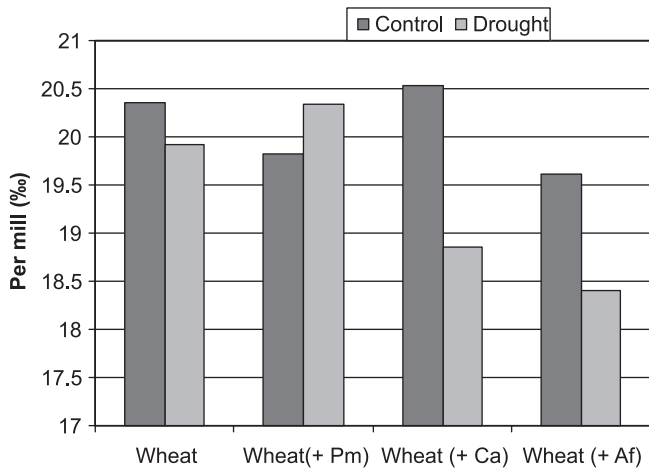


Fig 3 Interactive effect of drought and weed competition on carbon isotope discrimination ($\Delta^{13}C$) in wheat leaves

was because of the reason that the Δ was not much influenced by the stress but by the CO₂ enrichment (Fig 2). It was possible that difference in Δ due to association of different weeds could have been the product of differences in survival, and thus in competition with the crop. Variation in Δ due to competition among individuals has been reported earlier by Pita *et al.* (2001) suggesting the decrease in Δ due to increase in competition. The interaction between stress and elevated CO₂ (Fig 4) suggest that the stress had negative effect and the elevated CO₂ had positive effect on Δ . The decrease in Δ due to drought was about 1‰ under ambient CO₂, whereas, it was 0.4‰ under elevated CO₂ (Fig 4). The interaction between elevated CO₂ and weed association on the Δ (Fig 5) shows that wheat had gained competitive advantage over weeds under elevated CO₂ but, that was variable with its association with different weeds. The average reduction in Δ due to weed competition under ambient CO₂ was 1.9‰ and due to CO₂ enrichment the average increase in Δ against

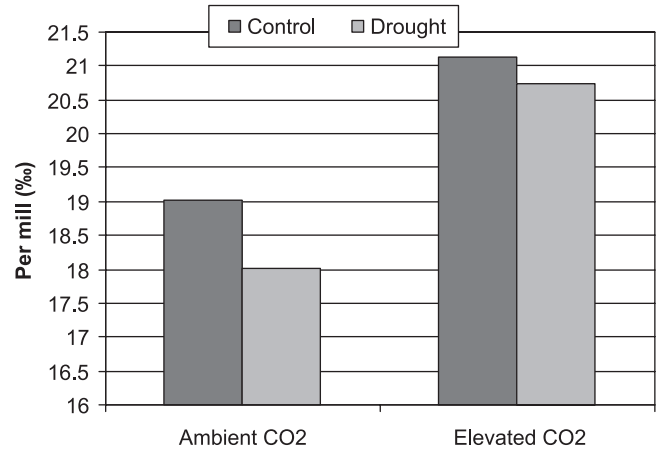


Fig 4 Interactive effect of drought and elevated CO₂ on carbon isotope discrimination ($\Delta^{13}C$) in wheat leaves

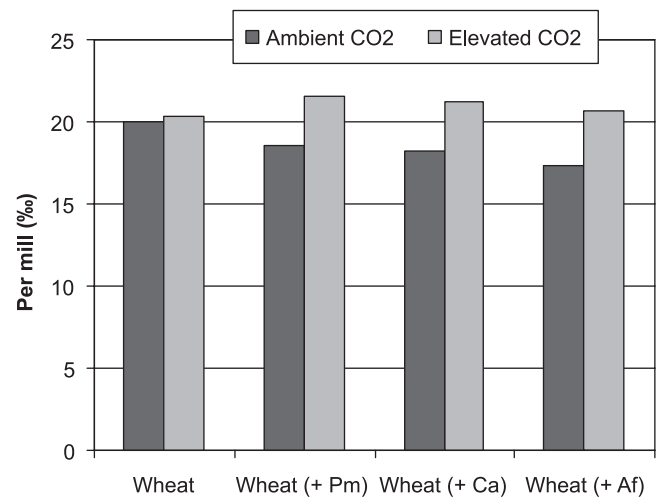


Fig 5 Interactive effect of elevated CO₂ and weed competition on carbon isotope discrimination ($\Delta^{13}C$) in wheat leaves

weed competition was 0.8‰ (Fig 5) indicating the competitive advantage to wheat over weeds due to elevated CO₂.

The relationship observed in this study between CO₂ concentration, drought, weed competition and $\Delta^{13}C$ indicate that impact of drought and weed competition on Δ was lessened by elevated CO₂ (Hamilton *et al.* 2008). The results conclude that Δ values are influenced by the presence of neighboring plants competing for water (Pita *et al.* 2001, McDowell *et al.* 2003). Impact of weed on Δ was similar to that of drought indicating that competition by weeds induces stress on crop. However, resource limitation due to weed competition is more an effect rather than a cause of competition.

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