

CO₂-mediated changes in mungbean chemistry: Impact on plant–herbivore interactions

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The effects of long-term CO₂ enrichment on the foliar chemistry of mungbean (*Vigna radiata* L. Wilczek) and the consequences of these chemical changes on the performance of the tobacco caterpillar (*Spodoptera litura*) were investigated. Foliage was collected from plants grown for kharif season under ambient or enriched CO₂ (average 350 ± 25 and 600 ± 50 µl l⁻¹, respectively) in outdoor, open top chambers at the Plant Physiology Division, Indian Agricultural Research Institute, New Delhi. Under enriched CO₂, level of leaf nitrogen (protein and non-protein nitrogen) declined and levels of starch and total soluble sugars (reducing and non-reducing) in leaves increased. Long-term bioassay (12 days) of tobacco caterpillar revealed that feeding by herbivores on the leaves of C₃ plants may increase due to poor nitrogen concentration and increased non-structural carbohydrate levels, and their growth rate may decrease as the level of atmospheric CO₂ rises. This change in feeding behaviour of herbivores due to enriched CO₂ may cause serious ecological disturbances.

THE continuing rise in the atmospheric CO₂ concentration has been projected to have widespread effects, particularly on plant metabolism and productivity^{1–3}. Leaf-eating insects as well as other herbivores may also influence plant productivity and the change in metabolism rates within the plants may alter insect feeding. Increased feeding by herbivores in elevated CO₂ regimes could reduce the potentially greater plant productivity.

Earlier studies have demonstrated that plant species with the C₃ photosynthetic pathway may exhibit enhanced photosynthetic rates when grown under CO₂ enrichment⁴. Increased availability of fixed carbon may not only enhance growth in some species, but also increase the proportions of leaf-soluble sugars and starch^{5,6}. The accumulation of carbohydrates is thought to dilute the concentration of foliar proteins⁷, making them a comparatively poorer food sources for phytophagous insects⁸. Generalist and specialist feeding insects may respond to the reduced nitrogen quality of their host leaves by increasing consumption rates^{9–11}, and/or suffer reduced

larval weights and prolonged developmental times^{12–14}. Carbon dioxide availability may affect leaf quality to herbivores through factors other than simple dilution of foliar nitrogen. Increase in soluble leaf sugars may be phagostimulatory to locusts¹⁵, while increased leaf storage carbohydrate levels may enhance digestibility of some herbivores¹⁶. On the other hand, CO₂ enrichment may act to increase leaf fibre content¹⁷, which may reduce leaf digestibility to herbivores.

There are many possibilities and interaction between plants and herbivores is a key determinant of community structure worldwide. This interaction is particularly important in tropical conditions where rates of herbivory are higher, plants are better-defended chemically and physically, and herbivores have specialized diets. As a consequence of these tight ecological linkages, the interplay between plants and herbivores in the tropics is more susceptible to perturbations of climate change. However, not a single study from Southeast Asia and only a few studies worldwide are reported regarding the ramification in plant–herbivore interactions under elevated CO₂ concentration.

In the present communication, we report influence of elevated atmospheric CO₂ on plant–herbivore interactions. We fed leaves from mungbean plants grown under two CO₂ concentration regimes to tobacco caterpillar larvae and measured their consumption and growth. The experiment also examines how the carbon supply rates of plants influenced herbivore feeding and growth.

Mungbean (*V. radiata* (L.) Wilczek cv PS16) was grown in 3.5 l earthen pots at the Plant Physiology Division, Indian Agricultural Research Institute (IARI), from 10 July 2000 to 18 September 2000. These pots were filled with sandy-loam soil (pH 7.8) and thoroughly mixed with farmyard manure. One week after germination all pots were thinned to five plants, and in each pot five plants were maintained throughout the growth period. In the experiment, a modified open top chamber (OTC – 1.8 m height and 1.6 m diameter), as described by Rogers *et al.*¹⁸ was developed to study crop responses to elevated CO₂. One group of plants (80 plants/set) was grown under ambient CO₂ (350 ± 25 µl l⁻¹) and another group of plants was grown under elevated CO₂ (600 ± 50 µl l⁻¹) in a naturally lit OTC. A total of 16 pots were used in each chamber for the treatment. The concentration of CO₂ in the chamber was monitored by an infra-red gas analyser (LiCOR 6200).

Leaflet blades of the same physiological age for analysing total sugar, starch and total nitrogen were sampled in July–August 2000 at 22–33 days after germination. All sampling days were mostly clear, bright and sunny. Leaves from the apex of five different plants in each chamber were harvested and carried to the laboratory in an ice-bucket. Total sugar content was estimated by Nelson's arsenmolybdate method¹⁹ using improved copper reagent of Somogyi²⁰. Absorbance was measured at

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630 nm in Spectronic-20 (Baush and Lomb, USA). Dried samples of the residue leaf after extraction for reducing sugars were used for starch content²¹.

Non-protein and protein nitrogen portions in the form of reduced nitrogen in the trichloroacetic acid (TCA)-preserved leaf material were determined by using N-Kjeltech Auto 1030 analyser, following the procedure detailed in the *Tecator Manual*²² (Tecator Company, Hoganas, Sweden).

Larvae of the tobacco caterpillar were reared on an artificial diet to avoid possible conditioning effects from food prior to the feeding trials²³. A laboratory colony was established using eggs obtained from the Division of Entomology, IARI. Eggs obtained within a two-day period were immediately placed on the diet. The larval stage lasted 15 days and it took the larvae 12 days from the hatching stage to reach the 5th instar.

The feeding trials up to 4th instar were carried out inside a controlled chamber at 26°C day, 20°C night with a 14-h day/10-h night and a light intensity of 550 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Twelve feeding trials using larva (from 1st to 4th instar) were performed; five replicates for both the CO₂ regimes. Thirty larvae were placed in separate petri dishes with one lateral leaflet inserted in moistened filter paper to maintain leaf turgidity. Lateral leaflets from matched plants were used to determine the dry weight and nutritional quality of the offered leaflets.

The initial weight of the leaves offered to the larvae was measured at the start of the feeding trial and the leaf material remaining at the end of the feeding trial (every 24 h) was also measured. The initial and final fresh weights of the larvae and their faecal matter were also measured using an electronic balance (Sartorius 1212 MP) for determining consumption of food material.

The food quality of the leaves differed among CO₂ regimes. We studied nitrogen in two parts – protein nitrogen and non-protein nitrogen. Non-protein nitrogen includes chlorophyll, amino-sugars, alkaloids, etc. In the

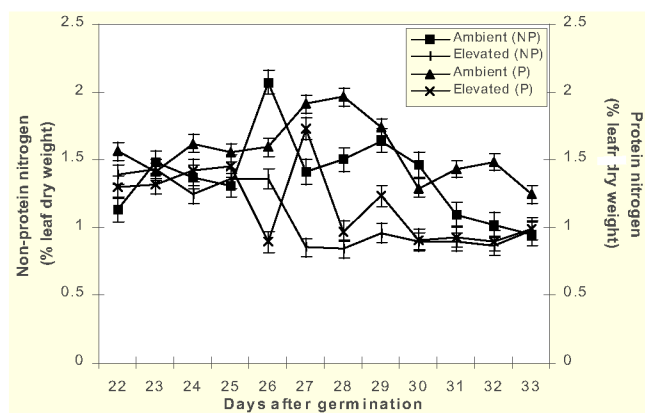


Figure 1. Mean values for non-protein and protein nitrogen in mungbean leaves from 22 to 33 days after germination under ambient and elevated CO₂ condition. Vertical bars on each column indicate SD ($P < 0.05$, $n = 5$).

present study, the non-protein and protein nitrogen in the leaves of elevated CO₂-grown plants were lower than in ambient CO₂-grown plants throughout the experimental period (22 to 33 days after germination) (Figure 1). CO₂ enrichment increased the concentration of leaf starch significantly from 22 to 33 days after germination (Figure 2 b). Similar to starch content, concentration of total soluble leaf sugars (reducing and non-reducing) also increased significantly throughout the vegetative period under CO₂ enrichment, but to a lesser degree than observed with storage carbohydrates (Figure 2 a).

Marked difference in the growth and consumption of *S. litura* was observed when fed with leaves grown at ambient and elevated CO₂ conditions. The larvae ate significantly more leaves of plants grown at high CO₂ than of the plants grown at ambient CO₂ concentrations. The consumption of high CO₂-grown leaves was more at all larval stages, but at the 3rd and 4th instar stages, the

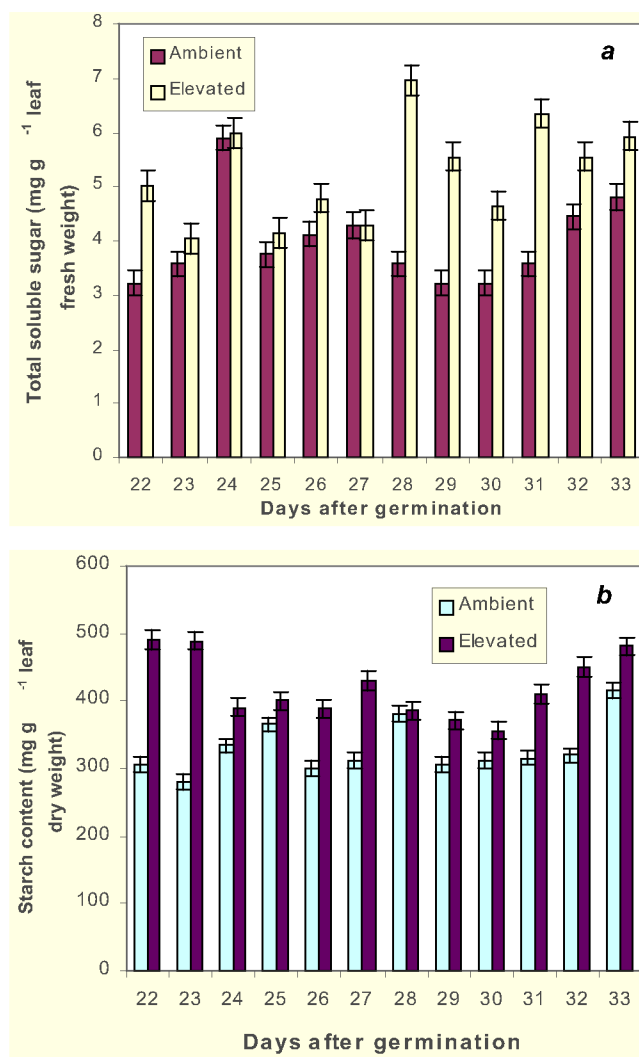


Figure 2. CO₂-mediated changes in (a) total soluble sugar content and (b) total starch content of mungbean leaves from 22 to 33 days after germination. Vertical bars on each column indicate SD ($P < 0.05$, $n = 5$).

consumption was significantly more. They also grew less when feeding on mungbean leaves grown at elevated CO₂ levels compared to performance on leaves from plants grown at ambient CO₂ concentrations (Table 1). Although consumption was more on host leaves grown under enriched CO₂ conditions, caterpillar faecal matter was also highest on the enriched CO₂ conditions. This shows that most of the food eaten remains undigested. However, the approximate digestibility of host leaves to *S. litura* was almost equal in both CO₂ conditions, and no consistent pattern could be obtained for digestion.

The increased feeding observed in this study may be a common feeding response of herbivores to the increasing concentration of atmospheric CO₂. Because the feeding response appears to be determined by leaf nitrogen (protein) level, herbivores, which are limited by nitrogen supply rates, should be the most influenced. Earlier studies have suggested that many herbivores are limited by the nitrogen supply in their food and adjust their feeding rate to maintain sufficient nitrogen intake^{11,24-26}. Therefore, the relative consumption and CO₂ regimes can be discriminated on the basis of leaf quality (i.e. nitrogen content) of the food. Low nitrogen content discriminates high CO₂ regimes and higher consumption. This illustrates the fact that changes in relative consumption between the CO₂ regimes are essentially nitrogen effects or perhaps an unmeasured factor also affected by CO₂.

In the past, studies conducted on phloem-feeding insects such as sweet potato whitefly showed no change in their

feeding behaviour when grown under CO₂-enriched conditions^{27,28}. This lack of response suggests that the composition of the phloem contents is not changed by atmospheric CO₂, in contrast to leaf composition, and the response to elevated CO₂ may be limited to leaf-eating herbivores. Furthermore, both C₃ and C₄ plants generally respond to elevated CO₂ levels with increased growth^{29,30}, but C₃ plants also exhibit increased photosynthetic rate and greater leaf thickness resulting in reduced nitrogen contents at higher CO₂ levels^{31,32}. Hence, increased feeding response of herbivores may be limited to the C₃ plants only. The degree to which increased rate of feeding will depress plant productivity has not been studied in the present case.

We observed increase in total soluble sugars and starch content of the leaves grown under high CO₂ throughout the study. Leaf starch and sugar balance may play an important role in herbivore nutrition, because carbohydrates are usually phagostimulant, highly digestible and represent an essential energy source to many insects³⁴. Although this study has suggested that CO₂ levels affect leaf nitrogen and herbivore response to it, other leaf constituents or even insects themselves maybe affected by CO₂ level. Leaf secondary chemicals via their effects on herbivore as attractants, repellents or toxins³⁴ may over-ride nitrogen effects on herbivore feeding.

In a nutshell, the nutritional quality of mungbean leaves declines substantially due to a dilution of nitrogen under enriched CO₂ atmosphere. The most dramatic and

Table 1. Growth and feeding characteristics of *Spodoptera litura* larvae-fed mungbean leaves from plants grown under ambient (350 ± 25 µl l⁻¹) and elevated (600 ± 50 µl l⁻¹) CO₂ conditions

| LGS | Treatment | Final larval weight (mg) | Initial larval weight (mg) | Weight gain (mg) | Food given (mg) | Leftover food (mg) | Food eaten (FE, mg) | Faecal matter (FM, mg) | Digested food (FE-FM) (mg) | Digestibility (%) |
|-----|-----------|--------------------------|----------------------------|------------------|-----------------|--------------------|---------------------|------------------------|----------------------------|-------------------|
| I | AC | 0.049 ± 0.004 | 0.006 ± 0.0003 | 0.042 ± 0.004 | 20.90 ± 0.54 | 9.38 ± 0.03 | 11.53 ± 0.51 | 0.14 ± 0.003 | 11.39 ± 0.51 | 98.77 |
| | EC | 0.078 ± 0.003 | 0.01 ± 0.0003 | 0.068 ± 0.004 | 42.91 ± 0.32 | 27.33 ± 0.07 | 15.58 ± 0.37 | 0.15 ± 0.005 | 15.45 ± 0.35 | 99.17 |
| | AC | 0.176 ± 0.008 | 0.049 ± 0.004 | 0.13 ± 0.011 | 42.45 ± 0.19 | 26.25 ± 0.06 | 16.20 ± 0.06* | 0.18 ± 0.001 | 16.00 ± 0.06 | 98.76 |
| | EC | 0.116 ± 0.012 | 0.078 ± 0.003 | 0.038 ± 0.013 | 45.76 ± 0.19 | 24.57 ± 0.03 | 21.19 ± 0.03 | 0.35 ± 0.01 | 20.84 ± 0.04 | 98.35 |
| | AC | 1.30 ± 0.10 | 0.176 ± 0.008 | 1.12 ± 0.11 | 212.90 ± 3.02 | 158.49 ± 1.44 | 54.41 ± 1.37* | 0.74 ± 0.02 | 53.67 ± 1.38 | 98.64 |
| | EC | 0.96 ± 0.03 | 0.116 ± 0.012 | 0.84 ± 0.03 | 182.22 ± 2.98 | 115.80 ± 1.73 | 66.42 ± 1.29 | 0.76 ± 0.01 | 65.66 ± 1.26 | 98.86 |
| II | AC | 4.96 ± 0.04 | 1.30 ± 0.10 | 3.66 ± 0.04* | 262.82 ± 3.40 | 173.95 ± 1.14 | 88.88 ± 3.43* | 2.38 ± 0.09 | 86.49 ± 3.81 | 97.32 |
| | EC | 3.47 ± 0.05 | 0.96 ± 0.03 | 2.51 ± 0.10 | 613.64 ± 4.46 | 487.81 ± 1.82 | 125.84 ± 4.45 | 3.04 ± 0.08 | 122.79 ± 4.01 | 97.58 |
| | AC | 11.60 ± 0.07 | 4.96 ± 0.04 | 6.64 ± 0.05* | 832.73 ± 3.42 | 621.33 ± 4.22 | 211.39 ± 4.42* | 8.49 ± 0.11 | 202.91 ± 4.38 | 96.69 |
| | EC | 9.02 ± 0.01 | 3.47 ± 0.05 | 5.55 ± 0.03 | 1007.14 ± 8.44 | 693.62 ± 3.17 | 313.52 ± 3.84 | 8.78 ± 0.14 | 304.75 ± 3.64 | 97.20 |
| | AC | 25.88 ± 0.45 | 11.60 ± 0.07 | 14.28 ± 0.09 | 766.79 ± 6.11 | 539.82 ± 3.33 | 226.97 ± 6.35 | 13.05 ± 0.11* | 213.92 ± 6.35 | 94.25 |
| | EC | 20.96 ± 0.13 | 9.02 ± 0.01 | 11.94 ± 0.09 | 773.09 ± 5.08 | 531.63 ± 8.00 | 241.67 ± 5.09 | 20.09 ± 0.15 | 221.58 ± 5.00 | 91.68 |
| III | AC | 42.64 ± 0.13 | 25.88 ± 0.45 | 16.76 ± 1.02* | 500.70 ± 1.14 | 229.59 ± 1.28 | 271.11 ± 1.19* | 17.56 ± 0.12* | 253.53 ± 1.21 | 93.52 |
| | EC | 30.08 ± 0.05 | 20.96 ± 0.13 | 9.12 ± 0.17 | 823.77 ± 1.02 | 388.99 ± 1.29 | 434.78 ± 3.36 | 21.62 ± 0.15 | 413.76 ± 3.38 | 95.17 |
| | AC | 63.72 ± 0.22 | 42.64 ± 0.13 | 21.08 ± 0.45* | 652.70 ± 2.18 | 289.20 ± 5.29 | 363.55 ± 4.36* | 20.09 ± 0.11* | 343.46 ± 4.31 | 94.47 |
| | EC | 47.57 ± 0.08 | 30.08 ± 0.05 | 17.49 ± 0.14 | 807.10 ± 6.38 | 390.29 ± 7.27 | 416.81 ± 7.53 | 29.65 ± 0.16 | 387.16 ± 7.50 | 92.89 |
| | AC | 112.81 ± 8.14 | 63.72 ± 0.22 | 49.09 ± 4.18* | 1100.00 ± 9.35 | 536.22 ± 1.77 | 563.78 ± 6.18 | 31.67 ± 0.12* | 532.11 ± 6.18 | 94.38 |
| | EC | 92.33 ± 9.14 | 47.57 ± 0.08 | 44.76 ± 4.44 | 1006.53 ± 6.80 | 430.99 ± 6.18 | 575.53 ± 7.50 | 40.27 ± 0.10 | 535.26 ± 7.50 | 93.00 |
| IV | AC | 153.88 ± 10.21 | 112.81 ± 8.14 | 41.07 ± 1.31* | 1045.67 ± 6.11 | 386.62 ± 3.33 | 659.05 ± 2.18* | 43.51 ± 0.47 | 615.48 ± 2.18 | 93.39 |
| | EC | 125.22 ± 8.15 | 92.33 ± 9.14 | 32.89 ± 2.32 | 1188.89 ± 9.09 | 379.63 ± 3.00 | 809.26 ± 3.55 | 43.88 ± 0.28 | 765.38 ± 3.59 | 94.58 |
| | AC | 205.64 ± 8.16 | 153.88 ± 10.21 | 51.76 ± 4.47* | 1309.94 ± 10.6 | 683.20 ± 8.19 | 626.74 ± 9.53* | 45.65 ± 0.29 | 581.09 ± 9.56 | 92.72 |
| | EC | 163.57 ± 8.29 | 125.22 ± 8.15 | 38.35 ± 2.33 | 1296.75 ± 11.3 | 583.04 ± 5.83 | 713.72 ± 8.53 | 47.86 ± 0.32 | 665.86 ± 8.50 | 93.29 |
| | AC | 264.78 ± 9.15 | 205.64 ± 8.16 | 59.14 ± 5.29 | 1413.83 ± 10.5 | 794.52 ± 6.55 | 619.32 ± 8.63* | 50.12 ± 0.98 | 569.20 ± 8.60 | 91.11 |
| | EC | 217.64 ± 9.11 | 163.57 ± 8.29 | 54.07 ± 4.31 | 1361.98 ± 9.35 | 668.38 ± 8.38 | 696.61 ± 8.18 | 52.34 ± 0.36 | 641.28 ± 8.20 | 92.46 |

LGS, Larval growth stages; AC, Ambient CO₂; EC, Elevated CO₂; Values are mean ± SD of five replications and each replicate consists of 30 larvae. Growth and feeding characteristics of single larva are given. *P < 0.05; n = 5.

robust effect of climate change on plant–herbivore interaction would change the feeding behaviour of *S. litura*.

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Thermomechanical structure of the central Indian shield: Constraints from deep crustal seismicity

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Intraplate seismicity in the Indian shield is confined to the upper 10–15 km except for the Jabalpur and Satpura events which occurred at a depth of 35–40 km in the region bounded by the Narmada–Son and Tapti lineaments, two major palaeo-rift-related tectonic features in the central Indian shield. Interestingly, high surface heat flow of 70–100 mW/m² has been suggested for the above region. Rheological models of continental crust in such a high heat flow regime do not support occurrence of deep crustal seismicity. In the present work we computed a range of rheological models for the region for different values of thermal parameters and analysed these in light of deep crustal seismicity. The study suggests that mantle-derived heat flow should be significantly low for the occurrence of deep crustal events in the above region and the excess surface heat flow could be a manifestation of fluid advection in the uppermost part of the crust, as is evident from the presence of many hot springs.

THE Indian shield has experienced many intraplate earthquakes of magnitude > 5.0 during the last fifty years. These include Anjar (1956), Broach (1970), Bhadrachalam (1969), Killari (1993), Jabalpur (1997), Koyna (1967), and Satpura (1938) events^{1–6}. The focal depths of these events are confined to the upper 10–15 km, except for the Jabalpur and Satpura events which occurred at a depth of more than 35 km in the region (hereafter called

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