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SPATIAL ADAPTATION AND DEVELOPMENTAL STRATEGY IN CARBON DIOXIDE ENRICHED MUSTARD PLANTS

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The morphological adaptation and developmental strategy of mustard plants, grown at 330 (atmospheric), 600 and 900 ppm CO_2 enriched atmosphere, are described. CO_2 enrichment evoked differential response pattern to the longitudinal and spatial adaptation. An increase in the atmospheric level of CO_2 resulted in increased plant height and greater number of branches. Development of assimilatory structures followed almost identical pattern corresponding to the plant height and branches. The absolute DM production was an increasing function of CO_2 concentration, but with no apparent set-back on the phasic development and pattern of DM distribution in different components indicating that increasing atmospheric CO_2 concentration also improved yield capacity through increased number of pods/plant and heavier seeds but with a consistent depression in harvest index.

Key words: CO, enrichment, Plant height, Area indices, DM accumulation, Harvest index.

Introduction

The atmospheric concentration of CO_2 is known to have increased from the beginning of twentieth century and is still increasing by more than 1 ppm per annum, mostly because of increased combustion of fossil fuels [1-5]. This increase in CO_2 concentration is causing the 'greenhouse effect' - a most talked about issue alarming the scientists around the globe for its predicted adverse effect upon the totality of the environment.

A change in CO_2 concentration also brings about a change in crop environment. The effect of such environmental change due to elevated CO_2 on plant growth is recognizable even under hydrophonic conditions [6] and varying (35 or 90%) relative humidity [7]. The direct effect of increased CO_2 is, however, beneficial for agro-ecosystem [8]. Eventually CO_2 enrichment has become one of the most spectacular ways of increasing yield in greenhouse and horticultural crops [9-11]. Even in field crop like mustard (*Brassica juncea*) an 8-10 days exposure to high CO_2 content (0.14%) brings about greater photosynthesis and nitrogen metabolism [12].

Most of the CO_2 enrichment experiments, conducted on various crops, are of short duration at different stages of growth and a very few of them from seedling to maturity. But such studies are of interest because there is little knowledge as to whether any long-term effect will emerge as feed-backs which can offset or reinforce the potential advantage in the performance of the plants. The present experiment with mustard plant was undertaken to follow the spatial adaptation and developmental strategy from seedling to maturity at atmospheric, 600 and 900 ppm CO_2 concentration. This

will allow a more reasonable extrapolation of the growth responses to the presently increasing concentration of CO_2 in the atmosphere.

Materials and Methods

Seeds of white mustard *Sinapis alba* cv. Bixley were sown on 24 May 1980 in plastic pots $(13 \times 9.5 \times 9.5)$ containing a mixture of peat and perlite under greenhouse condition with supplemental light. From 5-8 days after sowing (DAS) only one plant was allowed to grow in each pot. On 10 DAS 48 pots containing uniform plants were compacted in each of the three growth cabinets and were subjected to 330 (atmospheric), 600 and 900 ppm CO₂ contents. Each of the growth cabinet (90 x 90 x 90 cm) was made of iron frames to which glasses were fixed from all sides except bottom. The top and a vertical side had the provision of removable iron frames. The bottom was made of 3 cm wooden planket subtended by 15 cm wooden frame at the base and was placed about 25 cm above the floor of the greenhouse on four wooden pillars.

Air containing the required level of CO_2 entered the cabinets corresponding to an air renewal capacity of about 15 times per hour. The desired concentrations of CO_2 (supplied from a steel tank) were achieved by adjusting the low-flow rotameter and by continuous monitoring of the air with an infrared gas analyzer (type URAS 1, Hartman & Braun AG, FRG). The CO_2 level in the enriched chambers were controlled to 600 ± 30 and 900 ± 30 ppm, while in the atmospheric level it was 330 ± 10 ppm. When the cabinet doors were opened for watering, measurements etc. there was a large but brief deviation of CO_2 concentrations. The CO_2 enrichment was maintained from 06.00 to 18.00 hrs each day and continued until final harvest.

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The growth cabinets were naturally illuminated through the glass roof of the greenhouse (the natural illumination being 14 to 16 hrs, but each cabinet had supplementary light from a Philips HPLR 700 W Lamp suspended at a height of about 25 cm above the cabinet. The supplementary light was used during the period of CO, enrichment and was autocontrolled. This in addition to the natural light provided about 133 µmol m⁻² s⁻¹ photosynthetically active radiation (PAR) in the centre of the cabinet. The natural PAR both outside and inside of the greenhouse was measured on several occasions in both clear and cloudy days by quantum sensor attached to a Steady State Porometer (model LI-1600 from LI-COR, Inc. Lincoln, Nebraska, USA) to estimate the fraction of natural PAR on the growth cabinets. The relative amount of natural PAR on the cabinets was found to be a function of solar elevation with a maximum of 60% when the sun was high and reduced with increasing angle of incidence. However, on an average about 44% of the outdoor PAR was available on the cabinets.

The temperature in the chambers was partially controlled to ensure minimum by blowing the air through thermostatically controlled heating wires. Although the procedure effectively controlled the day/night minimum temperatures to about 22/18°C in the early experimental period, in June/July when the solar radiation was high, the day/night temperatures on some occasions exceeded 35/28°C. To avoid such excessive temperatures mist irrigation was applied at short intervals. Moreover, the roof of the greenhouse was provided with automatic devices to ventilate the excess temperature from the greenhouse whenever it exceeded 30°C. All other environmental parameters in the three growth cabinets were identical except CO₂ concentration, which was the only experimental variable.

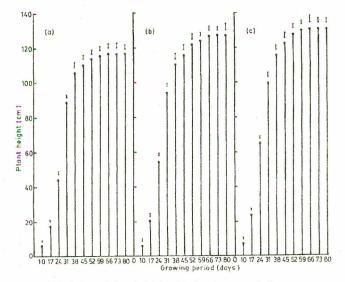
Crop sampling beginning from 10 DAS were made at weekly intervals until maturity, harvesting four pots at random from each of the three cabinets. With the advancement of crop growth the individual plant of each treatment was separated into components representing leaves, stem, branches, inflorescence etc. The height of the plant from soil level to the top of the individual plant was determined by a graduated scale. After separation the areas of the components of the individual plant except stem were determined by placing them in an electronic area meter (type LI-3000, Lambda Instrument Co., Nebraska, USA). The area of the stem was calculated by measuring base diameter, top diameter and the length of the stem in question.

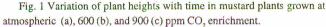
The dry matter (DM) determination of various components including roots were undertaken at each harvest after being oven-dried for 24 hrs at 80°C. At final harvest yield components like number of pods/plant and weight of seeds were also determined. All data were computed by Statistical Analysis System (SAS) according to Barr *et al.* [13] to derive the means of observation.

Results and Discussion

Plant height. The CO_2 induced spatial distribution of mustard plant has been evaluated in terms of plant height. The pattern of longitudinal growth was very much similar in all the treatments (Fig. 1). From emergence until 31DAS the stem elongation appeared to be exponential, although the values of the exponents were distinctly higher with increasing concentration of CO_2 . Thirty one DAS and with inflorescence initiation the stem elongation appeared to be some-what linear until attaining the final height. However, maximum heights of about 130 and 134 cm were observed in 600 and 900 ppm CO_2 treated plants respectively, compared to about 120 cm in the control plants. Further possible increase in plant height in CO_2 treated plants was arrested by the glass roof of the growth cabinets.

The increasing CO_2 enrichment had increasing apical dominance to produce greater plant heights. Such apical dominance was also reported in tomato plants grown in elevated CO_2 [10]. Since mustard is an indeterminate plant, where vegetative growth and flowering continue until about maturity, this variation in plant height may have a far-reaching consequence in the habitats of the plant. The greatest advantage of increased plant height in CO_2 induced mustard plants was probably associated with the leaves over-topping the neighbour and most obviously displayed flowers to the roving pollinators or wind. Unfortunately pollinators were absent during flowering period since, the plants were grown in growth cabinets placed in a greenhouse. Offsetting the advantage of height there were also disadvantages, the great length





of the stem could be a respiratory burden and finally under conditions of heavy bearing there was a great risk of lodging.

Branching. CO_2 enrichment evoked a differential response pattern in branching. The time of initiation of branching was not different among the treatments, which was first recorded 31 DAS concomitant with the inflorescence initiation (Fig. 2). CO_2 enrichment induced production of a greater number of branches than in the control plants. A maximum of about 5 branches per plant was observed in the control plants compared to more than 7 in CO_2 enriched plants. Although 900 ppm CO_2 treated plants ultimately produced a slightly higher number of branches than 600 ppm CO_2 plants, this difference was not statistically significant. The number of branches per plant declined in all the treatments with ages which was more pronounced in the control plants. This reduction was through the degeneration of smaller branches that could not compete until maturity.

Dring the vegetation and reproductive stages of growth many morphological changes occurred in the plants. Plant height and branching were the first steps in that direction to react to CO_2 enrichments. These and other associated changes led to the subsequent adaptation of functional organs of the plants.

Profuse branching is essential for increased yield in mustard plants [14]. The CO_2 enrichment not only played a dominant role in the longitudinal status of mustard plants (Fig. 1), but also in the status of branching (Fig. 2). However, most of the control of the extent of branching in mature plants, grown at atmospheric CO_2 , occured by both inhibition of their formation and degeneration of branches (Fig. 2). With CO_2

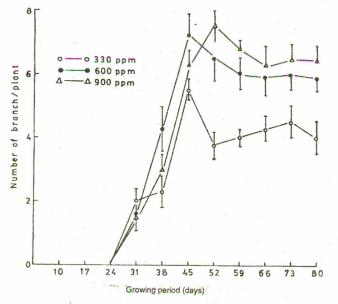


Fig. 2. Pattern of branching in mustard plant under the influence of increasing CO_2 concentrations. The vertical bar represent the standard error of means.

enrichment, although the degeneration of branches was not a rare event, formation of higher number of initial branches led to the superiority over the control plants.

Development of area indices. The expansion of foliar and other assimilatory structures is probably the most important measure for morphological adaptation in a plant. The ontogenetic variation in assimilatory structures due to the effect of CO_2 enrichment in mustard plants has been evaluated in terms of leaf, stem, branch, inflorescence and total green area indices and the results are presented in Fig. 3. During the vegetative stage of growth the leaf area indices (LAIs), from initial smaller values, sharply increased in an exponential manner to the maxima of 2.5, 3.0 and 3.4 in atmospheric, 600 and 900 ppm CO_2 treated plants respectively. Subsequently the LAIs steadily decreased until the complete senescence was apparent between 59 to 66 DAS. The leaf senescence, however, appeared to be faster in CO_2 treated plants.

The development of stem area indices (SAIs) followed more or less an identical pattern with the LAIs. The SAIs after attaining the maxima of 2.0, 2.3 and 2.5 in the atmospheric, 600 and 900 ppm CO_2 treated plants respectively at 38 DAS remained relatively unchanged in most period of vegetative growth. The SAIs then declined as the maturation approached, but with a faster rate in the control plants.

The development of inflorescence (IAIs) and branch area indices (BAIs) was marked at a time when the LAIs and SAIs were at their rapid phase of exponential growth and continued until complete senescence of leaves. However, CO_2 enrichment resulted in higher IAIs of 0.9 and 1.1 in 600 and 900 ppm CO_2 treated plants respectively compared to 0.7 in the control plants. The difference in BAIs among the treatments was apparently very small, appeared to be relatively unchanged

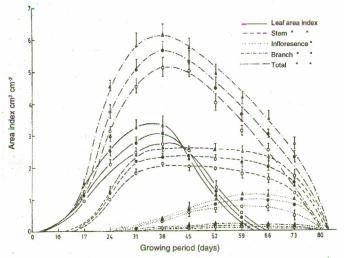


Fig. 3. Changing pattern of area indices of different components of mustard plants under atmospheric (•), 600 (o), and 900 (Δ) ppm CO₂. The vertical bar represent the standard error of mean.

and centred around 0.2 during the most active period of growth.

The integrated total area indices (TAIs) were maximum at a time when LAIs and SAIs were at their peak. However, the maximum TAIs were again among the CO_2 treated plants and was the contribution from higher area indices in most structures. The TAIs apparently had a reduction phase concomitant the beginning of leaf senescence, but the duration of TAIs was much longer than the LAIs due to the longer duration in other components.

It is apparent from Fig. 3 that the LAIs and TAIs were the continual changing function of time and none of them assumed any steady value in any treatment at any stage of growth. The SAIs, BAIs and IAIs on the other hand, appeared to be relatively unchanged after attaining the maxima in most periods of growth. They remained active. The variation in LAIs and TAIs with time was mainly ascribable to changes in leaf number per plant, the expansion and death of leaves. The initial increase is LAIs during the vegetative phase was the result of increased leaf number per plant and the subsequent expansion of leaves. With the production of maximum number of prime-order leaves (leaves on the main stem) the growing point of the stem eventually ceased to produce new leaves and became inflorescence, initials and lateral branches. At a time when second order leaves (leaves on the branches) were developing the older ones were senescing through age at higher rate than the production of second-order leaves. However, the leaf senescence was relatively faster in CO₂ treated plants (Fig. 3). This was probably due to the initial high expenditure of plant vigour for generating more foliar structures through faster growth, but lack of continuity with age [15].

The TAIs were the balance between senescing leaves and other existing green structures. Therefore, even at falling LAIs the extent and duration of TAIs (the sum of all other green organs) acted as light trapping apparatus in the ontogeny of mustard plants until senescence was apparent with physiological maturity. The reducing leaf areas were associated with increasing inflorescence areas. This can be explained from Watson's [15] proposition that the production of leaves ceases with the development of an inflorescence at a growing point. This is because the presence of a growing inflorescence has an inhibitory effect on the expansion of young leaves immediately below it.

The physiological analysis of variation of leaf area indices was accounted by both external and internal factors involving the availability of mineral nutrition and water, meristematic activity, rate of production of leaf area etc. [15]. CO_2 enrichment in mustard plants induced greater assimilatory structures through the increased leaf area in the vegetative

and through the greater stem and inflorescence area at the reproductive stages.

CO, enrichment and phasic development. The CO₂ induced DM production in mustard plants, considering to be composed of a series of successive exponential growth curves representing the growth of different organs, has been plotted as a series of straight lines (Fig. 4). An analysis of the curves presented in Fig. 4 recognized several growth phases. These phases roughly corresponded to the overall morphological changes of the plants. The initial phase, extended from germination to 24 days of growth, was characterized by a rapid growth rate and development of leafy structure. The second phase, from 24 to 38 days of growth, was marked by a moderate growth rate through stem elongation and leaf expansion and terminated with the attainment of maximum leaf area and rapid growth of inflorescence. In the third phase, from 38 to 66 days of growth, the growth rate gradually declined, but inflorescence gradually expanded at the expense of steep decrease in leaf area. The fourth phase, from 66 days to maturity, was a period of reduction of DM production mainly associated with respiratory losses in the absence of active photosynthetic organs and corresponded to the ripening of pods. This phase was characterized by a steady decrease in the still existing green structures due to the death of the green organs through maturity.

The theoretical concepts of phasic development in plants was introduced by the Russian plant physiologist Lysenko in 1935 and critically reviewed by Whyte [16]. According to

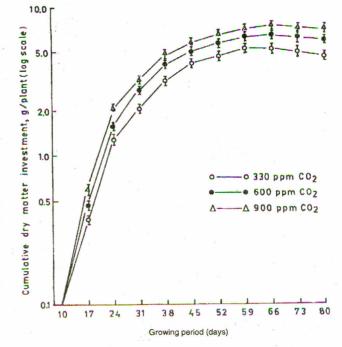


Fig. 4. Phasic development in mustard plants as a function of time and CO_2 enrichment. The vertical bar represent the standard error of mean.

MORPHOLOGICAL ADAPTATION AND DEVELOPMENT STRATEGY OF MUSTARD PLANTS

these concepts (i) the growth and development are not identical phenomena, (ii) the entire process of development consists of individual stages, (iii) these stages proceed in a strict sequence and the subsequent stage cannot set in until the preceding one has been completed and (iv) the different developmental stages require different environmental conditions for optimal growth. All of these stages, or at least most of them, are externally visible during the growth processes and some of them may not reflect any qualitative changes but still occurring in the life of a plant. In mustard plants too, these phases may have a real existence corresponding well to the actual events occurring during the ontogeny. However, CO, enrichment manifested apparently no set-back effect on the phasic development (Fig. 4). The increased DM production in CO, treated plants was the result of extended plant activity through greater assimilatory structure (Fig. 3) and increased net assimilation rate [17] and not due to the alternation of phasic development.

Accumulation, transloction and loss of DM. It has been attempted to relate DM accumulation with the translocation and loss of accumulated product in CO_2 enriched mustard plants, and the results are presented in Table 1. The amount of plant materials translocated or lost was calculated as follows [18].

Translocation (%) =
$$\frac{X_{max} - X \text{ maturity}}{X_{max}} \times 100$$

where, X_{max} = amount of DM in a plant component at a stage when it was maximum, and

X maturity = amount of DM in the same component at maturity.

It is apparent from Table 1 that there was an initial rapid increase in leaf, stem and root dry weight with the advancement of plant age which dropped after attaining the maximum. However, the DM accumulation in all the components was greater for CO, treated plants, while the decrease was maximum for the control plants. The apparent growth after 45 days in most components were practically halted except in inflorescence and branches. From a maximum DM accumulation at 45 days of growth the leaves, stems and the roots were loosing their weights, but the inflorescence DM was still increasing even after complete leaf senescence at 59 days of growth. The increase in inflorescence DM during this period was mostly accounted for by the photosynthetic contributions of growing pods [19, 20]. The contribution was, however, much higher for CO, treated plants as evident from higher inflorescence DM accumulation (Table 1).

As the maturation approached the control plants comparatively lost a higher amount of assimilated products from all the components than the CO_2 treated plants, but with a small increase in inflorescence DM. Therefore, there were reasons to believe that much of these materials were translocated for the growth of the pods when current photosynthesis was inadequate for rapid growth. The mobilization of assimi-

| TABLE 1. ACCUMULATION, TRANSLOCATION AND LOSS OF DM (g/PLANT) IN DIFFERENT COMPONENTS OF MUSTARD PLANTS AT |
|--|
| Successive Stages of Development Under Different Levels of CO ₂ – Enrichment. |

| Components | Growth day $ppm CO_2$ | 10 | 17 | 24 | 31 | 38 | 45 | 52 | 59 | 66 | 73 | 80 | %lost |
|------------|-----------------------|------|------|------|------|------|------|------|------|------|------|------|-------|
| Leaves | 330 | 0.05 | 0.31 | 0.63 | 0.74 | 1.01 | 1.81 | 1.04 | 0.93 | 0.64 | 0.52 | 0.51 | 56.78 |
| | 600 | 0.05 | 0.37 | 0.73 | 0.96 | 1.23 | 1.16 | 1.08 | 1.00 | 0.74 | 0.64 | 0.61 | 50.41 |
| | 900 | 0.05 | 0.47 | 0.91 | 1.21 | 1.41 | 1.26 | 1.09 | 1.02 | 0.74 | 0.72 | 0.71 | 49.64 |
| Branch | 330 | | | | 0.03 | 0.06 | 0.23 | 0.36 | 0.38 | 0.37 | 0.34 | 0.30 | 21.05 |
| | 600 | _ | | | 0.02 | 0.15 | 0.35 | 0.49 | 0.54 | 0.49 | 0.47 | 0.45 | 16 67 |
| | 900 | _ | | | 0.02 | 0.81 | 0.46 | 0.63 | 0.65 | 0.62 | 0.59 | 0.57 | 12.31 |
| Stem | 330 | 0.01 | 0.08 | 0.54 | 1.00 | 1.63 | 1.77 | 1.74 | 1.49 | 1.30 | 1.23 | 1.17 | 33.90 |
| | 600 | 0.01 | 0.11 | 0.72 | 1.50 | 2.10 | 2.41 | 2.32 | 2.13 | 1.90 | 1.85 | 1.82 | 24.48 |
| | 900 | 0.01 | 0.13 | 0.99 | 1.91 | 2.55 | 2.64 | 2.63 | 2.44 | 2.28 | 2.18 | 2.17 | 17.80 |
| Inflo | 330 | _ | | 0.09 | 0.26 | 0.49 | 0.96 | 1.46 | 2.26 | 2.91 | 2.88 | 2.72 | 6.53 |
| | 600 | _ | _ | 0.12 | 0.29 | 0.66 | 1.14 | 1.79 | 2.65 | 3.40 | 3.28 | 3.26 | 4.12 |
| | 900 | | | 0.16 | 0.31 | 0.70 | 1.41 | 2.18 | 3.06 | 3.78 | 3.70 | 3.62 | 4.23 |
| Roots | 330 | 0.01 | 0.08 | 0.21 | 0.31 | 0.45 | 0.52 | 0.48 | 0.46 | 0.41 | 0.36 | 0.33 | 36.54 |
| | 600 | 0.01 | 0.09 | 0.25 | 0.40 | 0.56 | 0.65 | 0.64 | 0.59 | 0.54 | 0.49 | 0.47 | 26.15 |
| | 900 | 0.01 | 0.11 | 0.31 | 0.47 | 0.59 | 0.68 | 0.71 | 0.69 | 0.61 | 0.57 | 0.54 | 23.94 |
| Total | 330 | 0.07 | 0.47 | 1.47 | 2.34 | 5.64 | 4.66 | 5.08 | 5.64 | 5.63 | 5.33 | 5.03 | 10.82 |
| | 600 | 0.07 | 0.57 | 1.82 | 3.17 | 4.70 | 5.71 | 6.32 | 6.91 | 7.07 | 6.73 | 6.61 | 6.51 |
| | 900 | 0.07 | 0.71 | 2.37 | 3.92 | 5.43 | 6.45 | 7.24 | 7.86 | 7.99 | 7.76 | 7.61 | 4.76 |

late in *Sinapis alba* has been demonstrated by ³²*p*-labelled phosphoric acid [21] and ¹⁴C-assimilates [22] at different stages of growth. However, a comparatively smaller loss of assimilated products in the CO_2 treated plants (Table 1) suggests that the current photosynthesis was enough to meet the demand of growing pods. Nevertheless, from the maximum TDM about 12 and 5% absolute losses were apparent in the control and CO_2 treated plants respectively. This loss was probably accountable to the respiration in the maturing plants when the net photosynthesis was practically nil after complete senescence of assimilatory structures.

Reproductive capacity and yield. The effect of CO_2 enrichment on the reproductive capacity of mustard plants has been evaluated in terms of number of pods, seed yield (mass/ plant), 100 seeds weight and their relation to biological yield and harvest index, and the results are presented in Fig. 5. The number of pods produced per plant, the seed yield and 100 seed weight were positively related to the increasing biological yield with increasing concentration of CO_2 in the atmosphere, but the harvest index was negatively related.

The number of pods produced per plant linearly increased from 69 to 77 and 84 in the control, 600 and 900 ppm, but the seed yield increased from 0.9g in the control plants to 1.6 and 1.7g in 600 and 900 ppm CO, treated plants respectively. The corresponding biological yield increased from 5.0g in the control plants to 6.6 and 7.6g in 600 and 900 ppm CO, treated plants, but with 6 to 11% decrease in the harvest index. In Indian mustard (Brassica juncea) the seed yield was reported to be positively correlated with the number of primary and secondary branches per plant, plant height, number of seeds per siliqua and 1000 seed weight [23, 24]. The present data on CO, enrichment agree well with the views expressed by these authors, but contradict with Mehrotra et al. [14] who reported a positive correlation between biological yield and harvest index with the number of pods per plant and seed yield. This differential response could be attributed to the poor fruit setting in the present experimental plants.

For maximum fruit setting a maximum pollination is essential. The mustard are both self and cross pollinated plants, where the basic pollinating agents are the winds and honeybees [25, 26]. Self and cross pollination in *Sinapis alba* are seriously affected when grown in isolation from pollinating agents under greenhouse conditions and the seeds produced from such plants are shorter and smaller than the normally grown field plants [27]. The seed production in white mustard plants caged with honeybee was about twice than the plants without honeybees [28]. All these evidences and the present experimental data suggest that mustard plants grown in isolation in the growth cabinets, where no pollinating agent was present, suffered a serious set-back for lack of pollination and resulted in reduced reproductive growth. Moreover, during the period of reproductive development the experimental plants experienced repeated infestation from mustard aphids. The seed yield was thus affected by both reduced number of pods/plant and reduced size of seeds with a consistent depression in harvest index despite a higher biological yield in CO₂ treated plants.

A somewhat higher yield in CO_2 treated plants was associated primarily with higher number of pods and heavier seeds (Fig. 5). This has been further evidenced from CO_2 mediated induction of pollen adhesion, germination, tube penetration, tube growth through the stylar tissue and seed setting in *Brassica compestris* [29]. Most of this reproductive

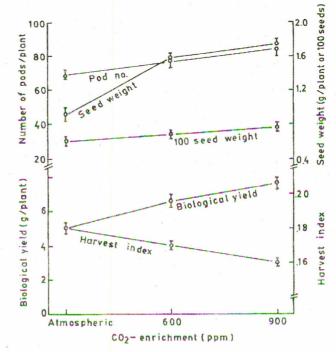


Fig. 5. Effect of CO_2 enrichment on the yield capacity of mustard plants. The vertical bar represents the standard error of mean.

growth occurred in the period of senescing leaves when the leaf, stem and root DM were departing from their maximum (Table 1). Thus the peak period of DM accumulation in most components did not coincide with the rapid growth in the inflorescence. In the control plants this rapid growth in the inflorescence was partially met by assimilate mobilization from other structures (Table 1), thus offering competition for assimilate utilization by seeds. The situation in CO₂ enriched mustard plants was different with reduced mobilization from other organs despite higher accumulation and most of the reproductive growth was the result of current photosynthesis after leaf senescence. Thus the present finding clearly demonstrates that the increasing atmospheric concentration of CO₂ although may have some promotive effects upon the vegeta-

tive growth should have no apparent set-back in the reproductive efforts of mustard plants.

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