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# CARBON DIOXIDE COMPENSATION CONCENTRATION IN RELATION TO PHOTORESPIRATORY ENZYMES IN PEA ($C_3$) AND SORGHUM ($C_4$) AS INFLUENCED BY STRESS AND NITROGEN

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## SUMMARY

Carbon dioxide compensation concentration ($CO_2CC$) in relation to photorespiratory enzymes viz., glycolate oxidase (GO) and catalase at various growth stages of Pea ($C_3$) and Sorghum ($C_4$) was studied. Attempt was made to relate nitrate reductase (NR) enzyme as marker to photo-respiration. Further, these investigations include study of $CO_2CC$ in changed environments like moisture stress and nitrogen fertilization. A positive relationship between $CO_2CC$ and NRA in pea was observed when nitrate was given as a sole source of nitrogen. In sorghum, $CO_2CC$ was related more to GO, whereas stress reversed these relationships.

## INTRODUCTION

The carbon dioxide released in photorespiration may be liberated by decarboxylation of glycine formed either by glycolate pathway through glycolate oxidase and catalase activities (Kisaki *et al.*, 1969; Zelitch, 1975) or by nitrogen assimilation pathway through nitrate reductase activity (Fair *et al.*, 1974 a; Lips and Avissar, 1972; Kalpan *et al.*, 1974). Lawlor and Fock (1976) studied water stress induced changes in photosynthesis, photorespiration and $CO_2CC$ of wheat and found that net photosytnhesis and photorespiration decreased with stress. Carbon flux through glycolate decreased. But respiration increased in light with stress, thus the total photorespiration remained large. Studies of Weissman (1972) on soybean and sunflower showed that NRA was inhibited in sunflower when ammonia was applied to roots whereas in soybean there was no such inhibition. Photorespiration is linked to nitrogen metabolism (Cresswell *et al.*, 1974).

Influence of moisture stress on $CO_2CC$ was studied in $C_3$ and $C_4$ plants by Glinka and Katchansky (1970), Heath and Meidner (1961), and O'toole *et al.* (1976). Few attempts were made to relate $CO_2CC$ with photorespiratory

enzymes in $C_3$ and $C_4$ plants, as influenced by growth stages, moisture stress and nitrogen fertilization. Hence, the present studies were undertaken.

## MATERIALS AND METHODS

Sorghum (*Sorghum vulgare* Pers.) and pea (*Pisum sativum* L.) were grown in summer and winter seasons repectively as described earlier (Chandra and Sirohi, 1983). $CO_2CC$ was measured by modified method of Sirohi and Srivatsava (1978). For estimating $CO_2CC$ in pea, branches with fully developed young leaves (3rd-5th leaf) from the top were collected. In sorghum, after anthesis, 2nd leaf below flag leaf was taken for $CO_2CC$ estimation. Sampling was done at 5.30 A.M.

Nitrate reductase activity was assayed *in vivo* following the method of Klepper *et al.* (1971). Glycolate oxidase activity was assayed by method of Mc Naughton and Fullen (1970) and Catalase activity was measured following the method of Teranishi *et al.* (1974.) There were 4 replications for each enzyme assay. For assaying NRA, GO and catalase, fully developed young leaves (leaflets in case of pea) preferably 3rd-4th leaf from top were used. Sampling was done at 10 A.M., allowing at least 2 hours of bright sunshine before sampling. Results were statistically analysed with the help of IBM-computer model 1620. As there was not much difference in results due to concentration, the data were pooled and given accordingly.

## RESULTS AND DISCUSSION

Carbon dioxide compensation concentration in pea increased over control when stress and nitrogen was applied (Table I). Ammonical form showed higher $CO_2CC$ values than nitrate form. A progressive increase in $CO_2CC$ with age was noticed except for low values at flowering in plants supplied with nitrogen (both $No^-_3$ and $NH_4^+$), under normal water supply (Table I).

In sorghum, a typical $C_4$ plant, the pattern of changes in different treatments was by and large similar for both the systems. Moisture stress increased $CO_2CC$ in sorghum also. Ammonia showed somewhat higher values of $CO_2CC$ than control, and nitrogen at all growth stages. $CO_2CC$ dropped at flowering stage in non-stress plants, but in stressed plants $CO_2CC$ was more at flowering stage than at seedling stages (Table I).

Nitrate reductase activity (NRA) in moisture-stress control pea plants showed a decline at flowering followed by a rise at later stages reaching a

Table I : Mean carbon dioxide compensation concentration at various stages of growth in pea and sorghum (expressed as ppm of $CO_2$ in enclosed air)

| Stages / Sub—Treatment | Seedling | | | Flowering/Anthesis | | | Pod/grain formation | | | Pod/grain maturity | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Non—Stress | Stress | Mean | Non—Stress | Stress | Mean | Non—Stress | Stress | Mean | Non—Stress | Stress | Mean |
| | | | | | | PEA | | | | | | |
| Control | 81 | 106 | 93 | 93 | 106 | 99 | 106 | 131 | 118 | 156 | 186 | 171 |
| $KNO_3$ | 103 | 131 | 117 | 78 | 157 | 117 | 124 | 152 | 138 | 162 | 171 | 166 |
| $(NH_4)_2SO_4$ | 134 | 134 | 134 | 102 | 249 | 175 | 137 | 193 | 165 | 146 | 214 | 180 |
| | | | | | | SORGHUM | | | | | | |
| Control | 12 | 43 | 27 | 03 | 50 | 26 | 24 | 56 | 40 | 43 | 81 | 62 |
| $KNO_3$ | 13 | 31 | 22 | 06 | 27 | 16 | 21 | 59 | 40 | 36 | 81 | 58 |
| $(NH_4)_2SO_4$ | 24 | 41 | 32 | 21 | 49 | 35 | 50 | 65 | 57 | 62 | 109 | 85 |
| C.D. at 5% level in Pea | ST=11.55 (S) INT=NS | | | ST=15.18 (S) INT=33.94 (S) | | | ST=8.8 (S) INT=NS | | | ST=16.18 (S) INT=36.18 (S) | | |
| C.D. at 5% level in Sorghum | ST=1.36 (S) INT=5.35 (S) | | | ST=3.99 (S) INT=8.92 (S) | | | ST=4.58 (S) INT=10.26 | | | ST=5.8 (S) INT=12.97 (S) | | |

ST=Subtreatment; INT=Interaction.

Table II: Mean nitrate reductase activity (NRA) at various stages in pea and sorghum expressed as (A) $\mu$ moles$^{-1}$/gm$^{-1}$ f. wt$^{-1}$/hr$^{-1}$, (B) $\mu$ moles$^{-1}$/gm$^{-1}$ d.wt./hr$^{-1}$.

| Sub-treatment | (A) 1 N.St | (A) 1 St | (A) 2 N.St | (A) 2 St | (A) 3 N.St | (A) 3 St | (A) 4 N.St | (A) 4 St | (B) 1 N.St | (B) 1 St | (B) 2 N.St | (B) 2 St | (B) 3 N.St | (B) 3 St | (B) 4 N.St | (B) 4 St |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | Pea | | | | | | | | |
| Control | 6.00 | 2.00 | 2.30 | 0.58 | 4.30 | 2.20 | 6.60 | 1.80 | 2 37 | 1.31 | 0.49 | 0.15 | 0.49 | 0.18 | 1.77 | 0.52 |
| $KNO_3$ | 5.50 | 3.55 | 4.53 | 2.72 | 4.72 | 1.55 | 11.85 | 3.98 | 1.09 | 2.85 | 1.35 | 1.67 | 0.40 | 0.16 | 2.20 | 0.59 |
| $(NH_4)_2SO_4$ | 6.15 | 2.95 | 5.13 | 2.12 | 6.65 | 1.43 | 7.35 | 2 42 | 1.53 | 1.82 | 2.35 | 1.40 | 0.56 | 0.10 | 1.78 | 0.78 |
| | | | | | | | | Sorghum | | | | | | | | |
| Control | 1.70 | 1.10 | 4.39 | 2.24 | 7.20 | 1.90 | 2.80 | 1.59 | 0.53 | 0.27 | 2.54 | 1.40 | 2.93 | 1.05 | 1.37 | 0.69 |
| $KNO_3$ | 5.35 | 3.55 | 9.33 | 4.08 | 16.10 | 7.15 | 3.78 | 2.12 | 2.10 | 1.21 | 5.60 | 2.44 | 6.68 | 5.09 | 1.51 | 0.94 |
| $(NH_4)_2SO_4$ | 5.05 | 3.73 | 7.88 | 4.76 | 15.60 | 8.35 | 3.12 | 1.51 | 1.79 | 1.22 | 3.57 | 2.20 | 7.30 | 5.13 | 1.18 | 0.62 |

| | | | | |
|---|---|---|---|---|
| Pea Plant | | | | |
| C.D. at | ST=0.13 (S) | 0.44 (S) | 0.19 (S) | 0.11 (S) |
| 5% level | INT=0.29 (S) | NS | 0.76 (S) | 0.41 (S) |
| Sorghum | | | | |
| C.D. at | ST=0.17 (S) | 0.13 (S) | 0.14 (S) | 0.17 (S) |
| 5% level | INT=0.38 (S) | 0.28 (S) | 0.31 (S) | 0.39 (S) |

1. Seedling stage; 2. Flowering/Anthesis stage; 3. Pod/grain formation stage;
4. Pod/grain maturity stage; N.St=Non stress; St=Stress.

Table III : Mean glycolate oxidase activity in pea and sorghum at various stages expressed as (A) $\mu$ moles$^{-1}$/gm$^{-1}$ f.wt/hr$^{-1}$, (B) $\mu$ moles$^{-1}$ glyoxylate/gm$^{-1}$ dr.wt/hr$^{-1}$

| Sub—treatments | (A) 1 N.St | 1 St | 2 N.St | 2 St | 3 N.St | 3 St | 4 N.St | 4 St | (B) 1 N.St | 1 St | 2 N.St | 2 St | 3 N.St | 3 St | 4 N.St | 4 St |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | Pea | | | | | | | | |
| Control | 80.4 | 45.6 | 44.4 | 62.4 | 31.2 | 48.0 | 40.8 | 50.4 | 31.75 | 29.95 | 9.50 | 15.66 | 3.50 | 3.84 | 10.93 | 14.51 |
| $KNO_3$ | 102.0 | 78.6 | 88.8 | 42.0 | 63.3 | 48.6 | 43.8 | 32.4 | 20.20 | 63.19 | 27.43 | 25.78 | 5.38 | 5.10 | 8.09 | 4.76 |
| $(NH_4)_2SO_4$ | 144.5 | 67.5 | 148.1 | 62.4 | 108.0 | 37.8 | 45.6 | 31.8 | 35.56 | 41.85 | 67.93 | 41.48 | 9.07 | 2.57 | 11.03 | 10.30 |
| | | | | | | | | Sorghum | | | | | | | | |
| Control | 28.5 | 15.0 | 2.4 | 24.0 | 12.0 | 16.8 | 26.1 | 34.7 | 8.95 | 3.70 | 1.39 | 15.02 | 4.89 | 9.35 | 12.74 | 15.16 |
| $KNO_3$ | 30.8 | 20.0 | 19.2 | 34.2 | 16.8 | 21.6 | 37.8 | 27.0 | 12.10 | 6.84 | 11.52 | 20.45 | 6.97 | 15.37 | 15.08 | 11.99 |
| $(NH_4)_2SO_4$ | 42.5 | 31.8 | 27.0 | 48.0 | 22.8 | 21.6 | 55.1 | 41.4 | 15.04 | 10.30 | 12.37 | 22.22 | 10.67 | 13.26 | 20.77 | 16.93 |

| | | | | |
|---|---|---|---|---|
| Pea | | | | |
| C.D. at | ST=9.79 (S) | 2.23 (S) | (NS) | 1.98 (S) |
| 5% level | INT=21.89 (S) | (NS) | (NS) | 4.44 (S) |
| Sorghum | | | | |
| C.D. at | ST=2.11 (S) | 0.85 (S) | (NS) | 4.59 (S) |
| 5% level | INT=8.27 (S) | 1.92 (S) | (NS) | 10.25 (S) |

1. Seedling stage; 2. Flowering/Anthesis stage; 3. Pod/grain formation stage; 4. Pod/grain maturity stage.

Table IV : Mean catalase activity in pea and Sorghum at various stages expressed as (A) M mole$^{-1}$/gm$^{-1}$ f.wt/min$^{-1}$, (B) M mole$^{-1}$/gm$^{-1}$ d.wt/mim$^{-1}$

| Sub—treatments | (A) 1 N.St | (A) 1 St | (A) 2 N.St | (A) 2 St | (A) 3 N.St | (A) 3 St | (A) 4 N.St. | (A) 4 St | (B) 1 N St | (B) 1 St | (B) 2 N.St | (B) 2 St | (B) 3 N.St | (B) 3 St | (B) 4 N.St | (B) 4 St |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | Pea | | | | | | | | |
| Control | 12.0 | 7.8 | 30.0 | 19.2 | 16.8 | 6.0 | 15.0 | 19.8 | 4.74 | 5.12 | 6.42 | 4.82 | 1.93 | 0.48 | 3.96 | 5.70 |
| $KNO_3$ | 12.3 | 7.2 | 10.8 | 20.9 | 56.9 | 51.0 | 25.8 | 20.7 | 2.43 | 5.79 | 3.33 | 12 83 | 4.83 | 5.35 | 4.80 | 3.04 |
| $(NH_2)_2SO_4$ | 15.0 | 10.2 | 30.6 | 10.2 | 91.8 | 54.0 | 31.4 | 13.5 | 3.70 | 6.30 | 14.05 | 6.78 | 17.71 | 3.65 | 17.64 | 4.37 |
| | | | | | | | | Sorghum | | | | | | | | |
| Control | 0 42 | 0.56 | 1.75 | 1.12 | 1.05 | 0.84 | 0.70 | 0.28 | 0,13 | 0.14 | 1.01 | 0.70 | 0.43 | 0.47 | 0.34 | 0.12 |
| $KNO_3$ | 0.87 | 0.53 | 1.29 | 0.84 | 1.04 | 0.80 | 0.70 | 0.70 | 0.34 | 0.18 | 0.77 | 0 50 | 0.43 | 0.57 | 0.28 | 0.31 |
| $(NH_2)_2SO_4$ | 1.05 | 0.56 | 1.55 | 0.84 | 1.22 | 0.66 | 0 77 | 0.70 | 0.37 | 0.18 | 0.71 | 0.39 | 0.57 | 0.41 | 0.29 | 0.29 |

| | | | | |
|---|---|---|---|---|
| Pea | | | | |
| C.D. at | ST=0.67 (S) | 1.55 (S) | 7.82 (S) | 1.99 (S) |
| 5% level | INT=1.50 | 3.44 (S) | NS | NS |
| Sorghum | | | | |
| C.D. at | ST=0.45 (S) | 0.13 (S) | 0.05 (NS) | NS |
| 5% level | INT=NS | 0.30 (S) | NS | NS |

1. Seedling stage; 2. Flowering/Anthesis stage ; 3. Pod/grain formation stage;
4. Pod/grain maturity stage; N.St=Non stress; St=Stress.

maximum at pod maturity (Table II). Nitrate treated plants showed decline in NRA at pod formation stage but a maximum at maturity as recorded in control. In ammonia treated plants unlike in control and nitrate treated plants, maximum NRA was noted at flowering stage and minimum at pod maturity stage. Increased NRA with nitrate application was already reported by many workers like Fair *et al.* (1974 a). Significant increase in NRA with ammonia at flowering stage was observed in the present study which may be attributed to increased growth of leaves (photosynthetic apparatus) which in turn increased NRA. In sorghum non-stress plants maximum NRA was recorded at grain formation stage in control and nitrogen treated plants followed by drop at maturity stage. Nitrogen as nitrate or ammonia contributed to maximum NRA at grain formation stage.

Even when water stress was given, nitrogen as both nitrate and ammonia increased NRA over control upto flowering stage in pea, whereas in sorghum increase in NRA with nitrogen treatment over control was noted at all stage of growth (Table II). With stress NRA was reduced at all stages in both pea and sorghum and such a decrease in NRA with stress was shown by Huffaker *et al.* (1970).

Glycolate oxidase activity (GO) decreased from seedling to pod formation stage followed by a rise at maturity in control plants (Table III). Both forms of nitrogen increased GO markedly at all stages except maturity. At maturity there was only slight increase over control in ammonia treated plants and no increase was noted with nitrate treatment. When moisture stress was given, nitrogen treatment increased GO only at seedling and flowering stages. Whereas the control plants recorded more GO than nitrogen treated plants at pod formation and pod maturity stage. Ammonical form of nitrogen was found to be more effective in increasing GO over nitrate from in non-stress and stress conditions (Table III). It appears that assimilation of ammonia and consequent amino acid formation may create a demand for more carbon skeletons which could have been derived through glycolate pathway.

In sorghum, unlike in pea, control and nitrogen treated plants showed a drop in Go at anthesis followed by an increase at later stages reaching a maximum at maturity. Increase in Go with nitrogen treatment in sorghum was not as significant as in pea. In sorghum, ammonical nitrogen recorded more GO than control and nitrate nitrogen treatment at all stages of growth and also when stress was given.

Increase in GO with ammonia in sin sorghum is in confirmation with the findings of Fair *et al.* (1974 a) in barley; Cresswel *et al.* (1974) in maize and sorghum.

In pea Catalase activity increased up to flowering stage followed by a drop at pod formation stage and again increase at maturity (Table 4). When nitrogen treatment was given, catalase increased up to pod formation stage reaching a maximum and there was no further increase at maturity. Ammonium treatment recorded more catalase than nitrate. With moisture stress, catalase decreased in both control and ammonia treated plants whereas nitrate treated plants recorded an increase, (Table 4).

In sorghum, both control and nitrogen treatments did not differ in catalase activity at grain formation and grain maturity stage. At anthesis control plants recorded maximum catalase whereas at seedling stage nitrogen treated plants recorded more catalase activity. Catalase was not influenced by form of nitrogen as both ammonical and nitrate showed similar response.

In pea $CO_2CC$ and NRA increased from seedling stage to maturity showing a positive relationship with each other (Tables 1 and 2). When nitrate nitrogen was given the relationship was more closer (Tables 1 and 2). An increase in NRA will generally lead to formation of glutamic acid, which in turn form glycine through transaminase reactions. Thus, the glycine formed through nitrogen assimilation pathway might have been decarboxylated leading to the release of $CO_2$ thus, increasing the $CO_2CC$. Fair *et al.* (1974 a), Kalpan *et al.* (1974) reported similar results.

When moisture stress was given, $CO_2CC$ increased in control and nitrogen treated plants (Table 1) from seedling to maturity. But NRA unlike in non-stress plants, reduced when stress was given. All nitrogen treatments particularly ammonium treated plants showed a peak in $CO_2CC$ at flowering stage with stress. But there was no peak in NRA, observed at flowering. Stress thus reversed the relationship between $CO_2CC$ and NRA.

In sorghum $CO_2CC$ was lowest at anthesis and maximum at maturity (Table 1). On the other hand NRA had a peak at pod formation stage followed by a drop at maturity (Table 2). Thus in sorghum, unlike in pea the relationship between $CO_2CC$ and NRA was negative.

In pea, GO was maximum at vegetative stage in control but in nitrogen treated plants maximum was at flowering stage Table 3). $CO_2CC$ increased with age reaching maximum at maturity stage (Table 1). Thus, the relationship between the two was negative. Normally one may expect that in pea, a $C_3$ plant GO be closely associated with $CO_2CC$ curve as glycolate accumulation and its further oxidation is related closely to photorespiration (Kisaki and Tolbert,

1969; Tolbert *et al.*, 1971). Though GO showed a peak at flowering when nitrogen was given in the form of ammonia or nitrate the relationship between GO and $CO_2CC$ remained negative (Tables 3 and 1).

In control, when moisture stress was given like $CO_2CC$, GO increased over non- stress control plants, thus showing a positive relationship. However nitrogen treated plants did not show such relationship (Tables 3 and 1).

In sorghum, both GO and $CO_2CC$ increased from seedling to maturity with a drop at anthesis stage (Tables 1 and 3). Thus, showing a positive relationship in non-stress series. In stress series also, such a positive relationship was maintained at all stages as $CO_2CC$ and Go increased at all stages (Tables 1 and 3). In sorghum, a $C_4$ plant (wherein general glycolate pathway enzymes are present in minimum quantity) the photorespiratory $CO_2$ released to increase $CO_2CC$ was derived from decarboxylation of glycine which is formed through glycolate path way. Sorghum having agranal bundle sheath chloroplast, (thus lacking PS II.), in general show lower GO. But the peroxides accumulated due to low activity of catalase (as shown in Table 4) might caused increased $H_2O_2$. This could have lead to the glycolate oxidation, thus showing increased GO with age of the plant. Similar findings were reported by Osmond (1971) and by Plaut and Littan (1971).

The relationship between $CO_2CC$ and catalase are varied, and are not constant at all stages of growth in both pea and sorghum (Tables 3 and 4). This indicates that catalase is not perfect marker for photorespiration, and this may be due to its universal presence in leaves, in peroxisomes, and cytoplasm.

Catalase was maximum at pod formation stage in pea when nitrogen was given either as nitrate or ammonia. Even when stress was given the same negative relationship was seen (Table 4). In sorghum plant $CO_2CC$ dropped at flowering whereas catalase increased, thus, showing negative relationship (Tables 4 and 1).

In conclusion, it can be said that $CO_2CC$ is linked to nitrogen metabolism and availability of nitrogen as shown by positive relationship of $CO_2CC$ and NRA in pea plant. It is also suggested from these studies that even a $C_4$ plant like sorghum synthesise higher level of photorespiratory enzymes. This is more visible when nitrogen is applied in the form of ammonia than in the form of nitrate.

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