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Increasing plant productivity through improved photosynthesis

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Abstract. The importance of increasing plant productivity through photosynthetic route and relevance of higher chain aliphatic alcohols in promoting photosynthesis in plants, resulting in increased yields in various crops is discussed. A mixture of aliphatic alcohols (C-24 to C-34) designated as "Mixtalol" was prepared and tested as seed soak and foliar spray at 1–2 ppm. It was found that the treatment resulted in a significant increase in root length and number of laterals, shoot fresh weight and shoot and root dry weight of various crop plants. Mixtalol treatment as seed soaking of paddy increased the chlorophyll content of leaves, which was higher at younger stages of development. The seed soak and foliar spray of Mixtalol also increased Fe^{++} content of tomato and paddy shoots. It also significantly increased the rate of photosynthesis in tomato and paddy. In tomato and barley leaves, a simultaneous decrease in photorespiration rates was also observed.

Foliar application of individual alcohols, (components of Mixtalol) indicated that excepting for C-28, C-22 to C-30 increased the rate of photosynthesis. A mixture of C-24 to C-30, in the same proportion as that of Mixtalol, increased the rate of photosynthesis in paddy but Mixtalol registered a higher rate than the mixture, probably, because of the presence of still unidentified components in the mixture. Extensive field trials with Mixtalol, have shown yield increases of 14–27% in paddy, 13–27% in wheat, 33% in maize, 20% in pearl millet, 21–29% in potatoes, 15–20% in groundnuts and 48% in sorghum fodder. The foliar application of Mixtalol on vegetables (tomato, brinjal, okra, beans, cauliflower, chilli, etc.) gave substantial increases in yield.

Keywords. Photosynthesis; photorespiration; chlorophyll; aliphatic alcohols; Mixtalol; *Lycopersicon*; *Oryza*; *Triticum*; *Zea*; *Pennisetum*; *Sorghum*; *Arachis*; vegetables.

1. Introduction

Plant productivity is dependent upon the interaction between genetic potentialities of crop plants and the environment in which they grow. Genetic variations, weather and cultural practice normally influence the physiological processes of the plant to control growth and yield. Unfavourable environmental factors like drought, temperature, cultural practices like soil fertility, pest attack, etc can only affect the yield by affecting physiological processes of the plant. Plant breeders produce high yielding varieties by having genotypes possessing combinations of efficient physiological processes capable of producing higher yields. An enormous amount of information has been collected on the effect of mineral nutrition, water relations, growth regulators and herbicides on various physiological processes for increasing crop productivity. However, specific attention to promotion of photosynthesis in plants as a means of increasing crop productivity has not been sufficiently stressed in agriculture. The biggest challenge for scientists in agriculture research is to find ways and means to meet world food requirements by the end of the century, when the population is expected to be 6 billion, particularly when the use of fertilizers is energy-intensive (a commodity increasingly in short supply), and, further, the genetic potential seems to be reaching a ceiling with respect to non-photosynthetic means of improvement in productivity.

Plants ingest maximally only about 2·6% of nitrogen and 0·31% of phosphorus from

the soil compared to over 90% of dry weight obtained through photosynthesis utilising CO_2 from air, water and sunshine (Russel 1973, table 1). Photosynthesis is absolutely essential even for the incorporation of nitrogen and phosphorus, as in proteins.

While increasing crop productivity by use of nutrients alone seems to have reached a plateau, there is enormous scope of improving the yields through the photosynthetic route. The upper limit for maximum photosynthetic efficiency for terrestrial plants has been calculated to be of the order of 6·6% (Bassham 1977, table 2), but most crop plants achieve photosynthetic efficiencies only of the order of 0·15 to 0·2% (Boardman 1980), suggesting a possibility of increasing the rate many folds more and, consequently, yields (table 3).

If the rate of net photosynthesis could be increased, the yields also would improve (Wade 1973). However, a number of authors had contended earlier that there was little likelihood of materially increasing the rate of photosynthesis in plants and the best way to increase yields was by increasing the leaf area index (Watson 1952). Nevertheless,

Table 1. Per cent content in dry matter.

	Wheat	Oats	Turnips	Cloves hay
Carbon	47·62	50·37	42·91	47·40
Hydrogen	5·47	5·85	5·49	5·00
Oxygen	40·42	37·96	42·30	37·80
Nitrogen	1·2	1·3	2·3	2·6
Phosphorus	0·22	0·21	0·31	0·28
Other minerals	5·07	4·31	6·69	6·92

(After Russel 1973)

Table 2. Maximum photosynthetic efficiency

	Per cent
Active radiation from the sun	100
Photosynthetically active radiation (400–700 nm)	43
Free energy stored in reaction per mole of CO_2	
$CO_2 + H_2O \xrightarrow[\text{photons}]{\text{eight}} (CH_2O) + O_2 = 114$ kcals	
8 Einsteins $= 8 \times 49{\cdot}74$ kcals	
Efficiency of photosynthetic reduction (aquatic) $= \frac{114}{8 \times 49{\cdot}74} = 0{\cdot}286$	
Total energy conversion $= 0{\cdot}286 \times 0{\cdot}43$	
$= 0{\cdot}123$	12·3
Canopy factor 0·80	
Respiration factor 0·67	
Upper limit for land plants $= 0{\cdot}286 \times 0{\cdot}43 \times 0{\cdot}80 \times 0{\cdot}67$	
$= 0{\cdot}066$	6·6

(after Bassham 1977)

Table 3. Photosynthetic efficiencies in plants.

Crop plants	Per cent
Sugarcane	1·0
Soybean	0·16
Napier grass	1·6
Cassava	0·8
Maize	0·2
Wheat, rice, etc	0·15
Forest trees	0·06

(After Boardmann 1980).

during recent years, there has been extensive research for search of plants with high rate of photosynthesis per unit leaf area and also investigations for more efficient mechanisms of photosynthesis (Staples and Kuhr 1980). Since C-4 carbon pathway is more efficient than the C-3 pathway, efforts could be made to modify the photosynthetic machinery through genetic engineering. However, this seems to be difficult as too many processes and too many genes are involved. Another approach involves the study of the possibility of conserving carbohydrates by finding a genetic or chemical method of reducing photorespiration (Zelitch 1975, 1979; Oliver and Zelitch 1977), which according to Servaites and Ogren (1977) can be accomplished without disturbing important internal protective mechanisms. The relationship between source and sink activity-demands on plant is a complex one and our knowledge of the regulatory processes involved is limited. Plant hormones or regulators are also involved in the regulation of physiological development by their action at the site of production and also by their transport to other sites (Wareing 1977). These activities can influence photosynthesis.

2. Importance of higher chain alcohols

The importance of higher chain alcohols in the transport and transposition of monomer of sugar and the synthesis of sugar polymers is, of late, being increasingly recognised. There is considerable evidence indicating the participation of Vitamin A (Retinol—a Tetraprenol) in sugar transfer reactions. Deprivation of Vitamin A has been shown to affect the synthesis of certain glycopeptides and glycolipids in the intestinal mucosa (DeLuca *et al* 1970, 1973), corneal epithelium (Kim and Wolf 1974) and liver (DeLuca *et al* 1975). This is also attested by the fact that one of the basic functions of vitamin A is the promotion of glycostasis in tissues. Leloir discovered the presence of a dolichol (a C_{100}-100α-saturated polyprenol) in various mammalian tissues (Parodi and Leloir 1979; Pullarkat and Reha 1982). Dolichols function in glycoprotein synthesis (Wacchler and Lennarz 1976; Lennarz 1975). Dolichols have now been found widely in plants as well. Similarly, polyprenols are present in bacteria and have been shown to act as lipid intermediates in the biosynthesis of bacterial cell wall polysaccharides (Ganguly *et al* 1980). The respective functions of retinol and dolichol in the transfer of sugar to acceptor proteins are presented in table 4 (DeLuca 1977). The presence of various growth factors, probably long chain aliphatic alcohols, in

Table 4. Mode of transfer of sugar to the acceptor proteins.

Retinol (4 isoprenol units)	Dolichol (~ 20 isoprenol units)
Functions in higher organisms only	Functions in virus, bacteria, plants and animals
Direct donor of mannose to glycoprotein without the build-up of oligosaccharide on itself	Builds up oligosaccharide chain on itself, after which the oligosaccharide is transferred to the acceptor protein
The mannosyl residue incorporated into an oligosaccharide chain (which is bound to a protein) is alkali labile and is probably O-glycosidic type of linkage	The sugar moiety (in say, ovalbumin) is attached to the asparginal residue of the protein by an alkali stable N-glycosidic bond

(After DeLuca 1977).

vertebrate saliva improving plant growth has been reported (Hollenberg and Gregory 1977; Detling *et al* 1980).

The higher chain alcohols seem to facilitate transport of sugar or passage of oligosaccharide, mostly from extracellular fluid into the cell interior, by providing a handle to the sugars, thus enabling them to cross the lipid membranes of cells as well as anchor the saccharide at specific regions of the membrane for subsequent action by membrane bound enzymes (Parodi and Leloir 1979). Vlitos and Crosby (1959) had reported the plant growth promoting activity of C-18 to C-22 alcohols and their acidic esters isolated from tobacco by the *Avena* first internode bioassay. Atkinson and Allen (1966) obtained a factor from cotton wax which was highly effective in stimulating the germination of self-inhibited wheat stem-rust uredospores. Mitchell *et al* (1967) found growth stimulating substances in the cotton fibre using bean internode bioassay. An oil product derived from Rape (*Brassica napus*) and designated as Brassins (Brassinolides) was shown by Mitchell *et al* (1970) to have plant growth-stimulating action. It consisted of five components of glyceridic structure, each having 12–26 carbon atoms (Mandava and Mitchell 1972). Yopp *et al* (1981) studied the activity of brassinolide in selected auxin bioassays.

The possible role of higher chain alcohols C-20 and above in facilitating sugar transport and synthesis attracted our particular attention to these alcohols in view of their possible role in improving physiological efficiency of the plants. Around this time we came across the work of Ries *et al* (1977) at Michigan State University, who reported that C-30 alcohol (triacontanol) extracted from alfalfa meal, when sprayed on the foliage or applied in nutrient culture, increased the growth of rice, corn and barley. Subsequently, Ries *et al* (1977, 1977a) and Ries and Wert (1977b) reported increases in leaf area and dry weight of maize and paddy treated with triacontanol. In studies with maize, rice and tomato seedlings, Jones *et al* (1979) observed that several analogues (C-16 to C-32) of triacontanol inhibited the response of plant seedlings to triacontanol, particularly C-28. Erickson *et al* (1981) noted a greater response to C-30 alcohol treatment in young tomato leaves, in which photosynthesis was less sensitive to oxygen concentration than control plants. In maize, no effect of C-30 treatment on dry weight was observed.

We considered the use of a mixture of higher chain alcohols to promote plant growth and productivity for the following reasons: Firstly, even dolichols vary in chain lengths

and different chain length alcohols have been reported to be present in various natural products. Secondly, we have taken the view that in biological systems, there is rarely present a single element deficiency, and even when such a deficiency occurs, it can rarely be treated by a single element alone, *e.g.* pellagra cannot be adequately treated with nicotinic acid alone though we know it is specific nicotinic acid deficiency. Similar is the case with beriberi (B_1 deficiency), glossitis (B_2 deficiency), achromotrichia (pantothenic acid deficiency) or pernicious anaemia (B_{12} deficiency). These conditions are all treated by administration of a mixture of B Vitamins or Vitamin B complex. It is in the nature of biological treatment therefore to resolve a deficiency state or promote improvements in nutritional/physiological state, not by a single missing nutrient but by a mixture of kindred nutrients. In this regard we considered prospects for the production of mixtures of higher chain alcohols to be used to improve physiological efficiency of plants.

3. Materials and methods

Waxy by-products of agriculture were used to obtain mixtures of a spectrum of aliphatic alcohols with chain lengths C-24 to C-34. This mixture of aliphatic alcohols was designated as "Mixtalol" and has the following composition (%): C-24 Tetracosanol: 7–10; C-26 Hexacosanol: 12–16; C-28 Octacosanol: 15–20; C-30 Triacontanol: 24–30; C-32 Dotriacontanol: 11–14; and C-34 Tetratriacontanol: 4–5.

3.1 *Preparation of Mixtalol*

Required dilutions of Mixtalol for seed soak or foliar application were prepared from 1% Mixtalol, emulsified in water using 1% each of Tween-40 and Tween-80.

3.2 *Bioassay*

Two types of bioassay were conducted to study bioeffectivity of Mixtalol as given below:,

3.2a *Root length measurement*: Root length was measured with paddy seeds (variety Jaya). The selected seeds were soaked in water for 26 hr before placing. The seeds (15–20) were placed on glass plates (9″ × 6″) covered with a moist filter paper held in place by rubber bands. Each glass plate was kept in a polythene bag containing 25 ml of distilled water. Two days later, the seedlings were selected based on the length of roots and too large or too small seedlings were discarded to overcome seed vigour variance. The seedlings were sprayed with test solutions (Mixtalol at 1–2 ppm). Test solution (4 ml) was sprayed on seedlings on each plate. Water-sprayed seedlings served as the control. Four days after the spray, their root lengths were measured and mean root length for each plate was calculated. There were 8–9 replicates for each of the treatments. The results were analysed statistically for their significance using students *t* test. Experiments were conducted at room temperature (25–29°C).

3.2b *Fresh and dry weight estimation*: Wheat (variety HD-2189) was used for fresh and dry weight measurements. Seeds were soaked in water for 24 hr before placing on

moist filter paper in glass petriplates 6 inches in dia. The seeds were allowed to grow for four days and made uniform by removing very large and very small seedlings. Twentyfive ml of full strength Hoaglands nutrient solution was given to each plate.

The seedlings were sprayed with 1·5 ppm Mixtalol solution. The solution (5 ml) was sprayed on each petriplate. Water-sprayed seedlings served as the control. Each treatment consisted of 5–7 replicates while each plate had 30–35 seedlings.

Four days after the spray, the seedlings were harvested. They were separated into shoot and root parts. Shoot fresh weight was recorded and later both shoot and root fractions were dried separately to a constant weight at 80°C in a hot air oven. Their dry weights were recorded. The results were analysed statistically for their significance using the students *t* test.

3.3 *Pot experiment*

Sieved soil was mixed with farm yard manure in the proportion 2 : 1 and filled in earthen pots (12 inches in dia). Seeds of tomato (*Lycopersicon esculentum* cv. Vaishali) and paddy (*Oryza sativa* cv. Jaya) were treated with the fungicide Bavistin (0·05 %) and sown in these pots. Doses of fertilizer (NPK) were applied at the rate of 100 : 100 : 60 kg/ha for tomatoes and 100:60:40 kg/ha for paddy in two split doses. In the case of paddy $ZnSO_4$ at the rate of 15 kg/ha was also applied. Weeding and other necessary plant protection measures were carried out as required. After the emergence of the seedlings, they were thinned to a uniform stand of 4 seedlings/pot. Both treated and control pots were regularly watered. Barley (*Hordeum vulgare*) seedlings were raised in paper cups (4 inches dia) for photorespiration studies and paddy, wheat and maize for root, shoot lengths and number of root laterals.

3.4 *Treatment*

Seed soaking and foliar spray were the two treatments given. In the first treatment, seeds were soaked in 1/1·5 ppm of Mixtalol for 24 hr and then sown in pots. Seeds soaked in distilled water for a similar period served as control. In the second treatment, first foliar spray of 1–2 ppm Mixtalol was given to the drip point when plants were four weeks old. The second foliar spray of the same concentration was similarly given four weeks after the first spray.

Plants were harvested and brought to the laboratory in moistened plastic bags. Fully expanded leaves were selected and used for the estimation of chlorophyll, net CO_2 fixation, photorespiration and Fe^{++} uptake.

3.5 *Field trials*

Random block design (RBD) was followed for replicated trials of Mixtalol on different crops. The quantity of spray used was at the rate of 500 l/ha. The first spray was made when the plants were at 2/3 leaf stage and the second spray four weeks after the first. The crop was harvested at maturity, separately threshed and grain yield/plot was recorded.

In large scale field trials, the farmers' fields were chosen and were divided in 4–6 plots of one acre each. These plots were separated by bunds. Equal doses of fertilizer (NPK) were given according to recommendations. In paddy, zinc sulphate at the rate of

15 kg/ha was applied in addition. Half the number of plots chosen at random were given Mixtalol treatment and the remaining half, served as control, which were sprayed with equal quantity of water. Weeding and other necessary plant protection measures were carried out in both control and treated plots as per requirements. At the time of harvest, produce of individual plots in treated and control was threshed separately and the weight of grains and straw recorded. The yield was reported at corrected moisture content.

3.6 *Estimation of chlorophyll*

The leaves were washed thoroughly with distilled water and blotted dry using Whatman filter paper. They were cut into small pieces (about 1·5 cm long) and 0·3 g fresh leaf tissue homogenised in 80 % acetone. The extract was centrifuged at 5000 rpm for 5 min and the supernatant decanted. The residue was washed with 80 % acetone and centrifuged again. The two supernatants were combined together and volume made to 30 ml. The absorbance was measured in a spectrophotometer at 663 and 645 nm and chlorophyll *a*, *b* and total chlorophyll content calculated by the method of Arnon (1949). The results are expressed as mg chlorophyll/g fresh weight. The values are mean of three replicates.

3.7 *Carbon dioxide fixation rates*

The CO_2 fixation rates were estimated by the method of Zelitch (1974) as modified for paddy and tomato plants.

In a 100 ml conical flask with one side arm and an inlet and an outlet for passing CO_2-free air, 5 ml Tris-HCl buffer (20 mM, pH 8·5) and 0·2 ml of $MgCl_2$ (25 mM) was taken. In the side arm 1 ml of 25 mM $NaHCO_3$ and 0·1 μCi labelled $NaHCO_3$ were taken. The leaves were washed thoroughly and blotted dry. They were cut into small pieces (about 1·5 cm long). Six such pieces were randomly selected, their fresh weight recorded and then placed in the conical flask.

The flask and the side arm were stoppered and CO_2 free air (by passing through 1 N NaOH) was flushed for 90 sec. The light source was put on (1000 W tungsten halogen lamp, 1400–1600 lux) and the leaf pieces were preilluminated for 10 min. Two ml of 6N HCl was added by a syringe to the side arm through the stopper and CO_2 released. The tissues were allowed to photosynthesize for 5 min after which the process was terminated by plunging the leaf pieces into boiling ethanol. The tissue was homogenized in ethanol and centrifuged at 5000 rpm for 5 min. The supernatant was decanted and made to 20 ml with alcohol. To 0·2 ml of this supernatant 10 ml Bray's scintillation cocktail was added and $^{14}CO_2$ counted in a liquid scintillation counter (Packard). The rates are expressed as μmol CO_2 fixed per g leaf fresh weight, per g dry weight and per mg chlorophyll per hr. The values are mean of three replicates.

3.8 *Photorespiration*

The fresh weight of six randomly selected leaf pieces was recorded and then they were allowed to photosynthesize for 10 min after liberating $^{14}CO_2$ as described earlier in the method for the estimation of CO_2 fixation rates.

After 20 min (at zero time), CO_2-free air was rapidly swept through the system and

$^{14}CO_2$ released by respiration trapped in 1 M ethanolamine for 15 min during illumination. The $^{14}CO_2$ content in the trap was determined by scintillation counting. Results were expressed as μmol $^{14}CO_2$ released per g leaf fresh weight per hour (Zelitch 1974).

3.9 *Estimation of iron*

Seedling shoot samples harvested at different days were dried in an oven at 80°C for 24 hr followed by ashing in a muffle furnace at 500°C for 2·5 hr. The ash was dissolved in 25 ml of 6 N HCl and the solution was filtered. The filtrate was made to a known volume and the iron content measured by atomic absorption at 248·3 nm using appropriate standards for comparison.

4. Results and discussion

4.1 *Effect on root length, number of laterals and shoot length of plants*

The concentration of application of Mixtalol was standardised in preliminary studies using from 0·01 ppm to 10 ppm and it was found that 1 to 2 ppm gave optimum results.

Mixtalol at 1 ppm concentration when used as a seed soak of paddy, wheat, jowar and maize produced a significant increase in root length, number of laterals and shoot length (table 5).

As shown in table 6, Mixtalol at 1 ppm spray on 4-day old paddy seedling produced a significant increase in the root length (table 6).

The shoot fresh weight increased by 8–10 %, the dry weight increased due to Mixtalol treatment (table 7).

Mixtalol application increased root length, shoot fresh weight and shoot and root dry weight. The increase in root length is dependent on water uptake since cell elongation is the primary mechanism responsible for extensive growth and water is

Table 5. Effect of seed soaking with 1 ppm Mixtalol on root length, number of laterals, and shoot length of crop plants (mean of 50 readings).

	Control	Treated
Paddy		
Root length (cm)	3·07 ± 0·17	3·94* ± 0·16
Shoot length (cm)	1·59 ± 0·09	1·62 ± 0·07
No. of laterals	2·24 ± 0·44	5·61* ± 0·99
Wheat		
Root length (cm)	6·84 ± 0·23	8·3* ± 0·52
Shoot length (cm)	6·0 ± 0·33	6·5* ± 0·37
Maize		
Root length (cm)	3·24 ± 0·16	3·66* ± 0·166
Shoot length (cm)	1·50 ± 0·07	1·34 ± 0·08
No. of laterals	2·18 ± 0·18	2·7* ± 0·19

*Significant at $P < 0·05$.

Table 6. Effect of Mixtalol on root length of paddy seedlings. (Treatment: 1·0 ppm spray 4 days after germination).

Sample	No. of observations	Mean (mm)	Mean difference ± SE (mm)
Control	91	123·24	5·60* ± 1·09
Treated	113	128·84	

*Significant at $P < 0·05$

Table 7. Effect of 1·5 ppm Mixtalol treatment (spray) on fresh and dry weights of shoots and roots of wheat seedlings (Water spray served as control).

Treatment	Shoot fr. wt. (g)	Shoot dry wt. (mg)	Root dry wt. (mg)
Experiment I			
Control	0·11 ± 0·004	12·8 ± 0·19	5·6 ± 0·55
Treated	0·12 ± 0·002	14·4 ± 0·23	6·9 ± 0·15
% Increase	10·3	12·5	25·1
Experiment II			
Control	0·11 ± 0·003	15·6 ± 0·58	6·9 ± 0·54
Treated	0·12 ± 0·002	17·3 ± 0·39	8·5 ± 0·21
% Increase	8·2	10·6	23·0

essential to maintain cell turgor leading to cell elongation. The increase in dry weight is mostly due to an increase in the level of carbon compounds, an increase easily explained by the observed increased rate of photosynthesis and decreased photorespiration rates (*vide infra*). It also indicates increased mitotic activity imparted either directly or possibly through change in endogenous levels of auxins/cytokinins due to application of Mixtalol.

4.2 *Effect on chlorophyll and iron content*

Mixtalol when applied as seed soak at 1 ppm for 24 hr in tomatoes (*Lycopersicon esculentum*) and paddy (*Oryza sativa*) produced an appreciable increase in the chlorophyll content of leaves (tables 8 and 9).

The effect of Mixtalol in increasing chlorophyll content (especially chlorophyll *a* content) of the leaves is higher at younger stage of development of paddy plants (table 9).

Soaking tomato seeds for 24 hr in 1 ppm Mixtalol increased chlorophyll content of leaves by 23·2% in 34-day old plants, 28·6% in 41-day old plants. However, on day 48, treated plants had only 3·5% increase over control (table 8). Similarly Mixtalol seed soak significantly increased the chlorophyll of paddy seedlings as well (table 9), where 17·4% higher chlorophyll *a* was recorded. There are no reports showing that chlorophyll content of leaves can be increased by application of growth regulators.

Table 8. Effect of Mixtalol on chlorophyll content of tomato leaves. (Treatment: Seed soaking at 1 ppm for 24 hr).

Age (days)	Treatment	Total chlorophyll (mg/g fresh wt.)	% Increase over control
34	Control	1·85 (±0·107)	
	Mixtalol	2·28 (±0·099)	23·2
41	Control	1·82 (±0·094)	
	Mixtalol	2·34 (±0·146)	28·6
48	Control	2·02 (±0·055)	
	Mixtalol	2·09 (±0·062)	3·5

Table 9. Effect of Mixtalol on chlorophyll content of *O. sativa* (var. Jaya)

Treatment	Chl. a	% Control	Chl. b	% Control	Total	% Control
Water (Control)	1·90 ±0·103	—	0·69 ±0·057	—	2·59 ±0·015	—
Mixtalol	2·23 ±0·160	117·4	0·67 ±0·031	97·1	2·90 ±0·189	112·4

Paddy seeds were soaked in 1 ppm of Mixtalol for 24 hr. Chlorophyll was measured on 7-day old plants and expressed as mg/g fresh weight.

Table 10. Effect of Mixtalol on Fe^{++} content of tomato and paddy shoots.

Plant	Treatment/ Concentration	Age of plants in days	Iron content (mg. g. dry wt^{-1})		% Inc.
			Control	Treated	
Tomato	Seed soak 1 ppm for 24 hr	29	2·35	3·90	66
Tomato	Foliar spray 1 ppm	44	1·07	1·32	23
Paddy	Seed soak 1 ppm for 24 hr	10	1·50	2·60	73

Since iron (Fe) is required for chlorophyll synthesis, the effect of treatment with Mixtalol on the Fe content of tomato and paddy shoots was undertaken. Foliar spray was done 10 days before Fe estimations in leaves. Data presented in table 10 show increased contents of Fe in leaves after treatment with Mixtalol both in tomato and paddy in line with the observed increases in chlorophyll content.

4.3 *Effect on rate of photosynthesis*

The results obtained on the effect of Mixtalol and individual alcohols on the rate of photosynthesis of tomato and paddy leaves are given in tables 11–14.

The treatment with Mixtalol, either as seed soak or as foliar spray has shown considerable increase in the rate of photosynthesis. The application of individual alcohols which are the components of Mixtalol have indicated that C-22 to C-30 registered an increase in the rate of photosynthesis except C-28 which has shown a depression. C-20 and C-22 are in very low quantity in Mixtalol (0·01 ppm). When C-20 itself was used at 1 ppm level, it had shown a depression in the rate of photosynthesis. The mixture of C-24 to C-30 in the same proportion as that of Mixtalol have also registered a higher rate of photosynthesis but Mixtalol promoted photosynthesis better. This may be due to the presence of small amounts of unidentified photosynthesis promoters in Mixtalol—the characterization of these chemicals is in progress.

Reviewing the hormonal control of photosynthesis and assimilate distribution Treharne (1982) stated that it is reasonable to suppose that some, if not all, classes of hormone present in leaves are involved in regulating photosynthesis and closely allied processes. Chloroplasts were shown to contain gibberellins (Railton and Reid 1974) and in many experiments involving gibberellin application, effects upon photosynthesis have ranged from enhancement (Gale *et al* 1974), undetectable changes in carboxylation and phosphorylation activities (Oben and Marcelle 1975), to a nil effect or depressions (Israelstam 1979). In cases of low gibberellin levels, application of GA promoted enzyme synthesis and photosynthesis (Treharne 1978). Ericksen (1981) reported increase in the rate of photosynthesis in tomato plants in air when treated with triacontanol whereas in another set of experiment, no change in the rate of photosynthesis was observed. He also observed no change in dark respiration in both the series.

Table 11. Effect of Mixtalol on photosynthesis by tomato leaves*.

Experiment No.	Rate of photosynthesis (μmol CO_2 fixed g.fr.wt^{-1} hr^{-1})		% Inc.
	Control	Treated	
1.	18·61	54·47	192·69
2.	19·11	61·08	219·54
3.	20·70	51·17	147·17
Mean	19·475 ±0·630	55·57 ±2·92	185·35

*Treatment consisted of 24 hr seed soak with 1 ppm Mixtalol. Leaves of 78-day old plants were used for measurements.

Table 12. Effect of Mixtalol on photosynthesis by tomato leaves*.

Treatment	Leaf photosynthesis (μmol CO_2 fixed)		
	g. fr. wt.$^{-1}$hr^{-1}	g. dry wt.$^{-1}$hr^{-1}	mg chlorophyll^{-1}hr^{-1}
Control (Water)	27·80 ±2·05	271·15 ±18·9	10·31 ±0·71
Mixtalol (1·5 ppm foliar spray)	48·33 ±4·12	475·75 ±80·6	18·37 ±0·71
% Inc.	73·84	75·46	78·18
P value	0·001	0·01	0·001

* 28-day old tomato plants were treated with Mixtalol at 1·5 ppm as foliar spray and measurements on photosynthesis were made after 10 days of treatment.

Table 13. Effect of Mixtalol on net CO_2 fixation in paddy leaves at different stages of growth.

Age (days)	Rate of photosynthesis (μm CO_2 fixed g. fr. wt.$^{-1}$hr^{-1})		% Increase in net CO_2 fixation
	Control	Treated	
95	15·8	32·18	103
104	21·2	31·37	48
116	18·6	26·41	42
125	41·2	42·3	Nil

(Treatment: 1st spray at 35 days and 2nd spray at 79-day old plants (1 ppm)).
Plants were harvested on the 130th day.

Table 14. Effect of individual aliphatic alcohols, their mixtures and Mixtalol on photosynthesis in paddy leaves.

Individual alcohols	Rate of photosynthesis (μm CO_2 fixed g. fr. wt.$^{-1}$ hr^{-1})		% Increase or decrease
	Control	Treated	
C-20	0·83 ± 0·072	0·74 ± 0·083	(−) 11
C-22	0·40 ± 0·056	0·44 ± 0·055	10
C-24	0·46 ± 0·070	0·55 ± 0·060	20
C-26	1·13 ± 0·200	1·34 ± 0·225	19
C-28	0·54 ± 0·070	0·54 ± 0·062	(−) 7
C-30	0·53 ± 0·044	0·65 ± 0·073	23
Mixture (C-24 to C-30)	0·83 ± 0·193	1·06 ± 0·269	28
Mixtalol	0·10 ± 0·027	0·16 ± 0·028	62

(7 days after 1 ppm spray of 30-day old plants).

The increased rate of photosynthesis shown due to the application of Mixtalol in tomato and paddy leaves could be attributed to enhanced carboxylation and phosphorylation activities besides increased chlorophyll content due to its application.

4.4 *Effect on photorespiration in C-3 plants*

Photorespiration is a group of processes by which C-3 plants release CO_2 in light at the cost of photosynthates. Zelitch (1975, 1979) has shown (table 15) that C-3 plants utilise almost 50% of the photosynthates as against only 0–6% in C-4 plants.

A search for plant growth regulators (PGR) to reduce photorespiration in order to enhance net photosynthesis will contribute to increased yields, as long as it is not harmful to the plant (Walker 1980). In fact, Zelitch (1979) reported that this process could be eliminated completely with benefits in terms of yields. Zelitch (1979a) and Lawler (1981) reviewed the prospects of regulation of photorespiration in plants by PGR. Although a number of chemicals have been reported to inhibit photorespiration a simultaneous dimunition was observed in the rate of photosynthesis in the presence of O_2 but not in the absence of O_2 suggesting that carbon from photorespiratory pathway may not be wholly able to recycle back into the Calvin cycle (Servaites and Ogren 1977).

A net promoter of photosynthesis may act either by increasing photosynthesis *per se* or by depressing photorespiration (Maugh 1981). The effect of Mixtalol on the rate of photorespiration on tomato and barley leaves is given in tables 16 and 17.

Besides increasing the rate of photosynthesis, seed soak treatment with Mixtalol was effective in decreasing the rate of photorespiration of tomato leaves. Soaking seeds for 24 hr in 1·5 ppm of Mixtalol decreased the rate of photorespiration from 6·45 to 4·7 μmol CO_2 released g.fr. wt^{-1} hr^{-1} as measured 74 days after the treatment. Spraying with 1·5 ppm of Mixtalol on 5-day old barley seedlings decreased photorespiration by 30% as measured 3 days after the spray (table 16). Decreased photo- and dark-respiration rates suggest improved physiological efficiency of treated plants in conserving photosynthates.

A number of chemicals have been reported to inhibit photorespiration (table 18)

Table 15. Photorespiration in plants.

Crops	Photorespiration as % of net photosynthesis
C-3 plants	
Alfalfa	36
Potato	50
Soybean	42–75
Sugar beet	34–55
Sunflower	27–31
Tall fescue	36–47
Tobacco	25–45
Wheat	17–69
C-4 plants	
Maize	0–6

Zelitch (1975, 1979).

Table 16. Effect of Mixtalol on photorespiration by tomato leaves (seed soaked for 24 hr in 1·5 ppm Mixtalol).

Treatment	Rate of photorespiration (PR) μmol CO_2 released g. fr. wt.$^{-1}$ hr^{-1}	% decrease in PR
54-days old plant		
Control	9·74	
Treated	3·58	63·1
71-days old plants		
Control	6·45	
Treated	4·70	27·1

Table 17. Effect of Mixtalol on photorespiration of barley leaves.

	μ mole $^{14}CO_2$ g. fr. wt.$^{-1}$ hr^{-1}		
Treatment	$^{14}CO_2$ released in light (L)	$^{14}CO_2$ released in dark (D)	L/D
Control	0·654	0·412	1·59
Mixtalol	0·461	0·130	3·55
% Change	(−) 29·5	(−) 68·5	

(Foliar spray of 1·5 ppm Mixtalol on 5-day old seedling and measured 3 days later).

Table 18. Effect of chemicals on inhibition of photorespiration.

Chemicals	Inhibitory action	Dose (mM)
α-hydroxy-2-pyridine methane sulphonic acid (α-HPMS)	Glycolate oxidase	10[1,2]
2-hydroxy-3-butynoic acid (HB)	Glycolate oxidase	0·1–0·5
Isonicotinic acid hydrazide (INH)	Conversion of glycine to serine	10–20
Aminoacetonitrile (AAN)	Conversion of glycine to serine completely	0·13
Glycine hydraxamate	Conversion of glycine to serine completely	0·24
Glycidate	Glutamate-glyoxylate aminotransferase	10–20
Mixtalol	Locus of action – not investigated	0·002

(After Keys *et al* 1982).
1. Murray and Bradbeer (1971) 2. Tee and Sin (1974).

apart from our finding of the effect of Mixtalol in the depression of photorespiration but none of them has shown to increase photosynthesis.

5. Field trials with Mixtalol on different crops

Detailed experiments conducted to establish the optimum concentration of Mixtalol for both seed soaking and foliar application have indicated that 1 to 3 ppm is effective in increasing the yields of various crops. Field trials were conducted in different locations (Andhra Pradesh, Punjab, Haryana and Uttar Pradesh). Replicated trials on various crops in different seasons indicated a significant increase in yields, which is summarised in tables 19–21.

5.1 *Paddy (Oryza sativa)*

Mixtalol trials were conducted both for *Kharif* season (July sowing) as well as *Rabi* season (October/November sowing). The first experiment was conducted in UP at Etah during 1978, which gave encouraging results and replicated trials were then conducted in AP at different locations from 1979 through 1982. During this period, a total of 889 trials were conducted. A summary of the results is given in table 19. The yield increases during these trials ranged from 14–27 % over the control. It is interesting to note that even at high levels of productivity (*Rabi* 1981), there was an increase of 23 % in the yields following Mixtalol treatment.

In order to see the effect of Mixtalol on increasing the number of tillers/plant and grains/panicle, experiments were conducted in *Kharif* 1981 at Bapatla, AP and the results are given in table 20. It can be seen that Mixtalol increases both the number of

Table 19. Effect of foliar application of Mixtalol (1–2 ppm) on yield of paddy (*Oryza sativa*).

Season	No. of trials	Yield kg/ha		% Increase
		Control	Treated	
Kharif 1979	23	3268	4156	27
Kharif 1980	18	4175	5036	21
Rabi 1980	228	4076	4634	14
Kharif 1981	203	5441	6597	21
Rabi 1981	415	7360	8960	23
Kharif 1982	2	4848	6033	24

Table 20. Effect of Mixtalol on tiller and grain number of paddy.

Treatment	No. of tillers/plant	Grains/panicle
Control	9·75	215·5
Treated	12·25	238·0
% Increase	25·0	10·4

(1–2 ppm spray at 35 days and second spray at 65 days after sowing).

Table 21. Effect of foliar application of Mixtalol (1–2 ppm) on yield of various crops.

Crops	Season	No. of trials	Yield kg/ha		% Inc.
			Control	Treated	
Triticum aestivum	*Rabi* 1979–80	6	2777	3518	27
	Rabi 1980–81	299	2733	3084	13
	Rabi 1981–82	678	3948	4660	18
Zea mays	*Kharif* 1980	6	2695	3576	33
Pennisetum typhoides	*Kharif* 1980	34	2160	2592	20
Sorghum vulgare (fodder crop)	*Kharif* 1982	1	34640	51360	48
Arachis hypogaea	*Rabi* 1980–81	6	2148	2702	25
	Kharif 1981	26	1591	1833	15

tillers/plant and also grains/panicle which are the yield components. Increase in tillers is indicative of initial vigour and as an effect of first Mixtalol application and increase in grains can be attributed to increase in rate of photosynthesis and decrease in photorespiration rates.

5.2 *Wheat (Triticum aestivum)*

Research and development trials with Mixtalol on wheat were confined to UP, Haryana and Punjab. An initial trial was conducted during *Rabi* 1979 at Etah registering a mean yield increase of 27%. Large scale field trials on the same pattern described under paddy, were conducted in 9 regions of Haryana and Punjab comprising of 229 trials during 1980–81 and 678 trials during 1981–82. The mean average increase in yield was recorded to the order of 13% and 18% respectively (table 21).

5.3 *Maize (Zea mays)*

Replicated trials were conducted to see the effect of Mixtalol (1–2 ppm) used as a foliar spray and results are given in table 21. It is interesting to note that a mean average increase in grain yield was 33%, which could be attributed solely to higher rate of photosynthesis as maize being a C-4 plant. Yield increases have also been recorded at various coordinated trials, following application of Mixtalol (under publication).

5.4 *Jowar (Sorghum vulgare)*

Jowar being used as fodder, effect of foliar spray of Mixtalol on fodder yield was studied. Replicated experiments were conducted in fields near Bombay during *Kharif* 1982 and it was found that 1 ppm spray of Mixtalol at 20 and 40 days after sowing increased 48% of the fodder yield in Sundhia variety (table 21).

5.5 *Pearl millet (Pennisetum typhoides)*

Mixtalol was used on three varieties of pearl millet *viz* CJ 104, BJ 104 and local and a total of 34 replicated trials were conducted in different regions. Local variety responded

better giving an average increase in yield to the tune of 24%. The overall mean average increase in the yield of pearl millet was 20% (table 21).

5.6 *Vegetables*

In the case of vegetables, being indeterminate crops, foliar application of Mixtalol contributed dramatic increases in yields. During 1980, a large number of trials were conducted on different vegetables in two regions, namely Etah in the North and AP in South India and the mean average yield is summarised in table 22. It can be seen from

Table 22. Effect of foliar application of Mixtalol (2–3 ppm) on vegetable yields.

Year	Crop	No. of trials	Yield kg/ha		% Inc.
			Control	Treated	
1980	*Lycopersicon esculentum* (Tomato)	7	5092	8570	68
	Solanum tuberosum (Potato)	11	8629	10468	21
	Ipomoea batatas (Sweet Potato)	1	8222	10222	24
	Solanum melongena (Brinjal)	2	3263	4657	42
	Abelmoschus esculentus (Okra)	1	4390	5660	29
	Phaseolus vulgaris (Beans)	1	1770	2026	15
	Brassica oleracea var. *botrytis* (Cauliflower)	3	11125	13765	24
	Allium sativa (Garlic)	2	3213	3612	12
1981	*Lycopersicon esculentum* (Tomato)	2	14277	22603	58
	Ipomoea batatas (Sweet Potato)	1	7800	13000	67
	Solanum melongena (Brinjal)	2	1500	2340	56
	Abelmoschus esculentus (Okra)	1	4600	8000	74
	Phaseolus vulgaris (Beans)	5	5870	8821	50
	Luffa acutangula (Ridged Gourd)	2	10992	18539	66
	Capsicum annuum (Chilli)	1	3375	5000	48
	Pisum sativum (Green Peas)	1	4530	6750	49
1982	*Lycopersicon esculentum* (Tomato)	4	5583	8611	54
	Solanum tuberosum (Potato)	4	2788	3594	29
	Solanum melongena (Brinjal)	1	7624	10861	42

the Table that tomato had increased in yield from 55 to 80 % as compared to control. All the vegetables registered a considerable increase in yield, when Mixtalol (2–3 ppm) was applied as foliar spray twice at an interval of 30 days. It was observed that the yield increases were due to more number of fruits indicating a possibility of its role in improving fruit set. The experiments on vegetables were repeated during 1981 and 1982 with similar results (table 22).

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