

Influence of Methanol on Sugarbeet Yield and Photosynthesis

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ABSTRACT

Foliar application of methanol has improved growth and productivity experimentally in a number of agricultural crops. To test the possibility that methanol application might improve sugarbeet yield, we conducted a replicated field study at Fort Collins, Colorado in 1994 with two commercial sugarbeet varieties (Monohikari, Beta 2398) and one public breeding line (FC709-2). Methanol was foliarly applied at about ten day intervals throughout the growing season starting at 40 dap. Plants were treated with 50% methanol plus 0.1% Triton-X surfactant, or 50% methanol plus 0.1% Triton-X plus 0.2% monosodium glutamate (MSG) as a nitrogen source. Control plants received no spray treatment. Two regimes of irrigation were included, one that provided water at a level typical of commercial growing practice and one in which about 50% as much water was applied on the same schedule, intentionally causing chronic water stress. Photosynthetic gas exchange was determined on August 26 and September 8 at mid-day on a subset of plots. Root yield and percentage root sucrose were determined at harvest, and sucrose yield was calculated from those values. The summer was warm and dry in 1994 and even plants in the higher irrigation regime were water-stressed (i.e., wilted at mid-day), and no significant differences in root yield, percent root sucrose, or sucrose yield occurred due to irrigation treatment. Significant differences for each of the three parameters occurred among varieties and for methanol treatments. Both methanol treatments re-

sulted in significantly lower root weight and sucrose yield than the control, and methanol plus MSG application resulted in significantly lower root weight and sucrose yield than application of only methanol. Percentage sucrose was statistically similar in control and methanol treatments, but treatment with methanol plus MSG resulted in lower percentage sucrose. Photosynthesis was increased in methanol treated plots, but this result was not consistent. If methanol treatment resulted in higher photosynthesis in the short term, this may have resulted in greater above-ground growth at the expense of root growth and root sucrose storage, which could account for the observed lower root and sucrose yield in the treated plots. If early-season methanol application timing and concentration could be adjusted to stimulate early canopy formation, so that maximal light interception could be achieved earlier in the season, this might lead to increased sucrose yield at harvest.

Additional Key Words: *Beta vulgaris*, root yield, sucrose, sugar yield, sugarbeet growth, photosynthetic rate, gas-exchange, partitioning

The use of foliar applications of methanol to increase biomass production and water-use efficiency of agricultural crops has received considerable attention. Such studies were stimulated by the initial report of Nonomura and Benson (1992a) that even a single foliar application of 10 to 50% methanol increased growth and development of a number of crops grown in an arid environment under high sunlight intensity. In a series of studies (Benson and Nonomura, 1992; Nonomura and Benson, 1992a, 1992b, 1992c), the feasibility of using methanol as a source of carbon in cultivated crops was examined. For a variety of C₃ plant species growing in direct sunlight, including rose (*Rosa* sp.), cabbage (*Brassica oleracea* L.), cotton (*Gossypium hirsutum* L.), tomato (*Lycopersicon esculentum* Mill.), strawberry (*Fragaria X ananassa* Duchesne), eggplant (*Solanum melongena* L.), palm (*Washingtonia robusta* H. Wendl.), watermelon [*Citrullus lanatus* (Thunb.) Matsum. & Nakai], and durum wheat (*Triticum durum*), methanol treatment resulted in higher turgidity and water use efficiency, and improved crop yield by up to 100%. Additionally, an increase in sugar accumulation, presumably due to a decrease in photorespiration (Benson and Nonomura, 1992) was noted. Subsequent reports have listed a number of other growth and yield responses to methanol. For example,

Devlin et al. (1994) found that foliar methanol application greatly stimulated the storage root growth of radish (*Raphanus sativus* L.). Root fresh and dry weights were 151% and 130% higher in plants treated twice with 10% methanol. Methanol also stimulated growth of wheat (*Triticum aestivum* L.) and pea (*Pisum sativum* L.) (Devlin et al., 1994); oilseed rape (*Brassica napus* var. *oleifera*) (Karczmarczyk et al., 1995); and geranium (*Pelargonium* sp.) and bachelor's button (*Centaurea cyamus* L.) (Devlin et al., 1995). Methanol applied to soybean [*Glycine max* (L.) Merr.] improved yield but not chlorophyll content or net photosynthetic rate (Li et al., 1995).

Methanol is rapidly metabolized as a carbon source during photosynthesis (Benson, 1951; Bassham et al., 1954; Quayle et al., 1954). In *Chlorella* and *Scenedesmus* rates of ^{14}C -methanol fixation were comparable to rates of $^{14}\text{CO}_2$ fixation (Calvin and Benson, 1949). Higher plants also fix methanol (Cossins, 1964). However, methanol apparently has no effect on C_4 plants (Nonomura and Benson, 1992a, 1992b). Photosynthesis in C_3 plants may be enhanced, photorespiration inhibited, and sink tissue stimulated by methanol treatment.

In laboratory experiments, methanol treatments resulted in higher photosynthetic gas exchange in spinach (*Spinacia oleracea* L.) and growth rates in soybean (*Glycine max* 'Corsoy') (Nishio et al., 1993). When soybean plants were water-stressed, methanol treated plants exhibited significantly lower water potential compared to controls, but remained turgid. The lower water potential was similar to drought or salt stress responses; however, in salt stress, leaves are smaller. Thus, it appears that methanol treatment may result in lower leaf osmotic potential, so uptake of available water continues longer than in non-treated plants. The turgidity may allow photosynthesis and growth to continue in treated plants when non-treated plants are wilted. Analysis of internal CO_2 concentration inside sugarbeet leaves suggested that methanol treatment may increase the internal CO_2 concentration in leaves (Nishio et al., 1993).

Some research has shown the application of methanol was not effective. Idso et al. (1995) reported that foliar application of methanol resulted in no clear differences in gas exchange measurements for the sour orange (*Citrus aurantium* L.). No influence on yield was reported for spring barley (*Hordeum vulgare* L.), winter wheat (*Triticum aestivum* L.), pea (*Pisum sativum* L.) (Albrecht et al., 1995); peppermint (*Mentha X piperita* L.) (Mitchell et al., 1994); potato (*Solanum tuberosum* L.) (Feibert et al., 1994; James et al., 1994); muskmelon (*Cucumis melo* L.), tomato, or watermelon (Hartz et al., 1994); or sugarbeet (*Beta vulgaris* L.) (Rykbost and Dovel, 1994). McGiffen Jr et al. (1995) reported that methanol did not increase yield or growth of creeping bentgrass (*Agrostis palustris* Huds.),

wheat, carrot (*Daucus carota* L.), lemon (*Citrus limon* L.), pea (*Pisum sativum* L.), radish (*Raphanus sativus* L.), or corn (*Zea mays* L.) in a variety of environments in California. Negative effects of methanol application were reported on growth of Kentucky bluegrass (*Poa pratensis* L.) (Crowe et al., 1994) and yields of romaine lettuce (*Lactuca sativa* L.) (McGiffen Jr et al., 1995). A detailed review of the literature has been provided by McGiffen, Jr. and Manthey (1996).

The objective of this study was to ascertain whether the storage root of sugarbeet would benefit from foliar methanol treatments under the hot, dry summer conditions on the Front Range of the Rocky Mountains. A stimulation of photosynthesis normally results in an increase in biomass. For this to be economically beneficial in sugarbeet, the increase must occur in root weight or root sucrose percent, and an increase in one of these must occur without a compensatory decrease in the other.

MATERIALS AND METHODS

This experiment was designed to test the effect of methanol application on root and sucrose yield of three sugarbeet varieties. Because supplementation with a nitrogen source appears to reduce methanol toxicity and allow sustained growth in methanol treated plants (Nonomura and Benson, 1992a, 1992b), we also included a treatment in which methanol was applied with nitrogen. We used MSG because it dissolved easily in methanol and was readily absorbed by the plant. To test whether drought stress affected the response of sugarbeet to methanol application, the experiment included two irrigation levels.

Plant material.

Sugarbeet was planted at Fort Collins, Colorado, on May 6, 1994. Cultural practices, including irrigation, employed throughout the year were similar to those used for commercial sugarbeet production. Three varieties were used: (1) Monohikari (Seedex, Inc.), a high sucrose diploid hybrid adapted for growth in the Great Plains; (2) Beta 2398 (Betaseed, Inc.), a high sucrose triploid hybrid adapted for growth in the Great Plains; and (3) FC709-2 (Panella, 1999), a multigerm *Rhizoctonia*-resistant germplasm developed by the USDA-ARS in Fort Collins. Seed was planted 5 cm apart in rows spaced 56 cm apart. Emerging seedlings were thinned to a plant spacing of 20 cm (approximately 5 plants m⁻¹). The soil type was a Nunn clay loam (Aridic Argiustoll; fine montmorillonitic, mesic).

Treatments.

Three treatments were applied to each of the varieties tested: (1) unsprayed control; (2) 50% (v/v) methanol plus 0.1% (v/v) Triton-X100 (a surfactant); and (3) 50% methanol plus 0.1% Triton-X100 plus 0.2% (w/v) monosodium glutamate (MSG) as a nitrogen source. This gave 18 treatment combinations, nine well-watered and nine water-stressed. Earlier experiments identified 50% methanol as the highest rate of methanol that did not result in some leaf necrosis (data not shown). The plants were sprayed with a hand-pumped sprayer until wetness (when the leaves dripped). This required 11 liters treatment⁻¹ or approximately 3.3 ml plant⁻¹ when the plants were first sprayed (at 40 days after planting) and had little leaf area. The plants were sprayed at approximately 10 day intervals until harvest of the south block; eleven applications were made (Figure 1a).

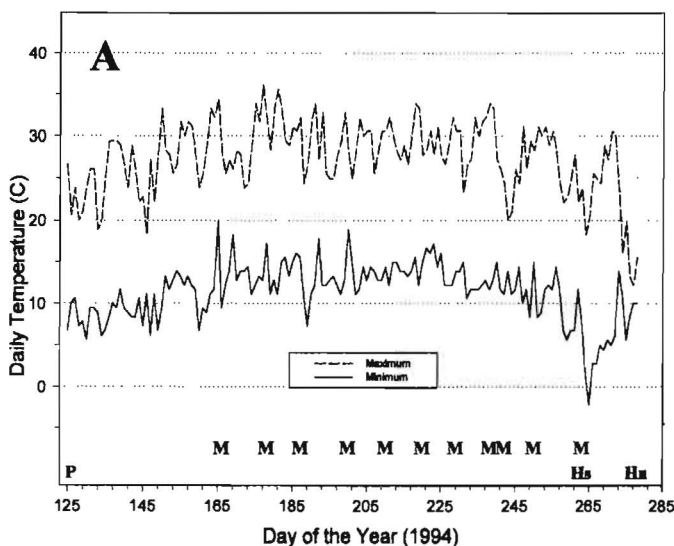


Figure 1A. Displays daily minimum and maximum temperatures, the date of planting (P), dates of harvest (Hs=southern block; Hn=northern block), and dates of methanol application (M).

Treatments ended about 15 days before harvest of the north block. As the leaf area index increased, the amount sprayed rose to a maximum of 26.5 liters treatment⁻¹ or approximately 8.0 ml plant⁻¹. Treatments were applied between 11:00 a.m. and 3:00 p.m. to occur during the hottest part of the day, because the largest effects were reported to have occurred under high sunlight intensity (1992a).

Design, harvest, and data analysis.

The experimental design was a randomized split block design with replicates nested within split blocks. Two blocks (north and south) were randomly split into well-watered and water-stressed treatments, each block containing three full replicates. Plots were 4 rows wide and 6 meters in length. The middle two rows were treated with methanol spray or left unsprayed as controls. Each of the two middle rows was harvested and analyzed separately; these values were averaged to produce a mean plot value for each variable. All roots 5 cm or greater in diameter were harvested from the south block on September 20th and from the north block on October 5th. Roots were counted, topped, washed, and weighed. Percentage sucrose was measured by standard procedures (Association of Official Agricultural Chemists, 1955). Sucrose yield plot⁻¹ was calculated as plot root weight times mean percent sucrose for the plot subsamples. An analysis of variance was performed on root weight, percent sucrose, and sucrose yield (SAS® Proc ANOVA).

Measurement of photosynthesis.

Replicated gas exchange measurements (LI-6200 portable gas exchange system, LI-COR, Inc., Lincoln NE) were made August 26 and September 8 on a subset of the field plots to determine the rate of photosynthesis. Three plants were measured in each plot when possible; at times all plants within a plot were wilted and no measurements were made, as plants exhibited net CO₂ evolution (respiration). The measurements were made during the heat of the day (between 11:00 a.m. and 2:00 p.m.) to increase the probability of observing an effect due to methanol application. An analysis of variance determined significant differences among treatments (SAS® Proc ANOVA).

Application of methanol.

We had a strong concern about potential health hazards when working with methanol. Each person spraying was made aware of the hazards and wore rubber boots, a rubber apron, a full face shield, and rubber gloves as protection against skin contact with methanol. The amount of methanol in air was monitored with a Sensidyne[®] pump kit no. 800, which measures methanol concentration in the air colorimetrically.

Water stress and water status monitoring.

Daily temperature maxima and minima, precipitation, and dates of irrigation were recorded. Generally, the stressed plots were irrigated for

half the time of the well-watered plots (6 versus 12 h in most cases). Additionally, eight neutron probe readings were taken throughout the season to monitor differences in soil water status between the well-watered and stressed treatments.

RESULTS

Concentration of methanol present.

Two samples of air were taken in the headspace of the methanol-containing can. Each indicated a methanol concentration of over 1000 pm. Air samples taken 18 inches above the spout of the can did not contain detectable methanol at the sensitivity of the pump kit ([methanol] \leq 10 ppm). Samples taken in the field directly above the plant (approximately 150 mm above the leaf surface) changed the color detector slightly when 400 ml of air was sampled (twice the normal sample volume), indicating that the methanol concentration present was not greater than 10 ppm. With the precautions taken against skin exposure described above, and the rapid dissipation of methanol documented by the measurements described here, minimal danger was present to the researchers because of exposure to methanol.

Analysis of variance of yield components.

The results of the analysis of variance (ANOVA) performed for root weight, percentage sucrose, and sucrose yield are shown in Table 1. In the ANOVA, the significance of an interaction between block and stress was first tested using Rep(block*stress) as the error term; if the interaction was significant, block*stress was used as the error term (i.e. root weight) to test for the significance of stress, otherwise the interaction term was dropped from the model and Rep(block*stress) with 9 df was used as the error term (i.e. percent sucrose and sucrose yield). Similarly the interaction of block, stress, variety, and treatment (16 df) was tested for significance; because it was not significant, this term too was dropped from the model and an error term with 80 degrees of freedom (df) was used.

The imposition of water stress did not result in statistically significant differences for yield components in comparison with well-watered plots. No interaction among variety, treatment, stress, or block was significant ($P=0.05$), although Beta 2398 was observed to wilt more readily under high temperature than the other varieties, and showed less sucrose production in the well-watered treatment (Table 2).

Table 1. The results of the analysis of variance performed on root weight, percent sucrose, and sucrose yield are shown below. In each instance, the source of the error term is indicated.

Source	Degrees of Freedom	Probability > F value		
		Root Weight	Percent Sucrose	Sucrose Yield
Block (blk)	1			
Stress (str)	1	0.43	0.14	0.37
Blk*str	1	error term		
Rep(blk*str)	8			
Blk*str+Rep(blk*str)	9		error term	error term
Variety (var)	2	0.0001	0.0001	0.0001
Treatment (trmt)	2	0.0001	0.0153	0.0001
Var*trmt	4	0.74	0.52	0.66
Str*var	2	0.73	0.10	0.08
Str*trmt	2	0.29	0.57	0.77
Str*var*trmt	4	0.93	0.78	0.90
Blk*str*var*trmt	16			
Blk*str*var*trmt +Error (64 df)	80	error term	error term	error term

Table 2. Root weight, sucrose percent, and sucrose yield for well-irrigated and water-stressed plots, averaged over block, replication, and treatment.

Variety	Treatment	Root Weight (kg plot ⁻¹)	Sucrose (%)	Sucrose Yield (kg plot ⁻¹)
Beta 2398	Well-watered	17.5	13.3	2.3
	Stressed	15.6	13.7	2.1
FC709-2	Well-watered	15.0	13.1	2.0
	Stressed	13.5	12.8	1.7
Monohikari	Well-watered	20.8	15.2	3.2
	Stressed	18.7	14.4	2.7

Highly significant differences ($P=0.01$) for root weight, percent sucrose, and sucrose yield were present among varieties and among treatments (Table 1). Root weight and sucrose yield for both methanol treatments were significantly lower than levels in the unsprayed control (Table 3). Percent sucrose at harvest did not differ between the controls and the methanol treated plots, but the control sucrose percentage was significantly greater than in the methanol plus MSG treatment (Table 3). An interaction between variety and water stress level was evident ($P = 0.104$, Table 1), probably because the water-stressed Beta 2398 variety had higher percentage sucrose than in well-watered plots of that variety, the opposite of what occurred in the other two varieties (Table 2).

Table 3. Root weight, sucrose percentage, and sucrose yield among treatments averaged over block, replication, stress, and variety. Means with the same letter are not significantly different ($P = 0.05$).

Treatment	Root Weight (kg plot ⁻¹)	Sucrose (%)	Sucrose Yield (kg plot ⁻¹)
Control	17.6 a	14.0 a	2.5 a
Methanol	16.9 b	13.7 ab	2.3 b
Methanol plus MSG	16.0 c	13.3 b	2.2 c

Analysis of variance of photosynthesis measurements.

Rate of photosynthesis did not differ among plots before methanol spray treatment (data not shown). After initiation of treatments, photosynthetic measurements were made on two dates with the same replicate measured on each date. Three plants were measured and averaged for a plot mean, and differences among plot means were tested by ANOVA. At both dates significant three-way interactions were present among stress regime, treatment, and variety. Therefore, the test error mean square was used to generate an LSD for comparisons among treatments within varieties within stress level (Table 4). Gas exchange measurements showed higher photosynthesis for those water-stressed plots sprayed with methanol or methanol plus MSG, but trends in differences were not consistent across variety or water stress level. Both FC709-2 and Beta 2398 showed a significant positive photosynthetic response to methanol in stressed plots; however, Monohikari's response to the methanol treatment was significantly lower photosynthesis or no significant difference from the control (Table 4). When MSG was present with methanol in the treatment mixture, however, significantly higher photosynthetic rates were found in comparison with the control only for Beta 2398, and only when the unsprayed control was wilted (net respiration was given a value of 0; measurements were not made on all wilted plants) on both sampling days in the stressed plots and on August 26 in the irrigated plot. In the one irrigated plot, when Beta 2398 was not wilted, the control had a significantly higher rate of photosynthesis than the methanol treatment, but not significantly higher than the methanol with MSG treatment (Table 4). Under stressed conditions, Monohikari showed a significantly higher rate of photosynthesis in the unsprayed control than the methanol treatment but not significantly different from the methanol with MSG treatment. In the irrigated plots, photosynthetic rates in the methanol or methanol plus MSG treated plants significantly exceeded that of controls in two of six or one of six comparisons, respectively (Table 4). When we visually examined the plants during the hottest part of the day, we frequently observed less wilting in plots treated with methanol or methanol plus MSG.

DISCUSSION

Summer temperatures in 1994 (Figure 1a) were consistently warm and rainfall was limited (Figure 1b). Although the field was irrigated seven times throughout the growing season, neutron probe readings showed that differences between the well-watered (subsequently, "irrigated") and

Table 4. Rate of photosynthesis in $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ sec}^{-1}$, measured on August 26 and September 8. Values are means of three plants measured in each plot. One of six field replicates was measured.

8/26	Stressed			Irrigated		
	Beta 2398	FC709-2	Monohikari	Beta 2398	FC709-2	Monohikari
Methanol	9.5	17.8	5.1	10.7	15.6	18.9
Methanol & MSG	11.0	8.1	13.2	12.4	14.9	12.5
Control	0.0 [†]	12.7	13.0	0.0	13.4	13.8
LSD _{0.05} = 3.0						
9/08	Stressed			Irrigated		
	Beta 2398	FC709-2	Monohikari	Beta 2398	FC709-2	Monohikari
Methanol	9.1	11.4	5.3	10.2	11.5	12.0
Methanol & MSG	6.2	8.0	6.4	12.9	9.2	10.5
Control	0.0	7.4	7.9	14.5	10.8	10.9
LSD _{0.05} = 2.3						

[†]A value of 0.0 was given when all plants in that plot were wilted and no measurement of photosynthesis was made, because plants exhibited net respiration.

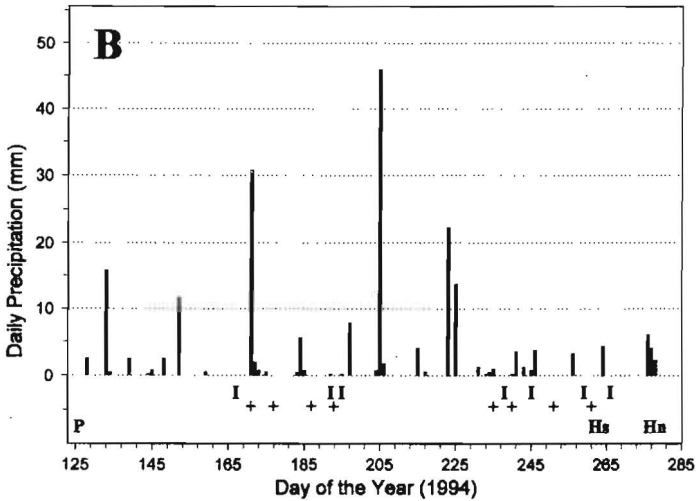


Figure 1B. Displays daily recorded precipitation, dates of irrigation (I), and dates of neutron probe readings (+). Generally, the stressed plots were irrigated for half the time of the irrigated plots.

water-stressed (“stressed”) treatments seldom exceeded 10% soil moisture at any depth (Figure 2). These were ideal conditions to test the effects of methanol, and even the plants in the higher irrigation plots were more stressed than would have been desired for optimum yields. Clear, significant differences in yield were present among spray treatments with very few interactions. Application throughout the growing season of methanol or methanol and MSG resulted in lower sugar production. In contrast, in an experiment with sugarbeet in an irrigated trial in Oregon, Rykboost and Dovel (1994) reported that three mid-season applications of 10, 20, 40, or 80 percent methanol had no effect on root yield, percentage sucrose, or sucrose yield at harvest.

The effect of methanol on the rate of photosynthesis measured was not so straightforward. Varietal differences were evident (Table 4). Beta 2398 appeared to be the most favorably responsive to the methanol treatments. In Beta 2398, the midday depression was attenuated by both methanol treatments, which led to enough retention of turgidity that measurable photosynthesis could occur during the high heat stress of midday, whereas the controls were wilted and exhibited net respiration. Beta 2398 was also the only variety that had significantly higher percentage sucrose. In the drought-stressed plots, FC709-2 had higher photosynthetic rates when

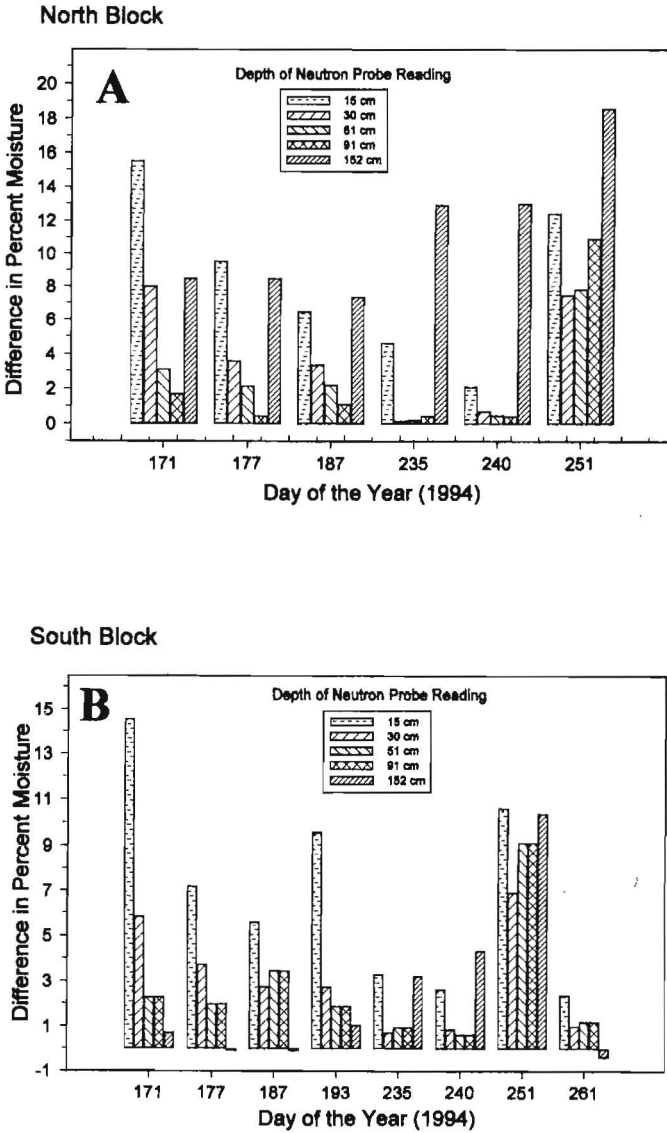


Figure 2. Differences in percent soil moisture between the irrigated and stressed treatments were calculated by subtracting the stressed values at different depths in the soil profile as measured by a neutron probe from the irrigated values at the same depth A) in the north block, and B) in the south block.

treated with methanol, but not in the plots treated with methanol plus MSG. The photosynthetic rate response to treatment was reversed in stressed Monohikari, where photosynthesis was lower in methanol-treated plots relative to controls, yet the plots treated with methanol plus MSG did not differ from controls (Table 4). Except for Beta 2398, in the well-irrigated plots, differences between treatments were small. Thus, the positive effect of methanol on photosynthesis appeared to be more apparent under the more stressful conditions.

Monohikari is considered well adapted to the northern high plains when grown under typical cultural conditions. Under water stress, the large leaf size and stomatal size of triploid beets such as Beta 2398 might be disadvantageous. However, data are limited concerning this possibility, and it does not explain the contradictory photosynthetic response to the two types of methanol treatment. Biochemical and metabolic differences among varieties should be examined. For example, varieties may differ in capacity for NO_3 and NH_4 metabolism. Also, little is known about genetic variation for response to water stress in sugarbeet and no information is available about potential genotypic variation for response to methanol. Plant architecture differs among varieties, including among those in this test, and could be related to the wilting and photosynthetic responses we observed.

Higher photosynthesis may have resulted in more above-ground growth at the expense of root growth and root sucrose storage. Sugarbeet root expansion and sucrose storage depend on the degree to which assimilate is partitioned to those functions in mid- to late-season. Excessive nitrogen fertilization is known to favor sugarbeet top growth at the expense of root growth and sucrose storage, which results in a lower percentage sucrose in the root (Draycott, 1993). Methanol treatment appeared to produce a lower sucrose percentage in the root (Table 3), perhaps for the same reason. The inclusion of MSG as a nitrogen source also could have stimulated foliar growth in late season; the fertilization scheme used provides adequate N for normal growth. In one study, radish storage root growth was highly stimulated by methanol application, but shoot length and fresh and dry weight also were stimulated significantly (Devlin et al., 1994). Perhaps sugarbeet foliar growth was stimulated by methanol application late in the growing season and this resulted in an more leaf biomass at the expense of sucrose storage in the root. A possible mechanism for such an event is provided by the observation of Karczmarczyk et al. (1995) that both leaf biomass and nitrate reductase activity were higher in methanol-treated oilseed rape. If nitrate reductase activity of sugarbeet were higher due to methanol treatment and additional late-season nitrogen were provided to tops, this might be expected to alter the distribution of photosynthate just as does excessive late-season uptake of nitrogen from the soil.

Although we did not measure canopy growth in this experiment, a future experiment could productively address this possibility, and studies on the effect of methanol on nitrogen metabolism may be useful in understanding the effect of methanol on photosynthesis and carbon partitioning.

The photosynthetic measurements suggest it would be worthwhile to determine if early-season methanol treatment will stimulate early canopy formation, perhaps through a combination of higher photosynthesis and more reduced nitrogen for incorporation into critical amino acids and enzymes. With early canopy closure, maximal light interception would be achieved earlier in the season, which in turn would lead to larger sucrose yield at harvest (assuming proper mid- to late-season nitrogen management is practiced) (Scott and Jaggard, 1993).

In summary, treatment with methanol or methanol plus MSG resulted in higher photosynthesis, but not consistently. The positive impact was more pronounced under stressful conditions, especially in Beta 2398. Methanol treatments caused statistically significant lower root yield, percentage sucrose and sucrose yield in this trial. A number of questions still need further investigation, particularly the action of late-season methanol application, which might indeed be increasing photosynthesis in water-stressed plants but with a biomass response occurring in tops rather than in roots or sucrose. More importantly for sugarbeet production, application of methanol during the early growth season could lead to early canopy closure and increased sugar yield during the majority of the growth season. Perhaps laboratory studies can provide a greater understanding of the physiological changes affecting sugarbeet after the foliar application of methanol. Such studies might also lead to useful information on the control of assimilate partitioning.

LITERATURE CITED

- Albrecht, S.L., C. L. Douglas Jr., E.L. Klepper, P.E. Rasmussen, R.W. Rickman, R.W. Smiley, D.E. Wilkins, and D.J. Wysocki. 1995. Effects of foliar methanol applications on crop yield. *Crop Sci.* 35:1642-1646.
- Association of Official Agricultural Chemists. 1955. *Official Methods of Analysis*. 8th ed. Pages 564-568. Washington D.C.
- Bassham, J.A., A.A. Benson, L.D. Kay, A.Z. Harris, A.T. Wilson, and M. Calvin. 1954. The path of carbon in photosynthesis. XXI. The cyclic regeneration of carbon dioxide acceptor. *J. Am. Chem. Soc.* 76:1760-1770.

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- Benson, A.A. 1951. Identification of ribulose in $C^{14}O_2$ photosynthesis products. *J. Am. Chem. Soc.* 73:2971-2972.
- Benson, A.A., and A.M. Nonomura. 1992. The path of carbon in photosynthesis: methanol inhibition of glycolic acid accumulation. *Photosyn. Res.* 34:196.
- Calvin, M., and A.A. Benson. 1949. The path of carbon in photosynthesis. IV: The identity and sequence of the intermediates in sucrose synthesis. *Science* 109:140-142.
- Cossins, E.A. 1964. The utilization of carbon-1 compounds by plants. I. The metabolism of methanol- C^{14} and its role in amino acid biosynthesis. *Can. J. Biochem.* 42:1793-1802.
- Crowe, F.J., D.D. Coats, and M.D. Butler. 1994. Performance of Kentucky bluegrass seed treated with methanol. Central Oregon Agricultural Research Center Annual Report, 1993. Pages 115-119. *In* Oregon State University Special Report 930, Agricultural Experiment Station, Corvallis, OR.
- Devlin, R.M., P.C. Bhowmik, and S.J. Karczmarczyk. 1994. Influence of methanol on plant growth. *PGRSA Quart.* 22:102-108.
- Devlin, R.M., S.J. Karczmarczyk, and P.R. Lopes. 1995. The effect of methanol on the growth and pigment content of bachelor's-button (*Centaurea cyanus*) and geranium (*Pelargonium hortorum*). *PGRSA Quart.* 23:127-136.
- Draycott, A.P. 1993. Nutrition. p. 238-279. *In* D.A. Cooke and R.K. Scott (ed.) *The Sugar Beet Crop: Science into Practice*. Chapman & Hall, London.
- Feibert, E.B.G., S.R. James, K.A. Rykbost, A.A. Mitchell, C.C. Shock, and F.J. Crowe. 1994. Methanol effects on potato yield, quality, and water use. *Proc. Potato Assoc. Am.* 78th Ann. Meeting:P24 (July 24-28, Calgary, Alberta).
- Hartz, T.K., K.S. Mayberry, M.E. McGiffen, M. LeStrange, G. Miyao, and A. Baameur. 1994. Foliar methanol application ineffective in tomato and melon production. *HortScience* 29:1087.

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- Idso, S.B., K.E. Idso, R.L. Garcia, B.A. Kimball, and J.K. Hooper. 1995. Effects of atmospheric CO₂ enrichment and foliar methanol application on net photosynthesis of sour orange tree (*Citrus aurantium*: Rutaceae) leaves. *Am. J. Bot.* 82:26-30.
- James, S.R., F.J. Crowe, and A.R. Mitchell. 1994. Methanol effects on potato yield, quality, and water use. *Proc. Potato Assoc. Am.* 78th Ann. Meeting:P23 (July 24-28, Calgary, Alberta).
- Karczmarczyk, S., R.M. Devlin, and I.I. Zbieć. 1995. (Effect of methanol on winter rape seedlings.) *Acta Agrobot.* 48:37-42. (In Polish, English abstract.)
- Li, Y. G., J. M. Gupta, J. M. Joshi, and A. K. Siyumbano. 1995. Effect of methanol on soybean photosynthesis and chlorophyll. *J. Plant Nutr.* 18:1875-1880.
- McGiffen Jr, M.E., and J.A. Manthey. 1996. The role of methanol in promoting plant growth: A current evaluation. *HortScience* 31:1092-1096.
- McGiffen Jr, M.E., R.L. Green, B.A. Faber, J. Downer, N.J. Sakovich, and J. Aguiar. 1995. Field tests of methanol as a crop yield enhancer. *HortScience* 30:1225-1228.
- Mitchell, A.R., F.J. Crowe, and M.D. Butler. 1994. Plant performance and water use of peppermint treated with methanol and glycine. *J. Plant Nutr.* 17:1955-1962.
- Nishio, J.N., S. Huang, T.L. Winder, M.P. Brownson, and L. Ngo. 1993. Physiological aspects of methanol feeding to higher plants. Pages 8-13. *In* L. Ferguson (ed.) *Proceedings of the Twentieth Annual Meeting, Plant Growth Regul. Soc. of Am.*
- Nonomura, A.M., and A.A. Benson. 1992a. The path of carbon in photosynthesis: improved crop yields with methanol. *Proc. Natl. Acad. Sci. USA* 89:9794-9798.
- Nonomura, A.M., and A.A. Benson. 1992b. The path of carbon in photosynthesis: Methanol and light. Pages 911-914. *In* N. Murata (ed.), *Research in Photosynthesis. Vol. III.* Kluwer Academic Publishers, Dordrecht, The Netherlands.

- Nonomura, A.M., and A.A. Benson. 1992c. The path of carbon in photosynthesis: stimulation of crop yields with methanol. *Photosyn. Res.* 34:207.
- Panella, L. 1999. Registration of FC709-2 and FC727 sugarbeet germplasms resistant to *Rhizoctonia* root rot and *Cercospora* leaf spot. *Crop Sci.* 39:298-299.
- Quayle, J.R., R.C. Fuller, A.A. Benson, and M. Calvin. 1954. Enzymatic carboxylation of ribulose diphosphate. *J. Am. Chem. Soc.* 76:3610-3611.
- Rykbost, K.A., and R.L. Dovel. 1994. Effects of foliar-applied methanol on sugarbeet production. Oregon State University Special Report 934, pp. 67-68, Agricultural Experiment Station, Corvallis, OR.
- Scott, R.K., and K.W. Jaggard. 1993. Crop physiology and agronomy. Pages 179-237. *In* D.A. Cooke and R.K. Scott (ed.) *The Sugar Beet Crop: Science into Practice*. Chapman & Hall, London.