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The Path of Carbon in Photosynthesis – XXVIII – Response of Plants to Polyalkylglucopyranose and Polyacylglucopyranose

Arthur M. Nonomura, Barry A. Cullen and Andrew A. Benson
Scripps Institution of Oceanography, University of California San Diego
USA

1. Introduction

A series of discoveries began 63 years ago through the collaboration of Melvin Calvin and Andrew Benson 1948. Paving the path (Benson 2002a) has since included the publications that have described the initial products of carbon fixation, from phosphoglycerate onward. From its inception, the program has followed a design that has been based on far-reaching interdisciplinary discourse, quoting the philosophy of Alexander Graham Bell, that, "Great discoveries and improvements invariably involve the cooperation of many minds." For example, investigations three decades ago by Wolf, Nonomura & Bassham 1985, established characteristics of the alga, "Showa," that accumulated the highest *in vitro* concentrations of hydrocarbons, 40% botryococcenes; from which gasoline and aviation fuels may be derived by catalytic hydrocracking in a conventional petroleum refinery. Studies of algal metabolism were as critical to the development of concepts of the Prize from 1948 through 1961, as they are today--special reference given to the lollipop (Nobelprize, 2011), a flat panel glass chamber that was designed by Benson and built by Harry Powell for controlled culture of *Chlorella* to track radiolabeled carbon metabolism in the laboratory --and thereby, paths converged, as Nonomura & Benson 1992 developed experimental methods for the feeding of single-carbon (C_1) fragments to "Showa." That led to foliar delivery into angiosperms of up to 15 M C_1 formulations supplemented with normally phytotoxic levels of ammoniacal nitrogen. When these applications were undertaken in sunlit fields, adjacent controls wilted by mid-afternoon, but rows treated with C_1 formulations remained fully turgid, showing no signs of wilt. Moreover, Benson & Nonomura 1992 discovered that treatments with these C_1 formulations inhibited glycolate formation, confirming their observations of long durations of reduced photorespiration. In addition to replicating increased yields, Ligocka et al. 2003 discovered corresponding increases of nitrate reductase and alkaline phosphatase by C_1 formulations. In the meantime, Gout et al. 2000 followed metabolism of the C_1 formulations by NMR to the identification of methyl-β-D-glucopyranoside; be that the case, little is known about glycosylation although it is a natural process in the metabolism of C_1 fragments. Thus, in our programs of experimental biology, we investigated responses of plants to substituted glycopyranosides (Benson, 2002a); and we recently showed that not only do substituted glycopyranosides improve productivity, they are transported in plants and metabolized (Benson et al., 2009; Biel et al., 2010;

Nonomura et al., 2011). For our current studies, we selected a polyalkylglycopyranose and we manufactured polyacylglycopyranoses as candidate compounds. Plant responses to formulations of 0.5 to 10 mM polysubstituted glucopyranoses were similar to those of growth enhancements from treatment with foliar formulations of 0.3 M methylglucopyranosides. Therefore, we conclude that when highly substituted sugars are appropriately formulated for application at optimal dosages, visibly discernible enhancement of vegetative productivity may be achieved that is statistically significant and highly consistent. Treatments with polyacylglucopyranoses resulted in significant enhancements of root and shoot growth without toxicity and we tracked putative metabolites of polyacylglucopyranoses and ammoniacal nitrogen. Finally, we gather evidence of mechanisms in which substituted glycopyranoses compete with sugars to release them from lectins.

2. Materials and methods

Plants were cultured in research facilities according to previously described methods (Benson et al., 2009). General supplementation of foliar formulations included the following: 10 - 50 mM ammonium salt; 1 - 6 ppm manganese, Mn-EDTA; and 1 - 6 ppm iron, Fe-HEDTA. For example, foliar solutions of 1,2,3,4-tetramethyl-β-D-glucopyranose, hereafter referred to as tetramethylglucopyranose, were formulated as follow: 23 mM ammonium sulfate, $(NH_4)_2SO_4$, 6 ppm Mn and 6 ppm Fe; and Nutrient Control contained 23 mM $(NH_4)_2SO_4$, 6 ppm Mn and 6 ppm Fe. We found the above supplements to be effective with polyalkylglucopyranoses and polyacylglucopyranoses, particularly, with Mn adding consistency of response to treatments. Moreover, our preliminary tests showed that without ammoniacal and Mn supplementation, the compounds were inactive. Solutions for foliar applications included phytobland surfactant blends applied at a concentration of 1 g/L made from a random block copolymer (Pluronic® L-62, BASF) with a polysiloxane wetter (Q2-5211, Dow Corning®) compounded at a 3:1 ratio. Controls were placed in the same location and all plants were given identical irrigation, fertigation, and handling. Plants were cultured in trays containing soil-less MetroMix® 560 media. Grasses were cultured in MetroMix® 560 blended with 25% calcined clay (Turface®). Plants were matched to control populations, treated after emergence of cotyledon and true leaves, and later harvested within one or two weeks for analysis. For biomass, plants were dried completely in ovens heated to 80°C and weighed. The performance of compounds was evaluated by comparing statistical means of individual weights of shoots and roots. Over the course of taking replicated corresponding measurements, we found that dry biomass gains were proportional to fresh wet gains, allowing us to exclude cell enlargement responses such as to gibberellin and to undertake exploratory surveys and dose response curves with wet weights. When the dosage was sufficiently narrowed, we obtained dry weights, as well. Individual plantings were cultured in plastic flats of identical volumes as needed for optimal growth for size and age within the same planting cycle. All potted plants were regularly given water-culture nutrients (Hoagland & Arnon, 1950). Foliar spray applications of identical volumes, either 100 or 186 liters/hectare (L/ha), were mechanically applied. Manual sprays were spray-to-drip volumes of approximately 800 L/ha. Isolation of metabolites of mixed polyacetylglucopyranoses was undertaken by methods of Biel et al. 2010 and modified by collecting numerous two dimensional chromatography strips, followed by C_{18} reverse phase column chromatography, and yielding 10 milligrams (mg) of

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the concentrate from 25% methanol:5% formic aqueous eluants. Isolates showed a chromatographic metabolite, R_f 0.34, identified by staining with ninhydrin. The isolated metabolite was dissolved in 100 ml of aqueous solution for treatment of roots. For all populations, means of different treatment groups were compared using Student's t-test with significance at the 95% probability level. Confidence intervals of the population means are "p" values, counts of population numbers are "n" values, and ± standard error is denoted, "SE." Specialty chemicals were from Sigma (St. Louis, MO), including the following: N^6-benzyladenine glucoside; tetramethylglucopyranose (TMG); tetraacetylglucopyranose (TAG); and methylglucopyranosides (MeG). A mixture of polyacetylglucopyranoses (MPG) was made by the authors with a modified chemical synthesis method of Hyatt & Tindall 1993, in which the extent of reaction was controlled by heating cycles. Vascular plants included Canola Nexera 500, *Brassica napus* L., a shoot crop; radish 'Cherry Bell' *Raphanus sativus* L., a root crop; rice, *Oryza sativa* L., a cereal crop; and corn TMF 114, *Zea mays* L. ssp. *Mays;* and these species were maintained as previously described (Benson et al., 2009).

3. Results

We initiated this investigation by surveying polysubstituted glycopyranoses formulated with nutrients to establish discernable trends of growth responses without deficiency. We started with tetramethylglucopyranose because of a consistency of response that we had experienced with methylglucopyranoside. Manual spray-to-drip foliar treatments were applied to even stands of 5 cm tall radish, formulated as follows: Nutrient Control 15 mM $(NH_4)_2SO_4$, 1 ppm Fe, 1 ppm Mn, 1 g/L surfactants; and 0.3 mM tetramethylglucopyranose and 1 mM tetramethylglucopyranose supplemented with 15 mM $(NH_4)_2SO_4$, 1 ppm Fe, 1 ppm Mn, and 1 g/L surfactants. The growth of radish shoots was not affected within the two week trial period and radish roots treated with foliar applications of formulations of Nutrient Control or 0.3 mM tetramethylglucopyranose showed no significant difference (n=36; SE 0.05; p=0.8) from controls. However, foliar applications of 1 mM tetramethylglucopyranose to radish shoots resulted in a significant (n=36; SE 0.07; p=0.05) 27% enhancement of mean weights of roots over those of Nutrient Control. Results of root analyses are displayed in Figure 1.

Following our establishment of an effective foliar dose that improved root yields, we developed a formulation for row crops that delivered 186 L/ha, less than a quarter the volume of manual applications to shoots. Foliar treatments to even stands of corn were of the following: Nutrient Control, 15 mM $(NH_4)_2SO_4$, 1 ppm Fe, 1 ppm Mn, 1 g/L surfactants; and 3 mM tetramethylglucopyranose, identically supplemented with the above nutrients. The results of this experiment can be seen in Figure 2, where the application of foliar 3 mM tetramethylglucopyranose resulted in a significant (n=18; p=0.03) increase over the Nutrient Control.

Tetraacetylglucopyranose (TAG) is similar to tetramethylglucopyranose except that the sugar is substituted around the pyranose-ring with four acyl-groups instead of alkyl-groups. The range of activity for polyacylglycopyranoses was unknown, therefore, 10 mM TAG was explored in these trials. Foliar 10 mM TAG, formulated in the same nutrient solution as Nutrient Control, was applied to shoots of radish and harvested a week later. Results of foliar application (Fig. 3) showed a significant (n=11, p=0.004) 27% increase of root mean dry weight as compared to Nutrient Control. The growth response of the roots of radish to foliar tetraacetylglucopyranose, therefore, was similar to that of tetramethylglucopyranose.
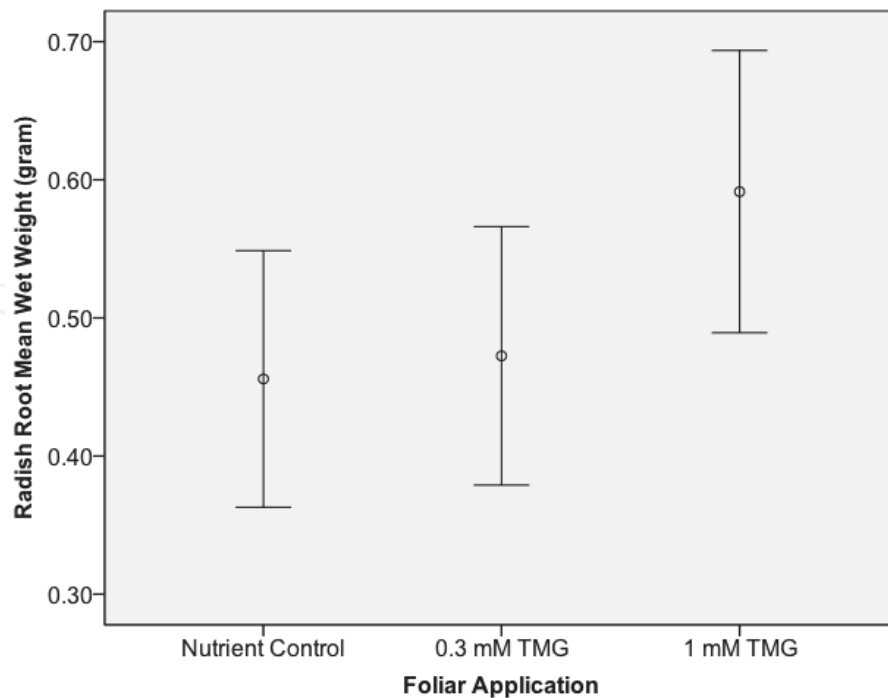
Fig. 1. Initial surveys of radish showed that applications of high volumes of 1 mM tetramethylglucopyranose formulations, 1 mM TMG, to shoots, significantly (n=36; p=0.05) enhanced root mean dry weights as compared to Nutrient Control. Means are marked as small open circles at the midpoint of error bars that indicate ±SE.
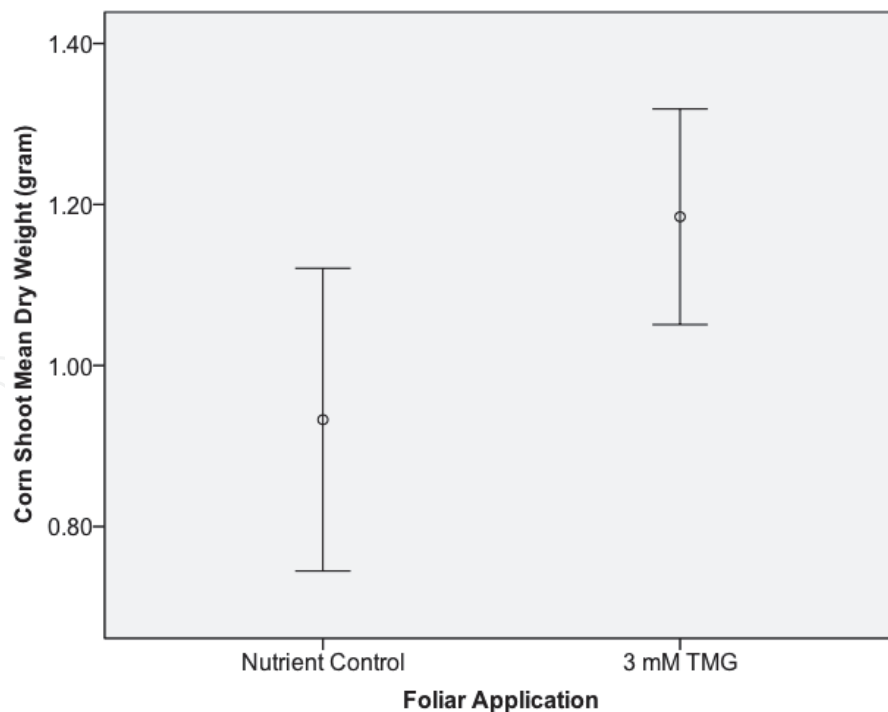

Fig. 2. As a result of foliar applications of 3 mM tetramethylglucopyranose, 3 mM TMG applied at 186 L/ha, a volume typical for row crops, shoot mean dry weights of corn improved significantly (n=11; p=0.004) as compared to Nutrient Control.
Error bars indicate ±SE.
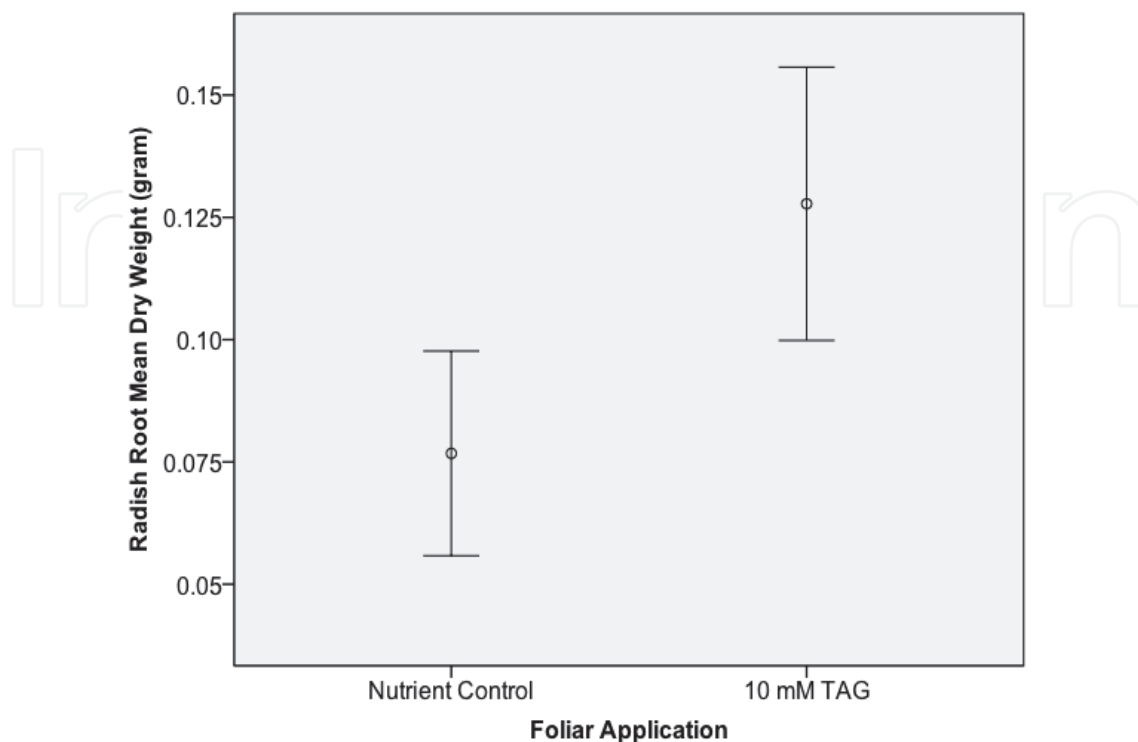
Fig. 3. Foliar application of tetraacetylglucopyranose, 10 mM TAG, to shoots of radish resulted in a significant (n=11; p=0.004) increase of root mean dry weight as compared to Nutrient Control. Error bars indicate ±SE.

We investigated a process for the chemical synthesis of our mixed polyacylglucopyranoses (MPG) at different temperatures to control the reaction; and results are summarized in Figure 4. Between 60° and 72° C, we succeeded in stocking supplies that we manufactured in 500 gram batches. We incorporated 4 mM and 8 mM tetraacetylglucopyranose (TAG) into our tests as positive controls to compare against the different 60° and 72° C batches of 4 mM, 8 mM and 12 mM MPG. Treatments with untreated Control, Nutrient Control, and 12 mM MPG resulted in no difference of growth. In contrast, 4 mM and 8 mM concentrations, showed significantly (n=36; p<0.05) higher vegetative yields than controls. With similar results from these two different batches comparable to tetraacetylglucopyranose, we extended tests to concentrations on various species of plants.

On Canola, responses to foliar applications of 3 mM mixed polyacetylglucopyranoses, 4 mM tetraacetylglucopyranose and 309 mM methylglucopyranoside were compared. All treatments contained 40 mM ammonium nitrate and surfactant blend, including Nutrient Control, and results are graphically depicted in Figure 5. Three treated populations each showed significant (p=0.000) shoot wet weight increases over Nutrient Control, as follow: 3 mM mixed polyacetylglucopyranoses, n=37, 18% increase; 4 mM tetraacetylglucopyranose, n=35, 20% increase; and 309 mM methylglucopyranoside, n=36, 14% increase. We have clearly demonstrated that the far lower concentrations of 3 - 4 mM polyacetylglucopyranoses than the ~100-fold higher dose of 309 mM methylglucopyranoside resulted in comparable growth increase responses from Canola.
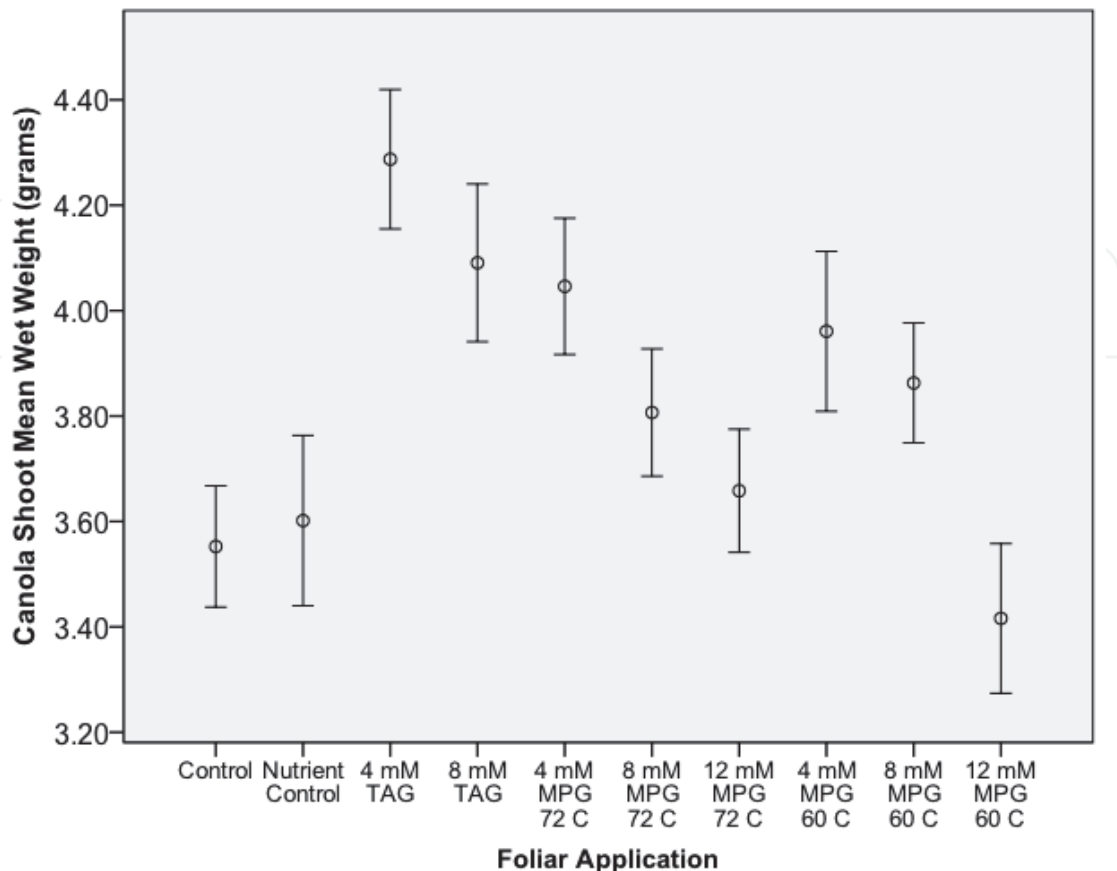
Fig. 4. Similar to nutrient-supplemented formulations of 4 mM and 8 mM tetraacetylglucopyranose (4 mM and 8 mM TAG), responses of populations of Canola to foliar applications of two different batches of mixed polyacetylglucopyranoses (4 mM MPG 72 C & 4 mM MPG 60 C) showed significantly higher (n=36; p<0.05) mean shoot weights than the untreated Control and the Nutrient Control. Error bars indicate ±SE.

A dose response curve of 1 – 3 mM mixed polyacetylglucopyranoses (MPG) was applied to roots of corn with treatments that were supplemented with identical nutrients to the control. Roots were saturated *in situ* with 5 ml of respective formulations per plant. Two weeks later, shoots were harvested and weighed. Statistical analyses showed trends in Figure 6, as follow: 1 mM MPG showed a signficant (n=21; p=0.006) increase in yield over Nutrient Control; 2 mM MPG showed a positive trend that was not significant (n=21; p=0.07); and 3 mM MPG showed a negative trend that may have resulted from exposure of roots to a critical concentration of the acidic mixed polyacetylglucopyranoses.

Treatments of roots of rice with mixed polyacetylglucopyranoses was compared to a treatment with a high concentration of methylglucopyranosides. All solutions were supplemented with identical nutrients including the following: 17 mM $(NH_4)_2SO_4$, 5 mM $(NH_4)_2HPO_4$ and 3 ppm Mn. Roots were saturated *in situ* with 10 ml of respective formulations per 100 cc culture vessel of each individual plant for two weeks. Roots exposed to formulations of 0.5 mM mixed polyacetylglucopyranoses and 50 mM methylglucopyranosides showed significant (n=27; p=0.000) increases in shoot yields of approximately 15% over controls. Results are graphically summarized in Figure 7.

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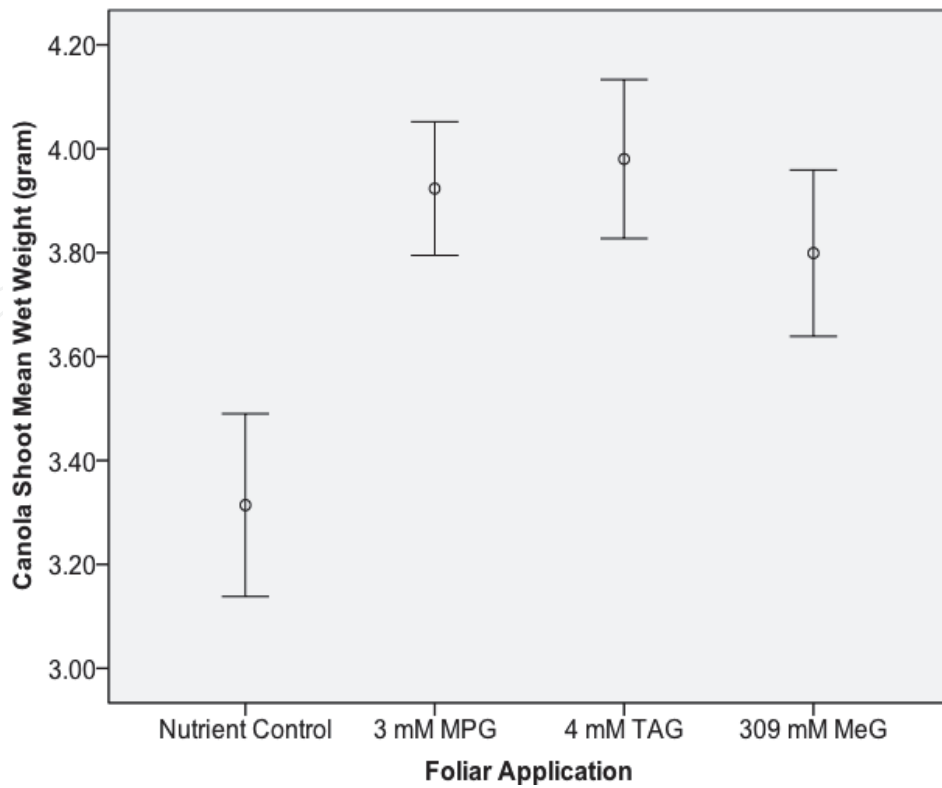to Polyalkylglucopyranose and Polyacylglucopyranose
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Fig. 5. Foliar applications with low concentrations of polyacetylglucopyranoses, 3 mM MPG and 4 mM TAG, were comparable to treatments with high methylglucopyranosides, 309 mM MeG, and resulted in significant shoot enhancements over Nutrient Control.
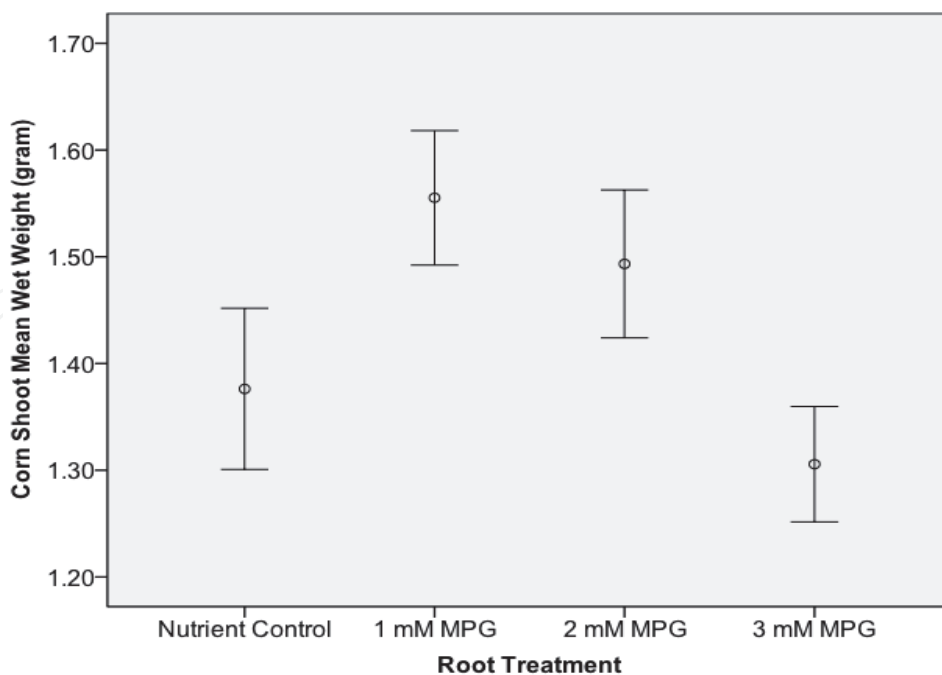

Fig. 6. Dose response of corn roots exposed to various concentrations of mixed polyacetylglucopyranoses (MPG) showed best results at 1 mM MPG with significant (n=2; p=0.006) shoot enhancement over Nutrient Control. Error bars indicate ±SE.
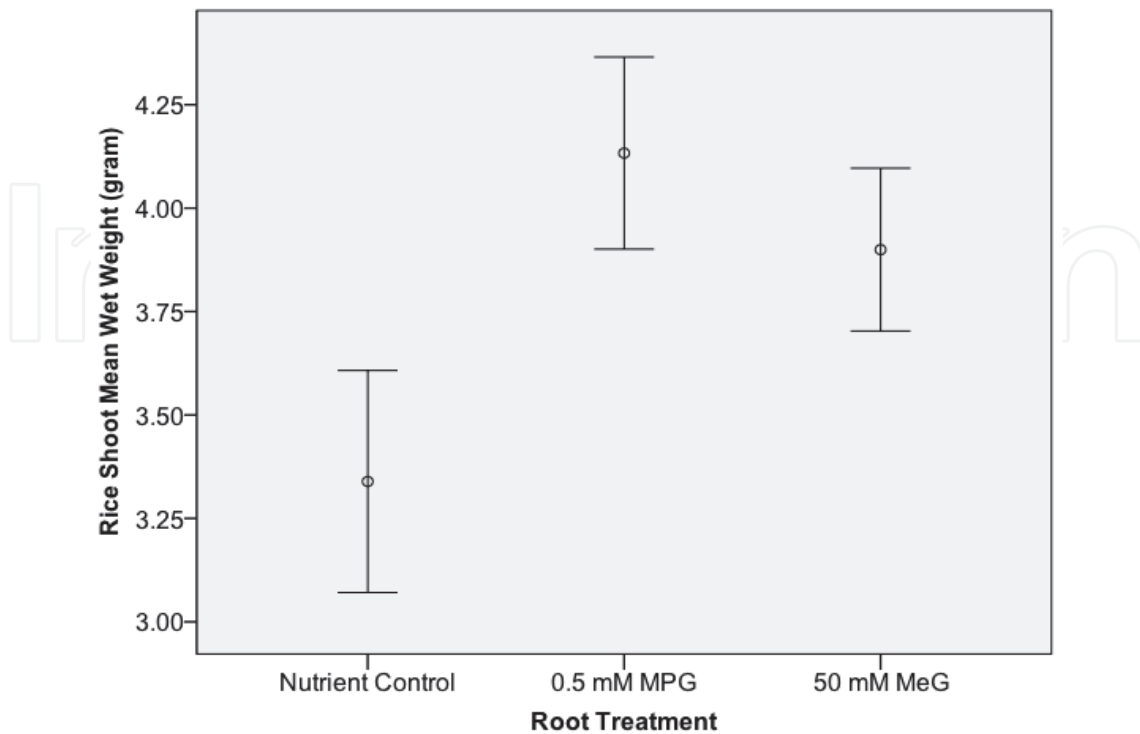
Fig. 7. Roots of whole rice plants exposed to 0.5 mM mixed polyacetylglucopyranoses (0.5 mM MPG) or 50 mM methylglucopyranosides (50 mM MeG), showed significant (n=27; p=0.000) shoot increases over Nutrient Control. Error bars indicate ±SE.

Roots of corn immersed in 1 mM mixed polyacetylglucopyranoses formulated with phosphate buffer to avoid artifacts associated with acidity, were additionally supplemented with the following: 23 mM $(NH_4)_2SO_4$, 5 mM K_2HPO_4, 3 mM KH_2PO_4 and 3 ppm Mn. Roots were saturated with 5 ml of respective formulations per 100 cc soil-less media per plant. The individual shoots of each of the rice plants were harvested after two weeks. Results are displayed in Figure 8 and show significant (n=21; Mean Wet Weight p=0.000; Mean Dry Weight p=0.006) increases of 12% in vegetative yields of shoots over the population of the Nutrient Control. Buffering the solution with phosphates may have nutritionally contributed to the rapid growths of the Nutrient Control and the active treatments while safening the solutions at the same time.

Treatment of roots with mixed polyacetylglucopyranoses resulted in enhancement of shoots, therefore, our hypothesis was that 100 L/ha foliar applications would similarly accelerate development of shoots. Foliar 1 mM and 7 mM mixed polyacetylglucopyranoses were compared to Nutrient Control, both solutions containing, 1 g/L surfactant blend, 23 mM $(NH_4)_2SO_4$ and 3 ppm Mn. Populations included the following: untreated control, n=20; Nutrient Control, n=20; 1 mM MPG, n=20; and 7 mM MPG, n=19; and with no significant difference between the untreated and Nutrient Controls. Foliar treatments of 1 mM and 7 mM mixed polyacetylglucopyranoses resulted in a significant (p=0.003) increase of shoot mean wet weight and a significant (p=0.002) 20% increase of mean dry weight as compared to the Nutrient Control. Shoot dry weights are summarized in Figure 9.
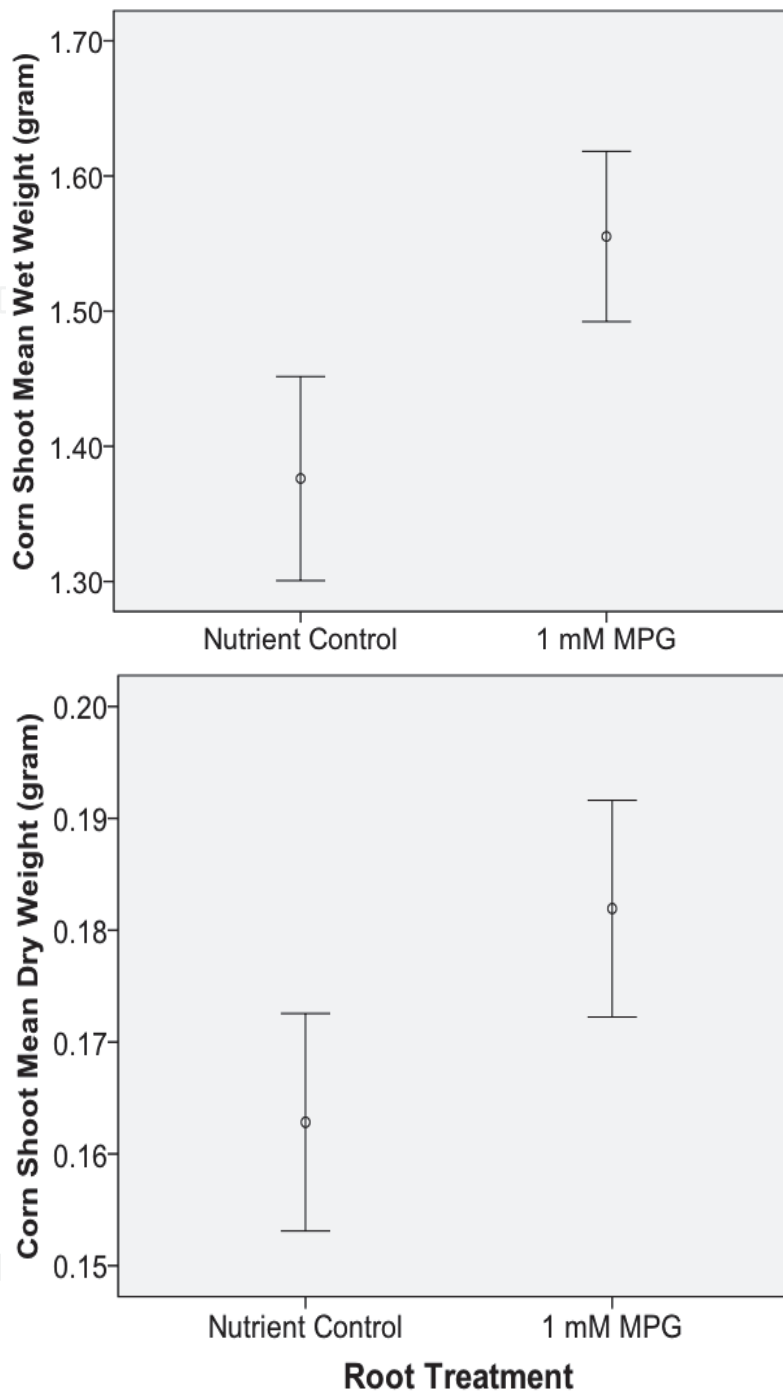
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Fig. 8. Top: Roots of corn exposed to 1 mM mixed polyacetylglucopyranoses (1 mm MPG) showed significantly (n=21; p=0.000) increased mean shoot wet weights. Bottom: Dry weights corresponded to wet weights, showing a significant (n=21; p=0.006) 12% increase of mean dry weight over Nutrient Control. Error bars indicate ±SE.

We collected sufficient samples of chromatographic isolates of putative metabolites (Isolate) of mixed polyacetylglucopyranoses (MPG) from aqueous extracts of host plants to undertake a comparison of activities. Mixed polyacetylglucopyranoses, 5 mM MPG, were positive controls. All aqueous solutions for the treatment of roots were adjusted to pH 6.5 and were made up with the following nutrients: 23 mM $(NH_4)_2SO_4$; 5 mM

$(NH_4)_2HPO_4$; and chelated 3 ppm Mn. For each corn plant, 5 ml of test solution was applied to saturate roots for 6 hours, according to the following doses: 5 mg mixed polyacetylglucopyranoses per plant; and 0.5 mg Isolate per plant. Entire plants were harvested after one week for whole weights of shoots with roots. A summary of data in Figure 10 shows treatment with 0.5 mg Isolate resulted in significant (n=21; p=0.005) 11% increase and treatment with mixed polyacetylglucopyranoses (MPG) resulted in significant (n=21; p=0.000) 15% increase of whole plant mean wet weight over Nutrient Control.
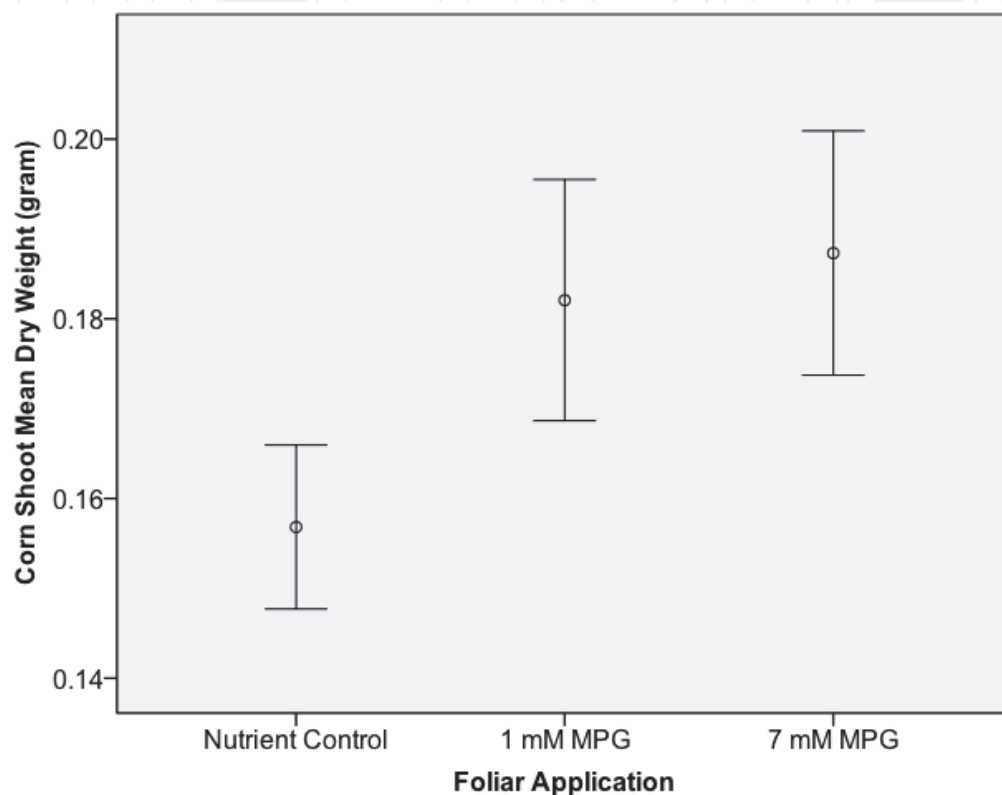

Fig. 9. Foliar applications of formulations of 1 mM and 7 mM mixed polyacetylglucopyranoses (1 mM MPG & 7 mM MPG) resulted in significant (p=0.002) increased shoot mean dry weights of approximately 20% over the population of the Nutrient Control. Error bars indicate ±SE.

The photograph of corn plants exhibited in Figure 11, was taken immediately prior to harvest, one week after treatment with the metabolite of mixed polyacetylglucopyranoses, 0.5 mg Isolate. The Isolate, right, in which the leaf tip reaches the top of the photograph, is visibly distinguishable from the Nutrient Control, left, of which the shoots reach approximately 1 cm below the top border of the photograph. This visual comparison of the generally larger plants of the Isolate, corroborates the 15% increase in the total mean weight of the plant as compared to the Nutrient Control.

Finally, N^6-benzyladenine glucoside chromatographed similarly to our metabolic Isolate of mixed polyacetylglucopyranoses. Therefore, these chromatographic results may suggest that supplementation of formulations with ammoniacal nitrogen may be suited to the incorporation of a nitrogen moiety into polyalkylglycopyranoses and polyacylglycopyranoses.
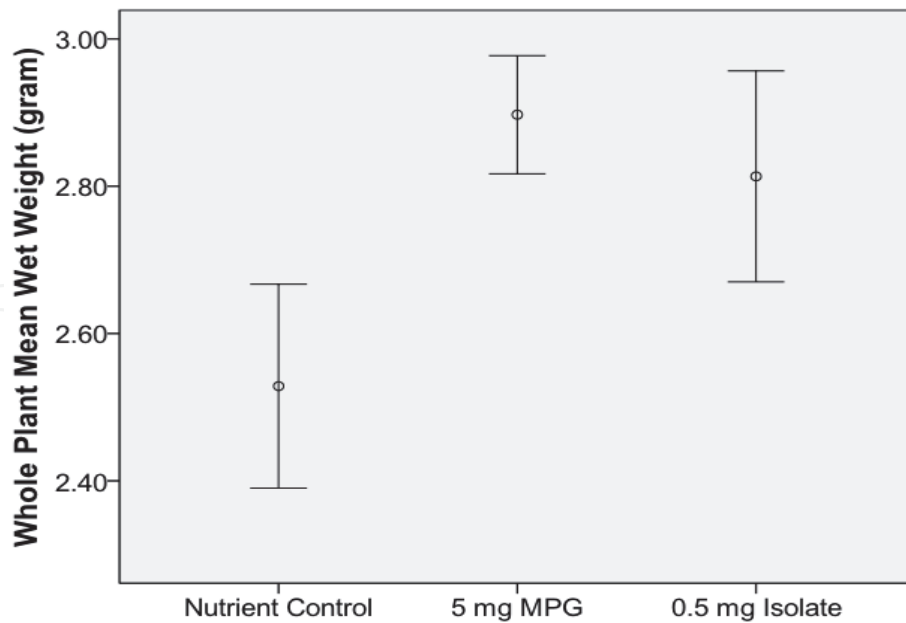
Fig. 10. Treatment of roots of corn with a metabolite of mixed polyacetylglucopyranoses, 0.5 mg Isolate, resulted in significant increases comparable to effects of treatments with ten times the quantity of mixed polyacetylglucopyranoses, 5 mg MPG. Error bars indicate ±SE.

Fig. 11. A chromatographically isolated metabolite of mixed polyacylglycopyranoses (Isolate) was applied to roots of young corn plants and, after a week, the experiment was photographed to show that the enhanced growth of plants treated with the Isolate was visibly discernable from Nutrient Controls. The population of 0.5 mg Isolate, right, is also tagged "Isol8," and Nutrient Control is separated, to the left. Scale = 1 cm.

4. Discussion

Whether to shoots or roots, nutrient applications of relatively low concentrations of polyalkylglycopyranose or polyacylglycopyranoses enhanced vegetative productivity of

plants as compared to control populations. For example, applications of polyalkylglucopyranose to shoots of radish resulted in significant root enhancements over controls; and, furthermore, applications of polyacylglucopyranoses to roots of corn resulted in significant increases of shoots as compared to controls, all of which were supplemented with identical carrier solutions. Similar to findings of our previous experiments with alkylglycopyranosides and C_1 fragments (Nonomura & Benson, 1992; Benson & Nonomura, 2009), polyalkylglycopyranose and polyacylglycopyranose required supplementation with nitrogen for active improvements of growth and our discovery of a ninhydrin-stained product of polyacylglycopyranose indicated incorporation of nitrogen into a highly active metabolite. To our knowledge, little is understood of the structure or functions of the metabolites of polyalkylglycopyranoses and polyacylglycopyranoses, however, a metabolized fraction of alkylglycopyranosides similarly stained with ninhydrin (Biel et al., 2010). These nitrogenous metabolites may be related to sugar-conjugated plant growth regulators (SPGRs) and in consideration of known pathways to conjugation and content of as much as 100 mM SPGRs in plants, Nonomura et al. 2011 reported significant growth enhancements from treatments with SPGRs, including 0.3 mM N^6-benzyladenine glucoside. Therefore, it may be useful to undertake similar investigations of polyacylglycopyranoses in the presence of various soluble nutrients to further elucidate roles of their metabolites (Nonomura and Benson, 1992), understand involvements of molecular networks regulated by carbon and nitrogen (Nonomura et al., 2011), and determine the nature of manganese requirement (Benson et al., 2009) for their potential and for their capacity as vehicles of crop improvement to be realized. Ammoniacal nitrogen sources, such as for example, ammonium sulfate, are substrates for NADPH:Cytochromes P450 reductase, and as such, may suggest a potential direction for investigation of the involvements of the Cytochromes P450, an offering of a tantalizing area for future research. Additionally, other pathways, such as those of site-directed alkylation and transmembrane transporters, have been shown to involve glycopyranosides (Nonomura et al., 2011) and, as it pertains throughout the eukaryotes, we suggest looking into similar models for photosynthetic organisms that are expanded to include polyalkylglucopyranoses (Kaback et al., 2007).

Inasmuch as the development and tracking of appropriate probes in our future investigations will most certainly shed light on the mode of activity of substituted sugars, the determination of their functions in diverse complexes and the elucidation of their mechanisms remain a goal. Thus, upon consideration of the accumulated results of our recent series of experiments, we have sought a system that involves competitive binding of sugars that would be both abundant and ubiquitous. That is, the system should occur in C_3 and C_4 plants because we have found that Canola and corn respond to treatments of MeG and TAG. Moreover, we have been looking for a system that could bind α-D-glycopyranosides and β-D-glycopyranosides. Upon careful examination, we found that plant lectins possess just these suitable features. In plants, up to a quarter of the protein content of seeds may be attributable to lectins as well as up to ten percent of the protein content of leaves, but even with such prominence, it had been held that vacuolar lectins served no endogenous role in plants (Lannoo et al., 2007). Notably, a number of lectins have been structurally defined to the extent that it has been generally established that manganese is required for competitive binding of methyl-α-D-glucopyranoside and glucose to occur (see, for example, Brewer et al., 1973), fulfilling yet another requirement of the system. Furthermore, based on Biel et al. 2010 showing that radiolabeled methylglucopyranoside is transported into leaves intact with a large portion of label in the protein fraction, we expect that our application of 309 mM methylglucopyranoside

to a shoot (Fig. 5) should be sufficient to saturate the system. Therefore, we propose that under conditions in which the cellular sugar concentration of a plant is diminished, chemical competition against substituted sugars acts to release sugar from lectin—and this is an essential process to sustain viability. Also, this act of competitive binding by lectins may naturally displace sugars on a regular basis allowing energy to be reapportioned for growth resulting from metabolism of the freed sugars. For example, we may assume that in the field, the concentration of methyl-β-D-glucopyranoside remains nearly constant in the plant (Aubert et al., 2004) and as a result of midday photorespiratory depletion of the concentration of glucose, competition for binding to lectin by the methyl-β-D-glucopyranoside arises and glucose is released. To an extent, the timely release of this free glucose may mitigate the effects of any impoverishment of glucose. Afterwards, under conditions more conducive to photosynthesis, perhaps later in the afternoon and morning, critical concentrations of glucose are rebuilt to sufficiently high levels that a surfeit of glucose outcompetes methyl-β-D-glucopyranoside, causing the substituted sugar to be displaced, while glucose wins by binding to the lectin. This cycle repeats itself on a daily basis, releasing sugar at each lengthy deprivation event, followed by the capture of fresh sugar upon resuming photosynthesis. Indeed, Nature's response to major environmental stimuli by means of chemical competition is well known. For example, photosynthesis turns to photorespiration strictly as a result of oxygen outcompeting carbon dioxide for binding to Rubisco. In our case, the higher the quantity of lectins residing in the plant, the more capable it may be of capturing and releasing sugars to endure prolonged periods of photorespiration. In contrast, when exogenous chemical competitors for binding sites on lectins are applied to plants, especially by the input of substrates, such as methyl-α-D-glucopyranoside, that do not naturally occur in plants, the duration of the effect may be substantially extended precisely because such foreign compounds may be selected for competitive advantages. Therefore, responses to treatments with substituted sugars must be carefully measured against the conformation of binding sites, biochemical structure, and their orders of preferences for prospective sugars. From another perspective, empirically formulated dosages of crops may possibly reflect the content and binding determinations of major lectins in a cultivar. For example, in the present investigation, our hypothesis is that the relatively low concentrations of tetraacetylglucopyranose required for the improved growth response of treated plants over controls evidently suggests a proportionally higher order of binding to lectins than methyl-β-D-glucopyranoside. Therefore, our search in the future will be focused on the details of descriptions of the functions of substituted sugars in relation to defining suitability to our proposed actions of lectins in the path of carbon, from which we are looking forward to elucidation of the most appropriate competitors, their quantities of application, and when to bind them. Across the broad field of photosynthetic ecosystem management, there exist numerous lectins, each variant with an array of binding characteristics that, hereafter, will further elucidate a competitive path of carbon in photosynthesis (Benson, 2002a & b).

5. References

Aubert, S., Choler, P., Pratt, J., Douzet, R., Gout, E. & Bligny, R. 2004. Methyl-β-D-glucopyranoside in higher plants: accumulation and intracellular localization in *Geum montanum* L. leaves and in model systems studied by ^{13}C nuclear magnetic resonance. *Journal of Experimental Botany* 55(406): 2179–2189

Benson, A. A. 2002a. Paving the Path. *Annual Review of Plant Biology* 53: 1-25.

Benson, A. A. 2002b. Following the Path of Carbon in Photosynthesis: A personal story. *Photosynthesis Research* 73: 29-49.

Benson, A. A. & Nonomura, A. M. (1992) The Path of Carbon in Photosynthesis: Methanol inhibition of glycolic acid accumulation, *in* Murata, N. (ed.), *Research in Photosynthesis 1, Proceedings of the IX International Congress on Photosynthesis,* Kluver, Nagoya, Japan, P-522.

Benson, A. A., Nonomura, A. M. & Gerard, V. A. (2009) The Path of Carbon in Photosynthesis. XXV. Plant and Algal Growth Responses to Glycopyranosides, *Journal of Plant Nutrition* 32(7): 1185-1200.

Biel, K. Y., Nonomura, A. M., Benson, A. A. & Nishio, J. N. (2010) The Path of Carbon in Photosynthesis. XXVI. Uptake and transport of methylglucopyranoside throughout plants. *Journal of Plant Nutrition* 33(6): 902–913.

Brewer, C. F., Sternlicht, H. , Marcus, D. M. & Grollman, A. P. (1973) Binding of ^{13}C-Enriched α–Methyl-D-Glucopyranoside to Concanavalin A as Studied by Carbon Magnetic Resonance. *Proceedings of the National Academy of Sciences, USA* 70 (4): 1007-1011.

Calvin, M. and Benson, A. A. (1948) The Path of Carbon in Photosynthesis, Science, 107: 476.

Gout, E., Aubert, S., Bligny, R., Rebeille, F., Nonomura, A., Benson, A. A. & Douce, R. (2000) Metabolism of methanol in plant cells. Carbon-13 nuclear magnetic resonance studies. *Plant Physiology* 123(1): 287-296.

Hoagland, D. R. and D. I. Arnon. 1950. The Water-Culture Method for Growing Plants without Soil. California Agricultural Experiment Station Circular 347, The College of Agriculture, University of California, Berkeley: 32 pp. URL: http://plantbio.berkeley.edu/newpmb/faculty/arnon/Hoagland_Arnon_Solution.pdf

Hyatt, J. A. & Tindall, G. W. (1993) The Intermediacy of Sulfate Esters in Sulfuric Acid Catalyzed Acetylation of Carbohydrates. *Heterocycles* 35(1): 227-234.

Kaback, H. R., Dunten, R., Frillingos, S., Venkatesan, P., Kwaw, I. , Zhang, W. & Ermolova, N. (2007) Site-directed alkylation and the alternating access model for LacY. *Proceedings of the National Academy of Sciences, USA* 104: 491-494.

Ligocka, A., Zbiec, I, Karczmarczyk, S. & Podsialdo, C. (2003) Response of some cultivated plants to methanol as compared to supplemental irrigation. *Electronic Journal of Polish Agricultural Universities,* Agronomy, Volume 6, Issue 1. URL: http://www.ejpau.media.pl

Lannoo, N., Vandenborre, G., Miersch, O., Smagghe, G., Wasternack, C., Peumans, W. J. & Van Damme, Els J. M. (2007) The Jasmonate-Induced Expression of the *Nicotiana tabacum* Leaf Lectin. *Plant Cell Physiology* 1–12 URL: http://www.pcp.oxfordjournals.org

Nobelprize.org. (2011) The Nobel Prize in Chemistry 1961. URL: http://nobelprize.org/nobel_prizes/chemistry/laureates/1961/

Nonomura, A. M. & Benson, A. A. (1992) The Path of Carbon in Photosynthesis: Improved crop yields with methanol. *Proceedings of the National Academy of Sciences, USA* 89(20): 9794-9798.

Nonomura, A. M., Benson, A. A. & Biel, K. Y. (2011) The Path of Carbon in Photosynthesis. XXVII. Sugar-conjugated plant growth regulators enhance general productivity. *Journal of Plant Nutrition* 34:(5): 653 — 664.

Wolf, F. R., Nonomura, A. M. & Bassham, J. A. (1985) Growth and branched hydrocarbon production in a strain of *Botryococcus braunii* (Chlorophyta). *Journal of Phycology* 21(3): 388-396.
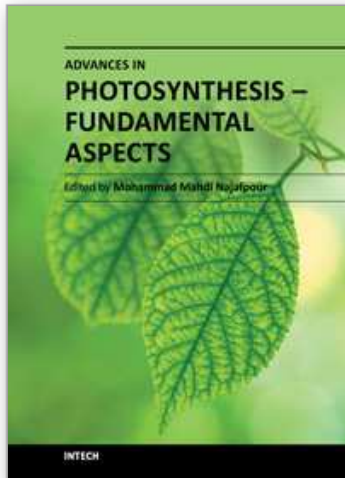
Advances in Photosynthesis - Fundamental Aspects

Edited by Dr Mohammad Najafpour

Photosynthesis is one of the most important reactions on Earth. It is a scientific field that is the topic of many research groups. This book is aimed at providing the fundamental aspects of photosynthesis, and the results collected from different research groups. There are three sections in this book: light and photosynthesis, the path of carbon in photosynthesis, and special topics in photosynthesis. In each section important topics in the subject are discussed and (or) reviewed by experts in each book chapter.

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