Effects of Growth-Regulatory Chemicals on the Action Spectra for ¹⁴C Assimilation and Transport in Sugarcane Leaves¹

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ABSTRACT

Pretreatment of sugarcane with the growth hormone gibberellic acid (GA₃) and the growth depressant Polaris [N,N-bis (phosphonomethyl) glycine] significantly altered the action spectra for ¹⁴C assimilation and transport by leaf tissues. Leaf segments enclosed in a ¹⁴CO₂ atmosphere were illuminated with discrete wavelengths of equal quantum flux from 400 to 710 nanometers (nm). Both compounds significantly lowered ¹⁴C assimilation in the blue, from 437 to 480 nm. Polaris accentuated a green depression at 550 nm while lowering assimilation peaks in the red at 600–640 nm and at 670 nm. Translocation of ¹⁴C, as percentages of the total nuclide assimilated, was vastly increased by both materials in the blue-violet (400 nm) and by GA₃ in the blue (437–480 nm). Polaris increased transport from the blue-green to yellow (520–600 nm). A high sensitivity of control plants to far-red light (710 nm) was unaffected by either material. These results support the theory that chemical ripening may involve sugar synthesis and transport processes in addition to growth-regulatory effects in sink tissues.

INTRODUCTION

Throughout the sugarcane world there is mounting interest in chemical ripeners as a means of enhancing natural ripening processes and to synchronize the period of highest quality with scheduled harvest operations. From an agronomic viewpoint the processes of chemical ripening are more or less synonymous with natural maturation and growth decline, and in fact the most successful agents to date have powerful growth-regulatory properties (2,19,20,23).

Less readily apparent is the fact that a ripened stalk is the culmination of diverse but interrelated events occurring along an intact source-to-sink continuum (9,13). In sugarcane, this system appears to include "push" and pressure flow mechanisms in leaf tissues (16,18) operating in conjunction with "pull" forces of storage tissues, the latter created and maintained by sugar utilization for growth and respiration (13). The processes of CO_2 assimilation, sucrose biosynthesis, vein loading, sugar transport, sugar storage, and retention of stored sugar must all contribute to ripening

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² Plant Physiologist, Agricultural Experiment Station, University of Puerto Rico, Mayaguez Campus, Río Piedras, P.R. and Professor Emeritus and former Director of the Biophysics Program, Department of Botany, Washington State University, Pullman, Washington. in conjunction with the sugar-consuming processes of tissue expansion and respiration. Within this context an authentic chemical ripener might induce or enhance ripening by altering a variety of source-to-sink activities operating at suboptimal levels.

During the present investigations the growth stimulant gibberellic acid (GA_3) and the growth depressant Polaris³ significantly altered the action spectra for ¹⁴CO₂ assimilation and initial transport of ¹⁴C-labeled photosynthate in sugarcane leaves. Each compound is a confirmed ripener of sugarcane when administered under carefully-controlled conditions. The study was made possible by a biological spectrograph offering unique resolution of white light and control of monochromatic light.

MATERIALS AND METHODS

SPECTROGRAPHIC

Resolution of white light into discrete spectral bands was accomplished with a spectrograph developed by Orlin Biddulph and described previously in detail (8,5). Key features of the instrument include a high-pressure, 6500 w Osram XBO xenon arc lamp, a 25-cm beam diffraction grating with 1200 ruled lines/mm, a diffracted light spectrum ranging from 225 to 775 nm, and a 4.8 m continuous focal curve along which plant materials can receive selected wavelengths of known range and controlled intensity. Energy level of the diffracted beam is regulated by adjusting the lamp's amperage input and the width of a slit passing light from lamp to grating.

In preliminary experiments radiant energy was diverted from the diffraction grating with a mirror, thereby offering a white light source with intensities up to 16.2 mv cm⁻² sec⁻¹. For the spectral experiments wavelength intensities were equalized with the wavelength of least quantum flux, i.e., 8.08 photons cm⁻² sec⁻¹ at 400 nm. Details of calculations leading to the correct thermopile reading for each test wavelength, and the amperage input to the lamp required to obtain each reading, are reviewed by Balegh (7).

PLANT MATERIALS

An interspecific hybrid, cv PR 980,⁴ was propagated with greenhouse and controlled-environment facilities at Washington State University, Pullman, as previously described (5). At 11 weeks of age, select plants were sprayed until runoff with aqueous solutions of GA₈ and Polaris (0.01 and 0.04 percent active material, respectively). Control plants received only

³ N, N-bis (phosphonomethyl) glycine, a product of the Monsanto Chemical Company.

*S. officinarum (11/16) \times S. spontaneum (3/16) \times S. sinense (2/16).

distilled water with wetting agent. Twenty days thereafter the plants were submitted to spectrographic analysis using equilibration and illumination methods described earlier (5).

PREPARATION AND ADMINISTRATION OF ¹⁴CO₂

 $^{14}CO_2$ was generated at the laboratory by uniting an excess of 15% perchloric acid with a carefully-weighed quantity of Ba¹⁴CO₃ enclosed in a tygon tube under a column of mercury (6). For storage, the gas was bled to a pyrex glass bulb partially filled with mercury and sealed at the base with a rubber gasket. The $^{14}CO_2$ resided as a bubble above the mercury and was withdrawn as needed with a syringe by passing the needle vertically



GENERAL OPERATION

FIG. 1.—Diagramatic representation of the air circulatory system used to administer ¹⁴CO₂ to sugarcane leaves.

through gasket and mercury. The Ba¹⁴CO₃ contained 0.127 mCi/mg, and 30 mg were used to prepare 3.404 ml of ¹⁴CO₂ containing 3,810.0 μ Ci. The standard dose was 0.040 ml, containing 44.8 μ Ci of ¹⁴C.

Radioactive CO₂ was administered to the apex region of leaf blades enclosed in a cylindrical lucite chamber having a stoppered volume of 0.420 l. Treatments were confined to leaf ranks +1 to +3 which showed least variation in preliminary tests. Slitted rubber stoppers, grooved slightly to accommodate the midvein, produced a gas-tight seal by virtue of their large mass and no supplemental sealing agent was needed. Tygon tubing was used to connect the leaf chamber with other components of the air circulation system, including a hose pump, flow meter, a G-M monitor and recorder, and a Ba(OH)₂ by-pass serving as a CO₂ trap (fig. 1). Total volume of the system was 0.589 l and air flow was constant at 1.5 l/min. Air temperature for the leaf chamber and ambient atmosphere was 22.5° C $(\pm 1^{\circ})$. The G-M tube was a continuous air-flow type, Nuclear Chicago No. D-34, having a thin mica window (1.4 mg/cm²) and about 8 percent efficiency at 900 v.

In operation, the leaf chamber with enclosed blade was carefully aligned along the focal curve so that the test wavelength coincided with the blade's midvein. All light was excluded from the facility except a monochromatic beam about 10 cm wide. This passed over the chamber and was mirrored downward at a right angle to the leaf surface. Equilibration time was 10 minutes. At this point the circulatory system was open and room air was being pumped through the leaf chamber. Energy output of the lamp was adjusted to the correct level. The system was then closed to the room atmosphere and 0.040 ml of ¹⁴CO₂ was withdrawn from storage with a microliter syringe fitted with a BD-25 needle. The dose was injected through a replaceable segment of tygon tubing, with the G-M counter monitoring at 650 v. Twenty minutes were allowed for ¹⁴CO₂ assimilation. This sufficed for roughly 30 to 60 percent depletion of the circulating ¹⁴CO₂, the remainder being trapped by a brief diversion through $Ba(OH)_2$. The system was reopened to ambient air when activity reached background level and an additional 40 minutes were allowed for transport of ¹⁴Clabeled photosynthate.

¹⁴C ANALYSIS

At the end of the treatment interval, premeasured blade segments (including the midvein) were removed from the enclosed treated tissues and at distances of 1 to 56 cm below the leaf chamber. These were quick-frozen, lyophilized, and extracted with 30 ml of boiling 95 percent ethanol. The extractions were twice repeated. Residual extracts were combined, brought to 2 ml volumes, and centrifuged 20 minutes at 5000 \times g. Samples of the condensed extracts were evaporated to dryness in stainless steel planchets and monitored with a Nuclear Chicago Model D47 gas flow counter operating at 1100 v. Each sample was counted for 10 minutes. Activity values were corrected for back-ground, instrument efficiency (40 percent), and self-absorption of the dried residues. Activity was computed as cpm/mg of lyophilized tissue, or as percentages of the total assimilated (ethanol-soluble) ¹⁴C obtained per mg of tissue.

STATISTICS

Eleven wavelengths were examined between 400 nm in the blue-violet and 710 nm in the far-red. For statistical purposes the 11 exposures to monochromatic light were taken as spectral treatments, and one complete pass along the focal curve constituted a spectral replicate. There were four replicates for each of the three chemical pretreatments. The distribution of test wavelengths along the focal curve, a permanent physical characteristic of the diffracted beams, conformed suitably to an incomplete randomized block design. Multiple range analyses were performed between the 11 wavelengths within each chemical pretreatment, and between the three pretreatments within each wavelength, in accordance with Harter (14).

RESULTS

TOTAL ¹⁴C ASSIMILATION

The action spectrum for total ¹⁴C assimilation, as established by control plants, was appreciably modified by GA₃ and Polaris in different regions



FIG. 2.—Action spectra for total ¹⁴C assimilation by sugarcane leaves pretreated with GA₃ and Polaris (CP 41845).

of the visible light spectrum (fig. 2). Assimilation rates were lowered significantly by both materials in the blue, from 437 to 480 nm (table 1). Assimilation peaks in the red at 600–640 nm and at 670 were also lowered by Polaris.

Other spectrograph studies have shown that ¹⁴C assimilated by Saccharum leaves is largely distributed in a 1:1 ratio between the hexose moieties of sucrose (to be reported elsewhere). It is important to note that the present control spectrum, representing ¹⁴C elaborated to the level of sucrose, approximates the net CO₂ assimilation spectrum for Saccharum species with its emphasis on blue utilization and two peaks in the red (5). The principal differences obtained with ¹⁴C are a blue maximum at 437 rather than 480 nm and a much accentuated green depression at 550 nm.

¹⁴C TRANSPORT

The control values for total transport, i.e., ¹⁴C obtained below the leaf chamber, were lowest in the blue-violet, green and far-red regions (400, 550 and 710 nm), and highest in the red at 670 nm (table 2). GA₃ increased significantly the blue-violet, green, and far-red responses, and in addition produced a new peak in the blue at 480 nm. Polaris reduced transport at 480 nm and vastly increased it at 520 nm while having no significant effect on responses to blue-violet and far-red light (table 2).

Wavelength (nm)	Pretreatment ¹			
	Control	GA,	Polaris	
	Assimilated 14C, cpm/mg dried tissue			
400	487 f ¹ *	306d ²	166 ² _{ef}	
437	3422a ¹	850°3	1273 ¹ _{bc}	
448	2140^2_{bc}	949°3	1364 _b ²	
480	2474 _b ¹	1104°3	1487 b ¹²	
520	1531^{1}_{cd}	1162°1	1693 ¹ _{ab}	
550	621 ¹ _{ef}	933°1	254 ² _{ef}	
600	1933 ¹ _{bo}	1181,2	678 ² _{de}	
620	1478 ¹ _{cd}	1174^{12}	706 _d ³	
640	1201 ² _{do}	1869 _b ¹	5533def	
670	3246 ¹	2782,2	1958 _n ³	
710	127,2	316 ₄ 1	124	

TABLE 1.—Action spectra for ¹⁴C assimilation by sugarcane leaves pretreated with gibberellic acid and Polaris

¹ Applied as aqueous foliar sprays 20 days prior to spectrographic analysis. Control plants received distilled water with wetting agent.

* Mean values in columns bearing different subscript letters, and mean values in rows bearing different superscript numbers, vary significantly (P < .05).

A different picture emerges with transport values expressed as percentages of the total ¹⁴C assimilated (table 3). GA₃ and Polaris tend to increase spectral proficiency from the blue-violet to yellow (400–600 nm), but do not increase the far-red response which is highly sensitive regardless of chemical pretreatment (fig. 3). Sensitivity to the blue-violet was enormously increased by both chemicals. Significant increases were produced by GA in the blue (437–480 nm), and by Polaris from the blue-green to yellow (520–600 nm).

DISCUSSION

Spectral changes produced by GA₃ and Polaris support the view that chemical ripeners may perform roles in sugar synthesis and transport

Wavelength (nm)	Pretreatment ¹			
	Control	GA3	Polaris	
	Translocated 14C, cpm/mg dried tissue			
400	37 ^{2*}	65 _b 1	26 ² _{bed}	
437	40^{12}_{dbed}	47 ¹ _{cd}	30^2_{bcd}	
448	43 ¹ _{abs}	49 ¹ _{cd}	34 ¹ _{bo}	
480	48^{1}_{ab}	81 _a ²	16d ³	
520	50^2_{ab}	41 ² _{cde}	90a ¹	
550	$29^2_{\rm cd}$	38 ¹ _{do}	27 ² bcd	
600	37 ¹ _{bcd}	31,1	33 ¹ _{bo}	
620	45 ¹ _{ab}	29°1	32^{1}_{bc}	
640	46 ¹ _{ab}	50^{1}_{ed}	23^2_{cd}	
670	55 _a 1	50°1	40 _b ²	
710	25d ²	71^{1}_{ab}	35 ² _{bo}	

TABLE 2.—Action spectra for ¹⁴C translocation in sugarcane leaves pretreated with gibberellic acid and Polaris

¹ Applied as aqueous foliar sprays 20 days prior to spectrographic analysis. Control plants received distilled water with wetting agent.

* Mean values in columns bearing different subscript letters, and mean values in rows bearing different superscript numbers, vary significantly (P < .05).

TABLE 3.—Translocated ¹⁴C, as percentage of total ¹⁴C assimilated, in sugarcane leaves pretreated with gibberellic acid and Polaris, and illuminated with discrete wavelengths of equal radiant flux density

Wavelength (nm)	Pretreatment ¹			
	Control	GA:	Polaris	
	Translocated ¹⁴ C as percent of total assimilated			
400	12.0 _b ^{2*}	28.2 ¹	18.4 _b 19	
437	1.3°5	5.8°1	2.3d ²	
448	2.4.2	5.2°1	$2.9^2_{\rm cd}$	
480	2.4°2	$14.4b^{1}$	2.5d ²	
520	3.3.2	3.6°3	7.5°1	
550	4.8.2	4.8.2	14.1_{b}^{1}	
600	2.1.2	2.6°2	5.8^{1}_{ed}	
620	3.6°1	2.8°1	$5.2^1_{ m cd}$	
640	4.5°1	3.3.1	4.3^{1}_{cd}	
670	3.3°1	1.6,2	2.1_{d^2}	
710	31.0 ¹	24.9	33.0.1	

¹ Applied as aqueous foliar sprays 20 days prior to spectrographic analysis. Control plants received distilled water with wetting agent.

* Mean values in columns bearing different subscript letters, and mean values in rows bearing different superscript numbers, vary significantly (P < .05).

which are physically and biochemically removed from growth-regulatory processes. While the potential contribution of such changes toward ripening cannot be defined from present evidence, several aspects of the data deserve comment: (a) The ability to utilize divergent wavelengths in carbon assimilation is highly sensitive to GA_3 and Polaris, but this ability does not appear to be increased by them; (b) sugar transport is equally sensitive and tends to be increased by chemical pretreatments; (c) persistently high sensitivity to the 710 nm wavelength suggests an efficient far-red control



FIG. 3.—Action spectra for ¹⁴C transport in sugarcane leaves pretreated with GA₃ and Polaris (CP 41845).

mechanism which is not enhanced by chemical treatment; and (d) spectral changes are more readily explained by changes in foliar pigment systems than by growth effects in sink tissues.

When administered under greenhouse conditions a consistent effect of GA_3 [(4), pp 458-467] and Polaris (2,3) is an increased sugar content of leaf and storage tissues. Their present effects on ¹⁴C assimilation were generally repressive across most of the visible spectrum, particularly against the large blue utilization enjoyed by control plants (fig. 2). This suggests that normal assimilation rates are more than adequate to meet plant needs. On the other hand, the chemical sensitivity of assimilation processes over a broad wavelength range may be an important regulatory factor under

conditions such that photosynthesis is excessive and detrimental to the overall source-to-sink operation.

In terms of total ¹⁴C transport the significant spectral differences produced by GA_3 were all increases, i.e., at 400, 480, 550 and 710 nm (table 2). Polaris produced an increase at 520 nm and decreases at 480, 640 and 670 nm. A more meaningful picture of wavelength influence on transport mechanisms is shown by the percentages of total assimilated ¹⁴C which were translocated from the fed area. In this case virtually all significant changes were increases (table 3), and they occurred at all test wavelengths shorter than 620 nm (fig. 3). This is interpreted to mean that a large segment of the visible spectrum—from blue-violet to yellow—may offer a suboptimal contribution to sugar transport, and that its efficiency can be improved by chemical treatment. The potential wavelength effects on initial movement of ¹⁴C are varied and obscure, but they might logically involve the evacuation of photosynthate from chloroplasts, vein loading, movement through leaf phloem tissues, or energy provision to support these processes.

The exceptional sensitivity of ⁴⁴C transport to far-red illumination at 710 nm (fig. 3) has also been observed in each of nine Saccharum clones having divergent speciation and evolutionary progression (to be reported elsewhere). This effect may be due to unidentified forms of phytochrome thought to control a variety of plant responses (10,21). Hartt (15,17), using incandescent lamps and sunlight as far-red sources, concluded that far-red light does not support sugar transport, but that a low-energy activating effect distinct from CO₂ assimilation processes (possibly relating to the polarity of sugar flow) might be mediated by phytochrome. Action spectra for CO₂ assimilation show significant increases at 710 nm in only one of nine Saccharum clones examined (5). Available evidence therefore suggests that a far-red control mechanism common to the genus Saccharum, affecting sugar movement rather than carbon assimilation, is operating at low illumination intensities in sugarcane leaves. Its efficiency is not improved by GA₃ or Polaris pretreatments (fig. 3).

Although sugarcane pigment systems remain obscure, the wavelengths herein examined generally coincide with known absorption bands for the chlorophylls, carotenoids or phytochrome (5). Changes in pigment content or performance may offer the best explanation of changes produced by chemical pretreatment. In terms of pigmentation the most difficult effect, to explain was the increased transport sensitivity at 400 nm produced by GA_3 and Polaris (fig. 3). This might be accountable to a minor chlorophyll *a* band with maximum absorption near 415 nm (12).

Attempts to explain the spectral changes in terms of growth-regulatory

effects is increasingly speculative. Present conceptions of the source-to-sink continuum concede a potential regulation of some source activities from sink regions (9,11,13), but in the case of GA₃ and Polaris such effects should be virtually opposite, i.e., increased and decreased demands, respectively, for fresh photosynthate. To the contrary, their main effects were the same in that they each reduced ¹⁴C assimilation and increased ¹⁴C transport. Their principal differences were a matter of degree and lay in the specific regions where wavelength sensitivity was affected. This is logically a function of leaf components and their capacity to utilize incident radiation. Moreover, the interpretation of source-to-sink growth effects is further clouded by the fact that chemical growth stimulation can be followed by a period of growth decline, as in the case of GA₃ (1,22), and growth repression by a period of excessive sucker and lala production.

RESUMEN

Los espectros de acción para la asimilación y transporte del ¹⁴C fueron alterados en hojas de caña de azúcar que fueron tratadas previamente con ácido giberélico (AG₃) y Polaris [N,N-bis (phosphonomethyl) glycine]. Ambos compuestos tienen potentes propiedades reguladoras del crecimiento y, además, inducen la madurez cuando se aplican bajo condiciones bien controladas. Empleando un espectrógrafo biológico, segmentos de hojas se colocaron en una atmósfera de ¹⁴CO₂ y se iluminaron con 11 ondas de igual flujo cuántico de 400 a 710 nanómetros (nm).

Los efectos principales de ambos compuestos fueron disminuir la asimilación total del ¹⁴C y aumentar la translocación. Las diferencias individuales fueron cuestión de grados y de las regiones específicas donde se afectó la sensibilidad de las ondas. La asimilación del 14C disminuyó por efecto de ambos compuestos en la región azul de 437 a 480 nm. Polaris intensificó una depresión en la región verde, a 550 nm y disminuyó las cimas de asimilación en la región roja a 600-640 nm y a 670 nm. Ambos compuestos aumentaron considerablemente la translocación del 14C en la región azul-violeta (400 nm), y el AG₃ en la región azul (437-480 nm). Polaris aumentó la translocación desde la región azul-verde a la región amarilla (520–600 nm). Se discute la evidente presencia de un mecanismo de activación de la translocación en el rojo extremo, que es insensitivo tanto al AG; como a Polaris. Los cambios espectrales producidos por AG; y Polaris se interpretaron en términos de pigmentación foliar y no de la actividad de crecimiento en los tejidos. Estos resultados sostienen la opinión de que los compuestos madurativos ejecutan funciones en la síntesis y translocación del azúcar, de las cuales son espacial y bioquímicamente apartadas de su actividad relacionada con la regulación del crecimiento.

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