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The Effect of Plant Hormones and Light Quality on the Invertase Activity in Maize (*Zea mays* L.) and Mung Bean (*Phaseolus radiatus* L.)

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Abstract

The effects of plant hormones (NAA, GA_3 and BA) and light qualities (white, red, green and blue light) on the changes of reducing sugar contents and invertase isozyme activities in leaves of maize (*Zea mays* L.) and mung bean (*Phaseolus radiatus* L.) seedlings were investigated. NAA accelerated the increase of reducing sugar contents and invertase isozyme activities, on the contrary, GA_3 had little effect in the accumulation of reducing sugar and in the increase of enzyme activities from the leaves of maize and mung bean seedlings. On the other hand, BA accelerated an increase in the activities of the invertase isozyme from the leaves of mung bean seedlings whereas it had little effect in the increase of the enzyme activities from those of maize seedlings. The accumulation of reducing sugar in leaves of both seedlings was promoted by red light irradiation compared to white light irradiation, while the activities of the enzyme were little affected by various light qualities. In the simultaneous applications of plant hormone and light quality, NAA with white light was very effective in the increase of reducing sugar contents and the enzyme activities from the leaves of mung bean seedlings, whereas NAA application with blue light showed a prominent enhancement in the reducing sugar contents and the enzyme activities from those of maize seedlings. These results suggest that plant hormone, particularly NAA, may be a more important factor than various light qualities in the stimulation of invertase activity.

Key words : acid invertase, alkaline invertase, maize, mung bean, NAA, GA_3, BA, light quality

1. INTRODUCTION

Sucrose known to be the predominant form in which carbohydrate is translocated in most plants, is synthesized in the cytosol of source organs, transiently stored in vacuole, and translocated via the phloem to sink organs. Invertase (β-D-fructofuranoside fructohydrolase, EC 3.2.1.26) plays a central role for the hydrolysis of sucrose to glucose and fructose available for energy and carbon requirements of plant cells. Therefore, invertase has been known to be a key enzyme for carbohydrate mobilization and partitioning (ap-Rees, 1984; Sturm and Chrispeels, 1990). Lauriere *et al.* (1988) has proposed that the transportation of invertase synthesized on the rough endoplasmic reticulum (ER) are regulated by Golgi complex. Plant tissues contain multiple form of invertase based on the pH required for maximum activity as well as its subcellular location. Invertase is subdivided into acid (pH 4.0-5.0) and alkaline

(pH 7.0-8.0) forms according to its pH optima (Chin and Weston, 1973; Matsushita and Uritani, 1974). The enzyme is also subdivided into extra- and intracellular forms on the basis of its subcellular location (Leigh *et al.*, 1979; Giaquinta *et al.*, 1983).

Invertase activity is affected by environmental stimuli, such as light and plant hormones, which play an important role for the growth and development of sink organs (Howard and Witham, 1983; Claussen *et al.*, 1986; Karuppiah *et al.*, 1989; Miyamoto *et al.*, 1992). Auxin applications result in closely correlated changes in expansion growth and invertase activity in bean internode segments, and the result is similar to that in other studies where the segments of oat coleoptile and sugar cane internode were used (Pressey and Avants, 1980; Morris and Arthur, 1984). Also, gibberellic acid is known to induce substantial rise in invertase activity in oat coleoptiles (Karuppiah *et al.*, 1989). Recently, it is proposed that soluble and bound invertase activities are regulated by gibberellic acid applications (Miyamoto *et al.*, 1992). On the other hand, in the detached radish cotyledons, the accumulations of reducing sugar that is, closely associated with invertase activity are enhanced by the irradiation of red light, and the accumulations are more significantly elevated by the cytokinin applications (Huff and Ross, 1975; Howard and Witham, 1983).

Very little information has been published on the invertase activities affected by interaction between light quality and plant hormones. In order to clarify the effect of plant hormones and light quality on the invertase activities in the seedlings of maize (*Zea mays*) and mung bean (*Phaseolus radiatus*) grown in different light quality with or without plant hormones, we describe the changes of reducing sugar contents and invertase activities in leaves of the seedlings treated with plant hormone and light quality.

2. MATERIALS AND METHODS

2.1. Plant materials

The seeds of maize (*Zea mays* L.) and mung bean (*Phaseolus radiatus* L.) were soaked in running tap water for 2 h and planted on the pot of soil, and grown in growth chamber at 28 ±1℃ with 70% humidity under dark condition for 2 days. The seedlings were grown under 18 h of different light quality / 6 h dark regime condition for 3 days. And 5 day-old seedlings were excised by razor blades and the detached leaves, grown hydroponically in MS solution with or without plant hormones under the

Table 1. Comparison of the hypocotyl length from *Phaseolus radiatus* grown hydroponically in MS solution contained three kinds of plant hormones for 48 h

Plant hormone Concentration (μM)	NAA	GA_3	BA
		Hypocotyl length (mm)	
5	5.69[a)]	5.80	6.82
5×10^{-1}	4.13	6.74	6.62
5×10^{-2}	6.31	8.45	6.23
5×10^{-3}	7.41	8.21	5.20
5×10^{-4}	6.11	6.48	6.62

[a)] The values are the average of results obtained from three independent experiments.

continuous irradiation of different light quality for 48 h, were used as the experimental materials.

2.2. Plant hormones and light treatments

The concentrations of NAA (naphthaleneacetic acid), GA_3 (gibberellic acid) and BA (benzyladenine) were ascertained to be 5×10^{-3}, 5×10^{-2} and 5 μM, respectively, which were chosen for optimal concentration obtained by the investigations on the length of mung bean hypocotyls (Table 1). These results are similar to those from oat, bean and *Solanum melongena* (Kaufman *et al.*, 1968; Morris and Arthur, 1985; Claussen *et al.*, 1986).

Light source was a white fluorescent light and shielded with selectively light enriched acrylfilters for red, green and blue light. Light intensities used for the growth of the maize and mung bean seedlings were 491 erg cm^{-2} sec^{-1} for white light, 47 erg cm^{-2} sec^{-1} for red light, 50 erg cm^{-2} sec^{-1} for green light and 65 erg cm^{-2} sec^{-1} for blue light with radiometer (Metrologic, 60-535, USA), and emission spectra of light sources obtained with Optical Multichannel Analyzer (EG & G PARU, 1640, USA) are shown in Fig. 1.

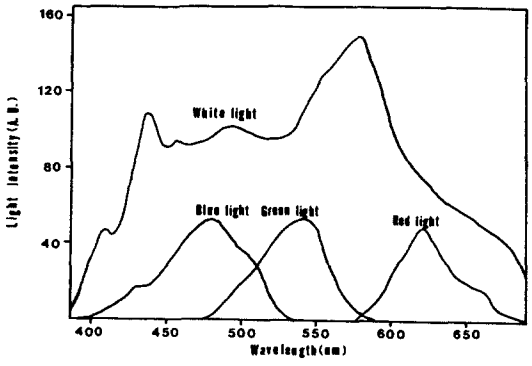

Fig. 1. Spectroradiometric scans of white, red, blue and green light used for growth of *Zea mays* and *Phaseolus radiatus*. A.U., Arbitrary unit.

2.3. Crude invertase extraction

Crude invertase extraction was performed by the modified Chen and Black method (1992). Detached leaves rinsed three times with distilled water were homogenized with Waring blender in initial plant extraction buffer consisted of 50 mM HEPES, pH 7.0, 1 mM Mg-acetate, 1 mM Na-EDTA, 1 mM DTT and 1 mM PMSF with ratio of 1 g of fresh leaves : 1 ml of the buffer. The homogenate was filtered through four layers of cheesecloth, and then centrifuged at 12,000 x *g* for 15 min. The supernatant was used as the crude extract. All procedures for crude invertase extraction were performed at 4 ℃.

2.4. Assays for invertase activities and reducing sugar

Invertase activity was determined by measuring glucose content formed from sucrolysis. For the assay of alkaline invertase, a 1.6 ml aliquot of reaction mixture contained 50 mM HEPES, pH 7.0, 1 mM Mg-acetate, 100 mM sucrose and a suitable amount of enzyme solution, whereas a 1.6 ml aliquot of reaction mixture, in the case of acid invertase, consisted of 50 mM phosphate-citrate, pH 5.0, 1 mM Mg-acetate, 100 mM sucrose and enzyme solution. The reaction mixture containing enzyme was incubated at 25 ℃ for 10 min, and then boiled for 3-5 min to cease the reaction. The amount of glucose formed was measured by the modified glucose oxidase-peroxidase method (Bergmeyer and Bernt, 1974). A 0.8 ml aliquot of the glucose oxidase-peroxidase mixture (0.8 unit of each enzyme) containing 400 μg of *o*-dianisidine dihydrochloride was added to reaction mixture and incubated for at least 30 min. After the addition of a 0.8 ml aliquot of 5 N HCl, the

amount of glucose was determined at 540 nm with spectrophotometer (Shimadzu, UV 240, Japan). A unit (U) is defined as the formation of 1 μmol of glucose from sucrose per min per 1 ml of enzyme solution at 25℃ at pH 7.0 and 5.0 for alkaline and acid invertase, respectively.

The amount of reducing sugar was determined according to the modified Somogyi-Nelson method (1944).

3. RESULTS

3.1 Changes in the contents of reducing sugar

Changes in the contents of reducing sugar from the leaves of maize and mung bean seedlings grown hydroponically in MS solution in the presence of 3 kinds of plant hormones under white light for 48 h were shown in Fig. 2. Control was defined as the leaves of the seedlings grown hydroponically in MS solution without plant hormones under the light. In maize seedlings grown in white light without plant hormones, the contents of reducing sugar were gradually decreased along with culture time, thus those of reducing sugar were given rise to a 55% decrease during the culture period investigated. NAA-treated leaves showed little changes in the contents of reducing sugar, while GA_3- and BA-treated groups led to 48 and 36 % decrease, respectively. The changes of reducing sugar contents in mung bean leaves were similar to those in maize leaves during the culture period investigated. In the NAA-treated group, however, reducing sugar contents increased to 1.03 times. These results suggest that NAA induces synergistic effect on the accumulation of reducing sugar while GA_3 and BA had little effect.

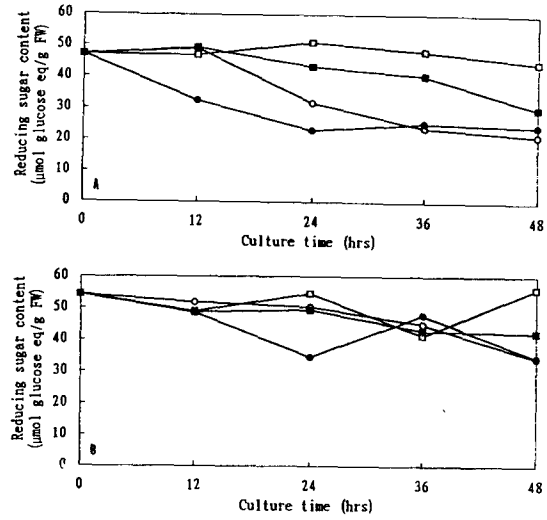

Fig. 2. Changes in the content of reducing sugar from the leaves of *Zea mays* (A) and *Phaseolus radiatus* (B) seedlings grown in the white light for 48 h. -○-, control; -□-, NAA; -●-, GA_3; -■-, BA.

The seedlings, grown in selectively enriched light quality for 3 days, caused the quantitative changes in the amounts of reducing sugar (Table 2). The maize seedlings grown in red and blue light contained about 1.4 and 1.3 times, respectively, in the contents of reducing sugar compared to those occurred in white light. The seedlings grown in green light were similar to those grown in white light in the changes of reducing sugar contents. In mung bean seedlings, red light alone caused significant accumulations of reducing sugar compared to white light. Huff and Ross (1975) proposed a similar possibility that red light induced the promotive accumulations of reducing sugar from detached radish cotyledons compared to dark conditions.

To elucidate the interaction between plant hormones and light quality on the accumulations

Table 2. Comparison of the content of reducing sugar from the leaves of *Zea mays* and *Phaseolus radiatus* seedlings grown for 5 days

μmol glucose eq/g FW

	White light	Red light	Blue light	Green light
Zea mays	47.1[a)]	63.5	61.2	53.1
P. radiatus	54.3	63.0	50.5	58.3

[a)] The values are the average of results obtained from three independent experiments.

of reducing sugar, the changes in the accumulation of reducing sugar were investigated when maize and mung bean seedlings were treated with plant hormones collaborated with different wavelengths of light for 48 h. As shown in Table 3, NAA-treated leaves of maize under blue light exhibited about 3.2-fold increase of the reducing sugar contents compared to control under white light, while mung bean leaves treated with NAA under white light contained 1.6 times as much the contents of reducing sugar as those treated without plant hormones under white light.

3.2 Changes in the activity of acid invertase

The activity of acid invertase, which plays an important role on the hydrolysis of sucrose, was linearly correlated with the reducing sugar contents during culture time investigated. The seedlings from maize and mung bean exhibited 47 and 49% decrease in the activity of acid invertase, respectively. But NAA-treated group of maize and mung bean had not pronounced changes in the activity of acid invertase throughout the culture time. Although BA-treated group showed 12% decrease in the activity of acid invertase in the seedlings of mung bean as compared to initial culture time, it produced 1.6-fold increase in the activity over the control (Fig. 3). From these results it is suggested that BA contributes to the signifiant promotion of acid invertase activity. NAA-treated group among plant hormone-treated groups showed the highest activity of acid invertase.

Table 3. Comparison of the content of reducing sugar from the leaves of *Zea mays* and *Phaseolus radiatus* seedlings grown in the medium containing plant hormones for 48 h

μmol glucose eq/g FW

Species	Hormone treatment	White light	Red light	Blue light	Green light
Zea mays	Control	21.4[a)]	36.5	61.7	51.9
	NAA	44.5	30.4	68.3	52.5
	GA_3	24.3	31.9	61.1	50.1
	BA	30.0	31.5	52.6	53.2
P. radiatus	Control	34.2	43.4	40.4	52.4
	NAA	55.9	42.6	48.3	47.1
	GA_3	34.5	44.3	41.3	54.4
	BA	42.2	44.8	41.6	47.5

[a)] The values are the average of results obtained from three independent experiments.

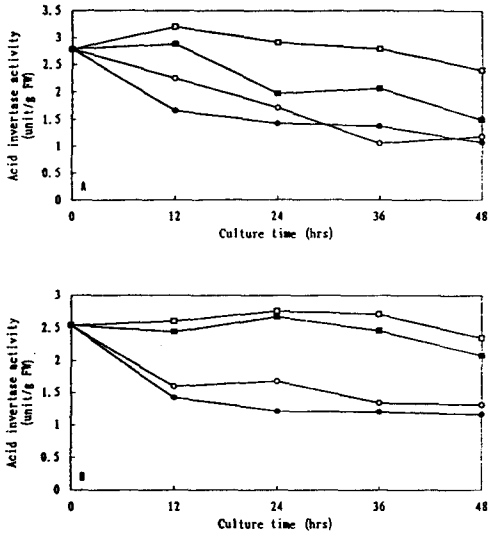

Fig. 3. Changes in the activity of acid invertase in the leaves of *Zea mays* (A) and *Phaseolus radiatus* (B) seedlings grown in the white light for 48 h. -○-, control; -□-, NAA; -●-, GA_3; -■-, BA.

The seedlings grown in red light exhibited 1.6-fold increase in the activity of acid invertase as compared to those grown in white light when maize seedlings were grown for 3 days, while red, blue and green light induced little changes in the activity of acid invertase from mung bean seedlings compared to white light (Table 4).

Table 4. Comparison of the activity of acid invertase from the leaves of *Zea mays* and *Phaseolus radiatus* seedlings grown for 5 days

unit/g FW

	White light	Red light	Blue light	Green light
Zea mays	2.78[a)]	4.48	3.42	3.04
P. radiatus	2.54	1.84	1.62	2.95

[a)] The values are the average of results obtained from three independent experiments.

Table 5 showed the changes in the activity of acid invertase from maize and mung bean seedlings treated with plant hormones collaborated with various light qualities for 48 h. NAA and BA under green light were more effective in inducing the activity of acid invertase from maize than other treatments. NAA-treated group grown in white light showed the highest value in the acid invertase activity in mung bean seedlings. These results suggest that NAA seems to be more effective in the increase of acid invertase activity than GA_3 and BA, and plant hormones may play an

Table 5. Comparison of the activity of acid invertase from the leaves of *Zea mays* and *Phaseolus radiatus* seedlings grown in the medium containing plant hormones for 48 h

unit/g FW

Species	Hormone treatment	White light	Red light	Blue light	Green light
Zea mays	Control	1.19[a)]	1.88	2.52	2.75
	NAA	2.41	1.77	2.46	2.87
	GA_3	1.09	1.57	1.77	2.65
	BA	1.50	1.93	1.56	2.89
P. radiatus	Control	1.31	1.70	1.15	1.47
	NAA	2.35	0.61	1.01	1.57
	GA_3	1.16	0.85	1.10	1.90
	BA	2.08	0.72	0.75	1.22

[a)] The values are the average of results obtained from three independent experiments.

important role compared to various light qualities.

3.3 Changes in the activity of alkaline invertase

When the seedlings treated without plant hormones were grown under white light for 48 h, the activity of alkaline invertase in the leaves of maize and mung bean seedlings was reduced by 61% and 49%, respectively. The activity of alkaline invertase from maize was reduced by 31% when NAA was applied, thus the activity increased about 1.8 times that of control. However, the activity from mung bean slightly increased during culture time (Fig. 4). The mung bean seedlings treated with BA also contained 1.8 times as much alkaline invertase activity as those treated without plant hormones. These results were similar to those obtained in the acid invertase activity.

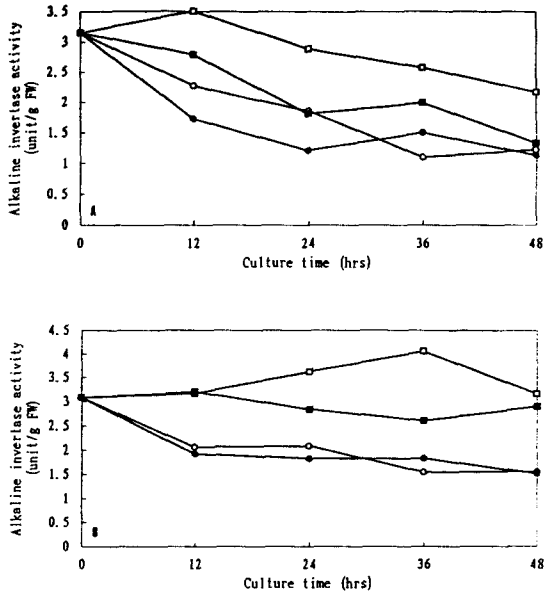

Fig. 4. Changes in the activity of alkaline invertase in the leaves of *Zea mays* (A) and *Phaseolus radiatus* (B) seedlings grown in the white light for 48 h. -○-, control; -□-, NAA; -●-, GA_3; -■-, BA.

Various light qualities such as red, blue and green light had little effect, as compared to white light, in the activity of alkaline invertase from maize and mung bean seedlings (Table 6). The changes of alkaline invertase activity from maize and mung bean seedlings to which plant hormones were applied in combination with the irradiations of various light qualities simultaneously for 48 h are shown in Table 7. NAA-treated group grown in blue light exhibited about 3.6-fold increase in the activity of alkaline invertase from maize, as compared to control under white light. Mung bean seedlings treated with NAA under white light contained about 2 times as much activity of alkaline invertase as those treated without plant hormones under white light.

Table 6. Comparison of the activity of alkaline invertase from the leaves of *Zea mays* and *Phaseolus radiatus* seedlings grown for 5 days

unit/g FW

	White light	Red light	Blue light	Green light
Zea mays	3.15[a)]	3.44	3.84	3.36
P. radiatus	3.08	2.26	3.41	3.85

[a)] The values are the average of results obtained from three independent experiments.

4. DISCUSSION

The contents of reducing sugar in leaves of maize and mung bean seedlings, grown hydroponically in MS solution under white light for 48 h, were gradually decreased along with culture time, and the activity of acid invertase was linearly associated with reducing sugar contents (Figs. 2 and 3). The correlation of reducing sugar and acid invertase is seemed to be consistent with a few studies that acid invertase plays an important role on the

Table 7. Comparison of the activity of alkaline invertase from the leaves of *Zea mays* and *Phaseolus radiatus* seedlings grown in the medium containing plant hormones for 48 h

unit/g FW

Species	Hormone treatment	White light	Red light	Blue light	Green light
Zea mays	Control	1.22[a)]	2.60	4.33	2.84
	NAA	2.17	2.64	4.33	3.17
	GA_3	1.13	2.64	3.92	2.77
	BA	1.33	2.56	3.41	3.24
P. radiatus	Control	1.57	1.21	2.96	1.58
	NAA	3.16	1.09	2.88	1.75
	GA_3	1.52	1.49	2.94	2.00
	BA	2.90	1.27	2.21	1.61

[a)] The values are the average of results obtained from three independent experiments.

accumulation of reducing sugar that is used for energy and carbon requirements of plant cell (ap-Rees, 1984). Alkaline invertase activity also exhibited a gradual decrease during culture period investigated (Fig. 4). These results are in general agreement with prior reports obtained from similar studies using *Solanum melongena* (Claussen *et al.*, 1986), although there are some reports that the activity of alkaline invertase from the leaves of barley seedlings shows little change during culture period (Lee *et al.*, 1992).

There are many reports on the promotive effect of plant hormones during plant growth and development (Pierik *et al.*, 1988; Venis *et al.*, 1990; Barbier-Brygo *et al.*, 1990; Lee and Kim, 1993), but little studies were carried out on the effect of plant hormones on the activity of invertase isozymes. When the maize seedlings were treated with plant hormones under white light for 48 h, NAA resulted in a substantial rise in the reducing sugar contents and invertase isozyme activities, while GA_3 and BA exhibited little effect. In the leaves of mung bean seedlings, on the other hand, BA accelerated invertase isozyme activities in the same way as NAA (Figs. 2, 3 and 4). Although some results argue that GA_3 gives rise to an increase in the activities of invertase isozyme from the growing subhook of pea (Miyamoto *et al.*, 1992), it had little effect on the increase of invertase isozyme activities as shown in previous reports in which bean internode segments were used (Morris and Arthur, 1984). Therefore, it is suggested that the effect of GA_3 on the activities of invertase isozymes may not be the same for all plants. These results agree with the observations that acid invertase activity is greatly enhanced by auxin applications in the segments of bean internode (Morris and Arthur, 1984). Other plant species also showed the similar changes in the activities of invertase isozymes (Howard and Witham, 1983). The promotion of invertase activity seems to be induced by NAA and BA, in which particularly NAA was more important, while GA_3 hardly affects the enzyme activity, although the physiological function of plant hormones on the activities of invertase isozymes has not been clarified.

When maize and mung bean seedlings were

grown in various light quality for 3 days, the amounts of reducing sugar were remarkably increased under red light as compared to under white light (Table 2). This result is consistent with the findings that red light induces the accumulation of reducing sugar in radish cotyledons (Huff and Ross, 1975). However, alkaline invertase activities were little affected by various light qualities such as red, green and blue light (Tables 4 and 6). These results suggest that light quality may not be an important factor on the activities of invertase isozymes, although the activities of invertase isozymes are more affected by light than by darkness. This is in agreement with other prior results obtained from radish cotyledons (Huff and Ross, 1974).

In the applications of plant hormones collaborated with different wavelength of light for 48 h, NAA application with white light was the most effective in the promotion of invertase isozymes activities and of reducing sugar contents from the leaves of mung bean seedlings. In contrast to this, in the leaves of maize seedlings NAA application under blue light had a prominent stimulation in the reducing sugar contents and the enzyme activities, and NAA and BA treatment collaborated with green light induced an increase of acid invertase activity (Tables 3, 5 and 7). It is considered, therefore, that NAA among plant hormones is more effective than GA_3 and BA, and plant hormones, particularly NAA, are more effective than various light qualities in the stimulation of reducing sugar contents and invertase isozyme activities, although these facts are insufficient to reflect a reciprocal effect of plant hormone and light quality.

Acknowledgements

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옥수수와 녹두의 Invertase Isozymes 활성에 미치는 식물호르몬 및 광선의 효과

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여러 파장의 광선(백색, 적색, 녹색 그리고 청색광)과 NAA, GA_3, BA 등의 식물호르몬을 옥수수와 녹두 유식물의 잎에 처리하여 환원당 축적과 invertase isozymes 활성에 미치는 효과를 조사하였다. NAA는 옥수수와 녹두 잎의 환원당과 invertase isozymes 활성의 증가를 촉진하였으나, GA_3는 환원당 축적과 효소의 활성증가에 효과적이지 못하였다. 한편 BA는 녹두 잎의 invertase isozymes 활성증가를 유도하는 반면, 옥수수 잎에 있어서는 큰 영향을 미치지 못하였다. 환원당의 축적에 있어서 적색광은 백색광에 비하여 효과적이었으나, invertase isozymes의 활성증가에 있어서는 여러 파장의 광선 모두가 촉진효과를 보여주지 않았다. 식물호르몬과 광선의 동시처리에 있어서 NAA와 백색광 동시처리는 녹두 잎의 환원당 축적 및 invertase isozymes의 활성증가에 매우 효과적이었으며 NAA와 청색광 동시처리는 옥수수 잎의 환원당 축적과 invertase isozymes의 활성증가에 매우 효과적이었다. 이상의 결과로 보아 옥수수와 녹두 잎의 환원당 축적 및 invertase isozymes의 활성증가에 있어서 식물호르몬, 특히 NAA는 여러 파장의 광선보다 더 중요한 요인인 것으로 사료된다.