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Effect of Growth Retardant BX-112 on Growth, Floral Initiation, and Endogenous GA Levels in Sorghum

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ABSTRACT

To define the relations between endogenous GA levels and growth and flowering in short-day plant sorghum, growth retardant BX-112 was applied to two sorghum genotypes, wild-type and phytochrome B mutant (*phyB-1*), which grows faster and flowers earlier than the wild-type. BX-112 and GA_3 were applied as a soil drench, and plant height, culm length, and date to floral initiation were investigated. Endogenous GAs contents were measured with GC-MS-SIM. BX-112 treatments inhibited shoot growth in both genotypes and drastically reduced GA_1 and GA_8 levels. With increasing BX-112 concentrations, GA_1 concentrations declined linearly, but caused the accumulation of intermediates from GA_{12} to GA_{20}. This result implies that GA_1 is the major active endogenous GA in shoot elongation in a short day plant sorghum. The inhibition of plant growth in both of wild type and *phyB-1* by BX-112 was very similar, while BX-112 effects on floral initiation in two types of plants differed significantly. Floral initiation of *phyB-1* was not affected by BX-112, but that of wild-type was delayed as BX-112 concentration increased. Because BX-112 treatment causes accumulation of biosynthetic intermediates between synthetic pathway from GA_{12} to GA_{20} and because *phyB-1* is altered in GA metabolism in this same region of the early C13-hydroxylation pathway, BX-112 may fail to block flowering of *phyB-1*.

Key words : growth retardant, BX-112, floral initiation, phytochrome B.

Sorghum bicolor (L.) Moench. is a short day (SD), quantitatively photoperiodic C-4 monocot. Four genes (Ma_1, Ma_2, Ma_3, and Ma_4) that regulate the critical night length necessary to promote floral initiation have been discovered in sorghum because of natural mutations, and three of them now exist in near isogenic lines. These genes are termed maturity genes (Quinby, 1967). The genes are inherited independently in a simple Mendelian fashion.

A systematic study of the growth and flowering behavior of these maturity genotypes, concentrating on the third maturity locus which has three known alleles (Ma_3, ma_3, ma_3^R), has been conducted during the past decade (William & Morgan, 1979; Pao & Morgan, 1986a; Beall et al., 1991; Childs et al., 1991; Childs et al., 1992; Childs et al., 1995; Foster & Morgan, 1995). These studies revealed that genotypes containing Ma_3 or ma_3 are very sensitive to photoperiod; flowering is significantly delayed by 12 h photoperiod and hastened by 10 h photoperiod. In contrast, ma_3^R-containing plants are different from the other genotypes. They flower very early and are relatively insensitive to the photoperiod, flowering in a wider range of photoperiodic conditions than non-ma_3^R plants. In addition, they are taller, contain less chlorophyll, exhibit greater shoot dry matter accumulation, develop fewer adventitious root, show greater apical dominance, and have elevated anthocyanin and gibberellin (GA) content than non-ma_3^R plants.

Genotypes containing ma_3^R allele showed increased GA levels; ma_3^R genotypes contain elevated levels of some of the native GAs and several-fold higher concentration of GA_1 than non-ma_3^R genotypes (Beall et al., 1991). The elevated GA content of ma_3^R genotype appears to account for much of its phenotype. When exogenous GA_3 is applied to Ma_3 or ma_3 genotypes, they become morphologically similar to the ma_3^R genotype and exhibit hastened floral initiation (Pao & Morgan, 1986b). Thus, it was proposed at first that the third maturity gene participates in the control of GA biosynthesis.

However, ma_3^R genotype contains higher amount of anthocyanin than non-ma_3^R genotype (Childs et al., 1991), and it is well known that anthocyanin biosynthesis is regulated by phytochrome. And, because anthocyanin biosynthesis was not changed by GA_3 or GA biosynthesis inhibitors in ma_3^R plants, the possibility of the primary lesion in phytochrome system in ma_3^R was tested (Childs et al., 1991 & 1992). Immunological assay revealed that ma_3^R genotype was missing the 123KD light stable, phyB-like phytochrome (Childs et al., 1992). Recently Childs et al. (1997) sequenced the phytochrome B gene from plants containing Ma_1 and ma_3^R and demonstrated that the mutant gene contains a single base pair deletion near 3′ end which results in a frame shift and stop codon in a region shown in phytochrome from other plants and necessary for dimerization and phytochrome activity (Cherry et al., 1993). Additionally, Ma_3 and *PHYB* were mapped to the same location on chromosome 1 in sorghum. Thus, Childs et al. (1997) concluded that plants containing the allele formerly designated as ma_3^R are

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mutants for phytochrome B. Ma_3 was redesignated as *PHYB* and ma_3^R as *phyB-1*.

Although GAs are not thought to be highly specific "florigen" hormones, there is an association between GA treatment or increase in GA content and flowering in a large number of species. Applications of GA_3 and other GAs substitute for the requirement for long day (LD) or low temperature vernalization in many species (Pharis & King, 1985). In addition, recent work on flowering mutants (*gal-3*) in *Arabidopsis* has clearly supported the involvement of GAs in mechanisms of flowering control (Wilson et al., 1992). The *gal-3* mutant which is defective in *ent*-kaurene synthesis never flowers in SD condition without treatment with exogenous GA. Of more than one hundred of known natural GAs and large number of GA-derivatives, only a small number are highly bioactive in growth and/or floral initiation (Evans et al., 1990; Evans & King, 1994).

Sorghum was found to contain the GAs of the early 13 hydroxylation pathway (GA_{12}→GA_{53}→GA_{19}→GA_{20}→GA_1→GA_8) which occurs in maize and rice (Beall et al., 1991). Application of GA_3 hastens floral initiation in sorghum (Williams & Morgan, 1979; Pao & Morgan, 1986b).

Growth retardant tetcyclacis has been shown to inhibit shoot growth and delay floral initiation in sorghum (Beall et al., 1991). Long day (LD) delays floral initiation but does not inhibit shoot growth in sorghum (Childs et al., 1995). However, shoot growth and floral initiation are clearly separated in LD plant where several growth retardants inhibit shoot growth but do not delay floral initiation (Talon et al., 1991). The existence of this marked difference needs to be confirmed more exhaustively. In this study, we used growth retardant acyclohexanetriones, BX-112, which blocks the late steps (3β- or 2β-hydroxylation) in the biosynthetic pathway which lead to active GAs, and defined the relation between endogenous GA levels and growth and flowering in short-day plant sorghum.

MATERIALS AND METHODS

Two sorghum maturity genotypes, *phyB-1* ($ma_3^Rma_3^R$) *and wild-type* (ma_3ma_3), were used in this study. Seeds were germinated and grown in pots (19 cm in diameter, 14 cm in depth) filled with a soil mix which was developed to minimize chlorosis problems in pot-grown sorghum. Plants were grown in a growth chamber under a 11 h photoperiod with 31℃ day and 21℃ night. The compositions of soil mix and other growth conditions have been described in Beall et al. (1991).

BX-112 (calcium 3,5-dioxo-4-propionylcyclohexanecarboxylate) were dissolved in distilled water. All treatments (3.16, 10, 31.6, 100, and 316 ppm) were applied as a soil drench in 50 ml of each solution per pot at 5 days after seeding (DAS). Every 7 days, another 50 ml was applied until the experiments were completed. This volume, method and timing of application was chosen based on preliminary experiments. To test whether or not GA_3 could overcome growth inhibition and delayed floral initiation by growth retardant in sorghum, combination of BX-112 and GA_3 were applied as a soil drench in 50 ml of each solution per pot. GA_3 (70.3% purity, Eli Lilly) was dissolved in 95% ethanol and then diluted to each concentration with distilled water.

Measurement of plant height (from soil to tip of tallest leaf) and culm length (height to the tallest leaf collar) were taken at 14 and 21 DAS. At 2- to 3-day intervals, floral initiation was determined by splitting the shoot of harvested plants and examining the apical meristem under a dissecting microscope. Floral stage 2 (visible flower primordia) was used as the criterion for floral initiation (Lane, 1963). After one plant in a population was recognized to have differentiated an inflorescence, several additional plants were examined to ensure that the response was typical.

For GA analysis, 14-day old plants treated with each BX-112 were harvested at 2:00-3:00 PM. Plants were cut at the root-shoot junction, and at the top of the tallest leaf sheath. The resulting shoot samples were frozen in liquid N_2 within 5 min following the removal of the plant from the growth chamber. After lyophilization, the three oldest leaves were removed from the culm. The samples were stored at −20℃ until extracted for GAs. The extraction of GAs followed the procedure of Lee et al. (1997). Following methanolic extraction, GA's were purified using a combination of preparatory chromatography (C_{18}, celite, SiO_2), solvent partitioning, and HPLC. GA's were quantified using GC-MS-SIM by calculating the area ratio of non-deuterated GA to deuterated [$^2H_2$]GA's which had been added during extraction.

RESULTS AND DISCUSSION

In exploratory experiments we have determined the method and timing of application and appropriate concentrations of growth retardant BX-112. BX-112 which mainly inhibits 3β-hydroxylation (the step GA_{20}→GA_1) was applied as a soil drench. Plant height at 14 and 21 DAS was progressively reduced by increasing the concentrations of BX-112 (Table 1). The inhibition of culm length also showed the same trend as plant height. Inhibition of culm length was more severe than that of plant height. The effect of growth retardants on height growth in *phyB-1* was duplicated on wild-type. GA_3 alone promotes growth over the control, and simultaneous application of 31.6 ppm of GA_3 almost completely relieved growth inhibition by the growth retardants. Further, plants growth was promoted by all treatments containing GA_3 (Table 1).

The inhibition pattern of plant growth by BX-112 was very similar in both *phyB-1* and wild-type, while BX-112 effects on floral initiation differed significantly. Floral initiation of *phyB-1* was not affected by BX-112, but that of wild-type was delayed as the BX-112 concentration increased (Table 2). This difference between two genoty-

Table 1. Plant growth of wild-type (WT) and *phyB-1* sorghum seedlings in response to exogenous BX-112 and combinations with GA_3.

Treatments†	Plant height (cm)				Culm length (cm)			
	14 DAS		21 DAS		14 DAS		21 DAS	
	phyB-1	WT	*phyB-1*	WT	*phyB-1*	WT	*phyB-1*	WT
Control	46.3	32.5	75.7	58.6	14.2	7.7	21.0	13.2
BX-112 3.16	46.2	34.1	75.0	58.1	14.1	7.6	21.1	13.0
BX-112 10	41.4	29.1	60.3	48.5	12.3	6.5	14.0	11.9
BX-112 31.6	30.3	21.9	42.0	37.4	8.2	5.1	11.2	9.3
BX-112 100	19.3	18.1	25.3	20.3	5.8	4.3	7.2	5.6
BX-112 316	19.0	13.1	24.2	20.5	3.8	2.6	5.6	4.3
GA_3 31	48.2	40.6	85.6	68.9	13.7	10.5	23.5	13.1
GA_3 31 + BX 3.16	49.6	43.5	84.4	69.5	13.6	8.7	22.3	12.0
GA_3 31 + BX 31	44.1	42.1	82.1	67.3	12.5	9.2	23.1	12.3
GA_3 31 + BX 316	40.9	41.3	80.4	61.3	11.3	10.2	23.5	10.6
GA_3 316	58.4	41.0	92.3	78.7	15.8	11.9	25.6	15.3
GA_3 316 + BX 3.16	53.7	41.8	94.3	81.2	15.1	12.9	27.3	18.9
GA_3 316 + BX 31	51.6	42.0	94.6	82.8	14.4	12.5	25.4	16.3
GA_3 316 + BX 316	55.9	44.9	93.7	81.5	13.9	13.4	23.9	15.2

† Treatment concentrations are given in ppm.

Table 2. Effect of BX-112 on floral initiation of wild-type and *phyB-1* sorghum.

Treatments†	Days to floral initiation	
	phyB-1	Wild type
Control	20	28
BX-112 3.16	20	28
BX-112 10	20	34
BX-112 31.6	21	40
BX-112 100	20	43
BX-112 316	19	49
GA_3 31	18	26
GA_3 31 + BX 3.16	18	25
GA_3 31 + BX 31	18	26
GA_3 31 + BX 316	18	28
GA_3 316	18	26
GA_3 316 + BX 3.16	17	25
GA_3 316 + BX 31	18	26
GA_3 316 + BX 316	18	26

† Treatment concentrations are given in ppm.

pes in response to BX-112 was differred from another group of growth retardant tetcyclacis which inhibited growth and delayed flowering (Beall et al., 1991). Tetcyclacis presumably lowered the GAs content by inhibiting biosynthesis early in GA production (Rademacher, 1989), and this lower GAs led to delayed flowering. Generally, rapid plant growth often occurs just prior to flowering in many species, and these two events appear closely linked. The use of BX-112 has allowed us to separate these effects; it was possible to inhibit growth without affecting flowering in *phyB-1*.

Delayed floral initiation in wild-type was almost completely relieved by simultaneous application of 31.6 ppm of GA_3. Further floral initiation was hastened by all treatments containing GA_3. The ability of GA_3 to reverse the effect of the inhibition on both growth and floral initiation in sorghum suggested a possible role of native GAs in sorghum flowering.

To demonstrate the relationship between endogenous GA content and growth and flowering in the SD plant sorghum, BX-112 was applied and the content of native GAs was measured. BX-112 reduced GA_1 and GA_8 levels dramatically, but in many cases they caused accumulation of intermediates from GA_{12} to GA_{20} (Table 3). Application of 10 ppm of BX-112 to *phyB-1* resulted in accumulation of about twice as much GA_{20} in treated plants. This is an evidence that BX-112 blocked the 3β-hydroxylation of GA_{20} to GA_1 in the late step of the GA biosynthesis pathway as shown previously by Nakayama et al. (1990, 1992). The wild-type genotype accumulated the GA_{12}→GA_{20} intermediates less than *phyB-1*, and treatment resulted in almost the same levels of GA_{19} as in control wild-type plants. Among these GAs, GA_{53} showed a different pattern of accumulation between the two genotypes; in *phyB-1* GA_{53} increased linearly with increasing inhibitor concentration, while it decreased in wild-type. With increasing BX-112 concentrations, GA_1 concentrations declined linearly. Plant height of sorghum treated with BX-112 was proportional to the level of GA_1 rather than to the total GA level.

The primary mode of action of the acyclohexadione inhibitors (BX-112, CGA 163 935, and LAB 198 999) has

Table 3. Effect of BX-112 on endogenous GAs levels in wild-type and *phyB-1* sorghum seedlings. GA levels were measured by GC-MS-SIM. Data are the means of three replicate samples.

Concentrations	Genotypes	GA_{12}	GA_{53}	GA_{19}	GA_{20}	GA_1	GA_8
		..... ng/g D.W.					
Control	WT	12.6±3.28†	60.0±6.31	124.8± 7.48	19.8±3.16	10.1±1.45	3.2±0.78
	phyB-1	17.8±3.44	33.2±2.31	95.4± 5.57	24.0±2.45	12.3±1.32	3.9±0.42
3.16 ppm	WT	6.1±1.78	54.4±4.33	129.3± 7.88	24.7±2.54	6.3±0.94	2.1±0.09
	phyB-1	10.5±2.17	23.2±2.68	111.1± 3.78	41.3±4.78	9.8±1.48	2.4±0.30
10 ppm	WT	4.9±0.24	46.5±3.47	102.4±12.32	30.4±3.71	4.3±0.53	1.8±0.23
	phyB-1	17.3±2.07	38.5±3.74	123.0±11.59	42.0±2.69	9.4±0.50	1.5±0.06
31.6 ppm	WT	8.3±1.25	43.3±1.75	123.1± 6.76	61.7±1.19	2.7±0.34	1.4±0.29
	phyB-1	17.6±1.52	44.9±2.56	121.8± 7.88	34.5±4.24	4.9±0.54	0.7±0.01
100 ppm	WT	10.8±2.45	37.7±1.45	137.3± 9.20	42.5±3.19	0.6±0.30	0.1±0.02
	phyB-1	12.0±2.36	59.1±5.46	146.0± 6.91	44.9±4.52	4.0±0.26	0.4±0.03
316 ppm	WT	10.5±0.36	41.5±3.60	130.4±10.40	29.9±3.61	0.5±0.21	0.1±0.01
	phyB-1	13.0±0.83	66.2±2.31	148.2± 5.67	34.8±1.22	1.3±0.72	0.1±0.01

† Mean ± standard deviation.

been suggested to be the inhibition of the 3β-hydroxylation of GA_{20}→GA_1 (Nakayama et al., 1990 & 1992). These compounds inhibited the steps of GA biosynthesis catalyzed by a soluble enzyme requiring 2-oxoglutarate, Fe^{2+} and oxygen. These steps include C-20 oxidation, conversion of C20 to C19-GAs, 3β-hydroxylation, and 2β-hydroxylation. Among these steps, the 3β-hydroxylation (GA_{20}→GA_1) appeared to be most sensitive to BX-112 (Nakayama et al., 1990). Inhibitors of late steps of GA biosynthesis, BX-112, reduce shoot elongation in rice, barley, maize, wheat, and rape (Hedden and Croker, 1992), as they do in sorghum.

In this study, we found that BX-112 delayed floral initiation in wild-type and not in *phyB-1*. GA_1 levels in *phyB-1* were 2, 3-fold higher than those in wild-type for BX-112 treatment at 10, 31.6, and 100 ppm. This difference in concentration of GA_1 in BX-112 treated wild-type versus *phyB-1* may explain why the treatment delayed flowering in the former but not in the latter genotype (Table 2 & 3). Thus, one possible explanation for this difference in floral initiation is that GA_1 levels are significantly lower in wild-type than in *phyB-1*, and a threshold treatment with BX-112 lowers GA_1 to a level too low to support floral initiation in wild-type but not in *phyB-1*. However, at the highest BX-112 concentration tested, GA_1 levels were reduced to very low and in distinguishable levels in both wild type and *phyB-1*. Meanwhile, the trend for BX-112 to delay floral initiation in wild type and have no effect in *phyB-1* continued to this concentration. A different hypothesis is that there is some aspect of gibberellin metabolism between GA_{12} and GA_{20} which influences floral initiation. Such a possibility may be supported by the recent finding about GA metabolism in these genotypes (Lee at al., 1998). In that study, *phyB-1* (58M) and wild type (90M and 100M) were compared from 9 sample times per day for 10, 14, 16, and 18 h photoperiod, and data were presented as average to investigate how phytochrome B control GA metabolism and flowering. Wild type contained consistently higher levels of GA_{53} and GA_{19} than *phyB-1* but less GA_{20}. Further, wild type, except for the sample from the floral initiation-favoring 10 h photoperiod, contained lower levels of GA_{12} than *phyB-1*. Thus, there is a reversal of levels of GAs between wild type and *phyB-1* from GA_{12} to GA_{53} and from GA_{19} to GA_{20}. This suggests that the step from GA_{12} to GA_{53} is retarded in *phyB-1* compared to wild type and the step from GA_{19} to GA_{20} is retarded in wild type compared to *phyB-1* (Lee et al., 1998). It is possible that the apparent differences in GA metabolism between wild type and *phyB-1* genotype at the GA_{12} → GA_{53} or the GA_{19} → GA_{20} steps might be related to the failure of the GA_{20} → GA_1 inhibitor to delay floral initiation in *phyB-1*. Therefore, treatment of GA_{20} → GA_1 inhibitor (BX-112) may impact the metabolism of upstream GAs biosynthesis pathway.

If this difference in floral initiation is due to the absence of phytochrome B effect on GA metabolism, one other possible hypothesis is that phyB modulate responses of GA_1 or/and other GAs such as GA_{12}, GA_{53}, GA_{19}, and GA_{20} for floral initiation like shoot elongation. However, although intermediates in the GA_1 biosynthesis pathway such as GA_{12}, GA_{53}, GA_{19}, and GA_{20} were accumulated in BX-112 treated plant (Table 3), those GAs show low or negligible activity in shoot growth and flowering (Pharis & King, 1985; Evans et al., 1990 & 1994). Nevertheless, a link between elevated endogenous GA_{12}~GA_{20} concentration and phyB has not yet been demonstrated, and therefore we cannot concluded definitely that elevated these GAs are not involved in promotion of flowering in *phyB-1* genotype.

Phytochrome-mediated GA-dependent response model was defined well in shoot elongation. In this model, GA is required for shoot elongation and phyB modulates the

degree of GA-dependent responses. This model has been deduced for the interaction of phyB-like phytochromes and GAs in pea (Weller et al., 1994), in cucumber (Lopez-Juez et al., 1995), and in *Arabidopsis* (Reed et al., 1996). These phytochrome B mutant exhibit increased sensitivity to applied GAs. However, responses model for floral initiation was not fully tested in other plant systems. We also did not investigate the possibility of the involvement of other GAs on floral initiation. Thus, it is difficult to explain that phyB definitively modulates GA responsiveness for floral initiation. Nevertheless, recent discovery about *FPF1* (flowering promoting factor 1) (Kania et al., 1997) which is involved in a GA-dependent signaling pathway and modulate a GA response in apical meristems during the transition to flowering may support this responses model of phytochrome in floral initiation in sorghum.

Effective growth retardation while promoting flowering with decreasing GA_1 levels was also observed by use of GA analogous (Foster et al., 1997). Modified GA (*endo*-DiHGA$_5$ and *exo*-DiHGA$_5$) inhibiting the 3β-hydroxylation of GA_{20} to GA_1 thereby reducing the GA_1 content, similar to the effects of BX-112 observed here, were shown to inhibit shoot growth but promote floral initiation slightly in *phyB-1* genotype.

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