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Comparison of the Seed Germination Effects of Synthetic Analogs of Strigol, Gibberellic Acid, Cytokinins, and Other Plant Growth Regulators

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Abstract. Four synthetic multiring analogs of strigol, a naturally occurring sesquiterpene lactone that promotes germination of dormant seeds of *Striga* (witchweed), were found to stimulate germination of dormant *Lactuca* (lettuce) seeds. The effects on light-sensitive and light-insensitive lettuce seeds were concentration-dependent and exceeded those produced by equimolar (0.1 mM) solutions of gibberellic acid. Strigol and epistrigol promoted lettuce seed germination to a lesser degree than did the synthetic analogs. The strigol group compounds had minimal effect on the germination of monocot seeds. The results indicate that the synthetic strigol analogs have plant growth regulatory activity in dormant seeds of genera beyond *Striga* in which germination stimulation by strigol and the synthetic analogs was first demonstrated.

Strigol, a sesquiterpene lactone which promotes germination of dormant seeds of *Striga* (witchweed) (Cook et al. 1966, 1972, Hsiao et al. 1981), has been isolated (Cook et al. 1966), identified (Cook et al. 1972), and synthesized (Heather et al. 1974, 1976, Brooks et al. 1987). In addition, a number of strigol analogs have been prepared (Johnson et al. 1981, Pepperman et al. 1982) and tested with positive results as germination stimulants for *Striga* (Babiker and Hamdoun 1982, Johnson et al. 1976, Pepperman et al. 1982, Stevens and Eplee 1979, Brooks et al. 1987), *Orobanche* (Johnson et al. 1976), and *Capsella bursa-pastoris* (Bradow 1986). *Striga* germination is also stimulated by

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thiourea (Brown and Edwards 1945), kinetin, and other 6-substituted aminopurines (Worsham et al. 1959, Yoshikawa et al. 1978). These same compounds promote germination in other seeds (Mayer and Poljakoff-Mayber 1982, Bewley and Black 1982), particularly lettuce (Mayer et al. 1958, Jones and Stoddart 1977, Thomas 1977, Poljakoff-Mayber and Mayer 1961, Reynolds and Thompson 1973). Like the synthetic strigol analogs, thiourea plus ascorbic acid, stimulated *Capsella* germination (Bradow 1986). These coincidences of seed germination stimulation in *Striga* and other species by strigol analogs and other plant growth regulators suggested that better understanding of the activities of strigol and the synthetic strigol analogs could be gained through a study comparing the stimulatory or inhibitory activities of strigol, multiring synthetic strigol analogs, thiourea, gibberellin (GA_3), and cytokinins, including kinetin, in a multiseed species germination assay. Ascorbic acid, alone and in combination with thiourea, was also included in these screening assays. This paper reports the results of these comparative assays and some concentration-dependent studies utilizing lettuce seeds.

Materials and Methods

Assay Seeds and Sources

The assay seeds, common names, seed sources, and the number of seeds per replicate are shown in Table 1. All undersize and damaged seeds were discarded, and assay seeds were preselected for uniformity of size and seed coat color in the case of the weed species.

Germination Assays

The multiseed assay protocol was the same 25°C/72 h/dark assay with eight replicates described by Bradow (1985), including the presence of 0.1% (v/v) dimethylsulfoxide (DMSO) added as an initial solubilizing agent to all test solutions and parallel controls, except those containing ascorbate or thiourea (Bradow 1986). Preliminary comparative experiments were performed to determine the effects of DMSO and 25°C/dark incubation on all assay seed lots. The concentration dependence studies using light-sensitive and light-insensitive lettuce seeds followed the same assay protocol used for *Capsella*, omitting the chilling procedure but retaining the germination evaluations after 72 and 168 h (Bradow 1986). Where necessary, test solution pH was adjusted to 6.8 with 0.1 N KOH. The osmolarities of all test solutions (<20 mOsm) were below that value found to be inhibitory of the most sensitive of the test seeds —i.e., tomato, lettuce, and carrot (preliminary characterization data not shown).

Chemicals

The chemical structures and molecular weights of the test compounds are

Table 1. Seeds used in screening assays.

Seed	Common name	Source[a]	No. seeds/ replicate
Allium cepa L.	Onion cv. Early Grano 501	1	20
Amaranthus palmeri S. Wats.	Palmer amaranth	4	25
Amaranthus retroflexus L.	Redroot pigweed	5	25
Avena sativa L.	Oat	3	15
Brassica napus L.	Rape	5	20
Bromus inermis Leyss	Smooth brome	5	20
Bromus secalinus L.	Cheat	5	20
Bromus tectorum L.	Downy brome	5	25
Capsella bursa-pastoris (L.) Medik.	Shepherdspurse	5	25
Cucumis sativus L.	Cucumber, cv. Marketmore	2	10
Daucus carota L.	Carrot cv. Danvers Half-Long	2	20
Echinochloa crus-galli (L.) Beauv.	Barnyardgrass	5	20
Eragrostis curvula (Schrader) Nees	Lovegrass	5	25
Lactuca sativa L.	Lettuce cv. Grand Rapids	2	20
	Light-insensitive lettuce	3	20
	Light-sensitive lettuce	3	20
Lepidium sativum L.	Garden cress	2	20
Linum usitatissimum L.	Flax	3	20
Lolium perenne L.	Perennial ryegrass	5	20
Lycopersicon esculentum Mill.	Tomato cv. Homestead	2	20
Medicago sativa L.	Alfalfa	3	25
Portulaca oleracea L.	Common purslane	5	25
Rumex acetosella L.	Red sorrel	5	25
Setaria italica (L.) Beauv.	Foxtail millet	5	25
Sida spinosa L.	Prickly sida	5	20
Sorghum bicolor (L.) Moench	Sorghum	3	15
Trifolium incarnatum L.	Crimson clover	3	20
Triticum aestivum L.	Wheat	3	15

[a] (1) Baxter's, Weslaco, TX 78596; (2) Burpee, Warminster, PA 18974; (3) Carolina Biological, Burlington, NC 27215; (4) R. M. Menges, USDA, Weslaco, TX 78596; (5) Valley Seed, Fresno, CA 93791.

shown in Fig. 1. Strigol, epistrigol, 2RAS, 3RAS (HM), and 3RAS (LM) were synthesized as described by Pepperman et al. (1982). The 3RAS isomers are resolved diastereomeric pairs (Connick and Pepperman 1981) from a mixture designated as GR7 by Johnson and co-workers (1981). GR24, also a racemic mixture, was a gift of A. W. Johnson, University of Sussex, England. The aniline-containing strigol analog (AMDF, 3-anilinomethylene-2,3-dihydrobenzo[α]furan-2-one) was prepared according to the procedure of Wolfbeis and Junek (1979). Gibberellic acid (GA_3, 90% pure), kinetin (KIN), 6-benzylaminopurine (BAP), and 6-benzylaminopurine riboside (BAPR) were all purchased from a commercial supplier (Sigma, St. Louis, MO 63178). Thiourea (TU) and l-ascorbic acid (AA) were analytical grade.

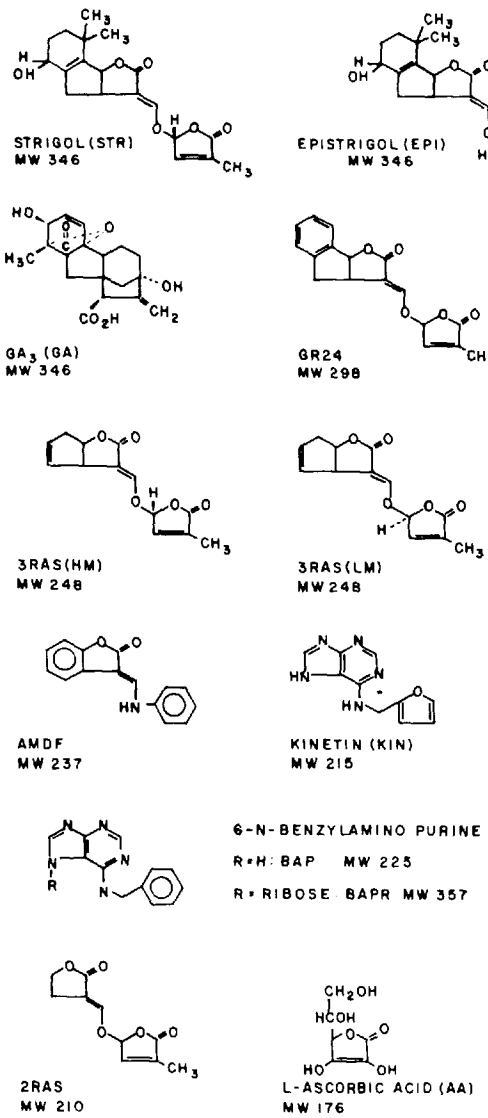

Fig. 1. Structures and molecular weights of cyclic compounds strigol (STR), epistrigol (EPI), gibberellic acid (GA), GR24, 3RAS (HM), 3RAS(LM), AMDF, kinetin (KIN), 6-N-benzylamino purine (BAP), 6-N-benzylamino purine riboside (BAPR), 2RAS, and ascorbic acid (AA) tested for germination stimulatory activity.

Statistical Analyses

Using a completely random design with eight replications, the count data from the various temperature and time treatments were normalized by the transformation, $(x + 0.5)^{0.5}$ (Sokal and Rohlf 1981). In the multiseed germination assay, data for each seed species were analyzed separately using one-way analyses of variance. Significant differences between compound effects were determined using the Waller-Duncan Bayesian k ratio (k = 100) t-test (Steel and Torrie 1980). Data from the concentration-dependent light-sensitive and light-

insensitive lettuce assays of the strigol group of compounds were compared in a 2 × 3 × 7 (cultivar × concentration × compound) factorial analysis of variance (Sokal and Rohlf 1981). One-way analyses of variance and Tukey's Honestly Significant Difference procedure (significance levels, $p = 0.01$) were used to examine the differences between the effects of three concentrations (0.01, 0.1, and 1.0 mM) of strigol, five strigol analogs, gibberellic acid, and single levels of ascorbic acid, thiourea, and thiourea plus ascorbic acid. (Sokal and Rohlf 1981). Data are presented as mean percent germination to facilitate comparison.

Results

Multiseed Germination Assays

Under the assay conditions used, most of the seeds germinated more than 65%. Those seed lots with control germination percentages below 50% under the assay conditions were tested for germination capacity under permissive environmental conditions—i.e., 20°C incubation, alternating 20–30°C temperatures or exposure to light (Maguire and Overland 1959, Steinbauer et al. 1955)—and only seed lots capable of at least 65% germination under permissive conditions were used in the assays. Where the assay environment reduced germination levels from those obtained under permissive conditions, those seed species were considered to have entered an environmentally induced dormancy (Simpson, 1978). Preliminary screening assays indicated that the presence of 0.1% DMSO in the incubation solution had no significant effect, compared to deionized water, on the germination of any of the seeds listed in Table 1 (data not shown).

Of the 28 seeds in Table 1, 13 showed significant responses to the test compounds. The mean germination percentages of the species significantly affected are shown in Table 2 (monocots) and Table 3 (dicots). The maximum standard error for the means shown in these tables was 2.1%.

Five monocot species listed in Table 1—*Allium, Avena, Echinochloa, Lolium,* and *Triticum*—were unaffected by any of the test compounds and have been omitted from Table 2. Under the assay conditions germination of *Bromus secalinus* and *B. tectorum,* but not *B. inermis,* was markedly reduced from that observed under permissive conditions, and the test compounds had contrasting affects on the germination of all three *Bromus* species. Nondormant *B. inermis* was unaffected by all the strigol group of compounds except 3RAS(HM), which inhibited, as did BAPR. Ascorbate plus thiourea allowed *B. inermis* to reach full germination potential. The two dormant *Bromus* species were further inhibited by ascorbate plus thiourea. Opposite effects were observed in *B. secalinus* and *B. tectorum* seeds exposed to 2RAS, 1.0 mM GA, BAPR, and thiourea.

Germination of the nondormant seeds of *Eragrostis* was significantly increased by four of the strigol analogs—epistrigol, GR24, and the two 3RAS compounds; GA, the three cytokinins, thiourea, and ascorbate plus thiourea inhibited germination. *Setaria* seeds were affected only by ascorbate, and only

Table 2. Comparison of the effects of 0.1 mM growth regulators, 1 mM Ga, 4.5 mM ascorbic acid, 50 mM thiourea, and ascorbic acid plus thiourea on the germination of monocot seeds.

Compound	Percent germination[a]					
	Bromus inermis	*Bromus secalinus*	*Bromus tectorum*	*Eragrostis curvula*	*Setaria italica*	*Sorghum bicolor*
STR	56.5 abc	23.6 abc	15.2 cd	58.2 bc	56.7 c	33.9 d
EPI	42.8 defg	22.0 bc	9.4 de	68.6 a	54.7 c	90.7 ab
GR24	49.7 cdef	17.7 cde	19.1 c	72.2 a	64.5 bc	82.9 ab
3RAS(HM)	39.0 fg	28.6 a	9.5 de	67.1 a	54.7 c	85.4 ab
3RAS(LM)	57.1 abc	19.8 bcd	17.2 cd	69.4 a	55.5 c	86.2 ab
AMDF	—	14.7 cdef	—	55.3 cde	—	88.1 ab
2RAS	42.6 defg	27.7 a	9.5 de	64.6 ab	54.9 c	89.7 ab
GA (1.0 mM)	41.0 efg	13.8 efg	57.1 a	51.8 def	70.0 ab	42.6 cd
GA (0.1 mM)	59.0 ab	11.6 fgh	14.2 cde	49.4 efg	71.8 ab	44.2 cd
KIN	45.5 cdefg	13.3 defg	19.7 c	46.7 gh	61.2 bc	89.8 ab
BAPR	36.7 g	9.6 gh	44.2 ab	34.8 h	61.6 bc	62.0 c
BAP	51.3 bcde	12.0 fg	11.4 cde	44.2 g	61.2 bc	94.1 ab
AA (4.5 mM)	54.0 abcd	21.4 bcd	0.0 f	55.9 cde	79.3 a	34.7 cd
TU (50 mM)	45.2 cdefg	6.1 h	36.3 b	48.2 fg	71.0 ab	31.0 d
AA + TU	67.1 a	9.8 gh	6.4 e	51.1 def	58.1 c	96.8 a
CTRL	51.8 bcde	21.1 bcd	21.2 c	58.6 cd	62.5 bc	75.7 b
Permissive CTRL	62.0[b]	93.0[b]	96.0[b]	67.8[b]	89.0[b]	89.4[b]

[a] Percent germination data are means of eight replications. Values in columns associated with a given seed and followed by the same letter(s) are not significantly different according to the Waller-Duncan Bayesian k ratio (k = 100) t-test.

[b] Alternating 20/30°C, 3-day incubation.

strigol, of the strigol-group compounds, inhibited *Sorghum*. *Sorghum* was inhibited by GA and BAPR, as well as ascorbate and thiourea separately. However, sorghum germination was significantly increased by ascorbate and thiourea in combination.

Ten dicot assay seeds from Table 1—*Brassica, Cucumis, Daucus, Lactuca sativa* cv. Grand Rapids, *Lepidium, Linum, Lycopersicon, Medicago, Rumex,* and *Portulaca*—were not affected by any of the test compounds and therefore do not appear in Table 3. Germination of seven dicot seeds was significantly affected by one or more of the test compounds (Table 3). Under the assay conditions six dicot seed species exhibited some degree of dormancy (*Amaranthus palmeri, A. retroflexus, Capsella, Sida,* and the light-sensitive (LSL) and light-insensitive (LIL) *Lactuca* seeds).

With the exception of a slight inhibition of LSL germination, 0.1 mM strigol and epistrigol had no effect on the germination of the dicot assay seeds. Both *Amaranthus palmeri* and *A. retroflexus* were partially dormant under the assay conditions, an environmentally induced dormancy that was partially relieved in both species by 2RAS and significantly increased by the three cytokinins. In addition, *A. retroflexus* germination was promoted by GR24 and reduced by AMDF and 1 mM GA, as well as ascorbate and thiourea separately. *Capsella*

Table 3. Comparison of the effects of 0.1 mM growth regulators, 1 mM GA, 4.5 mM ascorbate acid, 50 mM thiourea, and ascorbate plus thiourea on dicot seed germination.

	Percent germination[a]						
Compound	*Amaran. palmeri*	*Amaran. retroflex.*	Capsella *b-p*	*Lactuca sativa* Lt.-sens.	Lt.-insens.	*Sida spinos.*	*Trifolium incarnat.*
STR	35.1 bcd	20.0 d	10.0 de	50.1 e	64.7 de	15.3 bcd	72.2 bc
EPI	29.1 cd	23.6 cd	13.2 de	29.9 fg	47.3 f	16.7 bcd	66.8 cd
GR24	31.9 bcd	54.6 a	50.7 a	78.7 bc	95.5 ab	8.1 f	74.6 bc
3RAS(HM)	44.9 ab	38.0 bc	55.3 a	81.0 abc	95.5 ab	11.0 def	80.4 ab
3RAS(LM)	32.4 bcd	31.8 bc	49.4 a	87.9 ab	98.7 a	8.5 f	78.5 bc
AMDF	31.6 bcd	15.8 ef	14.2 de	68.3 cd	94.2 ab	11.5 def	65.5 cd
2RAS	50.7 a	43.5 ab	69.1 a	91.1 a	93.6 ab	17.6 abc	68.3 cd
GA (1.0 mM)	21.3 de	8.4 g	41.1 b	89.8 ab	89.6 abc	23.3 ab	68.2 cd
GA (0.1 mM)	26.6 bcd	31.8 bc	16.0 cde	52.0 e	81.2 bc	14.6 cde	54.9 de
KIN	10.5 e	6.0 g	17.8 d	58.5 de	97.5 a	24.3 a	45.6 e
BAPR	14.3 e	8.8 fg	27.3 c	89.7 ab	92.4 ab	23.0 ab	55.0 d
BAP	10.8 e	5.4 g	5.2 e	73.4 bc	91.6 ab	17.9 abc	59.4 d
AA (4.5 mM)	29.6 bcd	9.3 fg	4.9 e	36.7 f	74.3 cd	25.2 a	67.0 cd
TU (50 mM)	28.0 cd	16.1 e	6.9 de	94.9 a	98.1 a	21.0 abc	81.7 a
AA + TU	38.1 bc	33.3 bc	50.5 a	89.8 ab	98.8 a	9.5 ef	82.4 a
CTRL	31.4 bcd	25.4 cd	10.7 de	32.3 f	56.0 ef	14.3 cde	72.6 bc
Permissive CTRL	89.6[b]	70.5[b]	82.0[b,c]	77.4[c,d]	94.5[c]	65.3[b]	75.3[c]

[a] Percent germination data are means of eight replications. Values in columns associated with a given seed and followed by the same letter(s) are not significantly different according to the Waller-Duncan Bayesian k-ratio (k = 100) t-test.
[b] Alternating 20/30°C, 3-day incubation.
[c] 20°C, 3-day incubation.
[d] Light, 3-day incubation.

germination was increased by KIN and BAPR, as well as four strigol analogs, GA, and ascorbate plus thiourea, effects discussed further elsewhere (Bradow 1986). *Sida* germination was reduced significantly by GR24 and 3RAS(LM), whereas 1 mM GA, and 0.1 mM KIN, and BAPR increased *Sida* germination, but not to levels observed under permissive conditions. *Trifolium* was unaffected by any of the strigol group of compounds, and all three cytokinins decreased germination of these seeds. Germination of both LSL and LIL was increased by all five synthetic strigol analogs, both levels of GA, the three cytokinins, thiourea, and ascorbate plus thiourea. LIL germination was also increased by ascorbate alone. The concentrations of ascorbate (4.5 mM) and thiourea (50 mM) used in this study were the same levels found most promotive of lettuce (Mayer et al. 1958) and *Capsella* (Bradow 1986).

Lettuce Seed Assays

Of the seeds tested, *Capsella*, LSL, and LIL were the most sensitive to 0.1 mM strigol analog growth regulators. This concentration was not always optimal for the promotion of *Capsella* germination by strigol analogs or GA (Bradow 1986), and concentration studies of the responses of LSL and LIL seeds to 0.01, 0.1, and 1 mM solutions of strigol, the strigol analogs, and GA indicated differing concentration dependence profiles for lettuce seeds as well (Figs. 2, 3). The 50 mM thiourea plus 4.5 mM ascorbate used in the screening assays proved to be the optimal concentration in the LIL and LSL assays (data not shown), and the results at this level were included in the statistical analyses (one-way analyses of variance) that produced Figs. 2 and 3.

Light-Sensitive Lettuce

After 72 h incubation at 25°C, clear concentration effects were observed for all the strigol group of compounds and GA (Fig. 2). Strigol and the two 3RAS analogs had optimal promotive activity at the lowest concentration, while 1 mM epistrigol, GR24, and GA induced maximum germination promotion. Even at apparent optimal concentration, strigol and epistrigol were not as effective as the other analogs and GA. Supraoptimal concentrations of strigol, 2RAS, and 3RAS(LM) reduced LSL germination to that of the control. Alone, AA had no effect on LSL germination, but thiourea and ascorbate plus thiourea were as effective in promoting germination in the absence of light as optimal concentrations of GA or any of the strigol group of compounds. Exposure of both LSL and LIL seeds to thiourea with or without ascorbate produced bright yellow, somewhat distorted seedlings with excessively elongated hypocotyls. The pigmentation was not limited to the radicles, as has been reported (Poljakoff-Mayber and Mayer 1961).

An additional 96 h of incubation in the dark increased control germination only 3 percentage points while increasing germination of LSL seeds exposed to 0.1 mM strigol 10% absolute. Seeds exposed to 0.01 mM 2RAS and 0.1 mM GA germinated an additional 9% absolute. At both 72 and 168 h the analyses of

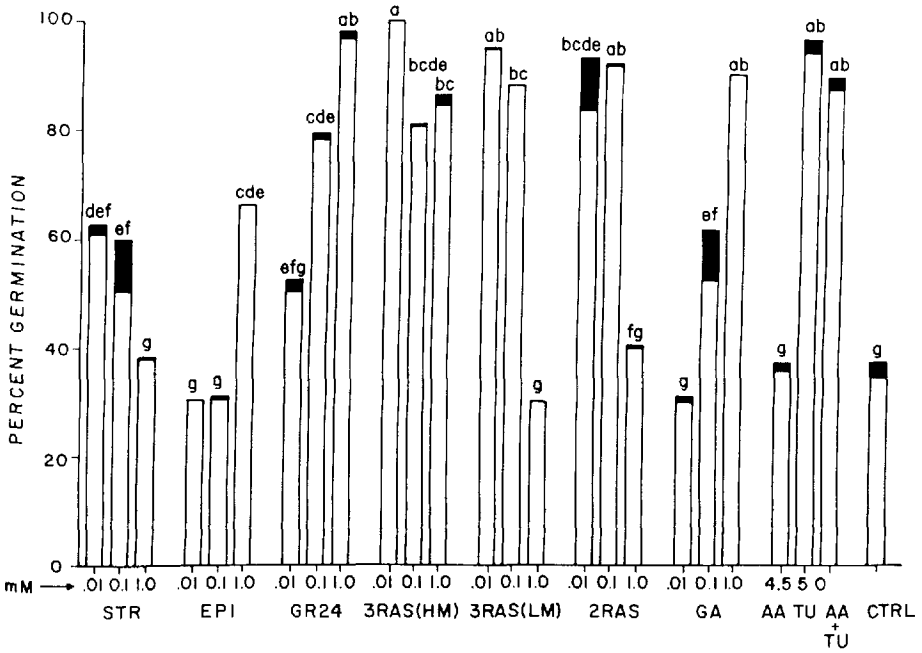

Fig. 2. The effect of strigol, epistrigol, GR24, 3RAS(HM), 3RAS(LM), 2RAS, GA3, ascorbate (AA), thiourea (TU), and 4.5 mM AA + 50 mM TU on 72-h dark germination of light-sensitive (LSL) lettuce seed. Columns associated with the same letters are not statistically different (p = 0.01). Shaded areas indicate additional germination after 168-h (total) incubation. (SE <2.0%.)

variance show strong interactions between the compounds and concentration as well as highly significant differences between test compounds.

Light-Insensitive Lettuce

While LIL controls germinated 20 percentage points more than the LSL seeds, LIL did not fully germinate in 72 h under the experimental conditions (Fig. 3). All the synthetic strigol analogs, epistrigol, GA, ascorbate, thiourea, and ascorbate plus thiourea significantly increased LIL germination, in comparison to the control. Some concentration dependence was apparent in these promotive effects. Supraoptimal millimolar levels of 3RAS(LM) and 2RAS reduced LIL germination to that of the control, whereas the lower levels of these compounds promoted germination. Millimolar epistrigol significantly increased LIL germination. Alone, ascorbate promoted LIL germination, but not to the extent that thiourea and ascorbate plus thiourea did.

An additional 96 h of incubation led to an additional 3% absolute LIL germination. After 168 h the only significant change in the presence of the test compounds was the 19% absolute increase in germination of LIL seeds exposed to 0.1 mM strigol. Again the analyses of variance showed strong interactions between the test compounds and concentration, but the differences between the

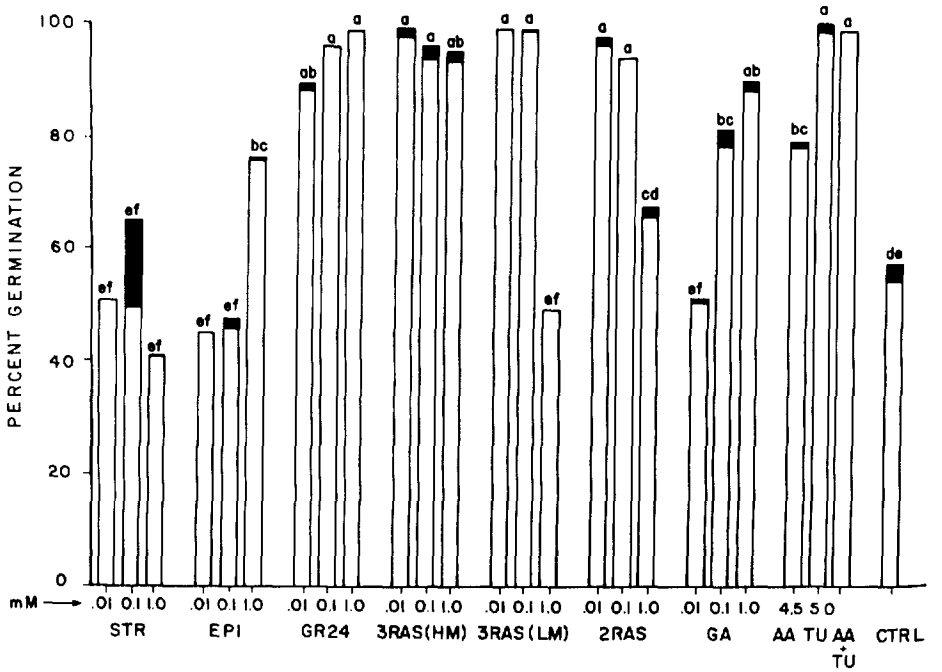

Fig. 3. The effect of strigol, epistrigol, GR24, 3RAS(HM), 3RAS(LM), 2RAS, GA3, ascorbate (AA), thiourea (TU), and 4.5 mM AA + 50 mM TU on 72-h dark germination of light-insensitive (LIL) lettuce seed. Columns associated with the same letters are not statistically different ($p = 0.01$). Shaded areas indicate additional germination after 168-h (total) incubation. (SE <1.8%.)

compounds were the most important factor, particularly after 7 days of incubation.

Discussion

In the screening assays with monocot seeds, there were no clear parallels between the effects of the strigol analogs, gibberellic acid, the cytokinins and ascorbate, thiourea, and ascorbate plus thiourea. Of the monocot species showing marked environmentally induced dormancy under the assay conditions (*Bromus tectorum, B. secalinus,* and *Setaria*), *B. secalinus* germination was not increased to permissive control levels by any of the test compounds, *B. tectorum* was promoted by 1 mM GA and 0.1 mM BAPR, and *Setaria* germinated most fully in the presence of ascorbate. The strigol group compounds had minimal promotive effect on these dormant monocots; only the germination of nondormant *Eragrostis* was significantly increased by several of the strigol group of compounds. In general, based on the minimal effects shown in Table 2, the compounds tested show little promise as regulators of monocot seed germination, at least in those monocot species used in these assays.

Of the seven dicot seeds that exhibited dormancy under the assay conditions, *Capsella*, LIL, and LSL were the most sensitive to GA and the strigol analogs. In both LIL and LSL, 0.1 mM or 0.01 mM solutions of the strigol analogs were more effective than equimolar solutions of GA. The optimal GA concentration for promoting lettuce and *Capsella* (Bradow 1986) seed germination was 1 mM.

The multiway analysis of variance in the lettuce seed germination data clearly indicated that the responses of LIL and LSL to the test compounds were different and that the major factor was the interaction between test compound and concentration. The general activity trends (increasing activity with increased concentration for epistrigol, GR24, and GA and decreasing activity with increased concentration for 3RAS(HM), 3RAS(LM), strigol, and 2RAS) are the same for LIL and LSL, but the concentration effects are more pronounced in the more dormant LSL. The greater the degree of seed dormancy (*Capsella* > LSL > LIL), the more apparent were the concentration effects. Strigol and epistrigol were less effective than the synthetic strigol analogs in promoting germination of dormant seed, having less effect than millimolar GA on LSL and LIL and no effect on *Capsella* (Bradow 1986).

One obvious explanation for the lower activities of strigol and epistrigol in these assays is their lower water solubility, even in the presence of DMSO. Millimolar solutions of these two compounds were near saturation, and chilling to 4°C caused precipitation. The aniline-containing strigol analog AMDF is so insoluble that the 0.1 mM solution was near saturation. For this reason AMDF was not included in the 0.01, 0.1, and 1 mM concentration dependence study. Before use of this multiseed assay, attempts were made to overcome the water insolubility of test compounds by the use of other dispersal agents such as acetone and detergents and by pretreatment with solutions of the test compounds dissolved in nonpolar solvents such as dichloromethane. Acetone levels sufficient to dissolve strigol decreased control seed germination significantly, particularly in the case of lettuce, and dichloromethane pretreatment greatly reduced germination in controls of several species, including *Sorghum*, *Avena*, *Triticum*, and *Cucumis*, compared to water controls. Of all the carriers and solubilizers tested, DMSO had the least effect on the fewest seed species.

The results above do indicate that the bioregulatory activity of the synthetic strigol analogs extends to dormant seeds of dicot genera other than *Striga*, the original target for germination promotion by these compounds. Low water solubility lowers the effectiveness of strigol and epistrigol, compared to that of the more hydrophilic analogs, which are effective at 10-fold lower concentrations than gibberellic acid.

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