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Germination Stimulation in Wild Oats (*Avena fatua* L.) by Synthetic Strigol Analogs and Gibberellic Acid

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Abstract. At concentrations of 0.01–1 mM, five synthetic multiring analogs of strigol were effective germination stimulants of intact and dehulled wild oat (*Avena fatua* L.) seeds. The effect was concentration-dependent and equaled or exceeded that produced by equimolar gibberellic acid (GA_3). The most effective strigol analog treatments induced 55–80% germination within 7 days in intact wild oat seeds and resulted in 63–86% germination and normal seedling growth over 14 days. Intact wild oat controls germinated 14% after 14 days. The stimulation of wild oat germination by these synthetic strigol analogs demonstrates that these compounds, initially developed as germination stimulants for the seeds of the parasitic weed, witchweed (*Striga asiatica* L. Kuntz.), have bioregulatory activity in dormant seeds of monocots, as well as dicots. None of the compounds tested significantly affected the germination of nondormant cultivated oat seeds (*Avena sativa* L.). The commonly used dispersal agent, Tween 20 (0.1%), was found to inhibit germination of cultivated oats, alone and in the presence of 2% acetone.

Many weeds, including wild oats (Banting 1966a,b) and witchweed (Saunders 1933), persist through a seed dormancy survival strategy. To effectively control such weeds, it is necessary to deplete the soil seed banks by stimulating germination of dormant seeds and then eliminating the seedlings with herbicides (Egley and Dale 1970; Eplee 1975; Eplee and Langston 1976; Foley 1987; Metzger 1983). As expected, the seed morphologies of the monocot, wild oats (Simpson 1978), and the parasitic dicot, witchweed (Egley 1972), differ considerably; however, physiologically, these two seeds are strikingly similar. Germination of both witchweed (Brown and Edwards 1944; Egley 1972) and wild oats (Atwood 1914; Foley 1987; Naylor and Jana 1976) requires seed after-ripening or ageing. Dormant embryos of both species can be induced to germinate by piercing the seed coat and/or aleurone layer (Atwood 1914; Egley 1972). Starch hydrolysis is an important germination factor following dormancy removal in both witchweed (Menetrez 1985) and wild oats (Simpson 1978; Simpson and Naylor 1962). Dormant seeds of both witchweed (Brown and Edwards 1944) and wild oats (Simpson 1978) are induced to germinate by a variety of exogenous substances, such as ethylene (Adkins and Ross 1981; Egley and Dale 1970), cytokinins (Tilsner and Upadhyaya 1985; Worsham et al. 1959; Yoshikawa et al. 1978), coumarin (Hsiao et al. 1981; Hsiao and Quick 1985), NaOCl plus gibberellin (Hsiao et al. 1981; Hsiao and Quick 1985), and gibberellin applied to seeds with scarified or punctured testae (Egley 1972; Naylor and Simpson 1961). Germination of wild oats is also stimulated by other gibberellin-like substances (Metzger 1983). Some of the synthetic analogs of strigol, a potent inducer of witchweed germination (Cook et al. 1966; Cook et al. 1972; Hsiao et al. 1981), also stimulate germination of witchweed (Babiker and Hamdoun 1982; Johnson et al. 1976; Stevens and Eplee 1979) and broomrape (*Orobanche ramosa* L.) (Johnson et al. 1976). Further, several of these multiring synthetic strigol analogs have shown gibberellin-like activity by inducing germination in dormant seeds of shepherdspurse (*Capsella bursa-pastoris* L.) (Bradow 1986) and lettuce (*Lactuca sativa* L.) (Bradow et al. 1988). This article compares the effects of five of the multiring strigol analogs and gibberellin (GA_3)

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on the germination of dormant dehulled and intact wild oat disseminules and nondormant cultivated oats.

Materials and Methods

Assay Seeds and Sources

The seeds of cultivated oats and a 1985 Montana-gathered wild oat crop were purchased from commercial sources (Carolina Biological, Burlington, NC, USA and Valley Seed, Fresno, CA, USA, respectively) and used in the spring of 1986.

Germination Assays

Paleae and lemmae were removed by hand from the wild oat caryopses for the "dehulled" treatments no more than 24 h before each assay and kept refrigerated (4 ± 1°C) until use. Intact wild and cultivated oats were stored at room temperature. No distinction was made between primary and secondary seeds, but immature (unfilled) and damaged seeds were discarded. All experiments were performed within 6 weeks, using the same wild and cultivated oat seed lots throughout.

Twenty seeds were placed in a plastic 10-cm petri dish lined with one 9-cm sheet of filter paper (Whatman No. 1) saturated with 5 ml of test solution (one replicate). Eight replicates per treatment were wrapped in aluminum foil, randomized, and incubated in the dark at 20 ± 1°C in sealed plastic storage boxes. Equivalent replicated dehulled and intact wild oat and cultivated oat controls were incubated with each set of treatments (total control replications = 96 for each type of seed). Germination evaluations were made after 3, 7, 10, and 14 days. Coleorhizal protrusion was the germination criterion. Separate counts of seeds showing coleorhizal or both coleoptile and coleorhizal protrusion were made as a measure of developmental abnormalities. Germinated seeds were removed after each evaluation. Seed manipulations and germination evaluations were performed under a dim green safe light.

All test solutions, including the controls, contained 2% (vol/vol) acetone and 0.1% (vol/vol) Tween 20 (polyoxyethylenesorbitan, Sigma, St. Louis, MO, USA) to aid in the dispersal of the test compounds (Metzger 1983). Each compound was tested as a tenfold dilution series from 10^{-3} to 10^{-10} M with the initial acetone and Tween 20 concentrations held constant. Deionized distilled water was used in solution preparation. Test solutions were adjusted to pH 5.0 with 6 N KOH when necessary, and all solutions were allowed to equilibrate for 48 h at 22°C before use. To investigate possible solvent effects in the cultivated oat assays using 2% acetone plus 0.1% Tween, 16 replicates of 20 wild or cultivated oats were incubated in 5 ml deionized water, 0.1% (vol/vol) dimethylsulfoxide (DMSO), 2% (vol/vol) acetone, or 0.1% (vol/vol) Tween 20 for 3 days and then evaluated as described above.

Chemicals

The chemical structures and molecular weights of the test compounds have been previously published (Bradow 1986; Bradow et al. 1988; Pepperman et al. 1981). Gibberellic acid (GA_3, 90% pure) was purchased from a commercial supplier (Sigma, St. Louis, MO, USA). The synthetic strigol analogs, 2RAS, 3RAS(HM), 3RAS(LM), and LD were synthesized as described by Pepperman et al. (1981). The 3RAS isomers are resolved diastereomeric pairs (Connick and Pepperman 1981) from a mixture designated as GR7 by Johnson and coworkers (1981). LD is the dimer, 5,5′-oxybis [3-methyl-2(5H)-furanone, designated D-7 by Pepperman and coworkers (1981). GR24, also a racemic mixture, was a gift from A. W. Johnson, University of Sussex, UK. All other reagents used were analytical grade and obtained from commercial suppliers.

Statistical Analyses

The germination count data (eight replicates per treatment) were normalized by the transformation $(x + 0.5)^{0.5}$ and subjected separately, according to evaluation date, to three-way factorial analyses of variance (Sokal and Rohlf 1981). Two-way analyses of variance were used to examine compound and concentration effects for each separate seed type at each evaluation date, and one-way analyses of variance were used to evaluate the concentration-dependent effects of each compound on the germination of each seed type and to compare the effects at each concentration across compounds. The control germination count replicates used in the one-way analyses of variance were the means of 12 control repetitions made for each type of seed during the 6-week duration of the experiment. Significant differences among compound concentration effects and among compounds at each concentration were determined using Tukey's Honestly Significant Difference Procedure. Concentration-dependence data were also examined by curvilinear regression analyses, using orthogonal polynomials. A significance level of $P = 0.01$ was used throughout. Data are presented as percent germination to facilitate graphical representation.

Results and discussion

Seed Lot Germination Characteristics

Controls (in 2% acetone and 0.1% Tween 20) consisting of intact seeds from the natural wild oat population germinated 13.8% after 14 days in the dark at 20°C (Table 1). This level of dormancy in intact seeds is comparable to that reported by others (Corns 1960; Fay and Gorecki 1978). Natural populations of wild oats are not homogeneous with respect to seed dormancy (Naylor and Jana 1976; Sawhney and Naylor 1980; Sawhney and Naylor 1982), and it has been suggested that inbred uniform wild oat populations be used for biochemical studies of seed dormancy (Simpson 1978). However, the objective of this work, the preliminary screening of a new group of growth regulators for field use potential, is more closely related to herbicide screening using natural populations (Metzger 1983; Thai et al. 1985); therefore, "generic" wild oat seeds were used.

Preliminary testing showed that dry storage for 48 h at 25–27°C increased dehulled wild oat control germination to 62.6% after 7 days. This is compa-

Table 1. Germination percentages of intact and dehulled wild oat and intact cultivated oat disseminules incubated in deionized water solution containing 2% acetone + 0.1% Tween and cultivated oats incubated in deionized water, and aqueous solutions containing 0.1% DMSO, 2% acetone, or 0.1% Tween.

Incubation solution	Percent germination[a]						
	Acetone (2%) + Tween (0.1%)			Water	DMSO (0.1%)	Acetone (2%)	Tween (0.1%)
	A. Fatua		*A. Sativa*				
	Intact	Dehulled	Intact	Intact	Intact	Intact	Intact
Day 3	0.7	12.4	13.1	70.6	56.9	65.0	23.1
Day 7	11.5	18.7	30.7	—	—	—	—
Day 10	13.6	24.6	34.9	—	—	—	—
Day 14	13.8	26.9	35.6	—	—	—	—
Max. SE	±1.5	±1.9	±2.1	±1.4	±2.1	±1.0	±1.9

[a] Percent germination data for the three seeds incubated in acetone + Tween are means of 96 replications, and data for *A. sativa* incubated in other solutions are the means of 16 replications.

rable to reported dormancy losses induced in wild oats by caryopsis wounding (Foley 1987). Dehulled wild oat controls refrigerated no longer than 48 h before use germinated 12.4, 18.7, 24.6, and 26.9% after 3, 7, 10, and 14 days incubation, respectively (Table 1). The germination of intact wild oats was significantly lower. Therefore, wounding and/or hull removal increased germination an average of 10.7% under the incubation conditions. There was no significant change in the germination of the regularly repeated wild oat controls over the 6-week duration of these experiments, but dormancy was completely lost after 1 year at room temperature.

Cultivated oat controls incubated in acetone plus Tween 20 germinated much less than expected from previous experiments using other solvent systems (Bradow 1985; Bradow et al. 1988). Under the conditions of this experiment, the cultivated oats germinated more than 70% in deionized water (Table 1). The cultivated oat germination percentages obtained in water, DMSO, and acetone alone were not significantly different from each other. In contrast, Tween 20 reduced cultivated oat germination to levels observed in the seeds incubated in acetone plus Tween 20. Germination of intact and dehulled wild oat disseminules was not significantly affected by Tween 20, DMSO, or acetone (unpublished observations). Clearly, any increased solubilization achieved by adding Tween 20 as a dispersal agent must be carefully weighed against the possibility of germination inhibition such as that observed here in cultivated oats.

Factorial Analyses of Variance

The three-way factorial analyses of variance (three seeds by six compounds by nine concentrations, including controls) indicated significant differences among seed types, compounds, and concentrations at all four evaluation times ($P = 0.01$). The first-order interactions, seed by compound and seed by concentration, were also significant throughout. The compound by concentration interaction was significant only after 14 days. The second-order interactions were not significant.

Significant effects for compound and concentration were observed in both the dehulled and intact wild oat data at all four evaluations. None of the test compounds had any significant effect at concentrations below 10^{-8} M. The data for 10^{-10} and 10^{-9} M are, therefore, not given.

When the data were examined by separate two-way analyses of variance for each seed type, cultivated oat data showed no significant effects due to compound, concentration, or compound by concentration interactions. After 14 days, maximum mean germination of treated cultivated oat was 56.4 ± 2.7% and the minimum mean was 23.9 ± 3.1%. Control germination was 35.6 ± 2.1%. Further presentation and discussion of cultivated oat data have been omitted on the bases of the universal insignificance of the treatment effects on this nondormant seed and the obvious dispersal agent interference cited above.

Germination of Intact Wild Oat Seeds

After an incubation of 3 days, intact wild oats germinated 0.7%. The strigol analogs, 3RAS(LM) (10^{-7}–10^{-3} M), 2RAS (10^{-6}–10^{-3} M), 3RAS(HM) (10^{-5}–10^{-3} M), and GA_3 (10^{-5}–10^{-3} M) signifi-

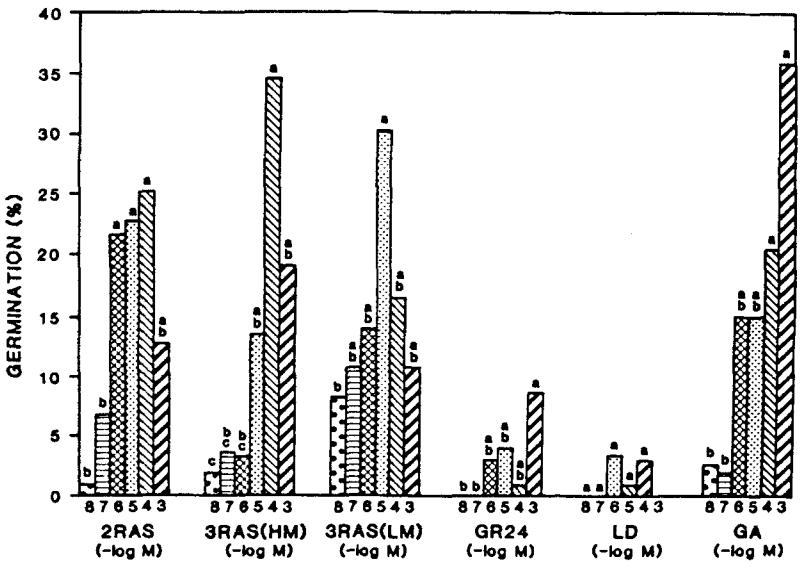

Fig. 1. Percent germination of intact wild oat disseminules incubated 3 days in 2RAS, 3RAS(HM), 3RAS(LM), GR24, LD, and GA_3 at 10^{-8}–10^{-3} M. Percentages associated with the same compound and same lower case letter do not differ significantly (P = 0.01). Germination of the control was 0.7%. SE <1.5%.

cantly increased intact wild oat germination in comparison to the control (Fig. 1). Germination promotion by the strigol analogs, 2RAS, 3RAS(HM), and 3RAS(LM), but not GA_3, showed an apparent, but nonsignificant, decrease at higher concentrations. Millimolar GR24 increased germination less than the strigol analogs and GA_3. The dimer, LD, had no significant effect on germination at any concentration.

After 7 days, the control germination increased to 11.5% (Fig. 2). The maximum germination observed in seeds treated by 2RAS, the two 3RAS diastereomers, and GA_3 exceeded 66%. GA_3 is significantly less effective than 2RAS at 10^{-7}–10^{-4} M. Millimolar GR24 significantly promoted intact seed germination, and LD had no effect. Treated intact wild oats germinated an average of 7.2% during the first 3 days. Most of the germination occurred between the 3rd and 7th day with little additional germination occurring thereafter (unpublished observations). Seedlings from treated and control seedlings developed normally.

Curvilinear regression analyses of the data from each evaluation indicated significant linear concentration responses of intact wild oats to 2RAS, 3RAS(LM), GA_3, and GR24. The response of intact wild oats to 2RAS also had a significant cubic factor, and that of 3RAS(LM) had an added significant quartic factor. The 3RAS(HM) response curve was best described by a combination of quadratic, cubic, and quartic factors. The patterns of wild oat germination response to concentration were consistent at each of the four evaluation times.

Germination of Dehulled Wild Oat Seeds

After 3 days, the dehulled wild oat control germinated 12.4%. The strigol analogs, 2RAS (10^{-7}–10^{-3} M), 3RAS(HM) and 3RAS(LM) (10^{-6}–10^{-3} M), GR24 (10^{-5}–10^{-3} M), LD (10^{-3} M), and GA_3 (10^{-6}–10^{-3} M) significantly increased germination of dehulled wild oats, compared to the control (Fig. 3). The effects of GA_3 and the three most active strigol analogs were not significantly different in the range, 10^{-5}–10^{-3} M. GA_3 was less effective than these three analogs at 10^{-6} M.

After 7 days, treated dehulled wild oat germination had increased an average of 6.3%, and the germination of the controls increased an added 6.3–18.7% (Fig. 4). Germination of the dehulled wild oat seeds occurred primarily during the first 3 days. After 14 days, the treated seeds had germinated an additional 10.2%, on the average. During that same period, dehulled wild oat control germination increased 12.5%. GA_3 was less effective than 2RAS and the two 3RAS analogs at concentrations below 10^{-6} M. All treatments produced normal seedlings, and coleorhizal and coleoptile development were the same in the treated seedlings and the controls (unpublished observations).

As in the case of intact wild oats, curvilinear regression analyses showed significant linear concentration dependence in the data obtained after each evaluation period for seeds treated with 3RAS(LM), GR24, and GA_3. The slopes of the linear regressions for GA_3 and 3RAS(LM) were not significantly different. The 2RAS response curve was best approximated by a quartic plot, and the curve for GR24 had an added significant cubic factor. These response patterns were consistent throughout the duration of the experiment.

The above results show that, at concentrations of 10^{-7}–10^{-3} M, three of the synthetic strigol analogs, 2RAS, 3RAS(HM), and 3RAS(LM) are as effective

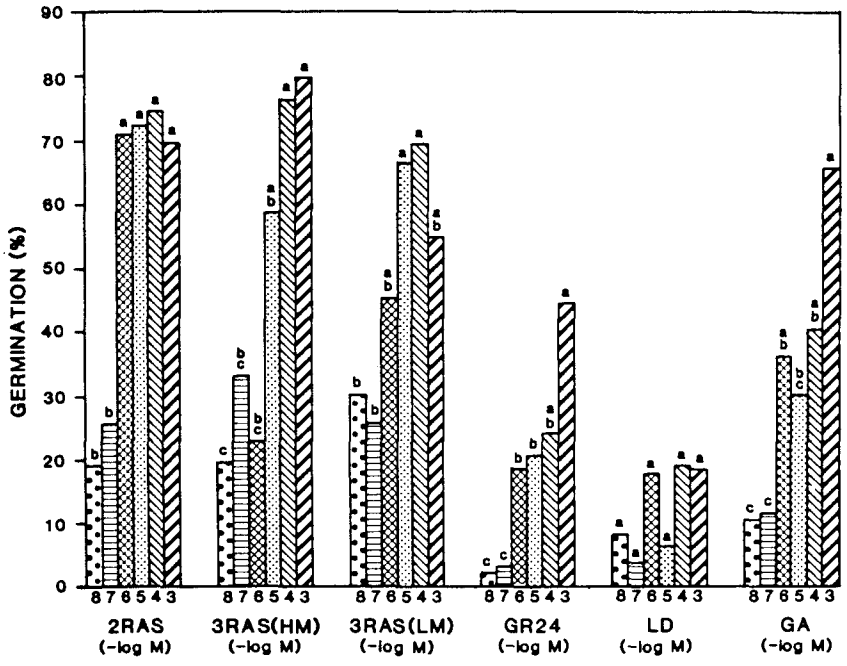

Fig. 2. Percent germination of intact wild oat disseminules incubated 7 days in 2RAS, 3RAS(HM), 3RAS(LM), GR24, LD, and GA_3 at 10^{-8}–10^{-3} M. Percentages associated with the same compound and same lower case letter do not differ significantly (P = 0.01). Germination of the control was 11.5%. SE < 1.4%.

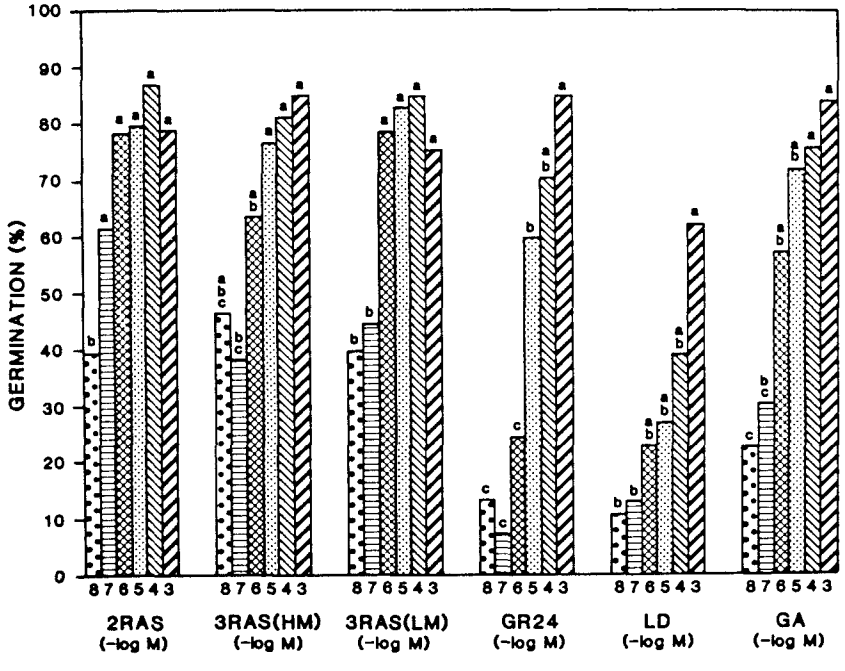

Fig. 3. Percent germination of dehulled wild oat disseminules incubated 3 days in 2RAS, 3RAS(HM), 3RAS(LM), GR24, LD, and GA_3 at 10^{-8}–10^{-3} M. Percentages associated with the same compound and same lower case letter do not differ significantly (P = 0.01). Germination of the control was 12.4%. SE < 1.8%.

as equimolar concentrations of GA_3 in promoting germination of both intact and dehulled dormant wild oat disseminules. After 7 days, germination of intact wild oats incubated in 10^{-6}–10^{-4} M 2RAS, 3RAS(HM), and 3RAS(LM) was 30% or more, higher than that of seeds incubated 14 days in equivalent concentrations of GA_3 or the substituted phthalimide, AC-94377 (Metzger 1983). The strigol analog, 2RAS, induced 71% germination in intact wild oats at 10^{-6} M, a concentration at which phthalimide was ineffective. The "supraoptimal" effect of 10^{-3} M 2RAS and 3RAS(LM) reduced intact wild oat germination to levels observed with 1.4×10^{-3} M AC-94377. A similar reduction in effectiveness at 10^{-3} M was observed in the promotion of *Capsella* germination by 2RAS, 3RAS(LM), and GR24 (Bradow 1986). Millimolar levels of GA_3, 2RAS, 3RAS(HM), and 3RAS(LM) also produced

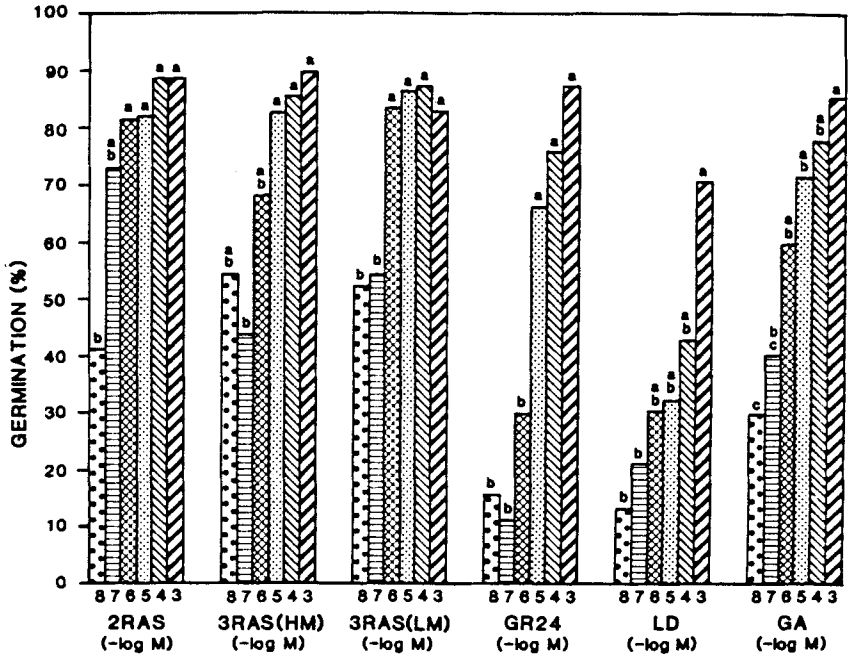

Fig. 4. Percent germination of dehulled wild oat disseminules incubated 7 days in 2RAS, 3RAS(HM), 3RAS(LM), GR24, LD, and GA_3 at 10^{-8}–10^{-3} M. Percentages associated with the same compound and same lower case letter do not differ significantly (P = 0.01). Germination of the control was 18.7%. SE < 1.9%.

seedling abnormalities (increased pigmentation and hypocotyl distortions) in *Capsella*, but wild oats germinating in the presence of all four compounds produced unpigmented seedlings with normal coleorhizae and coleoptiles.

As potential chemical stimulants for use in the reduction of dormant weed seed populations, these compounds, particularly the most water-soluble analog, 2RAS, have several advantages over GA_3 and the phthalimides. They are effective at lower, micromolar concentrations, the structures contain no acidifying carboxyl group, and the decomposition of these compounds leaves no halogen-bearing residues. Like ethylene and GA_3, these compounds induce germination in several monocot and dicot species (Bradow 1986; Bradow et al. 1988). Thus, these strigol analogs, developed to control a single parasitic plant genus, witchweed, meet the several criteria for germination stimulants for field use: (1) activity at low concentrations; (2) reasonable water solubility; (3) environmental safety; and (4) ability to promote germination in a range of species (Egley 1980). Further work, beyond the laboratory level, is required to reduce production costs and determine stability and mobility of the compounds in the soil; but the results presented here seem to indicate that these strigol analogs have definite potential as germination stimulants of dormant weed seed reservoirs in the soil, as well as use in germplasm maintenance and breeding programs where dormancy and other seed germination limitations are a problem.

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