Investigating the Cytokininlike Properties of Benomyl: Laboratory Growth Studies

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ABSTRACT

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Growth and development studies with seven vegetable crops in a controlled environment showed that benomyl 50WP was ineffective as a growth-promoting compound regardless of concentration and method of application (foliar spray or a root drench). Although benomyl exhibited a peak in stimulating chlorophyll synthesis in cucumber leaf disks at 1,000 mg a.i. L^{-1} there was no senescence (i.e., visible chlorosis and/or necrosis) retardation of leaf disks of the seven species floated on benomyl solutions ranging in concentration from 0 to 2,500 mg L^{-1}. Leaf disks floated on 2,500 mg L^{-1} showed earlier and more chlorosis and necrosis than the other treatments.

Benomyl (Benlate 50WP), a commercial fungicide, has been referred to as a cytokininlike compound (6,31,37) because it has been shown to retard chlorophyll breakdown in excised oat leaves (33), to maintain the green color of broccoli heads (21), to show cytokinin activity in the *Amaranthus* betacyanin bioassay (1), to suppress oxidant-induced chlorosis in bean leaves (14), and to enhance celery seed germination in the presence of GA_{4+7} (34). Structurally, benomyl closely resembles both kinetin and benzyladenine (16,31). Cytokinins are known to be involved as "mediators, promoters or inhibitors of growth, are involved in cell division, and can retard senescence" (36). Benomyl has been shown to decrease the growth of *Papaver bracteatum* (39), onions (2,3), mushrooms (13), *Agrostis palustris* Huds. (23), and potato tubers (11). Benomyl has also been shown responsible for increases in growth of tobacco (26), muskmelon (38), *Vitis vinifera* L. (29), *Poa pratensis* L., and *A. palustris* (37). Schreiber and Hock (27) have confirmed selectivity among plants in growth response to benomyl. The cytokininlike effects of benomyl appear to be associated with its method of application (e.g., foliar spray, root drench, or soil amendment), with the concentration applied (5,7), and with the types of rooting media used (22) as related to their organic matter content (28). We do not know whether benomyl is the translocated product from a benomyl application (12) or whether a breakdown product of benomyl (such as MBC among others) is the active translocated component causing effects similar to cytokinin responses (4,8,24,25,30).

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The purposes of this study were to determine whether benomyl produced growth and development effects in several vegetable crops and to note whether growth modifications, if any, were cytokininlike in nature. Avenues of entry studied were the foliage and the roots, and cytokininlike responses studied were growth, chlorophyll synthesis, and senescence retardation. Benomyl absorption and translocation have occurred with both methods of application (foliar spray and root drench) (15,17,20,32,35); however, few data exist comparing the growth effects of the two methods to indicate whether there are differential effects on the leaf area, the production rate of leaves (plastochron index), or the fresh or dry weights of various plant components.

MATERIALS AND METHODS

Growth studies. To study the effects of benomyl foliar sprays or root drenches on growth and development, plants were grown in controlled-environment chambers under baseline growth conditions (10,18) in 10-cm-diameter plastic pots with a 16-hr photoperiod with an abrupt light/dark change (6:00 A.M. and 10:00 P.M.), 72 ± 5% RH, 300–325 μmol m^{-2} s^{-1} photosynthetically active radiation, and a day/night temperature regime of 25/20 C. Plants were grown in the commercial rooting medium Pro Mix BX, which consists of sphagnum peat moss, vermiculite, and perlite (3:1:1). The following crops and cultivars were included: bean (*Phaseolus vulgaris* L. 'Kinghorn Wax'), radish (*Raphanus sativus* L. 'Cherry Belle'), cucumber (*Cucumis sativus* L. 'National Pickling'), sweet corn (*Zea mays* L. 'Golden Jubilee'), lettuce (*Lactuca sativa* L. 'Grand Rapids Forcing'), tomato (*Lycopersicon esculentum* Mill. 'Veemore'), and onion (*Allium cepa* L. 'Improved Autumn Spice').

Benomyl 50WP was applied either as a foliar spray (both adaxial and abaxial leaf surfaces until droplets coalesced without excessive runoff, about 2–3 ml per plant) or as a root drench (80 ml per pot until some solution leaked from the pot) at 0, 25, 250, or 2,500 mg a.i. L^{-1}. Each replicate consisted of one plant per pot per benomyl treatment. The experiment was conducted eight times. Plants were sprayed or roots drenched 14 days after planting for tomato, onion, and lettuce; 11 days after planting for bean, radish, and cucumber; and 9 days after planting for sweet corn. Sweet corn, bean, and radish plants were harvested 6 days after benomyl treatment, and tomato, onion, lettuce, and cucumber were harvested 12 days after treatment.

In another experiment, bean, radish, cucumber, and tomato plants were grown under the same conditions, except the medium was silica sand (no. 24) in order to investigate the effects of benomyl on shoot and root growth. Plants were sprayed with 0, 250, 2,500, 5,000, and 10,000 mg L^{-1} 10 days after planting for bean, 11 days after planting for cucumber and radish, and 14 days after planting for tomato. Plants were harvested 7 days after the benomyl spray treatment. Each replicate consisted of one plant per pot in each of two pots per benomyl treatment. The experiment was conducted four times.

Prior to a benomyl spray or root drench, the initial size of the plants was determined for use in analysis of covariance (19). These measurements included plastochron index, planar leaf area (19), height of the plant from cotyledons to the top of the growing point of the plant for tomato and bean plants, and height of the plant from the soil level to the top of the longest leaf for onion and sweet corn plants.

Cytokinin bioassay. The improved bioassay using National Pickling cucumber cotyledons (9) was used to detect the cytokinin activity of benomyl. In this bioassay, 7-day-old dark-grown cotyledons were incubated in solutions in petri dishes and then exposed to light. Test solutions of benomyl consisted of 0, 1, 10, 25, 250, 500, 1,000, 2,500, and 5,000 mg L^{-1}. Chlorophylls a and b were extracted separately and determined on a fresh-weight basis as described by Fletcher et al (9). Results are reported as total chlorophyll a and b. The extraction was repeated twice with two subsamples per benomyl treatment per replicate.

Cytokininlike activity of benomyl was

Table 1. Effects of benomyl foliar sprays on growth responses of cucumber, tomato, lettuce, sweet corn, onion, radish, and bean plants grown in commercial rooting medium

Plant	Benomyl treatment (mg a.i. L^{-1})	PA2[a]	PI2[b]	PA3[c]	PI3[d]	Height (cm)	Fr wt of leaves (g)	Leaf area (cm^2)	Dry wt of leaves (g)
Cucumber	0	307	4.54	···	8.14	···	44.0	1,107	3.49
	25	258	4.85	···	8.68	···	43.6	1,076	3.40
	250	294	4.87	···	8.74	···	43.9	1,076	3.54
	2,500	316	4.78	···	8.51	···	43.3	1,064	3.43
Tomato	0	192	6.24	···	9.21	···	30.9	729	2.66
	25	216	6.57	···	9.45	···	33.2	766	2.84
	250	216	6.53	···	8.96	···	30.5	701	2.55
	2,500	197	6.42	···	9.32	···	32.8	783	2.80
Lettuce	0	177	7.05	458	10.53	···	30.4	703	1.38
	25	172	6.38	431	10.33	···	29.5	667	1.46
	250	189	6.83	475	10.54	···	30.8	700	1.52
	2,500	151	6.85	478	10.85	···	30.9	689	1.45
Sweet corn	0	157	···	···	···	46.7	6.01	115	0.419
	25	139	···	···	···	47.4	5.52	118	0.405
	250	127*[e]	···	···	···	46.0	5.45	109	0.382
	2,500	142	···	···	···	46.6	5.61	113	0.389
Onion	0	27	···	39	···	21.3	0.630	7.35	0.035
	25	28	···	42	···	23.3	0.807	9.31	0.046
	250	25	···	41	···	23.6	0.780	9.53	0.047
	2,500	31	···	43	···	24.4	0.836	9.71	0.041
Radish	0	123	5.41	···	···	···	3.63	107	0.301
	25	128	5.54	···	···	···	3.95	108	0.292
	250	138	5.74	···	···	···	4.63	126	0.357
	2,500	129	5.64	···	···	···	4.26	118	0.341
Bean	0	···	6.99	···	···	67.0	21.9	851	2.47
	25	···	7.03	···	···	60.4	25.4	1,012	2.81
	250	···	7.30	···	···	66.7	31.8	1,009	3.08
	2,500	···	7.04	···	···	64.3	28.8	766	3.06

[a] Planar area measured 6 days after foliar sprays.
[b] Plastochron index measured 6 days after foliar sprays.
[c] Planar area measured 12 days after foliar sprays.
[d] Plastochron index measured 12 days after foliar sprays.
[e] Significance comparison is within a column and within a species. * = Significantly different (least-squares means test at $P \leq 0.05$) from plants treated with 0 mg a.i. L^{-1} benomyl. The experiment was conducted eight times for each species with one pot per benomyl treatment per replicate. Weight and area values are means per plant.

Table 2. Effects of benomyl foliar sprays on growth responses of cucumber, bean, radish, and tomato plants grown in silica sand

Plant	Benomyl treatment (mg a.i. L^{-1})	PI[a]	Fresh weight (g)				Leaf area (cm^2)	Height (cm)	Dry weight (mg)			
			Leaves	Stem	Hypocotyl	Roots			Leaves	Stem	Hypocotyl	Roots
Cucumber	0	3.53	5.12	1.31	···	3.61	167	···	483	69	···	132
	250	3.79	5.50	1.30	···	4.10	175	···	526	68	···	132
	2,500	3.55	5.19	1.21	···	2.90	163	···	505	63	···	129
	5,000	3.44	5.04	1.31	···	3.27	158	···	483	71	···	108
	10,000	3.72	5.06	1.26	···	2.86	163	···	489	57	···	120
Bean	0	4.48	5.28	1.67	···	2.99	220	9.0	551	188	···	171
	250	4.36	3.98	1.54	···	2.46	183	12.0	448	182	···	177
	2,500	4.57	5.68	1.94	···	2.98	239	12.1	573	191	···	172
	5,000	4.35	5.02	1.85	···	2.43	215	11.6	540	194	···	149
	10,000	4.39	4.39	1.41	···	2.40	180	8.5	462	150	···	151
Radish	0	5.74	3.18	···	3.98	···	87	···	273	···	245	···
	250	5.17	2.92	···	4.56	···	81	···	232	···	284	···
	2,500	5.28	2.92	···	4.05	···	82	···	241	···	234	···
	5,000	5.50	2.94	···	3.03	···	78	···	239	···	215	···
	10,000	5.50	2.92	···	2.12*[b]	···	74	···	249	···	193	···
Tomato	0	4.72	1.48	0.51	···	0.66	63	8.0	140	26	···	47
	250	4.91	1.68	0.60	···	0.82	69	8.6	158	32	···	45
	2,500	4.82	1.57	0.51	···	0.72	62	7.2	144	27	···	49
	5,000	4.73	1.31	0.47	···	0.58	48*	7.7	127	24	···	44
	10,000	5.01	1.24*	0.43	···	0.58	48*	7.2	122	23	···	40

[a] Plastochron index.
[b] Significance comparison within a column and within a species. * = Significantly different (least-squares means test at $P \leq 0.05$) from plants treated with 0 mg L^{-1} benomyl. The experiment was conducted four times with two pots per benomyl treatment per replicate. Weight and area values are means per plant.

Table 3. Effects of benomyl root drenches on growth responses of cucumber, tomato, lettuce, sweet corn, onion, radish, and bean plants grown in commercial rooting medium

Plant	Benomyl treatment (mg a.i. L^{-1})	PA2[a]	PI2[b]	PA3[c]	PI3[d]	Height (cm)	Fr wt of leaves (g)	Leaf area (cm^2)	Dry wt of leaves (g)
Cucumber	0	270	4.48	···	8.56	···	45.8	1,218	3.79
	25	286	4.57	···	8.82	···	41.7	1,112	3.73
	250	279	4.48	···	8.35	···	45.7	1,099	3.60
	2,500	221*[e]	4.22	···	8.23	···	35.0*	757*	2.67*
Tomato	0	230	6.59	···	9.46	···	37.5	851	3.19
	25	194	6.63	···	9.42	···	35.4	796	2.85
	250	238	6.66	···	9.71	···	37.7	849	3.22
	2,500	170*	6.40	···	9.16	···	21.8*	465*	1.80*
Lettuce	0	217	7.47	···	12.3	···	38.5	841	2.07
	25	224	7.57	···	12.6	···	39.9	881	1.98
	250	190	7.38	···	11.6	···	34.2	776	1.75
	2,500	162*	6.68*	···	10.8*	···	19.7*	528*	1.11*
Sweet corn	0	141	···	···	···	47.4	5.93	122	0.407
	25	147	···	···	···	46.8	6.31	127	0.434
	250	143	···	···	···	47.1	6.31	120	0.437
	2,500	130*	···	···	···	42.1*	4.56*	98*	0.323*
Onion	0	31	···	53	···	26.9	1.19	12.3	0.059
	25	31	···	52	···	25.5	1.10	15.9	0.060
	250	30	···	46	···	25.1	1.06	11.7	0.056
	2,500	28	···	44	···	22.1*	0.97	9.4	0.050
Radish	0	123	5.71	···	···	···	4.10	113	0.307
	25	161	5.47	···	···	···	4.47	122	0.348
	250	171	5.23	···	···	···	3.53	100	0.279
	2,500	105	5.27	···	···	···	3.64	96	0.296
Bean	0	···	6.11	···	···	49.2	24.3	931	2.44
	25	···	6.01	···	···	59.2	23.6	910	2.34
	250	···	6.18	···	···	50.2	24.3	896	2.40
	2,500	···	5.74	···	···	40.2	19.5*	653*	2.12

[a] Planar area measured 6 days after rooting medium drench.
[b] Plastochron index measured 6 days after rooting medium drench.
[c] Planar area measured 12 days after rooting medium drench.
[d] Plastochron index measured 12 days after rooting medium drench.
[e] Significance comparison is within a column and within a plant. * = Significantly different (least-squares means test at $P \leq 0.05$) from plants treated with 0 mg a.i. L^{-1} benomyl. The experiment was repeated eight times for each plant with one pot per benomyl treatment per replicate. Weight and area values are means per plant.

studied also using leaf disks (7 mm in diameter) from the unifoliolate leaves of bean, the first and second leaves of radish, the first leaf of cucumber, the second and third leaves of sweet corn, the third and fourth leaves of lettuce, and the first and second leaves of tomato as well as 10-mm-long pieces of the first and second leaves of onion.

Seeds of each plant were sown in ProMix BX. Plants were grown in controlled-environment chambers under baseline growth conditions (10,18) for either 2 wk (bean, radish, sweet corn, and cucumber) or 3 wk (onion, tomato, and lettuce) before leaf disks were removed. The leaf disks were placed in petri dishes containing benomyl at 0, 25, 250, or 2,500 mg a.i. L^{-1} and observed for eight consecutive days for the onset and amount of visible chlorosis and/or necrosis. The experiment was conducted four times with 10 leaf disks of each plant per petri dish and two petri dishes per benomyl treatment per replicate for a total of 20 leaf disks of each plant per benomyl treatment per replicate. Benomyl solutions in the petri dishes were changed daily throughout the observation period.

RESULTS

Growth studies. In the studies with the commercial rooting medium, no significant differences resulted from the benomyl foliar spray treatments in the harvest parameters measured for any of the plants investigated (Table 1) except for planar area of sweet corn plants treated with 250 mg L^{-1}. There was no visible foliar injury regardless of the benomyl foliar spray treatment. No significant differences were found regardless of the benomyl foliar spray treatment for cucumber or bean plants grown in silica sand (Table 2). Fresh weight of the radish hypocotyl was significantly reduced at 10,000 mg L^{-1}. In tomato, leaf fresh weight was significantly decreased at 10,000 mg L^{-1} and leaf area was significantly decreased at 5,000 and 10,000 mg L^{-1}. There was no visible foliar injury regardless of treatment.

All plants showed some growth modifications and injury caused by the root drench treatment at 2,500 mg L^{-1}, ranging from an inward curling of the leaves to chlorotic and/or necrotic flecking. Significant growth reductions occurred for all plants except radish (Table 3). Growth parameters for radish were not significantly affected by the root treatments at 2,500 mg L^{-1}.

Table 4. Concentration of chlorophyll a + b in National Pickling cucumber cotyledons treated with benomyl using the improved bioassay for cytokinins[a]

Benomyl treatment (mg a.i. L^{-1})	Chlorophylls a + b ± SD[b]
0	14.46 ± 0.76
10	15.94 ± 7.18
25	23.02 ± 3.79
250	28.32 ± 1.23
500	26.92 ± 0.22
1,000	32.51 ± 4.69
2,500	24.83 ± 11.95
5,000	18.55 ± 6.27

[a] From Fletcher et al (9).
[b] Fresh-weight basis (mg g^{-1}). Chlorophylls a and b were determined separately and then combined for data presentation.

Cytokinin bioassay. With the increase in benomyl concentration, total chlorophyll content also increased (Table 4), peaking at 1,000 mg L^{-1} and then declining at 5,000 mg L^{-1}.

When leaf disks were observed for the onset of visible chlorosis and/or necrosis, benomyl was found ineffective in retarding senescence in terms of both the time of onset and the amount of visible symptoms at 25 or 250 mg L^{-1} compared with the control (0 mg L^{-1}). Benomyl at 2,500 mg L^{-1} actually decreased the time to onset and increased the amount of visible chlorosis and necrosis in all species.

DISCUSSION

Despite the close structural resemblance of benomyl to cytokinins (31), its possible role as a cytokininlike compound (6), and the peak of cytokininlike activity at 1,000 mg L^{-1}, benomyl did not appear to have any senescence-retardation activity or any positive effects on growth of the seven crops studied under the controlled-environment conditions of these experiments. We feel that our data provide a reasonable assessment of the possible role of benomyl in stimulating growth and development and acting as a cytokininlike compound, since growth responses were measured at least 6 days after the benomyl treatment and the senescence studies were conducted for 8 days. There should have been time for demonstration of any benomyl-mediated effects in stimulating growth or retarding senescence, especially since plants in the growth studies were foliar- or root-treated during their exponential growth phase. Furthermore, covariate measurements were made to increase precision and help ensure that any real effects would be detected statistically.

Under the conditions of these experiments, benomyl had no effect or a negative effect on growth, depending on the mode and rate of application. Some researchers have reported this pattern of growth response (2,3,27), whereas others have reported increased growth (26,29,37,38).

This research does not represent an exhaustive study of growth responses to benomyl; only one environmental regime was used, and only young vegetative plants were studied. Experiments using different environmental conditions (light level, temperature, humidity, etc.) may demonstrate that positive effects are to be found only in certain environmental regimes. Also, plants carried further along to maturity may show effects of benomyl on flowering, fruit set, and various harvest parameters, such as fruit size and number. In addition, our research focused only on growth stimulation, chlorophyll synthesis, and senescence retardation as cytokininlike responses. Experiments designed to include several environmental conditions, many different plants, and a range of growth stages may serve to resolve the apparent contradictions in the extensive literature on the effects of benomyl on plants.

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