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Effects of Red Light on the Growth of Intact Wheat and Barley Coleoptiles[1]

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ABSTRACT

The final lengths of intact dark-grown coleoptiles vary with species and cultivar. The growth distribution pattern in the apical 25-mm growing zone and the absolute amount of growth in each zone depend on the age and species of the coleoptile. A comparative study of several cultivars of wheat, *Triticum vulgare*, and barley, *Hordeum vulgare*, indicates that the growth distribution pattern in 30- to 38-mm coleoptiles varies with the species and cultivar. In barley, there are two patterns of growth distribution among the several cultivars, whereas in wheat, all cultivars exhibit a common zonal growth pattern. The total growth of coleoptiles, initially 30 to 38 mm in length, during a 24-hour dark incubation period is the same in dark-grown coleoptiles as in those irradiated with 3 minutes of red (660 nm) light prior to the incubation period. The growth distribution pattern in the growing zone of this 30- to 38-mm coleoptile is, however, altered by red light. Growth of the apical 5-mm zone is stimulated by red light and the zonal growth 5 to 10 mm below the apex is only slightly affected, whereas growth in the zones 10 to 15 to 20, and 20 to 25 mm below the apex is inhibited. This growth distribution pattern in irradiated coleoptiles changes as the coleoptile increases in length. The response of a zone following exposure to red light is dependent upon the age of the seedlings irradiated. The over-all effect of red light on growth of the intact coleoptile varies with the length of the coleoptile. In young seedling 20 to 29 mm in length, the cells of the coleoptile can compensate for the effects of red light, with the over-all growth of the dark-grown and irradiated coleoptile about the same. As the seedling grows older, the cells of the coleoptile can no longer make up for the effects of red light, and the over-all effect changes from compensation to pronounced inhibition.

Previous studies dealing with the effects of red light on cell elongation in the intact coleoptile have been carried out. Most of these studies have used either oats or corn as the test plant material. In these latter studies, the oat or corn seedling was irradiated with red light at a very young developmental stage to suppress the growth of the mesocotyl. This procedure makes the experimental results difficult to interpret since the interaction between the mesocotyl and coleoptile is complex and poorly understood. The development of the oats coleoptile was expedited when the mesocotyl was suppressed with red irradiation (2, 8). A measurement of the growth of oats coleoptile in darkness and in red light showed that growth of the irradiated and dark-grown coleoptile were nearly the same in the linear phase of growth, even though their final lengths were markedly different (19). Another study (3) showed that the final length of the coleoptile was decreased by red light, but growth rates were not measured. In an experiment reported without details or data, a brief red irradiation of oats almost totally stopped cell elongation in the coleoptile (13). Other investigations showed that red light stimulated growth of the apical coleoptile cells and repressed cell elongation in the basal region of the coleoptile. No difference in the final length of the dark-grown and irradiated coleoptiles was found (Weintraub and D. S. Williams, personal communication).

Barley and wheat are two cereals which do not have a mesocotyl. Studies involving these species as test plants would not encounter the difficulty of preirradiation of the test seedling with red light to suppress mesocotyl growth. Studies of the effects of red light on cell elongation in the wheat coleoptile indicated that, in a single coleoptile, cells could be stimulated or repressed by red light or exhibit no response to irradiation. There was a definite zonal distribution in the response to red light, with growth of the apical cells promoted, growth of cells in the middle region unaffected, and growth of the more basal region suppressed. The final lengths of irradiated and nonirradiated coleoptiles were similar (16).

Although the experiments with oat, corn, and wheat coleoptiles indicate that red light does effect growth of the coleoptile, additional experiments are needed in a comparative study to determine the effects of brief exposures to red light on the zonal growth distribution and final lengths of coleoptiles of different species and different ages.

MATERIALS AND METHODS

Culture of Seedlings. Unimbibed grains of barley and wheat were sown on water-saturated Kimpak[3] contained in shallow aluminum trays. The trays were placed in dark cabinets at 25 to 26 C. Pans of water were placed in the cabinets to maintain the humidity at 65% or greater.

Safelight. All seedlings were selected and experimental techniques carried out under a green safelight constructed of a 15-w green fluorescent tube wrapped with Dupont yellow cellophane and No. P-42 bluegreen plastic film (Gelatine Products Co., Glencove, N. J.). The emission spectrum of the safelight was 490 to 550 nm, with a peak emission of 520 to 525 nm. Seedlings were exposed to low intensities of the safe-

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[3] Kimpak is an absorbent cellulose material supplied by Kimberly-Clark Mfg. Co.

light for only the time interval necessary to perform necessary manipulations with the test plants.

Selection of Plants. Consistent results were reproduced only through a critical selection of test plants. Within a single experiment, seedlings were chosen in a range of ±5 mm of the nominal value.

Marking and Transplanting. The apical 25 mm of the coleoptile was marked into 5-mm zones using Search fingerprint ink (Sirchie Fingerprint Laboratories, Moorestown, N. J.) and a marking device consisting of copper wires stretched over a plastic frame. The 5-mm zones of the coleoptile were designated *a, b, c, d,* and *e* in descending order from the apex of the coleoptile. Marked seedlings were transplanted into a Petri dish containing 20 ml of tap water, and the roots were covered with Kimpak to keep the seedlings upright in the dish and to prevent dessication.

Irradiation. Test plants were irradiated with monochromatic red (660 nm) light for a 3-min period with an incident intensity of 0.6 $mj \cdot cm^{-2} \cdot sec^{-1}$. The light source was a tungsten filament lamp in conjunction with a water cell and a red interference filter.

Growth Measurements. All test measurements were made with a millimeter ruler under a dissecting microscope. Growth measurements were determined to the nearest 0.5 mm.

RESULTS

Growth in Darkness. The final length attained by coleoptiles is maximum when they are grown totally in the dark. The length of the coleoptile at the time when the enclosed first leaf emerges through the tip of the coleoptile varies with the species and variety of the coleoptile (Tables I and II). Of 23 barley and 14 wheat test cultivars, the final lengths ranged from 60.2 to 92 mm and 76 to 116.9 mm, respectively.

The increase in growth is almost entirely restricted to the apical 25 mm. In coleoptiles 30 to 38 mm in length, no significant growth occurred beyond the *e* zone. The distribution of growth in this growing zone varies with the species and cultivar (Tables V and VI). In the barley coleoptile, two patterns of growth distribution are apparent. In the barley cultivars Atlas 68, Casbon, Knob, and Miller, growth is maximum in the *b* zone and least in the *e* zone, with growth in the *a, c,* and *d* zones intermediate between these two extremes. In all other barley cultivars, growth in the *a* and *b* zones do not differ significantly from each other, with growth decreasing in a progressive way from the *c* to the *e* zones (Table VI). In all wheat cultivars, the growth patterns are generally similar. Growth is maximum in the *b* zone and least in the *e* zone, with growth in zones *a, c,* and *d* intermediate between that of the *b* and *e* zones. The increase in length of the *a* and *c* zones is approximately the same in all wheat cultivars except Hercules (Table V). The total increase in length of the 25-mm growing zone is greater in the wheat coleoptile than the barley coleoptile for all cultivars studied. The barley varieties show more variability in growth, and the average elongation is only one-half that of wheat.

Table I. *Final Lengths of Coleoptiles of Intact Seedlings of Several Varieties of Barley Cultured in Darkness*

Means of 20 Plants	Length
	mm
Arimar	66.0 ± 1.6
Atlas 68	81.2 ± 1.1
Barsoy	60.0 ± 1.6
Benton	65.0 ± 1.0
Bonneville 70	81.5 ± 1.4
Briggs	73.0 ± 1.1
Casbon	83.6 ± 1.2
Cass	68.0 ± 1.5
Dickson	76.0 ± 1.6
Dover	71.0 ± 2.1
Godiva	80.0 ± 1.6
Hypana	90.0 ± 2.3
Jefferson	77.0 ± 1.6
Knob	66.8 ± 1.5
Luther	73.0 ± 2.0
McNair	65.7 ± 1.6
Miller	92.0 ± 2.4
Rapidan	60.2 ± 1.7
Steveland	80.8 ± 2.1
Tokak	75.0 ± 4.1
Tschermak	75.2 ± 1.5
Vale 70	81.4 ± 2.1
Woodvale	74.9 ± 1.1

Table II. *Final Lengths of Coleoptiles of Intact Seedlings of Several Varieties of Wheat Cultured in Darkness*

Means of 20 Plants	Length
	mm
Baart	116.9 ± 1.1
Bonanza	79.8 ± 1.0
Caprock	78.4 ± 1.2
Chanute	77.3 ± 0.8
Era	76.1 ± 0.7
Fletcher	98.7 ± 1.4
Fox	100.8 ± 1.5
Hercules	108.3 ± 2.4
Kenosha	77.3 ± 1.1
Paha	76.0 ± 0.8
Springfield	93.0 ± 1.6
Waldron	88.1 ± 1.6
Yukon	77.1 ± 0.8

To determine the extent to which the increase in length of the various regions of the growing zone varies with the length of the coleoptile, zonal increments were determined in various sizes of coleoptiles of wheat cv. Baart (Table III) and of barley cv. Bonneville 70 (Table IV). The total increase in length of the growing zone in both barley and wheat seedlings is greatest in coleoptiles 30 to 39 mm in length. Coleoptiles smaller or larger than 30 to 39 mm exhibit a growth increase less than that found in the 30- to 39-mm coleoptile. The zonal growth distribution pattern is the same for seedlings with coleoptiles 20 to 79 mm in length. For all size classes, growth is greatest in the *b* zone and decreases progressively to the *e* zone. In all cases, growth of the *a* zone is less than that of the *b* zone.

Effects of Irradiation. Regional growth in wheat coleoptiles is influenced by red light. When intact wheat seedlings 30 to 38 mm in length are exposed to 660 nm red light for 3 min prior to a 24-hr dark incubation period, growth of the *a* zone is stimulated, that of the *b* zone is only slightly affected, and that of the *c, d,* and *e* zones is inhibited. The growth pattern of all irradiated wheat cultivars is similar. The increase in length of the *a* and *b* zones is about the same, with growth decreasing progressively from the *b* to the *e* zones. The coleoptile 30 to 38 mm in length can compensate for the effects of red light, and the total amount of growth in irradiated and dark-grown wheat coleoptiles of this size is about the same (Table V). The effects of red light on growth distribution in the wheat coleoptile varies with the size of the seedling. In

Table III. *Comparison of Growth Distribution in Growing Zone of Dark-grown and Red-irradiated Wheat Coleoptiles of Various Lengths*

Apical 25 mm of coleoptiles of wheat cv. Baart of indicated size classes marked into 5-mm zones. Each set consisted of 15 plants.

Initial Length	Increase in Zone Length					Total
	a	*b*	*c*	*d*	*e*	
mm	*mm*					
20–29						
D[1]	4.0 ± 0.5	7.8 ± 0.7	10.8 ± 0.7	4.7 ± 0.5	2.4 ± 0.4	29.7
R[2]	6.9 ± 0.5	9.1 ± 0.7	10.6 ± 0.7	3.2 ± 0.4	1.2 ± 0.2	31.0
R/D	1.76	1.18	0.98	0.67	0.52	1.04
30–39						
D	8.6 ± 0.4	10.9 ± 0.7	7.9 ± 0.5	5.0 ± 0.3	1.4 ± 0.3	33.8
R	11.4 ± 0.4	11.6 ± 0.6	6.4 ± 0.4	2.7 ± 0.3	0.4 ± 0.2	32.5
R/D	1.32	1.06	0.80	0.54	0.28	0.90
40–49						
D	8.8 ± 0.3	10.3 ± 0.5	8.3 ± 0.3	3.2 ± 0.2	1.4 ± 0.2	32.1
R	9.6 ± 0.3	9.0 ± 0.5	5.4 ± 0.4	1.8 ± 0.3	0.4 ± 0.2	26.2
R/D	1.10	0.87	0.66	0.54	0.27	0.82
70–79						
D	5.0 ± 0.3	6.3 ± 0.3	5.4 ± 0.3	2.1 ± 0.2	0.8 ± 0.2	19.6
R	3.0 ± 0.3	3.7 ± 0.3	2.8 ± 0.3	0.8 ± 0.2	0.2 ± 0.2	10.5
R/D	0.60	0.57	0.51	0.39	0.25	0.54

[1] Increase in length of zones measured after 24 hr. of incubation in dark.

[2] Increase in length of zones measured after a 3-min. exposure to 660 nm radiation prior to 24 hr. of incubation in dark.

Table IV. *Comparison of Growth Distribution in Growing Zone of Dark-grown and Red-irradiated Barley Coleoptiles of Various Lengths*

Apical 25 nm of Barley cv. Bonneville 70 coleoptiles of indicated size classes marked into 5-mm zones. Each set consisted of 15 plants.

Initial Length	Increase in Zone Length					Total
	a	*b*	*c*	*d*	*e*	
mm	*mm*					
20–29						
D[1]	3.7 ± 0.5	5.2 ± 0.6	3.7 ± 0.6	2.4 ± 0.5	0.8 ± 0.3	15.9
R[2]	4.9 ± 0.5	5.4 ± 0.5	3.2 ± 0.5	1.6 ± 0.4	0.4 ± 0.2	15.5
R/D	1.32	1.02	0.88	0.67	0.50	0.96
30–39						
D	3.1 ± 0.4	5.6 ± 0.5	3.9 ± 0.5	3.8 ± 0.4	2.2 ± 0.2	18.6
R	3.4 ± 0.4	5.6 ± 0.5	3.2 ± 0.4	2.4 ± 0.3	1.2 ± 0.2	15.8
R/D	1.10	0.99	0.81	0.62	0.43	0.84
40–49						
D	1.5 ± 0.3	2.5 ± 0.3	1.2 ± 0.3	0.8 ± 0.2	0.5 ± 0.2	6.6
R	1.1 ± 0.2	1.6 ± 0.2	0.7 ± 0.2	0.4 ± 0.2	0.1 ± 0.1	3.9
R/D	0.86	0.66	0.57	0.43	0.26	0.60
50–59						
D	0.8 ± 0.2	2.6 ± 0.4	1.3 ± 0.4	1.1 ± 0.3	0.7 ± 0.2	6.5
R	0.4 ± 0.2	1.1 ± 0.3	0.5 ± 0.2	0.3 ± 0.2	0.2 ± 0.2	2.5
R/D	0.53	0.41	0.39	0.31	0.24	0.38
70–79						
D	1.1 ± 0.3	0.6 ± 0.3	0.4 ± 0.2	0.0	0.0	2.1
R	0.6 ± 0.2	0.2 ± 0.1	0.1 ± 0.1	0.0	0.0	0.9
R/D	0.48	0.33	0.24			0.9

[1] Increase in length of zones measured after 24 hr of incubation in dark.

[2] Increase in length of zones measured after a 3-min exposure to 660 nm radiation prior to 24 hr of incubation in dark.

Table V. *Comparison of Growth Distribution in Dark-grown and Red-irradiated Coleoptiles of Several Varieties of Intact Wheat Seedlings*

Apical 25 mm of 30- to 38-mm coleoptiles of 3-day seedlings was marked into 5-mm zones. Each set consisted of 15 plants.

Cultivar	Increase in Zone Length					Total
	a	*b*	*c*	*d*	*e*	
	mm					
Baart						
D[1]	8.4 ± 0.6	10.6 ± 0.7	8.8 ± 0.6	5.0 ± 0.5	0.4 ± 0.4	34.4
R[2]	11.2 ± 0.8	11.4 ± 0.8	6.6 ± 0.5	2.7 ± 0.5	0.4 ± 0.2	32.3
R/D	1.33	1.07	0.74	0.54	0.26	0.93
Bonanza						
D	7.6 ± 0.6	11.1 ± 0.7	7.7 ± 0.6	5.4 ± 0.5	1.8 ± 0.3	33.6
R	10.2 ± 0.8	11.2 ± 0.8	5.4 ± 0.6	2.8 ± 0.4	0.5 ± 0.2	30.1
R/D	1.33	1.01	0.70	0.51	0.27	0.89
Caprock						
D	8.7 ± 0.6	11.6 ± 0.9	8.6 ± 0.6	5.5 ± 0.4	2.0 ± 0.3	36.5
R	12.2 ± 0.9	12.4 ± 0.9	6.0 ± 0.6	2.9 ± 0.4	0.4 ± 0.3	33.9
R/D	1.39	1.06	0.81	0.53	0.20	0.93
Chanute						
D	8.1 ± 0.7	11.2 ± 0.9	8.3 ± 0.6	5.7 ± 0.5	2.6 ± 0.4	35.9
R	11.4 ± 0.9	11.7 ± 0.9	5.9 ± 0.5	2.6 ± 0.3	0.5 ± 0.2	34.1
R/D	1.41	1.01	0.72	0.44	0.19	0.89
Era						
D	8.5 ± 0.7	11.4 ± 0.9	8.6 ± 0.6	6.2 ± 0.5	3.0 ± 0.3	37.7
R	11.4 ± 0.9	11.7 ± 0.9	6.0 ± 0.6	2.2 ± 0.3	0.5 ± 0.2	31.8
R/D	1.34	1.02	0.70	0.36	0.16	0.84
Fletcher						
D	8.0 ± 0.5	11.2 ± 0.9	8.6 ± 0.7	5.6 ± 0.5	3.1 ± 0.4	36.3
R	11.6 ± 0.9	11.4 ± 0.9	5.5 ± 0.5	2.3 ± 0.3	0.4 ± 0.2	31.2
R/D	1.45	1.01	0.64	0.41	0.14	0.85
Fox						
D	7.6 ± 0.5	11.2 ± 0.9	8.0 ± 0.7	5.0 ± 0.5	1.8 ± 0.4	33.7
R	10.8 ± 0.8	11.2 ± 0.9	5.8 ± 0.6	2.2 ± 0.4	0.5 ± 0.3	30.6
R/D	1.41	1.00	0.71	0.46	0.27	0.93
Hercules						
D	8.9 ± 0.6	11.6 ± 0.9	7.6 ± 0.5	4.4 ± 0.5	2.2 ± 0.3	34.6
R	11.7 ± 0.8	11.8 ± 0.9	5.6 ± 0.6	1.8 ± 0.3	0.4 ± 0.2	31.3
R/D	1.31	1.01	0.74	0.41	0.20	0.90
Kenosha						
D	8.6 ± 0.6	11.5 ± 0.9	7.9 ± 0.6	5.3 ± 0.6	2.2 ± 0.3	35.5
R	11.6 ± 0.7	11.7 ± 0.9	5.6 ± 0.6	2.1 ± 0.4	0.4 ± 0.2	31.4
R/D	1.35	1.01	0.70	0.39	0.17	0.88
Paha						
D	8.4 ± 0.5	10.6 ± 0.8	7.4 ± 0.7	5.2 ± 0.5	2.0 ± 0.4	33.8
R	11.2 ± 0.8	11.5 ± 0.9	6.0 ± 0.6	2.3 ± 0.4	0.5 ± 0.2	31.5
R/D	1.33	1.09	0.81	0.43	0.25	0.94
Springfield						
D	8.0 ± 0.5	11.4 ± 0.9	8.4 ± 0.7	5.2 ± 0.5	2.4 ± 0.4	33.8
R	11.0 ± 0.8	11.4 ± 0.9	6.5 ± 0.6	2.2 ± 0.5	0.5 ± 0.2	31.6
R/D	1.31	1.00	0.76	0.42	0.21	0.88
Waldron						
D	8.0 ± 0.6	11.6 ± 0.9	7.6 ± 0.6	5.0 ± 0.5	2.3 ± 0.3	35.4
R	11.3 ± 0.9	11.6 ± 0.9	5.6 ± 0.5	2.3 ± 0.3	0.6 ± 0.2	31.4
R/D	1.41	1.00	0.74	0.46	0.26	0.94
Winoka						
D	8.6 ± 0.6	11.1 ± 0.9	7.8 ± 0.6	4.8 ± 0.5	2.4 ± 0.4	34.7
R	11.2 ± 0.9	11.5 ± 0.9	5.9 ± 0.5	2.2 ± 0.4	0.6 ± 0.2	31.4
R/D	1.31	1.03	0.75	0.45	0.26	0.91
Yukon						
D	8.2 ± 0.5	11.2 ± 0.9	8.1 ± 0.7	5.6 ± 0.5	2.2 ± 0.3	35.4
R	11.2 ± 0.8	11.8 ± 0.8	5.6 ± 0.5	2.6 ± 0.4	0.7 ± 0.3	32.1
R/D	1.35	1.05	0.70	0.48	0.31	0.90

[1] Increase in length of zones measured after 24 hr of incubation in dark.

[2] Increase in length of zones measured after a 3-min exposure to 660 nm radiation prior to 24 hr of incubation in dark.

Table VI. *Comparison of Growth Distribution in Dark-grown and Red-irradiated Coleoptiles of Several Varieties of Intact Barley Seedlings*

Apical 25 mm of 30- to 38-mm coleoptiles of 3-day seedlings was marked into 5-mm zones. Each set consisted of 15 plants.

Cultivar	Increase in Zone Length					Total
	a	*b*	*c*	*d*	*e*	
	mm					
Atlas 68						
D[1]	4.7 ± 0.4	6.2 ± 0.6	5.3 ± 0.5	4.3 ± 0.4	3.5 ± 0.4	24.0
R[2]	4.8 ± 0.4	5.3 ± 0.5	3.8 ± 0.4	1.9 ± 0.3	1.1 ± 0.3	16.9
R/D	1.01	0.99	0.85	0.73	0.71	0.84
Bonneville 70						
D	4.6 ± 0.5	5.3 ± 0.5	4.6 ± 0.4	4.1 ± 0.4	3.1 ± 0.3	21.7
R	4.6 ± 0.5	5.2 ± 0.5	4.0 ± 0.5	2.8 ± 0.3	1.8 ± 0.3	18.4
R/D	1.00	0.99	0.87	0.69	0.56	0.82
Casbon						
D	4.5 ± 0.4	5.8 ± 0.5	4.6 ± 0.5	3.5 ± 0.4	2.3 ± 0.3	20.7
R	4.6 ± 0.4	5.4 ± 0.4	4.2 ± 0.4	2.7 ± 0.3	1.4 ± 0.3	18.3
R/D	1.02	0.98	0.91	0.77	0.61	0.86
Knob						
D	3.0 ± 0.3	4.6 ± 0.4	3.1 ± 0.3	1.9 ± 0.3	1.0 ± 0.3	13.5
R	3.1 ± 0.4	3.8 ± 0.4	2.3 ± 0.3	0.8 ± 0.2	0.2 ± 0.2	11.3
R/D	1.03	0.82	0.73	0.67	0.56	0.92
McNair 601						
D	3.8 ± 0.3	4.1 ± 0.4	2.8 ± 0.3	1.4 ± 0.3	0.6 ± 0.2	12.7
R	4.2 ± 0.4	3.8 ± 0.4	2.3 ± 0.3	0.8 ± 0.2	0.2 ± 0.2	11.3
R/D	1.09	0.91	0.83	0.58	0.45	0.89
Miller						
D	4.2 ± 0.5	6.5 ± 0.6	5.6 ± 0.6	4.8 ± 0.5	2.0 ± 0.4	23.1
R	4.4 ± 0.5	6.0 ± 0.6	4.0 ± 0.5	3.0 ± 0.4	1.0 ± 0.3	18.4
R/D	1.05	0.92	0.71	0.63	0.50	0.80
Rapidan						
D	3.5 ± 0.3	2.5 ± 0.3	2.2 ± 0.3	1.6 ± 0.3	0.6 ± 0.2	10.4
R	3.8 ± 0.4	2.3 ± 0.3	1.8 ± 0.2	1.1 ± 0.2	0.3 ± 0.2	9.3
R/D	1.09	0.89	0.75	0.60	0.54	0.86
Steveland						
D	4.5 ± 0.4	4.1 ± 0.4	2.7 ± 0.4	1.8 ± 0.3	1.2 ± 0.2	14.2
R	4.9 ± 0.5	3.7 ± 0.4	2.3 ± 0.3	1.1 ± 0.2	0.6 ± 0.2	12.6
R/D	1.08	0.91	0.86	0.65	0.55	0.89
Tokak						
D	5.8 ± 0.5	5.4 ± 0.5	4.4 ± 0.5	3.8 ± 0.4	2.9 ± 0.4	22.3
R	6.1 ± 0.6	5.1 ± 0.5	3.5 ± 0.4	2.4 ± 0.4	1.4 ± 0.2	18.5
R/D	1.04	0.95	0.80	0.64	0.50	0.83
Tschermak						
D	3.9 ± 0.3	3.9 ± 0.3	3.2 ± 0.4	2.2 ± 0.3	1.1 ± 0.2	14.2
R	4.2 ± 0.4	3.6 ± 0.3	2.2 ± 0.3	1.6 ± 0.3	0.6 ± 0.2	12.2
R/D	1.08	0.93	0.86	0.71	0.59	0.90
Vale 70						
D	3.9 ± 0.4	3.8 ± 0.4	3.2 ± 0.3	1.8 ± 0.3	1.4 ± 0.2	14.1
R	4.3 ± 0.4	3.6 ± 0.4	2.7 ± 0.3	1.4 ± 0.2	0.8 ± 0.6	12.8
R/D	1.11	0.94	0.83	0.78	0.56	0.91
Woodvale						
D	4.5 ± 0.4	4.3 ± 0.4	3.3 ± 0.3	2.3 ± 0.3	1.5 ± 0.2	15.9
R	4.9 ± 0.5	3.9 ± 0.4	2.9 ± 0.3	1.6 ± 0.2	0.8 ± 0.2	14.1
R/D	1.09	0.92	0.86	0.71	0.52	0.89

[1] Increase in length of zones measured after 24 hr of incubation in dark.

[2] Increase in length of zones measured after a 3-min exposure to 660 nm radiation prior to 24 hr of incubation in dark.

coleoptiles 20 to 39 mm in length, red light promotes growth of the *a* zone, has only a slight effect on the growth of the *b* zone, and inhibits growth of the more basal regions. As the coleoptile increases in length, the effect of red light on growth of the *a* zone changes from strong stimulation to inhibition, growth of the *b* zone changes from slight stimulation to inhibition, while growth of *c*, *d*, and *e* zones shows a progressively more pronounced inhibition. The over-all response to red light by the coleoptile cells changes from compensation to a gradually increasing inhibition as the coleoptile increases in length (Table III).

Coleoptiles of barley also respond to red light; however, the response of barley and wheat coleoptiles of comparable size is somewhat different (Tables III, IV, V, and VI). Although the general picture of response to irradiation is similar in barley and wheat coleoptiles, the stimulatory effect of red light on the *a* zone is less in barley as compared to wheat coleoptiles of a similar size. At the same time, the degree of inhibition of the more basal regions is greater in barley than wheat cells in coleoptiles of the same size. It may be inferred that the compensated stimulation and repression occurs at a somewhat shorter length in barley than in wheat coleoptiles, although coleoptiles shorter than 20 mm were not studied.

Although both barley and wheat coleoptiles respond to irradiation, the degree of response varies with the species, the cultivar, the length of the coleoptiles, the position of the cells in the intact coleoptile, and the cells' development status (Tables III, IV, V, and VI).

DISCUSSION

The observed differences in final lengths of wheat and barley coleoptiles subjected to the same growing conditions suggest a varietal if not species variation in growth period and/or growth rate of the two cereals. A comparison of the growth distribution in dark-grown coleoptiles of barley and wheat cultivars shows two different patterns of growth response in the *a* and *b* zones for barley but only one for wheat (Table VI). If auxin stimulates the assembly of microtubule subunits (11), then the difference of elongation rates in the *a* and *b* zones of the two types of cultivars (*e.g.* Rapidan and Miller) may depend on the following: (*a*) the number of unorganized apical microtubule subunits available for auxin stimulation; and/or (*b*) the amount of unbound auxin in the apex available to stimulate a polarized organization of microtubule subunits for basipetal elongation.

An hypothesis to explain the action of red light on growth in the coleoptile follows. Phytochrome is free in the cytoplasm and is also located in the cell membrane (14, 18). Exposure to red light results in a small conformational change in the structure of photoreversible phytochrome (17) permitting the phytochrome to combine with the receptor site of a membrane-bound enzyme such as guanyl- or adenylcyclase. This interaction causes a configurational change in the catalytic site of the enzyme. This results in an activation of the cyclase, which catalyzes the production of a secondary messenger, such as cyclic AMP or cyclic GMP (15). The end results of the action of the cyclic nucleotide depend on the nature of the cell and the prevailing conditions in the cell. What is the possible mode of action of cyclic AMP or cyclic GMP in coleoptile cells? It is known that cyclic AMP acts allosterically to increase protein kinase activity (6, 9, 10). Isolated microtubule subunits then act as phosphate receptors for cyclic AMP-induced kinase (5). Actions of cyclic GMP are established via cyclic GMP specific kinases (6). Cyclic AMP affects microtubule subunit equilibrium (4) and promotes assembly of microtubules from the tubulin protein monomers (7). Tubulin is also known to bind the guanine nucleotide (1). Cytoplasmic microtubules maintain biological anisometry in order to direct and regulate the pattern of microfibril orientation in the plant cell wall (12). The amount and type of growth of a particular coleoptile zone would then depend on the amount of phytochrome per cell, the number of unorganized microtubule subunits available for assembly, the direction of microtubule assembly characteristic for that growth region, and prevailing conditions existing in the cell at any one time. The amount of phytochrome varies along the length of the coleoptile, being maximal in the apex of the coleoptile and decreasing basipetally (14). It has been suggested that specific microtubular sites are involved in assembly of subunits in both a lateral as well as a longitudinal direction (1). Under the influence of red light, phytochrome in the tip induces a stimulation of a pronounced longitudinal assembly of microtubule subunits relative to that of the dark control. Hence the irradiated tip shows a greater increase in length. In the middle zone of the coleoptile, however, cyclic AMP or cyclic GMP stimulates both longitudinal and lateral growth. The balance in the number of subunits assembled for longitudinal and lateral growth in the irradiated zone is sufficient to maintain an amount of growth equivalent to that of the dark control. At the base of the coleoptile, however, lateral growth predominates, and the basal zone shows an increase in length less than that of the dark control (*i.e.* inhibition). As the coleoptile ages, the ratio of longitudinal to lateral growth changes from the tip to the base, the percentage of lateral growth in each zone increasing with an increase in age of the coleoptile. Red light also affects the same zone in two species of coleoptiles, wheat and barley, differently. The fact that the *a* zone, for instance, shows less stimulation by red light than does the same zone in wheat suggests that the age of barley coleoptile when longitudinal growth is maximal is earlier than that of wheat. The ultimate effect, therefore, of red light on cell growth in the coleoptile relative to the dark control ranges from stimulation to inhibition, depending on the cell's position in the coleoptile, the age of the coleoptile, and the species of the coleoptile.

It becomes quite clear that in any study which involves a response of intact coleoptile cells to red light, there must be a critical selection of seedlings according to size, so that a uniform response to red light can be measured. At the same time, any comparison made between two sets of data derived from separate studies dealing with an over-all response of the coleoptile to irradiation can only be valid if the seedlings used in the separate studies are of the same species, variety, and length. If a further comparison is made between studies on the effects of red light on growth distribution in the intact coleoptile, two additional criteria are required. The cells must be of the same developmental status and be located in the same position in the coleoptile.

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