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EFFECT OF LIGHT QUALITY ON CANNABINOID CONTENT OF CANNABIS SATIVA L. (CANNABACEAE)

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Plants of a drug strain of *Cannabis sativa* L.—grown 33 days under daylight, shaded daylight conditions, filtered green, blue, and red light, and darkness—were analyzed by gas-liquid chromatography for their cannabinoid content. The highest content of cannabinoids, predominantly Δ^9-tetrahydrocannabinol (Δ^9-THC) in this strain, occurred in the youngest leaves of daylight-grown plants. Leaves at successively lower nodes of this control condition and all treated plants subsequently grown in daylight contained progressively lower levels of cannabinoids. Leaves from plants grown under filtered green light and darkness contained significantly lower levels of Δ^9-THC than those from plants grown in daylight. However, the Δ^9-THC content of leaves from plants grown under shaded daylight and filtered red and blue light did not differ significantly from the Δ^9-THC content in daylight controls, indicating that these conditions did not alter the synthetic rate of this cannabinoid. The cannabichromene (CBC) content of plants grown under filtered red and green light and darkness differed from the CBC content in plants grown in daylight, indicating that the formation of this cannabinoid was independent of Δ^9-THC. Leaves from plants grown under filtered red and green light and darkness recovered the capacity to synthesize typical levels of Δ^9-THC and CBC when placed under daylight conditions. Plants from all light and dark treatments, when subsequently placed under daylight conditions for 66 days, attained levels of cannabinoid synthesis comparable to the daylight controls.

Introduction

Both qualitative and quantitative variability in cannabinoid composition among numerous varieties of *Cannabis* have been reported (SMALL and BECKSTEAD 1973; TURNER et al. 1975; HEMPHILL, TURNER, and MAHLBERG 1980). Aside from artifactual differences induced by sampling techniques (FAIRBAIRN and LIEBMANN 1974; TURNER, HEMPHILL, and MAHLBERG 1977, 1978), the factors controlling the cannabinoid profile in plants are only partially understood. Both genetic and environmental influences probably contribute to their cannabinoid composition. The effects of light and, in a broader relationship, of the photosynthetic apparatus on cannabinoid production are incompletely understood. CROMBIE (1977) reported that albino and green tissues on green plants contained cannabinoids. Green plants placed in the dark continued to possess cannabinoids (FAIRBAIRN and LIEBMANN 1974; HEMPHILL, TURNER, and MAHLBERG, unpublished). VALLE et al. (1978) suggested that photoperiod can influence cannabinoid content in that increased daylength increased the tetrahydrocannabinol content in plants. Cyclic or rhythmic changes in cannabinoid content in plants have been reported to occur in which Δ^9-tetrahydrocannabinol (Δ^9-THC) content varied throughout the growing season in comparison with that for other cannabinoids (PHILLIPS et al. 1970; TURNER et al. 1975), although LANYON et al. (forthcoming) could not detect any rhythmic pattern for the production of cannabinoids in an in-depth 2-yr study of three clones.

The purpose of this study was to determine the effects of light quality on cannabinoid composition of *Cannabis*. Plant populations of a Mexican drug strain were used and examined periodically during a growth period under daylight, filtered red, blue, and green light, and darkness to assess the influence of light quality on cannabinoid formation.

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Material and methods

Plants of a Mexican drug strain of *Cannabis sativa* L. (HAMMOND and MAHLBERG 1977, 1978) were grown from seed in a greenhouse in a uniform soil mixture in peat pots maintained in flats, each containing ca. 50 plants. Plants were grown under different light treatments, including daylight, two conditions of shaded daylight, green, blue, and red filtered light, and darkness (tables 1, 2). For daylight conditions, flats were maintained on a greenhouse bench; the two shaded conditions were prepared by covering a frame around the flats with multiple layers of cheesecloth, which shaded plants to selected light levels. Green, blue, and red conditions were established by placing flats under cubic chambers, 30 inches on each side, made from Rohm and Haas Plexiglas (green, no. 2092; blue, no. 2045; red, no. 2444) that possesses spectral properties applicable in wavelength studies (RAGHAVAN 1973; GALSTON and SATTER 1974). Each filter chamber was placed over a 30-inch central opening in a light-tight wooden base, 48 inches square × 6 inches high. The base, open at the bottom, was placed on the gravel bed of a greenhouse bench. Air circulation in these chambers was provided by two light-baffled 4-inch ports in the

base. A 3-inch fan was mounted in one port and was in continuous operation during the experiments. All flats were watered from the exterior and received measured volumes of water periodically. All plants and chambers were maintained in an air-conditioned greenhouse with temperatures ranging between 20 and 30 C during the experiments. Plants grown in chambers were never exposed to white light. Plants grown in the dark were maintained in similar chambers covered with black cardboard and placed in a shaded area of the greenhouse.

Light level in the greenhouse at noon during spring on a sunny day measured an average of 1.5×10^5 ergs cm^{-2} s^{-1} with the thermistor shaded from direct sunlight (YSI-Kettering Radiometer, model 65). The two shaded conditions averaged 4.0×10^4 (condition A) and 3.2×10^4 (condition B) ergs cm^{-2} s^{-1}. Light level at noon under green, blue, and red light was adjusted to a similar level, 5.5×10^4 ergs cm^{-2} s^{-1}, with one or two 200-W incandescent bulbs suspended over the chambers. These bulbs were on from 10:00 A.M. to 2:00 P.M. to supplement normal daylight.

Leaves or shoot tips from ca. 10 plants in each treatment were harvested at night under dim green light after 33, 66, and 99 days of growth. All treatments at these times were sampled the same night without exposing the plants to white light. Harvested tissues were immediately oven dried at 60 C for 12–14 h. Dried tissues for each sample in each treatment were randomly divided into three lots, except that only one sample was available for green, blue, and red treatments at the 33-day interval. All samples were extracted for analyses of cannabinoids by gas-liquid chromatography (HEMPHILL et al. 1980). Each datum value in the tables represents the mean from analyses of the three lots for each sample, except where indicated below.

The remaining plants after the 33-day treatment were removed from the chambers and maintained under ambient daylight conditions along with daylight controls. Leaf samples from specific nodes (tables 2–4) of several to 10 plants were collected again after 66 and 99 days of growth (33 and 66 days in daylight, respectively, for plants from chambers). Leaf samples were collected and analyzed as described above.

This experimental study was repeated three times during a 2-yr period. Data presented in this report represent those derived from the third study; however, data and trends for cannabinoids were similar in the several studies. The *t*-test was used to examine significance of Δ^9-THC and total cannabinoids in tables 1 and 2.

Voucher specimens of several ages of the Mexican strain of *C. sativa* are deposited in the departmental herbarium.

Results

The cannabinoid content of 33-day-old plants grown in daylight possessed a characteristic distribution of cannabinoids for leaves along the vegetative axis (HEMPHILL et al. 1980). The youngest leaves at node 1 (N-1) contained the highest concentration of Δ^9-THC (2.24 mg/100 mg dry weight [DW]), as well as lower concentrations of cannabichromene (CBC), cannabidiol (CBD), and cannabinol (CBN) (table 1). Older leaves on subjacent nodes (N-2 through N-5) contained progressively lower concentrations of Δ^9-THC and other cannabinoids.

In plants grown for 33 days under different light conditions, those grown under daylight contained an average of 0.77 mg Δ^9-THC/100 mg DW tissues (table 2). This value represented the average content for leaves from all nodes, N-1 through N-5 (table 1). The youngest leaves on the daylight control plants (N-1 and N-2) contained considerably greater quantities of Δ^9-THC (2.24 mg and 0.95 mg/100 mg DW, respectively) than leaves on lower

TABLE 1

CANNABINOID CONTENT IN VEGETATIVE LEAVES OF CANNABIS AFTER 33 DAYS OF GROWTH IN DAYLIGHT

	mg CANNABINOIDS/100 mg DW				
NODE	CBD	CBC	Δ^9-THC	CBN	Total
N-1 (top) ...	.40	.80	2.24	.41	3.85
N-2	.07	.34	.95	.04	1.40
N-3	.01	.20	.47	.01	.69
N-4	.03	.08	.16	*t*	.27
N-5 (bottom)	*t*	.09	.05	*t*	.14
Average	.10	.30	.77	.09	1.27

NOTE.—*t* = trace (1 μg or less/100 mg DW).

TABLE 2

EFFECT OF LIGHT QUALITY ON CANNABINOID CONTENT IN VEGETATIVE LEAVES OF CANNABIS AFTER 33 DAYS OF GROWTH

	mg CANNABINOIDS/100 mg DW				
TREATMENT	CBD	CBC	Δ^9-THC	CBN	Total
Daylight[a] ...	.10	.30	.77	.09	1.27
Shaded A ...	nd	.25	.41	.02	.68
Shaded B ...	nd	.24	.33	.01	.58
Green	.02	.30	.12	nd	.44
Blue.....	.11	.28	.21	.01	.61
Red	.16	.69	.57	.02	1.44
Dark[b]	nd	.21	.01	nd	.22

NOTE.—nd, not detectable.

[a] Cannabinoid value is mean from table 1.

[b] Epicotyls from plants grown in dark 20 days.

nodes. The average value of Δ^9-THC for daylight controls was compared with the total Δ^9-THC content for other experimental conditions because it was not possible to distinguish among leaf nodes on plants under all treatments at the end of 33 days.

Partial shading of plants grown in daylight (shaded A, 0.41 mg Δ^9-THC; shaded B, 0.33 mg Δ^9-THC) resulted in a trend toward a decreased cannabinoid content (table 2). Young leaves (N-1) of daylight plants had a significantly greater quantity of cannabinoids (as Δ^9-THC) than shaded plants, but when the average (0.77 mg Δ^9-THC) was compared with Δ^9-THC content in shaded plants, there was no significant difference for this cannabinoid between these sets of plants.

The cannabinoid concentrations in plants grown 33 days under filtered light and in the dark showed a trend toward a lower concentration of Δ^9-THC compared with the daylight controls. The Δ^9-THC content in the top node of the daylight control was significantly greater than the content in leaves from all filter treatments as well as for plants grown in darkness. However, the average Δ^9-THC content in the daylight controls did not differ significantly from levels present in plants grown under red and blue filtered light.

The level of CBC, another prominent cannabinoid in this strain, remained comparable to daylight controls under most treatments, including those plants grown in the dark. Under red filtered light, the plants contained over twice the level (0.69 mg) of CBC present in the daylight controls (0.30 mg). Under daylight and shaded daylight conditions, the Δ^9-THC content always exceeded the CBC content. However, the ratio of CBC to Δ^9-THC became reversed under all filtered light and dark conditions. A relatively high level of CBC, but very low level of Δ^9-THC, occurred in plants grown in the dark (table 2).

Leaf tissue of plants from all treatments, after being placed in daylight for 33 days, was collected and analyzed for cannabinoid composition to determine whether treated plants could recover from imposed light-stress conditions (table 3). Sufficient

TABLE 3

EFFECT OF LIGHT QUALITY ON CANNABINOID CONTENT IN VEGETATIVE LEAVES OF CANNABIS AFTER 66 DAYS OF GROWTH

TREATMENT AND SAMPLE NO.[a]	mg CANNABINOIDS/100 mg DW				
	CBD	CBC	Δ^9-THC	CBN	Total
Daylight ⟶ daylight:					
Sample 1	.17	.57	2.20	.13	3.07
Sample 2	.15	.42	1.42	.05	2.04
Sample 3	nd	.31	.79	.02	1.12
Shaded A ⟶ daylight:					
Sample 1	.33	.72	2.42	.74	4.21
Sample 2	.17	.59	1.41	.03	2.20
Sample 3	.06	.15	.35	.01	.57
Shaded B ⟶ daylight:					
Sample 1	.29	.32	1.08	.07	1.76
Sample 2	.13	.15	.53	.02	.83
Sample 3	.09	.12	.31	.01	.53
Green ⟶ daylight:					
Sample 1	.06	.31	1.08	.09	1.54
Sample 2	.22	.45	1.28	.10	2.05
Sample 3	.07	.10	.32	.01	.50
Blue ⟶ daylight:					
Sample 1	nd	.93	3.22	.17	4.32
Sample 2	nd	.57	1.81	.08	2.46
Sample 3	nd	.26	.82	.02	1.10
Red ⟶ daylight:					
Sample 1	.67	1.41	3.88	.38	6.34
Sample 2	.34	.83	2.15	.11	3.43
Sample 3	.09	.36	.96	.03	1.44
Dark ⟶ daylight:[b]					
Sample 1	nd	.65	2.27	.11	3.03
Sample 2	nd	.34	.98	.02	1.34
Sample 3	nd	.19	.29	nd	.48

NOTE.—nd, not detectable.

[a] Sample 1 contains leaves from N-1–2 at shoot tip; sample 2 contains leaves from subjacent three nodes; and sample 3 contains mature leaves from lower nodes from all treatments.

[b] Plants grown in darkness for 20 days before light treatment.

leaf material had developed on all plants during the 33 days of growth in daylight to make it possible to analyze leaves from three nodal positions: young leaves from nodes near apex (table 3, sample 1), leaves from subjacent middle nodes (sample 2), and leaves from lower nodes (sample 3).

Total cannabinoid and Δ^9-THC content in young leaves (sample 1) contained increased levels for these compounds in all treatments (cf. tables 2, 3). Plants derived from red and blue light treatments showed a trend toward higher total levels of cannabinoids than daylight-grown plants, while those from green light and shaded B conditions contained lower cannabinoid levels than other treatments (table 3, sample 1). Samples 2 and 3 contained progressively lower cannabinoid and Δ^9-THC levels under all treatments, a trend consistent for plants grown under daylight conditions (table 3, samples 2 and 3). CBD and CBN synthesis are typically low in this strain. However, for plants grown under blue filters and in darkness, no CBD was detectable, while plants grown under red filters synthesized appreciably greater quantities of both CBD and CBN than other treatments (table 3, sample 1).

Sample 3 for plants originally under filters and in the dark represented leaves that had formed during the first 33 days of treatment and subsequently enlarged when exposed to daylight for the second 33-day growth period. Some Δ^9-THC synthesis occurred in these leaves upon exposure to light during this second growth period since the CBC to Δ^9-THC ratio, greater than 1.0 in filter- and dark-treated plants (table 2), was restored to the more typical less than 1.0 ratio (table 3, sample 3).

Plants were maintained for 66 days in daylight (99 days of total growth) and again analyzed for cannabinoid contents to determine whether plants after an extended growth period in daylight developed a pattern of cannabinoid synthesis comparable to daylight-grown plants. Sufficient new growth had occurred on plants during their 99-day growth period to provide leaf materials from different nodal positions for analysis (table 4).

TABLE 4

EFFECT OF LIGHT QUALITY ON CANNABINOID CONTENT IN VEGETATIVE LEAVES OF CANNABIS AFTER 99 DAYS OF GROWTH

TREATMENT AND NODAL POSITION	mg CANNABINOIDS/100 mg DW				
	CBD	CBC	Δ^9-THC	CBN	Total
Daylight → daylight:					
Nodes 1–3[a]	.15	.98	3.48	.38	4.99
Nodes 7–9	nd	.38	1.30	.02	1.70
Nodes 17–19	nd	.09	.37	.01	.47
Shaded A → daylight:					
Nodes 1–3	1.49	.81	2.79	.40	5.49
Nodes 7–9	.94	.28	.88	.03	2.13
Nodes 17–19	.19	.07	.33	.01	.60
Shaded B → daylight:					
Nodes 1–3	.34	.70	2.76	.44	4.24
Nodes 7–9	.33	.39	1.33	.16	2.21
Nodes 17–19	.17	.13	.46	.01	.77
Green → daylight:					
Nodes 1–3	nd	.68	2.95	.25	3.88
Nodes 7–9	nd	.33	1.24	.05	1.62
Nodes 17–19	nd	.04	.18	*t*	.22
Blue → daylight:					
Nodes 1–3	nd	.46	2.26	.14	2.86
Nodes 7–9	nd	.34	1.37	.04	1.75
Nodes 17–19	nd	.10	.42	.01	.53
Red → daylight:					
Nodes 1–3	.28	.59	2.92	.28	4.07
Nodes 7–9	.21	.19	.94	.02	1.36
Nodes 17–19	.05	.13	.51	.01	.70
Dark → daylight:[b]					
Nodes 1–4	nd	.32	2.27	.04	2.63
Nodes 7–10	nd	.12	.71	*t*	.83
Nodes 12–13	nd	.09	.36	nd	.45

NOTE.—nd, not detectable; *t* = trace.

[a] Includes leaves from axillary branches on mature plants.

[b] Plants grown in darkness for 20 days before placing in light treatment.

Leaves from nodal regions at three different levels along the axis, including those from N-1–3, N-7–9, and N-17–19 (table 4), were sampled for cannabinoid composition. Plants transferred to daylight from the dark remained somewhat smaller than other plants, and leaf samples were derived from nodal positions indicated in table 4. The total cannabinoid and Δ^9-THC contents in young leaves (N-1–3) in most treatments were similar (no significant differences) and were also similar to these values for plants in table 3. Plants transferred to daylight from blue filter treatment and darkness contained somewhat lower cannabinoid levels than those from other treatments.

The cannabinoid contents for daylight-grown plants (3.48 mg Δ^9-THC and 4.99 mg total, table 4) are comparable, within the range of sample variation, to the contents of N-1, N-2, and N-3 of young plants grown in daylight (3.66 mg Δ^9-THC and 5.94 mg total, table 1).

CBD, in blue filtered light and dark treatments, remained undetectable in plants subsequently grown for 66 and 99 days in daylight (tables 3, 4). The CBD concentration decreased in plants previously grown under green filters as well as in daylight after a total growth period of 99 days (table 4). Factors contributing to this altered CBD content remain unknown.

Discussion

Results from this study show that light quality and quantity affect cannabinoid synthesis in the growing plant. The effects were evident on the concentration of the principal cannabinoid component (Δ^9-THC) of this strain, although other cannabinoids, particularly CBC, also were influenced by light. Cannabinoid content decreased progressively and rapidly with aging of leaves for plants grown 33 days under experimental conditions. The Δ^9-THC content of the youngest leaves in the daylight controls was significantly greater than for young leaves of treated plants. However, when the average Δ^9-THC content of the control was compared to treated plants, no significant differences were evident among most treatments. Only under green filtered light was cannabinoid synthesis significantly reduced (0.05 level) over controls. Decreased light level may reduce the pool of precursor substrates available for cannabinoid synthesis. The factors influencing the progressive decrease in cannabinoid content in successively older leaves for all treatments, as shown here and reported in other studies (HEMPHILL et al. 1980; TURNER, HEMPHILL, and MAHLBERG 1980), require further study.

Presence of cannabinoids in plants grown in darkness indicated that their synthesis can occur in the absence of light since mature nongerminated seeds of this strain lack detectable cannabinoids (HEMPHILL et al. 1980). Substrates for cannabinoid synthesis in leaves apparently were derived from seed storage materials. CBC was the most prominent component in dark-grown plants, whereas Δ^9-THC was the only other detected cannabinoid. Synthesis of Δ^9-THC in darkness, although very low, indicates that light is not essential for formation of this cannabinoid.

Synthesis of cannabinoids occurred under each light condition in this study. Accumulation of a high level of CBC, in particular, resulted in an altered ratio between this cannabinoid and Δ^9-THC in plants under green, blue, and red filtered light as well as darkness. The synthesis of each of these cannabinoids is independent of that of any other, which supports the interpretation that they represent products of an alternate pathway derived from cannabigerol (CBG) (MECHOULAM 1973; SHOYAMA et al. 1975). The pathway leading to CBC is little affected by the presence or absence of light, although the enhancement noted for filtered red light requires further study. The significant reduction of Δ^9-THC under filtered green light and in the dark indicates an active, but imprecisely known, role for light in Δ^9-THC synthesis.

New leaves that developed on all plants after 33 and 66 days under daylight conditions, following their transfer from filtered light treatment, synthesized cannabinoids in a pattern typical for leaves grown in daylight. Only plants grown previously under the blue filter and in darkness did not appear to attain levels of Δ^9-THC synthesis recorded for other treatments. In general, the leaves at different nodal levels showed the typical decreasing trend for each cannabinoid and their total content from young to maturing leaves.

Young leaves, originally formed under filtered light and darkness and then exposed to daylight, retained the metabolic mechanism to synthesize typical levels of cannabinoids even during the protracted period of stress treatment. Leaves initiated under filtered light conditions and darkness and subsequently exposed to daylight increased their Δ^9-THC content and altered the ratio of Δ^9-THC to CBC so as to reflect the typical levels of cannabinoids present in leaves developed under daylight conditions.

Light quality influenced the ratio of CBC to Δ^9-THC accumulation in leaves. The high ratio of CBC to Δ^9-THC under filtered light conditions and the very high ratio for dark-grown plants indicated that the CBC pathway functioned under light-stressed conditions. CBC production was maintained at comparable or greater levels than those in daylight and shaded conditions. Importantly, these same leaves, when exposed to white light, were capable of Δ^9-THC synthesis, resulting in the reversal of the CBC:Δ^9-THC ratio. Synthesis and accumulation of Δ^9-THC, therefore, can occur independently of these processes for CBC. VALLE et

al. (1978) also reported a change in the ratio for these cannabinoids in plants grown under different daylength conditions. The change in ratio between 33 and 66 days of daylight may be a reflection, in part, of increased daylength under greenhouse conditions during our study. However, the basis for the differential between plants formerly grown in the dark (1:7) and those grown in daylight (1:3.5) after 66 days in daylight may relate to a more direct effect of the presence or absence of light.

Thus, the mechanism for cannabinoid synthesis can be partially inactivated in light-stressed leaves but can be reactivated when such leaves are placed in daylight, resulting in the production of a cannabinoid profile characteristic of the plant strain. The protoplasmic site of cannabinoid synthesis, as yet unknown, is under study at this time.

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