



# Temperature response of photosynthesis in different drug and fiber varieties of *Cannabis sativa* L.

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**Abstract** The temperature response on gas and water vapour exchange characteristics of three medicinal drug type (HP Mexican, MX and W1) and four industrial fiber type (Felinq 34, Kompolty, Zolo 11 and Zolo 15) varieties of *Cannabis sativa*, originally from different agro-climatic zones worldwide, were studied. Among the drug type varieties, optimum temperature for photosynthesis ( $T_{opt}$ ) was observed in the range of 30–35 °C in high potency Mexican HPM whereas, it was in the range of 25–30 °C in W1. A comparatively lower value (25 °C) for  $T_{opt}$  was observed in MX. Among fiber type varieties,  $T_{opt}$  was around 30 °C in Zolo 11 and Zolo 15 whereas, it was near 25 °C in Felinq 34 and Kompolty. Varieties having higher maximum photosynthesis ( $P_{N\ max}$ ) had higher chlorophyll content as compared to those having lower  $P_{N\ max}$ . Differences in water use efficiency (WUE) were also observed within and among the drug and fiber type plants. However, differences became less pronounced at higher temperatures. Both stomatal and mesophyll components

seem to be responsible for the temperature dependence of photosynthesis ( $P_N$ ) in this species, however, their magnitude varied with the variety. In general, a two fold increase in dark respiration with increase in temperature (from 20 °C to 40 °C) was observed in all the varieties. However, a greater increase was associated with the variety having higher rate of photosynthesis, indicating a strong association between photosynthetic and respiratory rates. The results provide a valuable indication regarding variations in temperature dependence of  $P_N$  in different varieties of *Cannabis sativa* L.

**Keywords** *Cannabis sativa* · Photosynthesis · Transpiration · Stomatal conductance · Internal CO<sub>2</sub> concentration · Water use efficiency · Temperature response

## Abbreviations

$P_N$	Net Photosynthesis
$P_{N\ max}$	Highest Rate of Photosynthesis
$R_D$	Dark Respiration
$T_R$	Transpiration
$C_i$	Internal CO <sub>2</sub> Concentration
$g_s$	Stomatal Conductance for CO <sub>2</sub>
$C_i/g_s$	Ratio of Internal CO <sub>2</sub> Concentration to Stomatal Conductance

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## Introduction

*Cannabis sativa* L. (marijuana) is an annual herb which is the natural source of cannabinoids, a unique class of terpeno-phenolic compounds which accumulate mainly in the glandular trichomes of the plant (Flemming et al. 2007). Besides its psychoactivity, the major biologically active

compound,  $\Delta^9$ -tetrahydrocannabinol ( $\Delta^9$ -THC) commonly referred as THC possesses analgesic, anti-inflammatory, appetite stimulant and anti-emetic properties making this cannabinoid a very promising drug for therapeutic purposes, especially for cancer and AIDS patients (Sirikantaramas et al. 2007). Synthetic  $\Delta^9$ -THC (dronabinol) is currently available in the US market in the form of soft gelatin capsules for oral intake known as Marinol<sup>®</sup>, for the control of nausea and vomiting in cancer patients receiving chemotherapy (approved by United States food and drug administration-FDA, in 1985) and as an appetite stimulant for AIDS patients (approved by FDA, USA in 1992). However, due to its high demand and the complexity of the synthetic process, extraction of natural THC from *Cannabis* plant can be a viable inexpensive alternative for production of bulk active drug. Finding a quality starting material for natural THC however, has always been a key issue and efforts have been directed toward screening and mass propagation of this species using conventional and biotechnological tools (Chandra et al. 2009, 2010; Lata et al. 2009a,b, 2010a,b). The demand of any plant based biologically active compound can be met by increasing its cultivation area or, a better option would be to screen for high yielding clones and to grow them under the most suitable climatic conditions.

Among various factors, temperature is one of the major environmental factor influencing the growth, survival, productivity, and natural geographic distribution of plants. It is reported that temperature above 30 °C has an adverse effect on photosynthesis and growth of a high THC yielding Mexican variety (MX) of *Cannabis sativa* (Chandra et al. 2008). Considering the climatic variations during various seasons in different parts of the Himalayas, Joshi and Palni (1998) have reported significant variations in temperature response in photosynthesis of tea clones. Therefore, improvement in the yield would depend on the proper selection of clone/variety which is better suited to the prevailing climatic conditions.

Photosynthesis plays a prominent role in the logistics of plant growth (Chandra 2003a, b, 2004). There is a close correlation between plant yield and their photosynthetic rate since more than 90 % of dry matter of live plants is derived from photosynthetic CO<sub>2</sub> assimilation (Zelitch 1975; Joshi et al. 2007). However, photosynthesis, being one of the first physiological processes to be greatly affected by temperature (Berry and Bjorkman 1980) is widely used as a tool for indicating temperature stress (Larcher 1994) and for the rapid selection of plants most suitable for different habitats (Joshi and Maikhuri 1996).

Furthermore, with predicted increase in global air temperature induced by greenhouse effect, photosynthetic response of plant species to variations in temperature has become a major area of concern (Rustad et al. 2001; Hikosaka et al. 2006). In general, temperature dependence

of photosynthesis is reviewed by several authors in different plant species (Sage and Sharkey 1987; Borjigidai et al. 2006; Hikosaka et al. 2006; Nagai and Makino 2009). However, such information is lacking for the medicinal drug (high  $\Delta^9$ -THC yielding) and industrial fiber (very low or no  $\Delta^9$ -THC yielding) type *Cannabis* varieties and therefore, the present investigation was undertaken to determine the variation in temperature response of photosynthesis, if any, in different varieties of *Cannabis sativa* L.

## Material and methods

### Plant material

Plants of three drug type – (1) HPM (from Mexico), (2) MX and (3) W1 (from Switzerland) and, four fiber type varieties – (1) Felinq 34 and (2) Kompoly (from Switzerland), (3) Zolo 11 and (4) Zolo 15 (from Ukraine) of *C. sativa* were grown from seeds (30 seeds of each variety) in the indoor growing facility at the University of Mississippi. Since female plants of this species contain higher concentration of THC, male plants were removed after onset of flowering and only female plants were kept for the experiment. Five female plants from each variety were selected and five cuttings were made from each plant for the photosynthetic study. Throughout the study, all the plants were kept under controlled environmental conditions (25±3 °C temperature and 55±5 % RH). Indoor light (18 h light, ~ 700±24  $\mu\text{mol m}^{-2}\text{s}^{-1}$  at plant canopy level, measured by LI-COR quantum meter, model LI-189, Lincoln, Nebraska, USA) was provided with seven full spectrum 1,000 watts HID (high intensity discharge) lamps in combination with seven 1,000 watt high pressure sodium bulbs (Sun Systems, CA), hung over the plants covering 350 square foot area. A hot air suction fan was attached to each light. The HID bulbs were kept at least three to four feet from the plants to avoid overheating. All the plants were grown in the equal size plastic pots (30 cm diameter×28 cm height) containing 1:1:1 ratio of top soil, sand and manure, and were watered equally and regularly to maintain identical growth condition. Out of 25 cuttings of each variety, 3 healthy and well established female randomly selected clones were used for the photosynthetic measurements and comparison.

### Photosynthetic measurements

To study the temperature response of photosynthesis in the different varieties of *C. sativa*, leaves of each variety were exposed to 20 °C, 25 °C, 30 °C, 35 °C and 40 °C under controlled photon flux density (PPFD, 1,500  $\mu\text{mol m}^{-2}\text{s}^{-1}$ ,

this light intensity is reported near optimum, Chandra et al. 2008), humidity ( $55 \pm 5$  %) and  $\text{CO}_2$  ( $350 \pm 5 \mu\text{mol mol}^{-1}$ ) concentrations. All the measurements were carried out on three upper intact, undamaged, fully expanded and healthy leaves of each plant with the help of a portable photosynthesis system (Model LI-6400; LI-COR, Lincoln, Nebraska, USA). Light was provided using an artificial light source (Model LI-6400-02; light emitting silicon diode; LI-COR), fixed on the top of the leaf chamber (cuvette size, 3 cm L  $\times$  2 cm W) and recorded using a quantum sensor kept in the range of 660–675 nm, mounted at the leaf level. The rate of dark respiration was measured by maintaining the leaf cuvette at zero irradiance. To avoid any radiation from outside the leaf chamber was covered with a black cloth during the measurements. Temperature of the cuvette was regulated by the integrated Peltier coolers, which is controlled by the microprocessor. Controlled  $\text{CO}_2$  concentration was supplied to the cuvette of the climatic unit (LI-6400-01, LI-COR Inc., USA) by mixing pure  $\text{CO}_2$  with  $\text{CO}_2$  free air and were measured by infrared gas analyzer. All the measurements for gas and water vapour exchange were first recorded at the lowest temperature condition and then subsequently at increasing levels of these parameters. Air flow rate ( $500 \mu\text{mol s}^{-1}$ ) and relative humidity ( $55 \pm 5$  %) were kept nearly constant throughout the experiment. Since steady state photosynthesis is reached within 30–45 min (Joshi and Palni 1998; Bag et al. 2000; Joshi 2006; Miyazawa et al. 2006 and Chandra et al. 2008), the leaves were kept for about 45–60 min under each set of temperature conditions before the observations were recorded. Four gas exchange parameters viz., photosynthetic rate ( $P_N$ ), transpirational water loss (E), stomatal conductance ( $g_s$ ) and intercellular  $\text{CO}_2$  concentration (Ci) were measured simultaneously at steady state condition under controlled light and temperature conditions. Water use efficiency (WUE) was calculated as the ratio of the rate of photosynthesis and transpiration.

#### Pigments content

Leaves used for the photosynthetic gas exchange measurements were harvested afterwards for the determination of pigments content (chlorophyll a, b and carotenoids) following the method described by Hiscox and Israelstam (1979). Three samples (50 mg leaf tissue each sample) were collected from each plant. These samples were individually extracted in 10 ml of dimethyl sulfoxide solvent incubated at 55–60 °C for 4–5 h or till tissue became colorless. The absorbance of the extracts was measured with a UV/visible spectrophotometer (Model Cary-50, Varian Inc., Palo Alto, California, USA) at 664, 648 and 470 nm, and the concentrations of Chl a, Chl b and carotenoids were calculated, respectively (Chappelle et al. 1992).

#### Statistical analysis

Results on the gas and water vapour exchange parameters ( $P_N$ ,  $R_D$ ,  $g_s$ , Ci, Ci/ $g_s$  and WUE) as dependent variables on temperature (20, 25, 30, 35, 40 °C) of different *Cannabis* varieties were analyzed using LSD (SYSTAT-11, Systat Software Inc. San Jose, CA, USA).

#### Results and discussion

The temperature dependence of  $P_N$ ,  $R_D$ , E,  $g_s$ , Ci/ $g_s$  ratio and WUE and, pigment content in drug and fiber type varieties of *Cannabis sativa* collected from different agroclimatic zones is shown in Table 1. *Cannabis* varieties, whether drug and fiber, differ significantly ( $p \leq 0.05$ ) not only in regards to the optimum temperature, but also with respect to temperature range of optimum photosynthesis. Among the varieties, the highest rate of photosynthesis,  $P_{N \text{ max}}$  was measured in the drug type Mexican variety HPM in the range of 30 to 35 °C, followed by the fiber type Zolo 11 and Zolo 15, Ukrainian varieties at 30 °C. Hence, HPM appears to be more suitable for planting in the areas experiencing higher temperature conditions. On the other hand, the Swiss varieties Felinq 34, Kompolty and MX have shown  $P_{N \text{ max}}$  at 25 °C. Another Swiss variety W1 has however, formed a plateau for  $P_{N \text{ max}}$  at the temperatures ranging from 25 °C to 30 °C. Due to heat stress, about 16 %, 23 %, 16 %, 16 %, 27 %, 19 % and 38 % reduction in the rate of  $P_N$  was noted in HPM, Felinq 34, Kompolty, MX, W1, Zolo11 and Zolo15 respectively at 40 °C as compared to their respective  $T_{\text{opt}}$  values. The varieties having greater maximum photosynthesis ( $P_{N \text{ max}}$ ) had higher Chlorophyll content as compared to those having lower  $P_{N \text{ max}}$ . Similarly, the *Cannabis* varieties also differed in their leaf carotenoids content. Drug type varieties exhibited comparatively higher carotenoids content as compared to those of fiber types. The total carotenoids content was found highest ( $0.40 \text{ mg g}^{-1}$ ) in HPM, a drug type Mexican variety and lowest ( $0.13 \text{ mg g}^{-1}$ ) in Kompolty, a fiber type variety from Switzerland. Higher carotenoids content is reported to enable several plant species in maintaining their greater efficiency of carbon assimilation under the adverse environmental conditions through protecting the photosynthetic apparatus against photodamage (Bartley and Scolnik 1995; Streb et al. 1998; Ort 2001). Given the fact that these plants were grown under controlled environmental conditions the differences in pigments content and photosynthetic response may be due to their basic genetic makeup. In studying the photosynthesis of four populations of *Cannabis sativa*, Bazzaz et al. (1975), have suggested that those populations can be grouped into different ecotypes, generally adapted to

**Table 1** Pigments content ( $\text{mg g}^{-1}$  fresh weight) and, temperature response of photosynthesis ( $P_N$ ), dark respiration ( $R_D$ ), transpiration (E), stomatal conductance ( $g_s$ ), mesophyll efficiency ( $C_i/g_s$  ratio) and water use efficiency (WUE) in different drug and fiber type varieties of *Cannabis sativa* L.

		<i>Cannabis</i> varieties							LSD $P < 0.05$
T ( $^{\circ}\text{C}$ )	Drug type			Fiber type					
	HP Mexican	MX	W1	Felinq 34	Kompoly	Zolo 11	Zolo 15		
Pigments content									
Chl a		2.44±0.22	1.82±0.42	1.44±0.20	1.23±0.19	1.49±0.15	1.22±0.23	1.63±0.13	0.72
Chl b		0.71±0.07	0.53±0.05	0.49±0.06	0.48±0.05	0.52±0.03	0.49±0.06	0.51±0.07	0.48
Chl a/b ratio		3.28±0.92	3.32±0.89	2.78±0.63	2.61±0.52	2.81±0.32	2.44±0.44	3.14±0.31	0.12
Total Chl		3.16±0.63	2.38±0.62	1.90±0.54	1.76±0.32	2.08±0.45	1.70±0.38	2.18±0.37	1.54
Carotenoid (Car)		0.40±0.06	0.36±0.03	0.22±0.02	0.17±0.03	0.13±0.04	0.28±0.05	0.19±0.02	0.17
Total Chl/Car		6.66±0.97	6.42±0.48	8.48±0.62	9.78±0.62	15.27±1.03	5.78±0.62	10.78±1.24	4.32
$P_N$	20	15.24±2.42	14.30±2.34	13.76±2.51	14.89±1.32	15.54±2.11	12.38±3.21	17.45±2.13	1.65
	25	19.32±1.98	21.62±2.44	22.22±2.32	22.76±1.48	20.23±1.23	23.46±1.24	21.76±2.42	0.76
	30	26.34±2.73	20.16±3.12	22.32±1.24	21.23±2.12	19.31±1.62	24.83±2.22	23.93±2.41	1.11
	35	26.42±1.27	18.30±2.38	18.92±1.42	19.82±2.23	17.45±1.41	22.35±2.31	18.78±1.88	2.04
	40	22.12±2.18	18.22±2.14	16.32±1.44	17.54±2.11	16.94±1.22	20.12±2.16	14.76±1.67	1.58
LSD, $P < 0.05$		3.76	3.29	4.12	2.15	3.12	4.78	3.44	
$R_D$	20	1.81±0.24	1.37±0.16	1.12±0.42	1.32±0.19	1.45±0.29	1.00±0.22	1.21±0.32	0.32
	25	2.42±0.14	2.65±0.32	2.14±0.32	2.56±0.32	2.76±0.33	1.98±0.43	2.12±0.37	0.14
	30	2.80±0.22	2.78±0.41	2.76±0.33	2.58±0.44	2.77±0.25	2.62±0.33	2.48±0.32	0.18
	35	2.79±0.37	2.72±0.44	2.77±0.39	2.94±0.39	2.97±0.38	2.61±0.21	2.41±0.44	0.20
	40	2.72±0.19	2.71±0.31	2.75±0.28	2.99±0.27	2.78±0.26	2.58±0.37	2.39±0.29	0.41
LSD, $P < 0.05$		0.25	0.13	0.41	0.21	0.19	0.22	0.15	
$g_s$	20	35.01±2.34	63.81±6.38	41.26±3.45	61.75±5.23	53.15±3.78	33.86±4.29	34.56±5.23	4.92
	25	43.97±3.76	86.15±7.22	53.15±5.82	84.94±6.92	57.78±4.92	40.69±4.01	39.81±4.92	7.16
	30	64.93±4.22	56.49±7.17	53.08±4.42	56.60±6.66	50.91±5.57	53.69±4.99	49.30±4.12	8.12
	35	69.92±5.89	51.24±3.93	50.19±6.37	47.79±6.38	42.33±4.44	51.18±3.92	47.72±3.97	6.54
	40	59.00±8.23	42.53±4.75	35.45±3.15	40.37±4.23	40.89±4.12	48.31±5.01	43.59±4.11	4.98
LSD, $P < 0.05$		5.65	4.28	5.55	5.76	4.11	4.98	5.17	
$T_R$	20	2.65±0.22	3.73±0.32	3.27±0.30	3.24±0.42	2.85±0.22	4.14±0.38	3.98±0.40	0.80
	25	2.74±0.31	4.12±0.38	3.76±0.40	4.65±0.51	3.20±0.31	4.96±0.42	4.75±0.33	1.54
	30	3.71±0.33	4.35±0.41	4.12±0.43	5.12±0.49	3.98±0.29	5.62±0.49	4.80±0.34	1.32
	35	4.15±0.41	4.76±0.28	4.37±0.37	5.38±0.38	4.64±0.37	5.67±0.46	4.89±0.41	0.98
	40	4.25±0.39	4.85±0.42	4.54±0.44	5.88±0.47	4.65±0.39	5.78±0.52	4.98±0.38	0.87
LSD, $P < 0.05$		1.08	0.75	0.66	0.78	0.68	0.72	0.65	
$C_i$	20	300±22.42	298±19.23	288±20.21	268±18.76	278±12.99	258±15.29	262±18.37	18.12
	25	270±22.23	280±18.77	278±21.82	265±18.69	276±21.23	249±18.12	258±20.55	12.47
	30	261±25.76	270±19.29	276±22.13	240±19.78	253±14.76	240±13.87	245±19.23	14.78
	35	258±19.98	268±22.13	265±21.22	238±15.12	240±15.23	239±13.23	239±21.76	9.88
	40	249±21.37	245±21.28	240±22.32	220±14.23	238±19.22	228±20.12	228±22.19	12.94
LSD, $P < 0.05$		1.24	0.56	1.02	0.74	0.69	0.77	0.59	

**Table 1** (continued)

		<i>Cannabis</i> varieties							
T (°C)		Drug type			Fiber type				
		HP Mexican	MX	W1	Felinq 34	Kompoly	Zolo 11	Zolo 15	LSD <i>P</i> <0.05
<i>C<sub>i</sub>/g<sub>s</sub></i>	20	8.57±0.44	4.67±0.66	6.98±0.32	4.34±0.38	5.23±0.41	7.62±0.34	7.58±0.24	1.52
	25	6.14±0.34	3.25±0.42	5.23±0.38	3.12±0.34	4.78±0.32	6.12±0.37	6.48±0.32	2.11
	30	4.02±0.43	4.78±0.32	5.20±0.42	4.24±0.45	4.97±0.38	4.47±0.34	4.97±0.37	1.30
	35	3.69±0.41	5.23±0.27	5.28±0.27	4.98±0.43	5.67±0.42	4.65±0.29	5.01±0.34	1.22
	40	4.22±0.22	5.76±0.43	6.77±0.35	5.45±0.37	5.82±0.33	4.72±0.41	5.23±0.39	1.74
	LSD, <i>P</i> <0.05	2.01	1.15	1.04	0.96	0.55	0.47	0.63	
WUE	20	5.56±0.46	3.83±0.29	4.20±0.36	4.59±0.46	5.45±0.43	2.99±0.22	4.38±0.27	0.76
	25	7.05±0.65	5.24±0.48	5.91±0.45	4.88±0.29	6.32±0.52	4.72±0.34	4.58±0.44	0.54
	30	7.10±0.59	4.74±0.37	5.41±0.48	4.14±0.28	4.84±0.49	4.41±0.39	4.98±0.32	1.34
	35	5.75±0.43	3.84±0.29	4.34±0.39	3.68±0.41	4.31±0.40	3.94±0.33	3.84±0.36	1.22
	40	4.19±0.44	3.75±0.40	3.59±0.42	2.98±0.30	3.90±0.46	3.48±0.28	2.96±0.21	0.74
	LSD, <i>P</i> <0.05	1.24	0.56	1.02	0.74	0.69	0.77	0.59	

their respective environments. Differences among varieties were also noted with regard to dark respiration (*D<sub>R</sub>*) which invariably, though inconsistent, increased with temperature up to 35 °C. The magnitude of increase, however, was higher in the range of lower (20–25 °C) temperatures as compared to upper temperatures (30–40 °C) in all varieties. Except Kompoly, a saturation in *D<sub>R</sub>* was observed in these varieties at temperatures ranging from 35 °C to 40 °C. A slight decrease of about 6.40 % was measured in Kompoly in this temperature range.

In all the varieties, *T<sub>R</sub>* was enhanced with increasing temperature up to the highest level. Among the varieties, the lowest rate of *T<sub>R</sub>* was observed in the drug type Mexican variety, HPM at all the temperatures and the highest *T<sub>R</sub>* was noted in the fiber type Ukrainian variety, Zolo11 at 20 °C, 25 °C, 30 °C and 35 °C. Whereas at 40 °C, *T<sub>R</sub>* was slightly higher (1.70 %) in Zolo11 as compared to the Swiss variety, Felinq 34. The stomatal conductance (*g<sub>s</sub>*) was increased with temperature to a maximum value and then declined at higher temperature in all the varieties. It is interesting to note that the maximum values of *g<sub>s</sub>* corresponded fairly well with *P<sub>N</sub>* (*max*) in all varieties. However, the variations in *g<sub>s</sub>* in response to changes in the *T<sub>R</sub>* were variety dependant. Corresponding to their *P<sub>N</sub>* (*max*), MX and Felinq 34 showed the highest (86.15 and 84.94 mmol m<sup>-2</sup>s<sup>-1</sup> respectively); while Kompoly, Zolo11, W1 and Zolo15 exhibited the lowest values of *g<sub>s</sub>* (57.78, 53.69, 53.15 and 49.3 mmol m<sup>-2</sup>s<sup>-1</sup> respectively). A comparatively intermediate value for *g<sub>s</sub>* was observed in HPM (69.92 mmol m<sup>-2</sup>s<sup>-1</sup>) at *P<sub>N</sub>* (*max*).

Intercellular CO<sub>2</sub> concentration (*C<sub>i</sub>*) in leaf tissue is considered to be a set point to determine how plants are responding to the fluctuating environment (Ehleringer and Cerling 1995). This provides a mean to assess the relative importance of stomatal and mesophyll processes in controlling *P<sub>N</sub>* (Renburg and Kruger 1993). In the present study, all the *Cannabis* varieties showed a pattern of decreasing *C<sub>i</sub>* with increasing temperature (Table 1). At the lowest temperature, the highest value of *C<sub>i</sub>* was observed in HPM followed by MX, W1, Kompoly, Felinq 34, Zolo 15 and Zolo 11. Intercellular CO<sub>2</sub> concentration was decreased by 17 to 18 % in HPM, Felinq 34, MX and W1, whereas it decreased by 12 to 14 % in Kompoly, Zolo 15 and Zolo 11 as temperature increased from 20 °C to 40 °C. The *C<sub>i</sub>/g<sub>s</sub>* ratio, which reflects the mesophyll efficiency of the plants (Sheshshayee et al. 1996) was calculated for each variety at different temperatures (Table 1). The *C<sub>i</sub>/g<sub>s</sub>* ratio was considerably higher at the lower temperature in HPM, Zolo 11 and Zolo 15 whereas, variety MX and Felinq 34 and Kompoly exhibited high values of this ratio at higher temperature. However, there was a comparatively stable *C<sub>i</sub>/g<sub>s</sub>* ratio in W1 with variation in temperature (Table 1). The trend of *g<sub>s</sub>* and *C<sub>i</sub>* in *Cannabis sativa* at different temperatures indicates that the mechanism of control of photosynthesis by temperature differs with the varieties. Both stomatal and mesophyll factors seem to be responsible for the differences in temperature dependence of photosynthesis, however, their magnitude varied with varieties.

The water use efficiency (WUE) in different *Cannabis* varieties and temperatures was calculated as a ratio of the net photosynthesis to transpiration. Similar to *P<sub>N</sub>*, WUE in these

varieties increased with temperature up to a certain level followed by a decrease at higher temperatures. Differences in water use efficiency (WUE) were observed within and among the drug and fiber type plants. The magnitude of differences however, varied with varieties and became less pronounced at higher temperatures. Among the drug type varieties, HP Max had the highest WUE in the temperature range of 25–30 °C, whereas Zolo 15 had the highest value among the fiber varieties at 30 °C. In all other varieties, the highest WUE was observed at 25 °C. Interestingly, HP max has maintained the highest  $P_N$  and lowest  $T_R$  and therefore, high WUE at higher temperature conditions. According to Jones (1992) and Zang et al. (1996), plants with high rate of  $P_N$  and WUE exhibit better potential to grow faster and yield more as compared to the species/varieties with low  $P_N$  and WUE under fluctuating environmental conditions. Therefore, cultivation of a variety of a species with higher WUE would be beneficial for better productivity in dry tropical and sub tropical areas where occurrence of long dry spells/partial drought during the summer is quite common. With the higher WUE and lower  $T_R$  as compared to other *Cannabis* varieties HP max, thus may be suitable for growing in dry and exposed cultivated areas for better yield. In general, the decrease in WUE at higher temperatures in *Cannabis* varieties appears to be due to the increase in transpirational water loss and the decrease in the  $P_N$ .

In conclusion, there was a considerable variation in temperature response of photosynthetic characteristics in different drug and fiber types of *Cannabis* varieties. However, variations were more variety-specific as compared to types (drug and fiber). Since these plants were grown under controlled and identical environmental conditions, variations in photosynthetic response represent the differences in their genetic make up and reflect their inherited tendency for preferred growth temperature.

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