FLOWERING AND VEGETATIVE GROWTH IN OPIUM POPPY AS AFFECTED BY PHOTOPERIOD AND TEMPERATURE TREATMENTS

Acock, M. C.
USDA-ARS Remote Sensing and Modeling Laboratory

Wang, Z.
USDA-ARS Remote Sensing and Modeling Laboratory

Acock, B.
USDA-ARS Remote Sensing and Modeling Laboratory

出版情報：BIOTRONICS. 25, pp.11-21, 1996-12. Biotron Institute, Kyushu University
バージョン：
権利関係：

BIOTRONICS **25**, 11–21, 1996

FLOWERING AND VEGETATIVE GROWTH IN OPIUM POPPY AS AFFECTED BY PHOTOPERIOD AND TEMPERATURE TREATMENTS

M. C. Acock, Z. Wang and B. Acock

USDA-ARS, Remote Sensing and Modeling Laboratory, BARC-West, Beltsville, MD 20705, USA

(Received June 19, 1995; accepted November 21, 1995)

Acock M. C., Wang Z. and Acock B. *Flowering and vegetative growth in opium poppy as affected by photoperiod and temperature treatments.* BIOTRONICS 25, 11–21, 1996. Estimating yields of illicit opium poppy requires knowledge of how climate and geography affect the crop. This experiment provided part of the database needed to predict flowering time and shoot biomass of poppy (*Papaver somniferum* L., 'album DC') for any geographical location. Plants were grown in chambers under a 12, 13, 14, or 24-h photoperiod and a 12-h thermoperiod of 25/20℃. Plants at 10 or 20 days after emergence (DAE) were transferred to separate chambers and treated for 48 h with either (a) 10℃ and a 12-h photoperiod or (b) continuous light and a 12-h thermoperiod of 25/20℃. The 48-h interruption of each photoperiod treatment with continuous light decreased days to flower (DTF) for photoperiods $<$ 24 h for both seedling ages, the effect being more pronounced at 10 DAE and for the 12-h photoperiod. The 48-h 10℃ interruption had no effect on DTF. The poppy flower was an increasingly larger proportion of the shoot biomass (from 6 to 15%) as photoperiod increased from 12 to 24 h. DTF, plant height and shoot dry weight showed the same pattern of response to photoperiod, having minimum values in the 24-h photoperiod treatment and increasing in values with photoperiods $\leq$ 14 h. Critical photoperiod, P_c, was calculated as 14.8 h, by plotting DTF against photoperiod as two straight lines and determining their point of intersection. A similar approach using the reciprocal of DTF gave a P_c of 16 h. Shoot dry weights from all treatments were found to be an exponential function of DTF. Results indicate that plant biomass at flowering can be estimated simply by knowing how photoperiod and temperature affect DTF. This result presupposes that the number of photosynthetically active days between plant emergence and flowering is the primary determinant of biomass. If environmental conditions irretrievably limit photosynthetic activity during this period, biomass would be overestimated.

Key words: *Papaver somniferum*, vernalization, long day plant.

INTRODUCTION

The environmental variables that most influence flowering times in plants are temperature and photoperiod. Temperature often controls flowering time because of its effect on a multitude of metabolic processes. The optimum

temperature range for crop growth and development in most cultivated crops covers about 5℃ and usually starts somewhere between 20 and 30℃ (*1*). Temperature can also affect crop development through a process called vernalization. Vernalization promotes flowering and occurs when susceptible plants experience a prolonged period of cold temperatures. The winter strain of *Secale cereale* (Petkus rye), for example, will flower faster if seeds are cold-treated (*12*) and *Hyosyamus niger* (henbane) will flower faster in long photoperiods if 10 day old rosette plants experience cold temperatures (*4*). Optimum temperatures for vernalization are species-dependent but generally range between 2 and 12℃(*3, 5*). The length of time required for maximum response to vernalization depends on the 'conditioning' temperature but can vary between seven days (*8*) and several months (*9*). Typically, lower vernalizing temperatures must be given for longer periods, but they hasten flowering more than slightly higher vernalizing temperatures do (*8*). Vernalization can be reversed by high temperatures (*13*) and can be influenced in a variety of ways by light (*11*). Poppy is a cool-season crop and commonly experiences temperatures near 0℃ during its life cycle. Therefore, vernalization could be an important factor in the phenological development of the plant, if it is susceptible.

Photoperiod is the other environmental variable that plays a major role in flower development for many plants. Flowering in opium poppy occurs most rapidly in long photoperiods. Its critical photoperiod, P_c, (i.e., the photoperiod below which flowering time is delayed) has not been determined precisely but is somewhere between 14 and 16 h according to Gentner et. al. (*6*). Gentner et al. also observed that flowers were initiated in plants >50 days old by two or more long photoperiods or by a single period of light longer than 24 h, but that plants in photoperiods ≤ 12 h did not initiate flowers.

The purpose of this work was to increase our understanding of how the opium poppy responds to photoperiod and temperature so that we can predict the effects of geographical location and temperatures during the growing season on days to flower (DTF) and plant size at flowering. The main objectives were to derive a relationship between flowering time and photoperiod, to determine whether flowering in opium poppy might be hastened by cold temperatures typically experienced by the plants, and to determine whether plants were susceptible to photoperiod and/or vernalization when they were as young as 10 days old.

MATERIALS AND METHODS

Seed of *Papaver somniferum* (var. album DC, bi-colored flower petals of red and white) which had been stored at 4-5℃ were sown in 3.75 liter black plastic pots filled with a growing medium consisting of 1 part Sphagnum peat moss and 1 part medium grade vermiculite (by volume). A starter solution with a proprietary formula of N, P, K and the following micronutrients: Bo, Mg, Cu, Zn, Mo, Fe, and Ca was sprayed onto the medium. Dolomitic lime was added to

adjust the pH of the medium to 6.0.

Six reach-in controlled environment chambers (Environmental Growth Chambers, Inc., Chagrin Falls, OH, USA) were used. Four chambers were set at a photoperiod of either 12, 13, 14 or 24 h. Light intensity was maintained at 1000 ± 200 μmol m^{-2} s^{-1} at the top of the plant canopy. Temperatures were controlled at 25±2℃ during the first 12 h of light, and 20±2℃ for the next 12 h in all four chambers. Thirty plants were placed in each chamber and watered as needed in the early stages of growth. Soluble fertilizer (20.0N-8.74P-16.6K) was applied when needed to each pot in 250 ml of irrigation water at a concentration of 100 mg L^{-1} of N beginning at the three leaf stage.

Plants were thinned to one per pot at 28 days after emergence (DAE) and harvested on the day of first flower. At that time, plant height was measured from the soil line to the top of the immature seed capsule. Each plant was divided into stem, leaves, and flower and each part was oven-dried at 75℃.

Ten plants from each of the four chambers were removed at either 10 or 20 DAE. Five from each chamber were placed in another chamber with continuous light and 12 h of 25℃ followed by 12 h of 20℃. The other five were placed in a chamber with a 12-h photoperiod and a temperature maintained at 10℃. After 48 h, these plants were returned to their original chambers. At least five plants (controls) remained in the original chambers until the day of flowering.

RESULTS AND DISCUSSION

Photoperiod Effect on Days to Flower

Three values are important to characterize the photoperiodic effect on flowering time: (a) the minimum DTF, (b) the critical photoperiod, P_c, and (c) the rate of change in DTF with photoperiods$<P_c$. By plotting DTF as a function of photoperiod, we can fit two equations of straight lines:

$$y=y_{min}\text{; for } P \geq P_c$$

$$y=y_{min}+\alpha\ (P_c-P)\text{; for } P<P_c$$

where y_{min} is the minimum DTF, P is photoperiod, and α is the slope of the photoperiod effect for $P<P_c$. The value of y_{min} was determined from the 24-h photoperiod treatment as 29.4 days, α was found to be 9.31 days h^{-1}. These two straight lines intersect at P_c which has a value of 14.8 h (Fig. 1).

Another technique used (*7, 14*) for characterizing the photoperiodic effect and determining P_c is to fit the same two equations but using the reciprocal of DTF (1/DTF). The results are expressed in terms of rates of progress toward flowering. The two equations are:

$$y=R_{max}\text{; for } P \geq P_c$$

$$y=R_{max}-\alpha(P-P_c)\text{; for } P<P_c$$

where R_{max} is the maximum daily progress toward flowering. The values generated by this approach are: $R_{max}=0.03404$ day^{-1}, $\alpha=0.00378$ $day^{-1}h^{-1}$, and

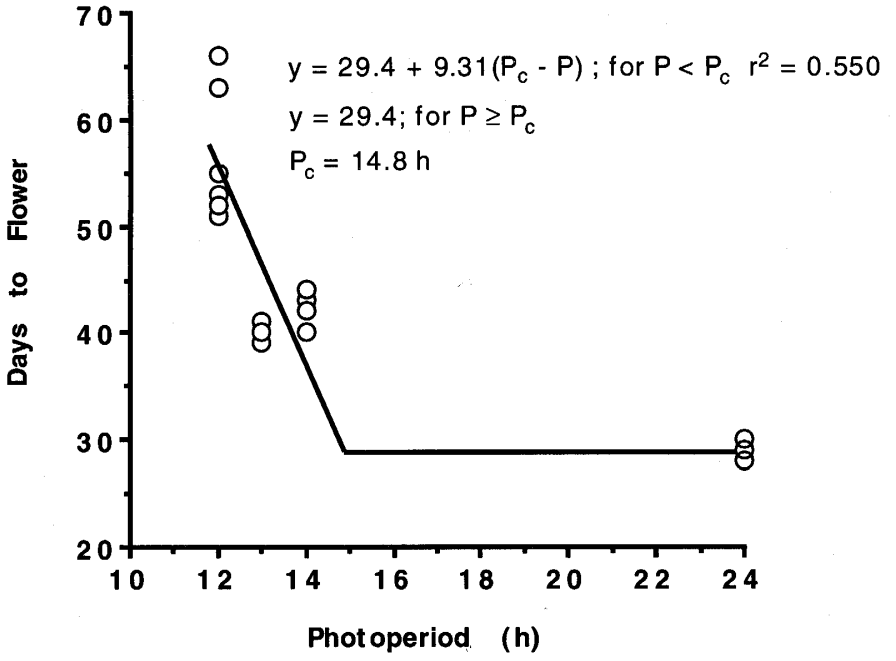

Fig. 1. Effect of photoperiod (h) on days from emergence to first open flower for plants grown in controlled environment chambers with a 12-h thermoperiod of 25℃/20℃.

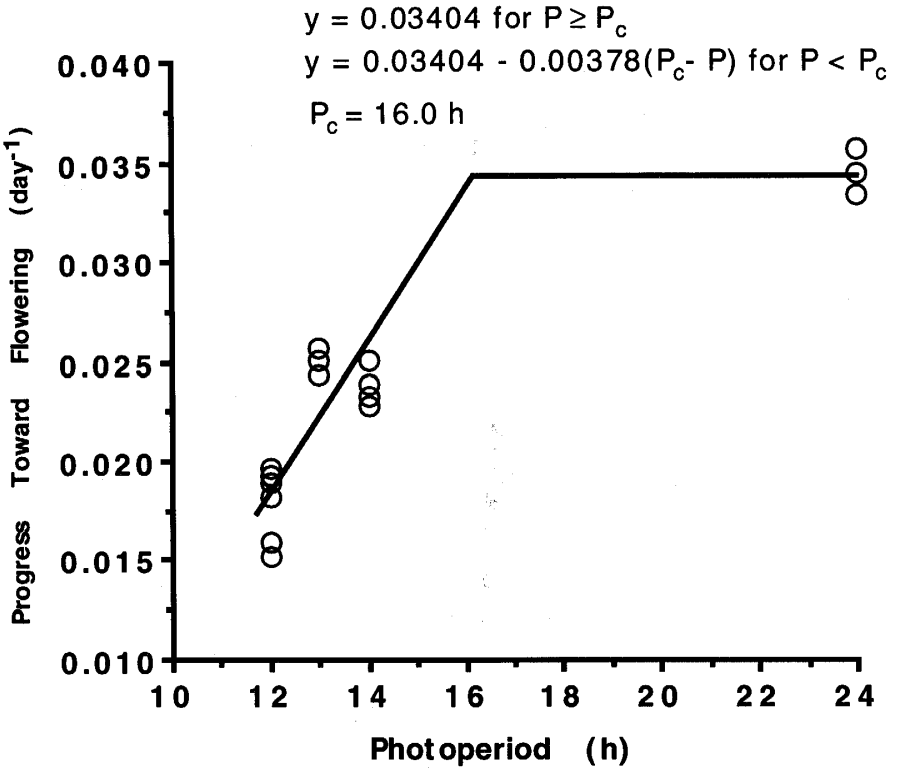

Fig. 2. Effect of photoperiod (h) on the reciprocal of days to flower for plants grown in controlled environment chambers with a 12-h thermoperiod of 25℃/20℃.

Table 1. Means of days to flower, and various plant attributes at flowering: plant height, shoot dry weight, and flower: shoot dry weight ratio, as a function of photoperiod and one 48 h interruption of either 10℃ and a 12-h photoperiod or continuous light and a 12-h thermoperiod of 25/20℃ given to plants when they were 10 or 20 days old. Mean separation within rows by LSD at $p<0.05$

Photoperiod (h)	*Control*	*48 h of light*		*10℃ and 12-h photoperiod for 48 h*	
		10 days	20 days	10 days	20 days
	Days to flower				
12	57.9 a	46.8 b	52.4 a	60.8 a	59.2 a
13	39.8 b	37.0 c	39.6 b	40.8 ab	52.0 a
14	42.2 ab	39.2 c	40.6 bc	43.6 a	43.0 ab
24	29.4 b	30.4 ab	30.2 ab	30.8 ab	31.8 a
	Plant height (cm)				
12	73 a	52 b	67 ab	78 a	77 a
13	41 c	40 c	43 bc	48 ab	52 a
14	47 ab	42 b	42 b	49 a	49 a
24	27 a	30 a	31 a	30 a	29 a
	Shoot dry weight (g plant^{-1})				
12	7.94 ab	4.76 b	6.67 ab	9.43 a	8.26 ab
13	4.05 b	3.33 b	4.43 ab	5.57 a	5.57 a
14	3.04 ab	2.85 ab	2.69 b	3.74 a	3.72 a
24	1.05 a	1.30 a	1.23 a	1.46 a	1.74 a
	Flower: shoot dry weight ratio				
12	.06 a	.09 a	.06 a	.07 a	.06 a
13	.06 b	.09 a	.06 b	.06 b	.07 b
14	.10 a	.12 a	.10 a	.09 a	.10 a
24	.15 a	.05 a	.15 a	.13 a	.14 a

P_c=16.0 h (Fig. 2). Both results are in accord with the findings of Gentner *et al.* (*6*) who reported a P_c between 14 and 16 h for the opium poppy they investigated.

The interruption of the prevailing photoperiod with 48 h of continuous light significantly reduced DTF for all photoperiods other than 24 h, but only if it was given at 10 DAE (Table 1). Results demonstrate that, not only are plants sensitive to photoperiod as early as 10 days, but early treatment is more effective at reducing DTF. Because the 48 h of continuous light was more effective at 10 DAE than at 20 DAE, it may not be possible to describe the influence of photoperiod on flowering accurately without specifying the stage of development of the plant.

Temperature Effect on Day to Flower

Plants given a 48 h period of 10℃ and a 12-h photoperiod took longer to flower compared with control plants but the effect was not significant (Table 1). Only the plants grown in 13 and 24-h photoperiods and then placed in 48 h of

10℃ and a 12-h photoperiod at 20 DAE had significantly longer flowering times than controls and it is impossible to determine whether the delay in flowering was the result of low temperature or the shorter photoperiod, both of which were found to delay flowering. However, it is clear that two days at 10℃ coupled with a 12-h photoperiod during the first 20 days of growth does not hasten flowering for plants grown in and returned to photoperiods from 12 to 24-h. Our results are consistent with those of Mika (*10*) who found that time to flower increased linearly with a decrease in daily mean temperature over the range of 9-28℃ (*10*).

There was no evidence from our results that opium poppy is susceptible to vernalization. However, our data are insufficient to draw any firm conclusion because a 48 h period of 10℃ may not be long enough or low enough to trigger any response. Also older plants may respond to the low temperature differently from younger ones. More research is needed to clarify the quantity and quality of cold temperature treatments needed to have short term and long term effects on plant development and/or growth.

Photoperiod Effect on Plant Height, Shoot Dry Weight and Dry Matter Partitioning

Plant height and shoot dry weight followed the same pattern of response to photoperiod as DTF (Figs. 3 and 4). Plant height and shoot dry weight changed little between 14-h and 24-h photoperiod treatments but increased for photoperiod treatments < 14 h. Using the same technique of two linear fits to

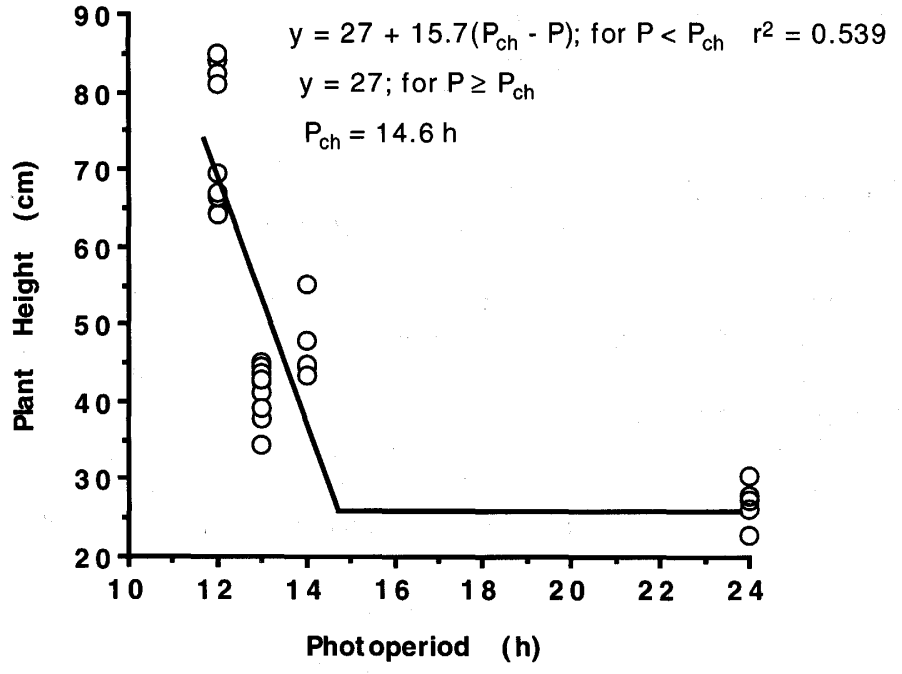

Fig. 3. Effect of photoperiod (h) on plant height at time of flowering for plants grown in controlled environment chambers with a 12-h thermoperiod of 25℃/20℃.

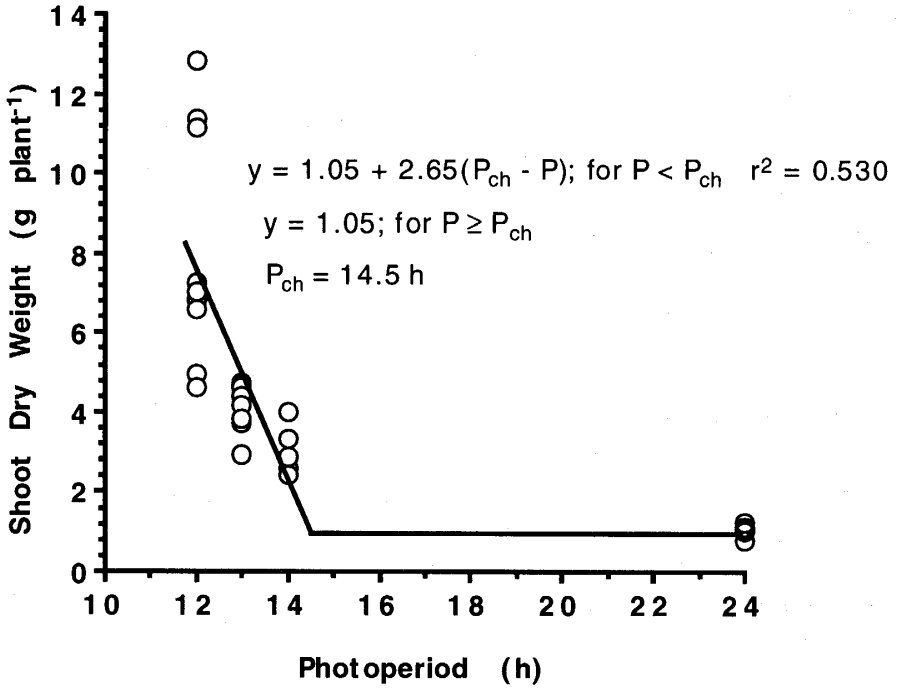

Fig. 4. Effect of photoperiod (h) on shoot dry weight at time of flowering for plants grown in controlled environment chambers with a 12-h thermoperiod of 25℃/20℃.

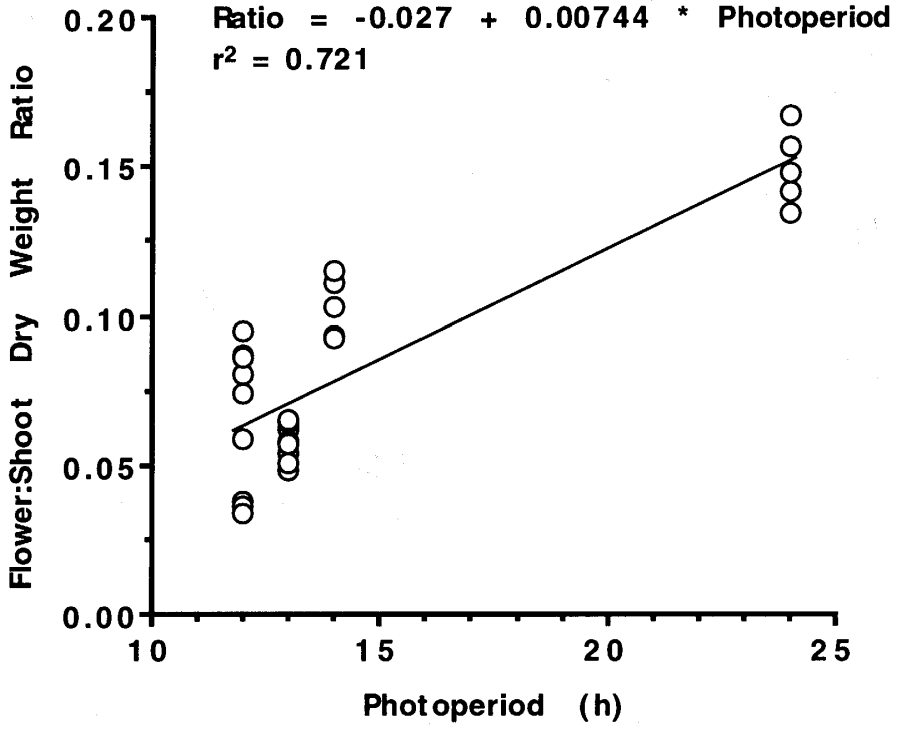

Fig. 5. Effect of photoperiod (h) on flower : shoot dry weight ratio at time of flowering for plants grown in controlled environment chambers with a 12-h thermoperiod of 25℃/20℃.

the data, the intersection of the two lines occurred at 14.6 and 14.5 h for plant height and shoot dry weight respectively. We refer to the value of the x-coordinate at the intersection of these lines as P_{ch}.

Exposure of 10 or 20 day old plants grown in photoperiods of 13 h or 14 h, to 48 h of continuous light had no effect on plant height or shoot dry weight (Table 1). Such exposure did significantly reduce the height of plants grown in a 12-h photoperiod if they were treated with continuous light at 10 DAE (Table 1).

The proportion of the shoot that developed into flower was a positive linear function of increasingly long photoperiods (Fig. 5). The special treatment of 48 h of continuous light significantly increased the flower: shoot ratio for 10 day old plants that were grown in and returned to a 13-h photoperiod (Table 1). Ten day old plants from 12 and 14 h photoperiods also showed increased partitioning to the flower when given 48 h of continuous light but the differences were not statistically significant.

Temperature Effect on Plant Height, Shoot Weight and Dry Matter Partitioning

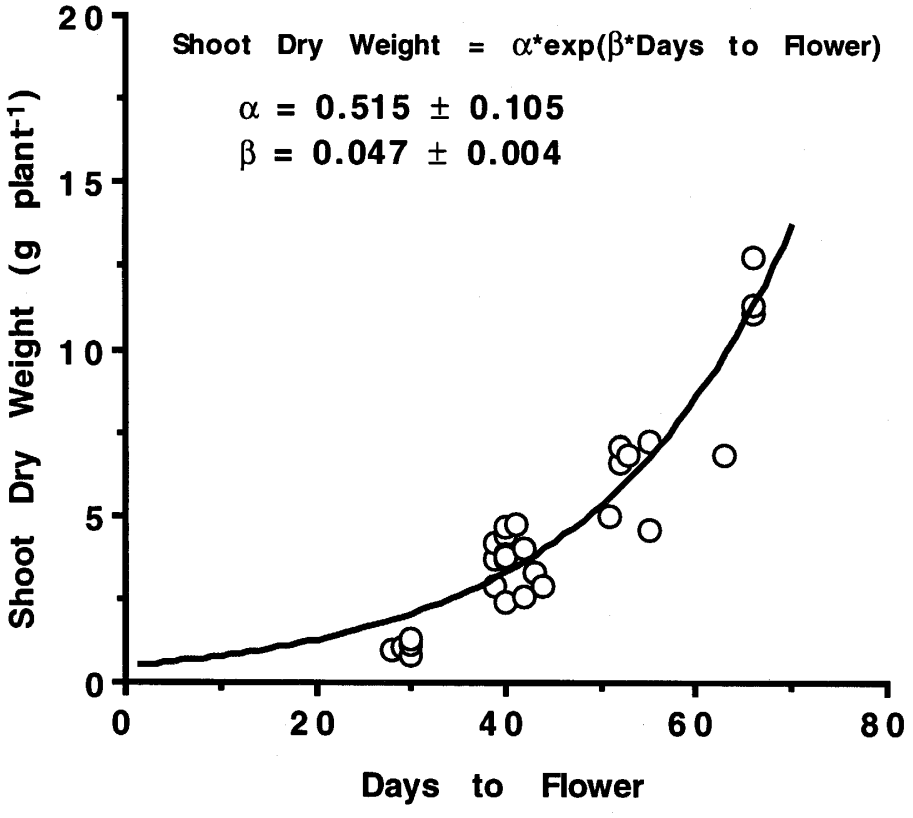

Fig. 6. Effect of days from emergence to flowering on shoot dry weight at time of flowering for plants grown in controlled environment chambers with fixed photoperiods of 12, 13, 14 or 24 h and with a 12-h thermoperiod of 25℃/20℃ in all chambers.

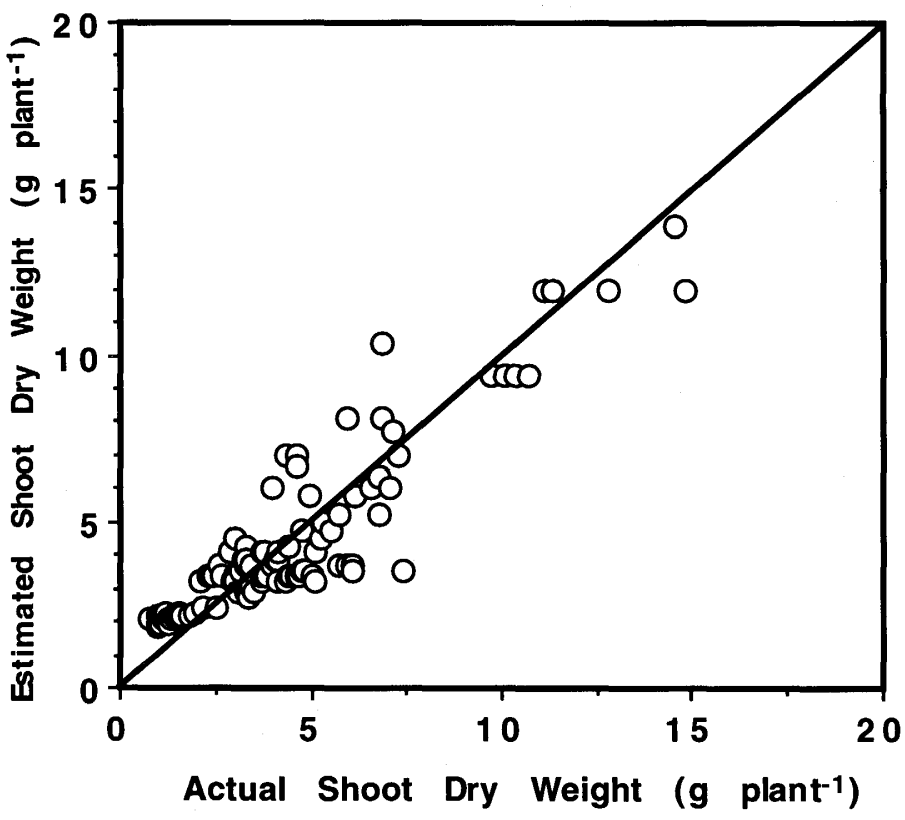

Fig. 7. Actual shoot dry weight compared with estimated shoot dry weight using the equation: shoot dry weight=0.515×exp (0.047×days to flower) (n=110).

The special treatment of 48 h at 10℃ and 12-h photoperiod had no notable effect on plant height or shoot dry weight (Table 1) nor did it affect the flower: shoot ratio when compared with the 12-h photoperiod control plants. This is the only comparison where temperature effects are independent of photoperiod. Differences arising in other photoperiod treatments could be attributed to the shorter 12-h photoperiod rather than the 48 h at 10℃, because these effects were confounded.

Flowering Time and Shoot Dry Weight at Flowering

We found we could estimate shoot dry weight from DTF using an exponential function with two parameters (Fig. 6). Parameter values were fitted from data on control plants (plants that remained in a fixed photo-and thermo -period until flowering) and then tested against all plants in the experiment (Fig. 7). This equation should not be used outside the bounds of growing conditions as defined by the experiment because there are many other factors that could affect this relationship. For example, Bernath and Tetenyi (1979) found that low light intensities reduced growth and delayed development of poppies (*2*). However, we would suggest that temperature and photoperiod are

strong determinants of plant biomass under field conditions because they determine the number of growing days and that other factors are minor by comparison.

CONCLUSIONS

We cannot say unequivocally that opium poppy is not susceptible to vernalization, only that there was no evidence from plants treated during the seedling stage with 10℃ for 48 h in a photoperiod of 12 h. The cold period of 48 h may have been too short or the return of the plants to normal temperatures of 25/20℃ may have nullified the effect of the cold treatment.

Photoperiod, on the other hand, had a dominant influence on DTF and this influence was observable after one 48 h period of continuous light. The minimum flowering time was 29.4 DAE. The value of the critical photoperiod, P_c, ranged from 14.8 h to 16.0 h, depending on whether days to flower or its transformation (1/days to flower) was used to calculate it. Abrupt changes in plant height and shoot dry weight were inferred at 14.6 h for plant height and 14.5 h for shoot dry weight by using two intersecting straight lines to interpret the data.

Sensitivity to photoperiod was observed on seedlings as early as 10 days old.

Shoot dry weight at flowering can be estimated from DTF when the daily growth rate is not irretrievably limited by environmental conditions. DTF is largely a function of photoperiod.

REFERENCES

1. Acock B. and Acock M. C. (1993) Modeling approaches for predicting crop ecosystem responses to climate change. Pages 299–306 *in* D. R. Buxton, R. Shibles, R. A. Forsberg, B. L. Blad, K. H. Asay, G. M. Paulsen, and R. F. Wilson (eds) *International Crop Science I.* Crop Science Society of America, Madison, Wisconsin, USA.
2. Bernath J. and Tetenyi P. (1979) The effect of environmental factors on growth, development and alkaloid production of poppy (*Papaver somniferum* L.). I. Responses to day-length and light intensity. *Biochem. Physiol. Pflanzen.* **174,** 468–478.
3. Brewster J. L. (1987) Vernalization in the onion—a quantitative approach. Pages 171–183 *in* J. G. Atherton (ed) *Manipulation of flowering.* Butterworths, London.
4. Chouard P. (1960) Vernalization and its relations to dormancy. *Ann. Rev. Plant Physiol* **11,** 191.
5. Dennis, Jr. F. G. (1987) Two methods of studying rest: temperature alternation and genetic analysis. *HortScience* **22,** 820–824.
6. Gentner W. A., Taylorson R. B. and Borthwick H. A. (1975) Responses of poppy, *Papaver somniferum,* to photoperiod. *U. N. Bull. on Narcotics* **27** (2), 23–31.
7. Hammer G. L., Vanderlip R. L., Gibson G., Wade L. J., Henzell R. G., Younger D. R., Warren J., and Dale A. B. (1989) Genotype-by-environment interaction in grain sorghum. II. Effects of temperature and photoperiod on ontogeny. *Crop Sci.* **29,** 376–384.
8. Lang A. (1951) Untersuchungen uber das Kaltebedurfinis von zweijahrigem *Hyoscyamus niger. Der Zuchter.* **21,** 241–243.
9. Krekule J. (1987) Vernalization in wheat. Pages 159–169 *in* J. G. Atherton (ed) *Manipulation of flowering* Butterworths.
10. Mika E. S. (1955) Studies on the growth and development and morphine content of

opium poppy. *Bot. Gaz.* **116,** 323–339.
11. Napp–Zinn K. (1984) Light and vernalization. Pages 75–88 *in* D. Vince–Prue, B. Thomas, and K. E. Cockshull(eds) *Light and the flowering process.* Academic Press, London.
12. Purvis O. N. (1934) An analysis of the influence of temperature during germination on the subsequent development of certain winter cereals and its relation to length of day. *Ann. Bot.* **48,** 919.
13. Purvis O. N. and Gregory F. G. (1965) The physiological analysis of vernalization. *Encyc. Plant Physiol.* **15,** 76–122.
14. Summerfield R. J., Roberts E. H., Ellis R. H. and Lawn R. J. (1991) Towards the reliable prediction of time to flowering in six annual crops. I. The development of simple models for fluctuating field environments. *Expl. Agric.* **27,** 11–31.