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GROWTH AND DEVELOPMENT OF OPIUM POPPY (*PAPAVER SOMNIFERUM* L.) AS A FUNCTION OF TEMPERATURE

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Acock M. C., PAUSCH R. C. and Acock B. *Growth and development of opium poppy (*Papaver somniferum* L.) as a function of temperature*. BIOTRONICS 26, 47–57, 1997. The U.S. State Dept. annually estimates yields of opium poppy (*Papaver somniferum* L.) and other narcotic crops around the world. When field sampling is possible, objective methods are used to estimate yields. However, field sampling is expensive and can be dangerous so other techniques are being sought. One method is to simulate crop performance using a computer model. To develop such a model, crop response to soil conditions, weather, and management practices must be understood. The first step in this process is to examine the influence of individual factors by growing the crop in controlled environments, keeping all factors except one at optimum levels, and varying that factor over a wide range. Temperature is a major weather variable. To study its effects on opium poppy, young seedlings were grown in controlled environment chambers in a 12 h photoperiod at a light intensity of $1000 \pm 100 \mu\text{mol m}^{-2} \text{s}^{-1}$ with day/night temperatures of 12/7°C, 16/11°C, 20/15°C, 24/19°C and 28/23°C. Dry weights of plant parts and specific leaf area (SLA) were measured at various stages during plant development. The optimum mean temperature for poppy growth was between 16 and 20°C. Development rate was reduced at lower temperatures but remained relatively constant over the 20/15, 24/19, and 28/23°C treatments. SLA was sensitive to temperature, maximizing at 19.5°C. Variation in SLA could explain some of the differences in relative growth rate and growth rate associated with temperature. Gum yield could be estimated from capsule dry weight or capsule volume using a linear regression model ($r^2=0.71$ and 0.75 respectively). Analyses of these data represent an important first step in quantifying the effects of temperature on poppy growth, development, and gum yield.

Key words: *Papaver somniferum*, long day plant, relative growth rate, growth rate, dry matter partitioning, specific leaf area, opium gum yield.

INTRODUCTION

Temperature has profound effects on growth and development of most crops, controlling the development rate through a multitude of metabolic processes.

The processes of flower initiation, development, anthesis, and fruit development can all be highly affected by temperature, depending on the sensitivity of the particular crop under investigation. The optimum temperature range in most cultivated crops is about 5°C and usually occurs somewhere between 20 and 30°C (1). In studying the effects of temperature on opium poppy in a 12 h photoperiod, Bernath and Tetenyi (4) found that the "low" temperature program, which varied from 12.5/7.5°C for the first five weeks to 18.5/11.5°C after 18 weeks, delayed development, prolonged the growth period, resulted in taller plants, and brought about more partitioning of dry matter to the leaves compared with their "high" temperature program that had the same starting temperatures but increased to 26.0/16.0°C after 18 weeks. This study strongly suggests that poppy is a cool-season plant, and though the temperature regimes employed followed the kind of warming trends a crop might experience over the season, it is difficult to know from this study what temperature was optimum for poppy.

The purpose of this work was to provide various stable thermoperiods from an early growth stage to 24 days after flowering and to describe time to flower, plant growth, and gum yield as a function of temperature. It represents a first step in identifying important plant variables that influence growth, development, and yield and in developing equations that describe the effects of temperature on these variables. Once all the important variables affecting yield have been studied, it should be possible to write a set of equations that will predict flowering time and gum yield under field conditions, at various geographical locations under known weather conditions, provided sowing or emergence dates, and cultural practices are known or can be estimated.

MATERIALS AND METHODS

Seeds of *Papaver somniferum* 'album' collected from a poppy with red & white petalled flowers in Thailand during the early part of 1992 were sown into 4-liter pots in a greenhouse at Beltsville, MD (latitude 39°N) on 1 Sep 1992 and emerged six days later when the daylength was 12.8 h). The growing medium consisted of 0.5 m³ vermiculite and 0.5 m³ Sphagnum peat moss amended with 4.03 kg dolomitic lime, 5.57 kg of a 9-month slow release fertilizer containing 13–5.7–10.8 (N–P–K), and 1.06 kg Micromax containing (g kg⁻¹) 120 S, 120 Fe, 25 Mn, 10 Zn, 5 Cu, 1 B, and 0.5 Mo. The thermostat in the greenhouse was set to maintain an air temperature of 20°C and controlled perimeter hot water radiators. Side and roof ventilation was manually operated. Night temperatures rarely went below 20°C but day temperatures reached above 35°C on occasions. On 28 Oct 1992 (Daylength=10.7 h), all plants were thinned to one per pot and additional fertilizer was given in 100 ml of irrigation water containing a water soluble nutrient mix of 20–8.6–18.6 (N–P–K) at an N concentration of 100 mg L⁻¹. Once the poppy seedlings had reached a dry weight of about 0.25 g (ca. 51 days from emergence), plants of uniform size were transferred to five reach-in controlled environment chambers (Environmental Growth Chambers, Inc.,

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Chagrin Falls, OH, USA). Sixteen plants were placed in each chamber with a 12 h photoperiod and day/night temperature of 12/7°C, 16/11°C, 20/15°C, 24/19°C, or 28/23°C. These treatments will subsequently be referenced by daily mean temperatures: 9.5, 13.5, 17.5, 21.5, and 25.5°C. Of the 16 plants assigned to each chamber, four plants were randomly selected for harvesting at each of the four stages of development: (a) flowerbud (FB) stage when the terminal flowerbud extends beyond the foliage, (b) day of flowering (F), (c) 7 days after flowering (F+7), and (d) 24 days after flowering (F+24). At each destructive harvest, plants were divided into roots, stems, leaves, and capsules and dried in an oven at 80°C. Leaf areas and leaf dry weights were recorded on samples of leaves from the harvested plants to obtain specific leaf area (SLA=a leaf area to leaf dry weight ratio). Those plants destined to be destructively harvested at F+24 were used to measure opium gum yields. Opium gum was harvested according to the procedure used in the Thailand study (2). To harvest the gum, the capsules were lanced: a series of four cuts that penetrated the capsule wall up to 1 mm were made with a three-bladed knife. The gum was left to exude and solidify overnight, then collected from the capsule and dried in an oven at 80°C the next day. Lancing was initiated on a capsule 7–10 days after flowering and was repeated every 3 to 4 days until the capsule had been lanced a maximum of five times.

All parameter values in the regression equations were estimated using the non-linear iterative fitting routine in JMP (SAS for the Macintosh, SAS Institute, 1989).

RESULTS AND DISCUSSION

Development.

There were no significant differences in time of flowerbud appearance between the three highest temperature treatments: 17.5, 21.5, and 25.5°C (Fig. 1). Flowerbud appearance was progressively delayed at temperature treatments below 17.5°C. An exponential function with an asymptotic value was chosen to describe the time of flowerbud appearance resulting from the low temperature treatments. The equation was:

$$\text{Days to flowerbud} = 93.3 \times \exp(-0.174 \times T) + 25.3$$

where T=mean daily temperature in °C and days to flowerbud is the number of days from the start of the temperature treatment to flowerbud appearance.

The asymptotic value of 25.3 days to flowerbud appearance was obtained in a 12 h photoperiod and is highly dependent on photoperiod (3).

A continued delay in development rate up to first open flower was observed in plants given the lowest temperature treatment. This amounted to about 9 days in addition to the normal 24 days between flowerbud and flowering in the 12 h photoperiod. The same exponential form of the equation was used to fit the effect of temperature on time to flower (Fig. 1):

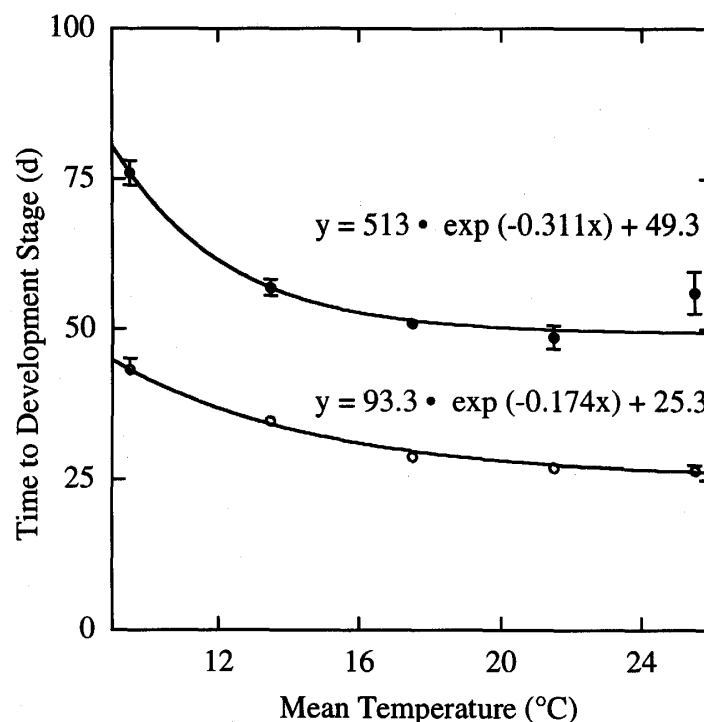


Fig. 1. Effect of temperature on time from start of treatments (51 days after emergence) to flowerbud appearance (open circles) and to first open flower (filled circles) \pm s.e.

$$\text{Days to flower} = 513 \times \exp(-0.311 \times T) + 49.3.$$

This equation does not fit the data for the 25.5°C treatment well but it was chosen because the delay in time to flower for the 25.5°C treatment was assumed to be the result of necrosis. Normally, the mainstem flowers first. When the mainstem flowerbud is killed or severely damaged, the plant flowers later, from branches. The necrosis appeared at the tip of the mainstem and on the youngest developing leaves when rapid elongation began. The 25.5°C treatment sustained the most damage. The damage was related to high humidity and over or underwatering. It was assumed that, if this necrosis had not occurred, the time to flower would have been similar to that in the moderate temperature treatments.

The function describing the effect of temperature on development may be reasonably reliable, but the parameter values undoubtedly depend on photoperiod and could be influenced by early growth in the greenhouse. Further refinements to the equations are required before they can be used in a simulation model to describe development under a variety of temperature and photoperiod conditions.

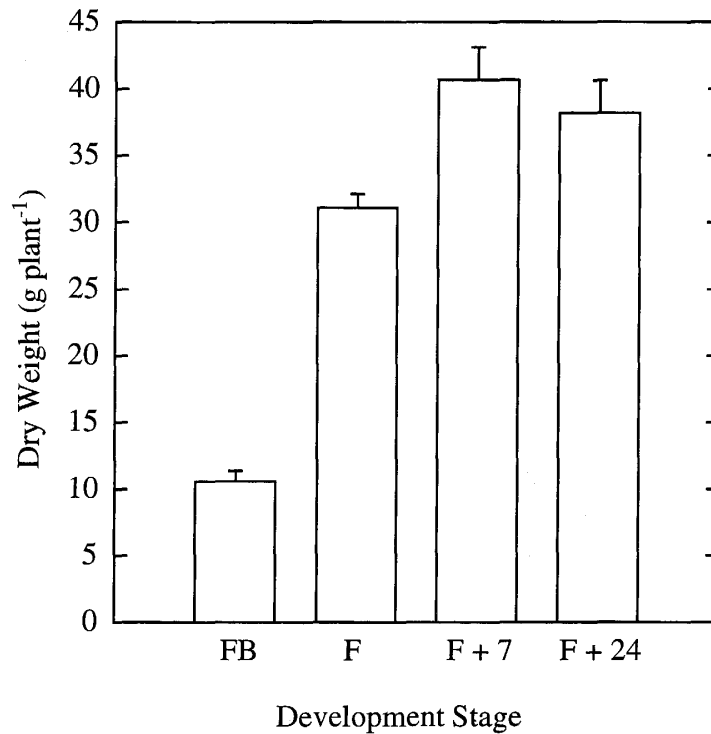


Fig. 2. Mean plant dry weights at flowerbud appearance (FB); at first open flower (F); 7 days after flowering, (F+7); and 24 days after flowering, (F+24) \pm s.e.

Growth.

Plant dry weight was greatest at F+7 (Fig. 2). To model these changes in dry weight, three growth periods were considered: (a) early growth (from the beginning of temperature treatment to FB), (b) FB to F+7, and (c) F+7 to F+24.

Early growth: The influence of temperature on plant dry weight gain prior to FB was modeled by fitting an exponential function (5) to the data,

$$W_t = W_o \times \exp(rt)$$

where, W_t = plant dry weight at the flowerbud stage (g plant^{-1}), W_o = plant dry weight at the beginning of the temperature treatment (g plant^{-1}), r = relative growth rate ($\text{g g}^{-1} \text{d}^{-1}$), and t = time (days). The effect of the temperature treatments on relative growth rate, r , can be described (Fig. 3) using the equation,

$$r = 0.134 - 0.000394 \times (T - 19.8)^2.$$

This equation estimates a maximum relative growth rate of $0.134 \text{ g g}^{-1} \text{d}^{-1}$ occurring at a temperature of 19.8°C .

Growth from FB to F+7: Dry weight gain from the flowerbud stage to seven days after flowering was linear for all temperature treatments. The growth

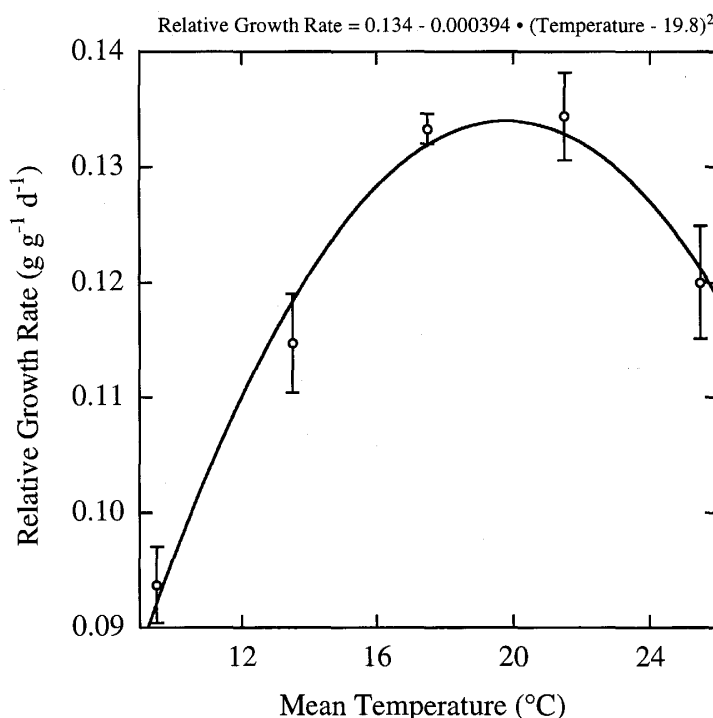


Fig. 3. Relative growth rate \pm s.e. prior to flowerbud stage as a function of mean temperature.

rates (slopes of the the linear functions) can be described as a function of temperature (Fig. 4) using the equation,

$$\text{growth rate} = 0.966 - 0.00852 \times (T - 17.0)^2.$$

The equation estimates a maximum growth rate of $0.966 \text{ g plant}^{-1} \text{ d}^{-1}$ at a temperature of 17.0°C .

Growth from F+7 to F+24: Total dry weights of the plants reached a maximum around 7 days after flowering and then declined slightly (Fig. 2). Some leaves began to senesce during this period, while the capsules enlarged (Tables 1 and 2).

The possibility that observed differences in growth rates generated by the temperature treatments could result from changes in the partitioning pattern and/or SLA was examined. Changes in partitioning of dry matter to the leaves and SLA could have a profound effect on early growth because these variables impact the light interception capability of the plant. When young plants with leaf area indices (LAI) much less than 1.0 have higher SLA, there is a concomitant rise in the ability to intercept light per unit of leaf dry weight and therefore more growth potential.

Partitioning.

Partitioning is highly dependent on the development stage of the plant. When the plant is young and vegetative, any preferential partitioning of dry

Table 1. Mean organ dry weights and dry matter partitioning of poppy grown in a range of day/night temperatures and under a 12 h photoperiod. Plants were harvested at 7 days after flowering. Each value is a mean of up to four observations. Means within columns followed by the same letter are not significantly different (Student-Newman-Keul's Multiple Range Test $p < 0.05$).

Mean temperature (°C)	Roots	Stems	Leaves	Capsules	Total
Dry weight (g plant ⁻¹)					
9.5	4.10a	13.60a	14.40a	2.93a	35.03a
13.5	3.96a	17.63a	15.94a	5.14a	42.67a
17.5	2.71a	23.80a	12.08a	5.33a	43.92a
21.5	3.68a	18.48a	13.70a	4.06a	38.19a
25.5	3.75a	14.43a	6.88a	1.07b	24.36b
% total plant dry weight					
9.5	11.7a	38.7a	41.3a	8.4a	100
13.5	9.7a	41.3a	37.1a	11.9a	100
17.5	4.3a	47.1a	35.8a	12.7a	100
21.5	7.5a	46.6a	35.9a	10.0a	100
25.5	16.4a	51.6a	26.6a	5.4a	100

Tabel 2. Mean organ dry weights and dry matter partitioning of poppy grown in a range of day/night temperatures and under a 12 h photoperiod. Plants were harvested at 24 days after flowering. Each value is a mean of four observations. Means within columns followed by the same letter are not significantly different (Student-Newman-Keul's Multiple Range Test $p < 0.05$).

Mean temperature (°C)	Roots	Stems	Leaves	Capsules	Total
Dry weight (g plant ⁻¹)					
9.5	3.85b	12.12c	9.35b	3.92c	29.24c
13.5	4.49a	17.55ab	12.73a	13.21b	47.97a
17.5	3.24c	15.60b	6.61c	18.34a	43.78ab
21.5	2.69c	19.39a	5.88c	13.37b	41.32b
25.5	2.55c	13.77c	4.33d	3.02c	23.65d
% total plant dry weight					
9.5	13.0a	41.2c	32.0a	13.8c	100
13.5	9.3b	36.5d	26.7b	27.5b	100
17.5	7.5c	36.2d	15.7d	40.7a	100
21.5	6.5c	47.0b	14.3d	32.2b	100
25.5	10.5b	57.0a	19.2c	13.3c	100

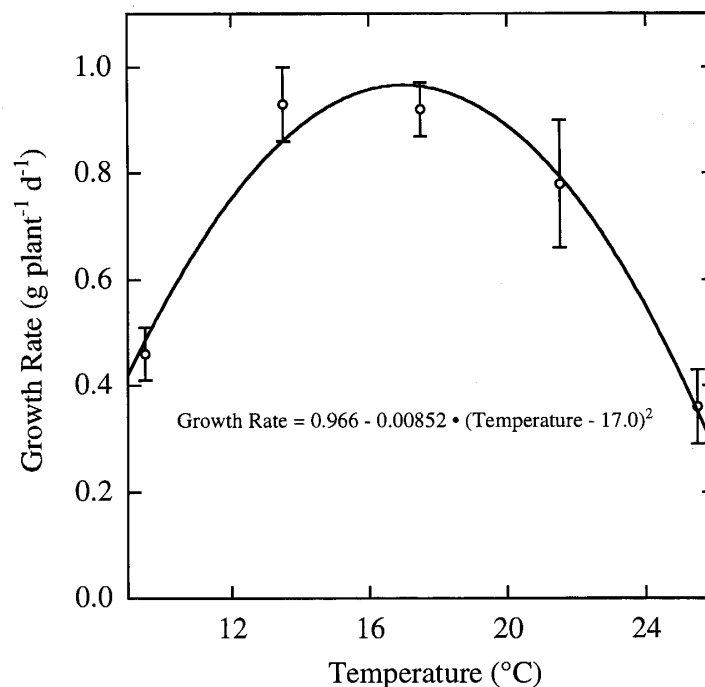


Fig. 4. Growth rate \pm s.e. from flowerbud appearance to 7 days after flowering as a function of temperature.

matter into leaves resulting in a corresponding increase in leaf area would enhance light interception, leading to a rapid growth potential. Such potential should continue until leaves in the upper part of the canopy begin to shade lower leaves.

Temperature had no significant effect on dry matter distribution at F+7 (Table 1) but differences were observed by F+24 (Table 2). There was a larger percentage of plant dry matter in leaf tissue under the coldest temperature treatment. This may be a result of leaves being retained or senescence occurring more slowly in the cold temperatures. Alternatively, low temperature may have prolonged the vegetative period and delayed development after flowering. If low temperature does prolong the vegetative stage, one might expect more leaves on the mainstem. In fact, leaf numbers were not higher in the low temperature treatments, so the evidence points towards some other explanation. A greater distribution of dry matter to the leaves at low temperatures has also been observed in soybean (6).

The partitioning of dry matter to the capsule was greatest in the 17.5°C treatment at F+24 (Table 2). Capsule dry weight was also highest in 17.5°C, indicating near optimal conditions for capsule development. Partitioning of dry weight to the stem was greater in the two highest temperature treatments. This was accompanied by higher dry weights in the 21.5°C treatment but not in the 25.5°C. The higher proportion of dry weight in 25.5°C along with a lower absolute dry weight may have been a result of injury. Whatever the reason,

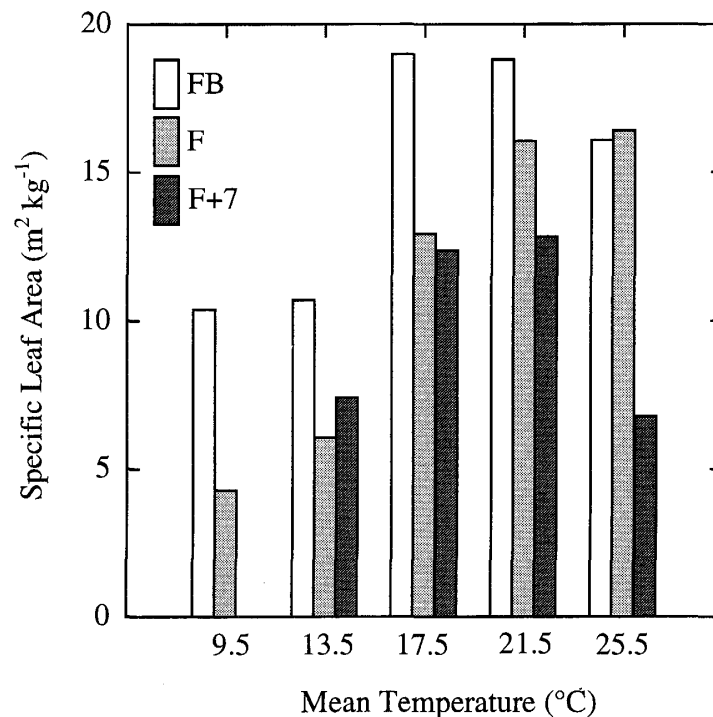


Fig. 5. Specific leaf area as a function of temperature and time of harvest.

higher temperatures do favor partitioning to the stem. Wang *et al* have also reported greater partitioning to the stems in soybean at higher temperatures (6).

Specific Leaf Area.

The amount of leaf area generated per unit of dry weight partitioned into leaf tissue determines the efficiency with which leaf tissue can intercept light. Temperature can change that efficiency if SLA is temperature dependent. Fig. 5 indicates that SLA changes with temperature in a similar manner to growth (Figs. 3 and 4), suggesting that changes in SLA may have been, at least partly, responsible for changes in growth. The two lowest temperature treatments had much reduced SLA values compared with the other temperature treatments. SLA had its maximum value in the 17.5°C treatment. Stage of development also influenced SLA but the early phase of growth (up until flowering) is most important because this is the period when canopy cover is incomplete (Fig. 5). An equation that expressed the effect of temperature on SLA at the flowerbud stage and fitted all but one data point well was:

$$\text{SLA (m}^2 \text{ kg}^{-1}\text{)} = 19.3 - 0.0889 \times (T - 19.5)^2$$

Effect of temperature on gum yield, capsule dry weight, and capsule volume.

Three closely related variables: gum yield, capsule dry weight, and capsule volume had maximum values in the 13.5°C or 17.5°C treatment. The effects of temperature on these plant variables can be described by the equations:

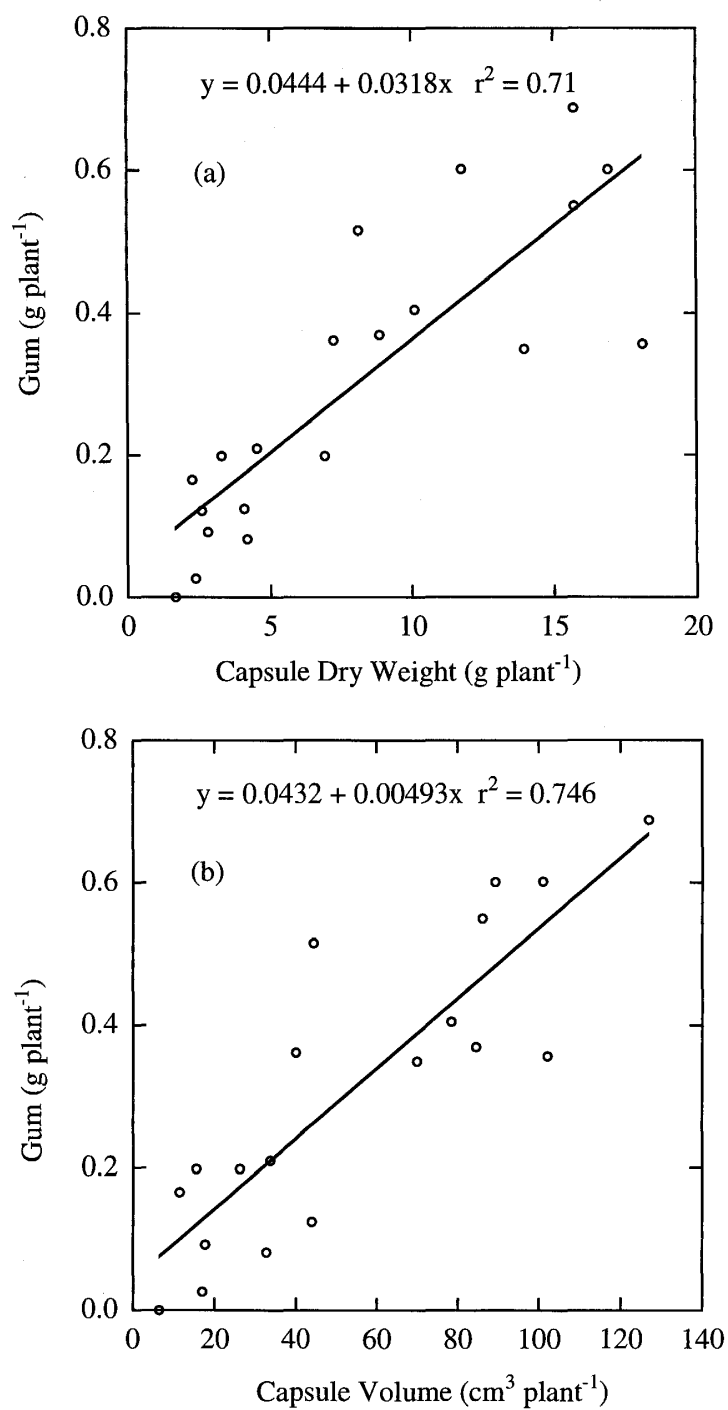


Fig. 6. Total opium gum yield per plant as a function of (a) capsule dry weight and (b) capsule volume.

$$\text{gum weight (g plant}^{-1}\text{)} = 0.474 - 0.00539 \times (T - 17.2)^2,$$

$$\text{capsule weight (g plant}^{-1}\text{)} = 13.1 - 0.156 \times (T - 17.1)^2,$$

$$\text{capsule volume (cm}^3 \text{ plant}^{-1}\text{)} = 82.4 - 0.900 \times (T - 16.2)^2,$$

From these equations, the maximum gum yield was estimated to be 0.474 g plant⁻¹ at a temperature of 17.2°C (planting density was 14.4 plant m⁻²), the maximum capsule dry weight was estimated to be 13.1 g plant⁻¹ at a temperature of 17.1°C, and the maximum capsule volume was estimated as 82.4 cm³ plant⁻¹ at a temperature of 16.2°C.

According to this study, the optimum temperature for growth and development of poppy appears to be between 16 and 20°C, with no serious reduction in growth rate from thermoperiods of 13.5°C to 21.5°C and little delay in development from thermoperiods 17.5°C or above.

This study confirmed the strong relationship observed in a Thailand study (2) between gum yield and capsule dry weight and also between gum yield and capsule volume (Fig. 6).

Understanding the response of the poppy plant to temperature is the first step in developing a simulation model to describe plant performance under field conditions. However, poppy development rate is partly controlled by photoperiod and development rate affects partitioning, which in turn affects growth rate. Therefore, the effects of photoperiod must be incorporated into the model before it can be used to estimate yields adequately. Work on the response of poppy to photoperiod is in progress.

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