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REFOLIATION OF *ERYTHROXYLUM COCA* VAR. COCA. II. EFFECT OF TEMPERATURE

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Acock, M. C. *Refoliation of* Erythroxylum coca *var. coca.* II. *Effect of temperature.* BIOTRONICS **28**, 97–107, 1999. The coca plant regenerates readily after being stripped of its leaves. Leaf regrowth may depend on past environmental conditions as well as current ones. The purpose of this study was to determine (a) how temperature affected the refoliation process and leaf yield and (b) whether there was any after effect of temperature on subsequent refoliation and yield. Coca plants grown under near optimum temperatures were defoliated and placed in controlled environment chambers at constant day/night temperatures of 17, 18, 19, 20 or 21℃. Some plants remained in the greenhouse at a mean daily temperature of 21.9℃. The number of leaves per growing point was closely associated with leaf yield. The change in canopy cover was a three parameter, logistic function of time with two temperature-sensitive parameters: canopy cover at the end of a flush and the time required for 50% canopy cover. Coca refoliation was similar for temperatures≥19℃ but fell off sharply at 18℃ and practically stopped at 17℃.

After the second defoliation, plants were placed under similar environmental conditions. Plants previously grown at low temperatures had higher canopy cover 11 d after defoliation than other plants but this difference quickly disappeared. All plants initiated similar numbers of leaves by the end of the first flush. The rate of leaf initiation and the completion of the second flush were similar for all plants. However, the beginning of the second flush was a linear function of prior temperature treatment. Plants from the lowest temperature began the second flush earliest. This ability to eliminate yield differences caused by low temperature by the next harvest suggests that coca plants are resilient to sub-optimal temperatures and that annual yields may be relatively stable even though yields for individual harvests throughout the year may fluctuate.

Key words: narcotic, leaf yield, canopy cover, yield assessment.

INTRODUCTION

The coca plant is a tropical, perennial shrub that is totally defoliated every two to four months once it has reached harvestable size (eight months to two years). Its ability to regenerate leaves after such a loss attests to its proficiency in activating meristematic tissue and in storing energy for regrowth. The typical refoliation process for coca when air temperature is within the optimal range for growth begins in 10 d (*2*). The progress in canopy cover, defined as the increase over time in the ratio of intercepted to incoming solar radiation, can be described by the equation:

$$C = C_{fn}/[1 + (t_{0.5}/t)^a]$$

where C_{fn} is the canopy cover achieved at the end of flush n, $t_{0.5}$ is the time in days to reach 50% C_{fn}, a describes the rate of increase in C during flush n, and t is the independent variable time in days.

Some evidence suggests that *Erythroxylum coca* var. coca will practically stop growing at air temperatures below 20℃ (*1*). This rationale was used in a simulation model (unpublished) to develop an equation that would reduce the increase in C in response to low, non-optimum temperatures. The temperature factor varied between 0 and 1. The change in the value of the temperature factor (TF) was described as:

$$TF = 1/[1 + (T_a/19.0)^a]$$

where $a = -25$, and T_a is the average daily air temperature (℃). Using this equation, the value of TF is near zero between 0 and 16℃, then rapidly rises to 0.5 at 19℃ and is near one at $\geq$22℃.

The equation for estimating TF was based on the differences in leaf yield of coca plants grown in air temperatures of 18 or 19℃ and those grown in 23℃. The purpose of the first experiment described here was to obtain a more complete dataset of temperature response over the range where maximum differences in growth seemed to occur in order to refine the model in terms of temperature response to refoliation.

To study the after effect of temperature treatment, all experimental plants were placed under similar environmental conditions in a greenhouse and allowed to refoliate. Differences in refoliation were attributed to prior temperature treatments. The hypothesis was that the low temperature treatments with reduced leaf yield would have more energy rich compounds stored. Grown under more favorable temperature conditions, these plants might demonstrate an enhancement in leaf yield for the next harvest compared with plants grown continuously under favorable temperature conditions.

MATERIALS AND METHODS

Twenty-four plants were selected from those described in the first paper of this series (*2*). Plants were separated into four groups based on leaf fresh weights at the first defoliation just before the start of this experiment. A plant within each group was assigned at random to one of five environmental growth chambers (Environmental Growth Chambers, Inc., Chagrin Falls, Ohio) or to the greenhouse on 8 Dec 1998 at latitude 39.0°N.

The six chambers were set at a photoperiod of 12-h. Each chamber was provided with a combination of six high pressure sodium and six metal halide lamps that were arranged alternately in three rows. Photosynthetic photon flux density (*PPFD*) inside the growth chambers was maintained at $500 \pm 100 \mu$mol $m^{-2} s^{-1}$ at the top of the plant canopy by introducing a neutral shade cloth between the lights and the plants. In the growth chambers, temperatures during the entire experimental period were controlled at 17, 18, 19, 20, 21±1℃. In the greenhouse, temperatures were monitored at a mean of 21.9±0.5℃ for the period of growth. The range in daily mean temperatures was 17.4±0.7℃ to 29.9±0.5℃, and the absolute range in temperature for any 15-minute period in the greenhouse was 7 to 37℃. Plants were fertilized and watered as described in Part I of this series (*2*).

On 21 Jan 1999, (45 d after defoliation) the temperature during the light period in the chambers having the two lowest temperature treatments was increased to 19℃ because the rate of refoliation was so slow at these temperature treatments.

Because of the good relationship between number of leaves per growing point and leaf area index, canopy cover was calculated using an exponential function similar to that used for calculating leaf area index. In this case,

$$C = 1 - e^{-KN}$$

where C is canopy cover, N is the number of leaves per growing point, and K has a value of 0.40. The value for K was based on data in which canopy cover had a value of 0.92 when there was a mean of 6.3 leaves per growing point (*2*).

A dataset was generated for canopy cover based on leaf number per growing point. To describe the changes in canopy cover with time, equations were fitted to the calculated values for canopy cover. A logistic approximation was selected for describing the data after inspection of the graph showing change in C with time.

$$C = C_{fl} / [1 + (t_{0.5}/t)^{a}] \qquad (1)$$

where C_{fl} is the value of C achieved at the end of the first flush, t is the number of days after defoliation, $t_{0.5}$ is the number of days required for C to reach 50% of C_{fl}, and a indicates the rate at which canopy cover is achieved.

To monitor progress in C, the number of leaves initiating over time was recorded on five selected growing points per plant. On 1 Mar 1999 all experimental plants in the chambers and in the greenhouse were defoliated. The leaves were dried at 70–75℃ and weighed.

On 4 March 1999 all experimental plants were transferred to the greenhouse (located at latitude 39°N) where they were grown for 81 d before the next leaf harvest. During this period, the absolute range in temperature experienced by the plants over a 15-minute interval was 22.2 to 40.6℃, the mean daily temperature was 27.6±0.2℃, the maximum daily mean was 30.7℃, and the minimum daily mean was 24.1℃. Leaf initiation rate was measured daily. All experimental plants were defoliated on 24 May 1999.

The same type of equation used above was fitted to the data for the first and second flush of growth.

$$C=C_{fn}/[1+(t_{0.5}/t)^{a}]$$

where C=canopy cover, $C_{fn}=C$ at the end of flush n, $t_{0.5}$ is time to half way to end of flush n, t is time in days, and a is a parameter describing the rate of change in C.

RESULTS AND DISCUSSION

First refoliation.

The refoliation process for plants grown under various constant temperature is shown in Fig. 1. As can be observed from these curves, temperatures of 18℃ or below depressed refoliation whereas plants grown in temperatures of 19℃ or above had similar refoliation patterns. The effect of temperature on coca refoliation can be described by one equation with three parameters, two of which were found to be sensitive to temperature: $t_{0.5}$ and C_{fl} (Fig. 2). The points were obtained by estimating C_{fl} and $t_{0.5}$ for each temperature separately and fitting the data to the equation:

$$C=C_{fl}/[1+(t_{0.5}/t)^{4.77}] \quad (2)$$

The curves on Fig. 2 show results of fitting equations to these points. The curves are graphs of the logistic equation:

$$C_{fl}=0.732/[1+(17.28/T)^{32.1}] \quad (3)$$

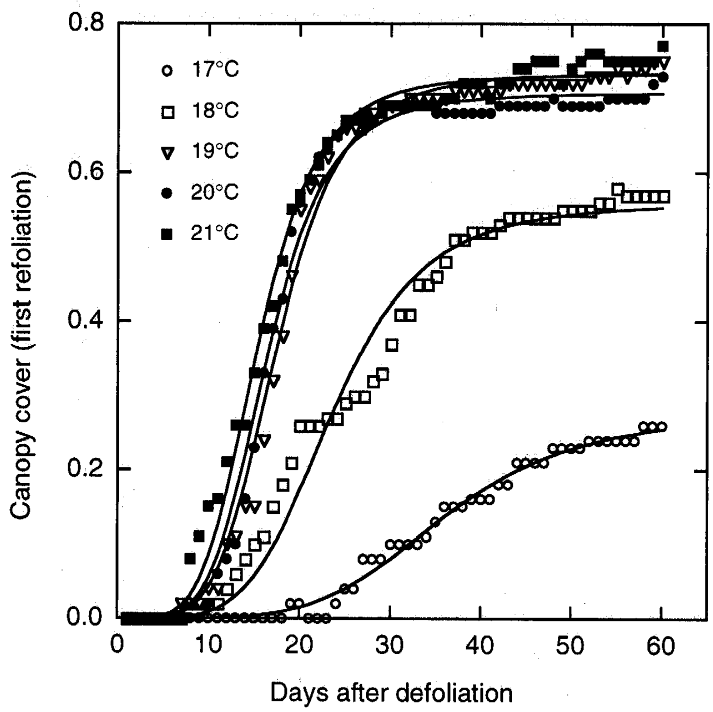

Fig. 1. Change in canopy cover as a function of time. Canopy cover is defined as $1-e^{-KN}$ *where* K is 0.40, and N is the number of leaves per growing point.

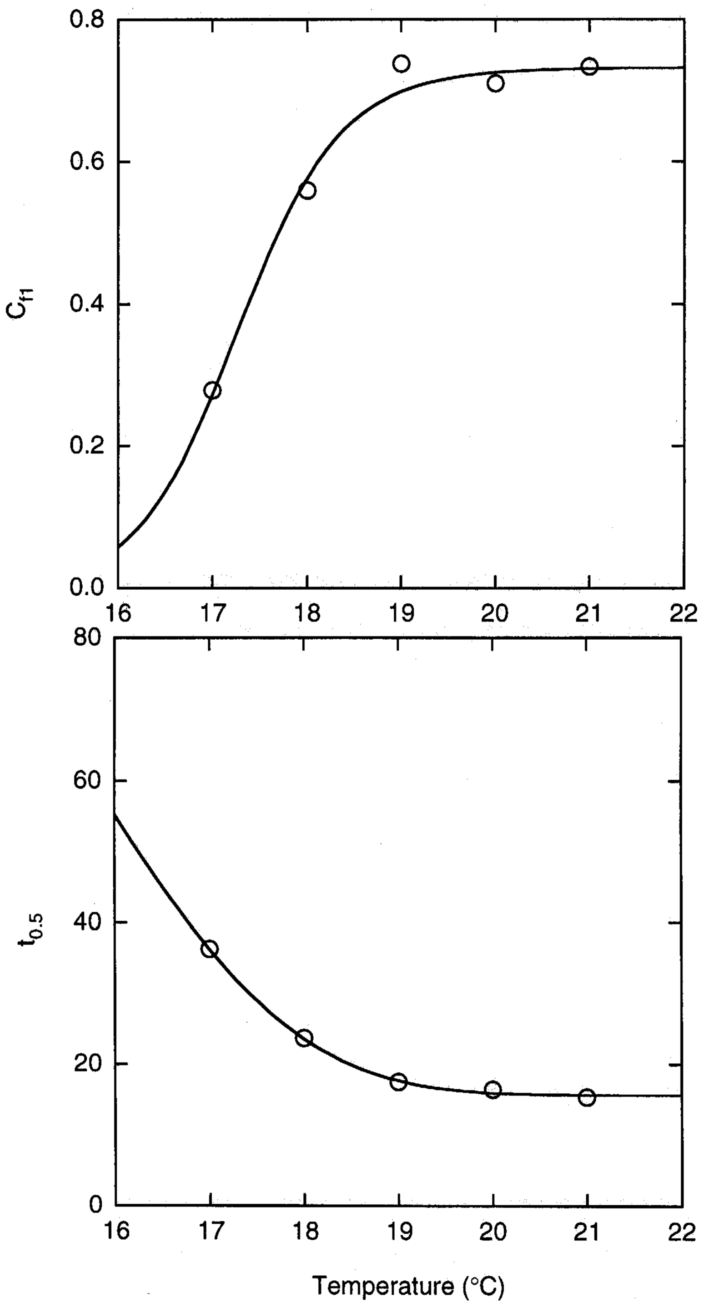

Fig. 2. Graphs of (a) the logistic curve $C_{fl}=0.732/[1+(17.28/T)^{32.1}]$ and (b) the Weibull equation $t_{0.5}=15.67+125\ \exp[-(T/15.7)^{7.42}]$ where T is temperature in ℃ showing the change in values of the parameters, C_{fl} and $t_{0.5}$, with temperature.

and of the Weibull equation:

$$t_{0.5}=15.67+125\ \exp[-(T/15.7)^{7.42}] \qquad (4)$$

where T is temperature in ℃

The one-to-one correspondence between measured and calculated values of

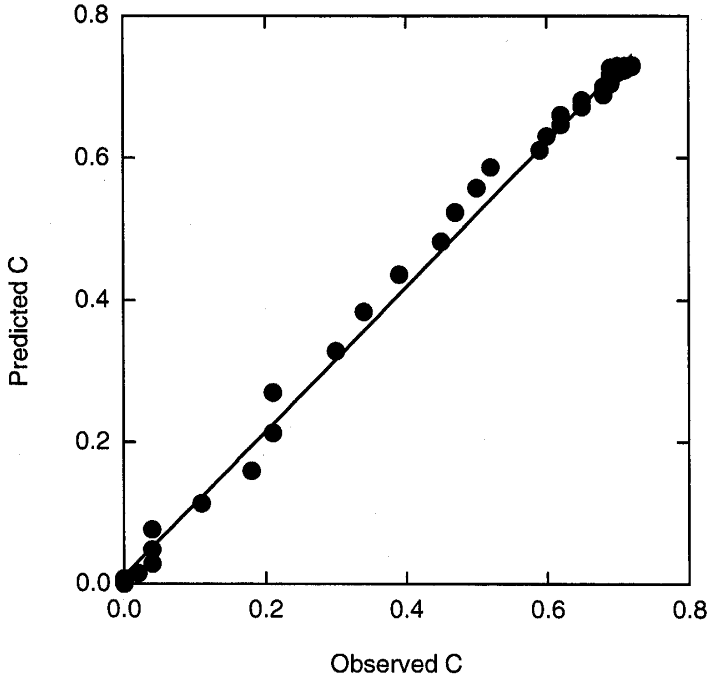

Fig. 3. Plot of calculated values of canopy cover based on observations made on coca plants grown in the greenhouse at a mean daily temperature of 21.9℃ and predicted values of canopy cover based on a 3-parameter logistic equation.

C with Eq. (2) is shown in Fig. 3. The mean daily temperature over the period of growth in the greenhouse was used to calculate values for C_{fn} and $t_{0.5}$. The coefficient of determination was $R^2=0.997$. The slope of the regression line was 1.02 ± 0.008 and is not significantly different from 1.0, the intercept of the regression line was 0.011 ± 0.004 and is not significantly different from zero. These results lead to the conclusion that the model fits the data well. The validation of the selected equations using a greenhouse dataset where air temperature varies, indicates that this model may be suitable for field conditions where air temperature fluctuates.

Leaf yields after first refoliation.

The number of leaves per growing point was closely associated with leaf dry weight (Fig. 4) for this group of plants which had similar leaf yields at the start of the temperature treatments (Table 1). The higher leaf dry weights for plants grown at 19 and 20℃ suggests that the optimum temperature for leaf growth is very narrow, occurring over a 2℃ range.

Second refoliation.

All plants, regardless of prior treatment, were nearing the end of their flush of growth approximately 17 d after defoliation (Fig. 5). There was no significant difference in canopy cover at the end of the first flush for the coca

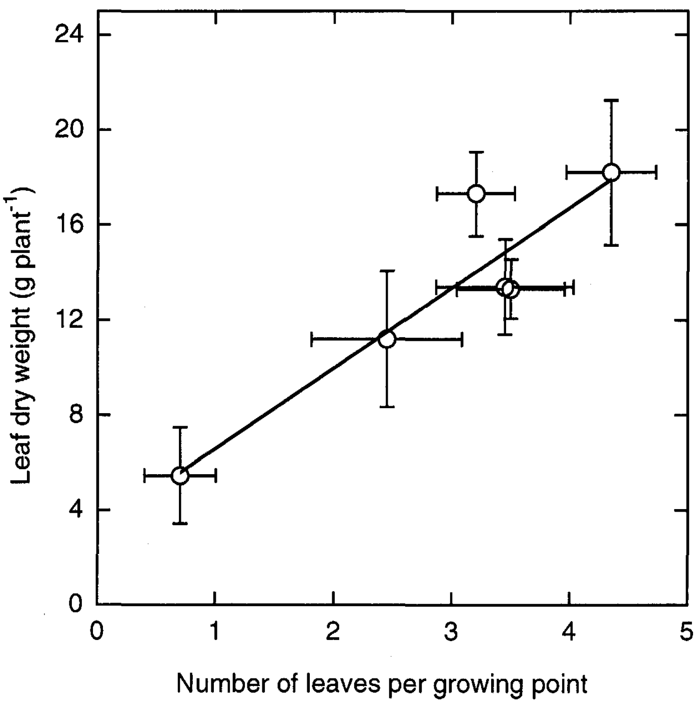

Fig. 4. Leaf dry weight described as a function of the number of leaves per growing point on *Erythroxylum coca* var. coca. The standard errors for the number of leaves and for the leaf dry weight are given for each temperature treatment.

Table 1. Effect of temperature on leaf yield of *Erythroxylum coca* var. coca for plants that had undergone defoliation prior to treatment and had grown for 101 d before the next defoliation (replications=4).

Temperature Treatment (℃)	First harvest (g/plant)	Second harvest (g/plant)	Leaf number/ grow point±s. e.
17	11.99 a[z]	5.47 b	0.70±0.30
18	12.83 a	11.15 ab	2.45±0.64
19	13.32 a	18.22 a	4.35±0.38
20	12.95 a	17.30 a	3.20±0.33
21	12.92 a	13.43 ab	3.45±0.58
21.9±0.5	13.76 a	13.26 ab	3.50±0.46

[z]Means followed by same letter within columns are not significantly different at $p<.05$, Student–Newman–Keuls' Test

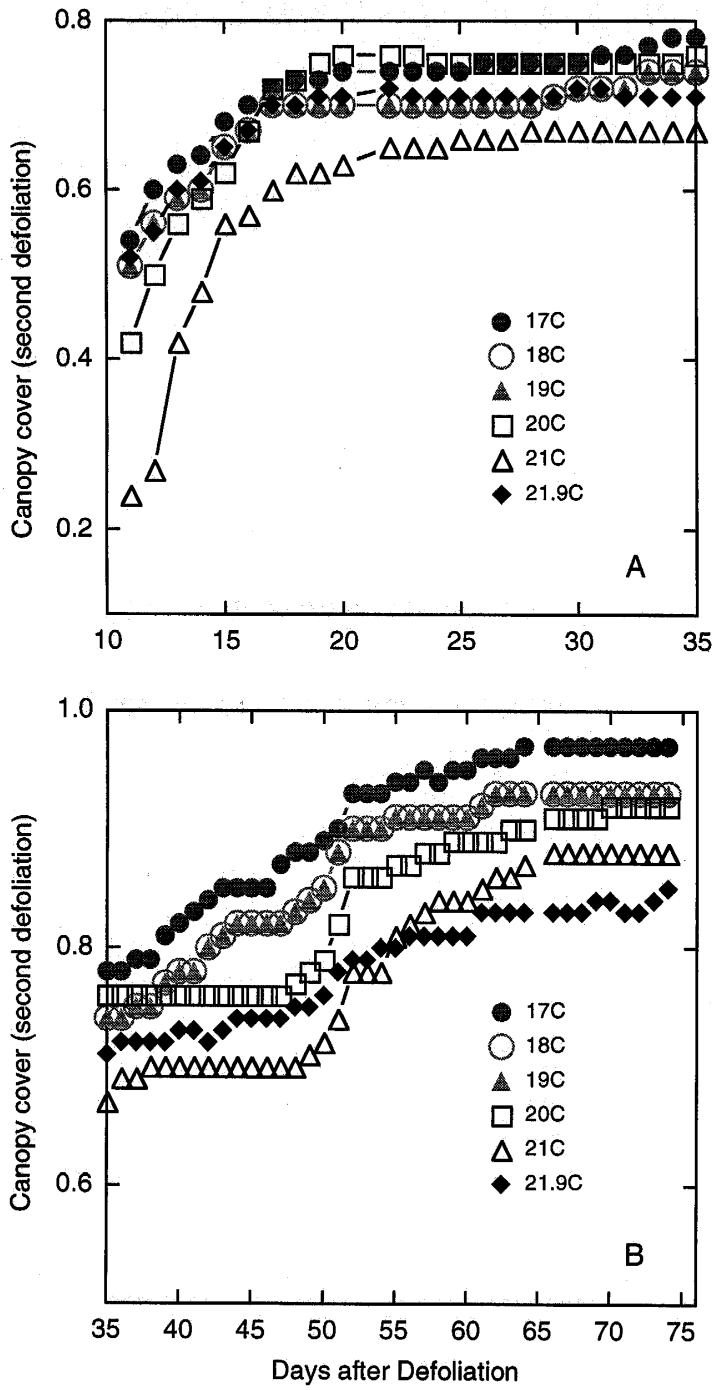

Fig. 5. Change in crop cover of *Erythroxylum coca* var. coca with time (days) for plants that had received various temperature treatments prior to being defoliated (A) from 10 to 35 days after defoliation and (B) from 35 to 75 days after defoliation.

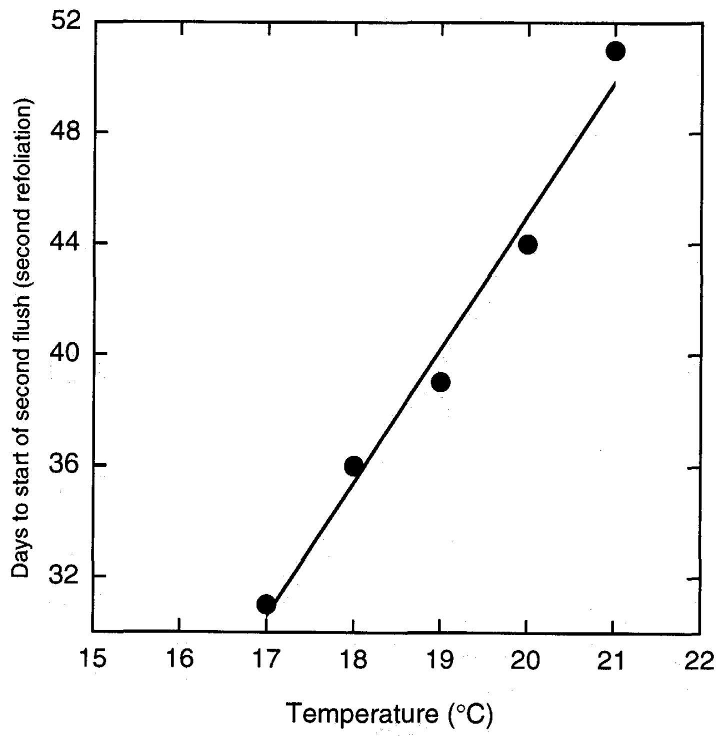

Fig. 6. Plot of days to the beginning of the second flush of leaf growth of *Erythroxylum coca* var. coca plants as a function of temperature treatment received prior to the start of the whole refoliation period.

Table 2. Predicted and observed canopy cover at the end of the second flush (second refoliation) assuming all plants reach the same canopy cover at the end of the first flush, the second flush ends at 65 d after defoliation for all plants, the rate of increase in canopy cover with the second flush is linear and is the same for all plants (0.007 d^{-1}), and that the timing of the second flush depends on prior temperature treatment.

Temperature (℃)	Observed LC_{f2}	Predicted LC_{f2}
17	0.97	0.971
18	0.93	0.937
19	0.91	0.904
20	0.88	0.870
21	0.83	0.836
21.9	0.87	0.806

plants, regardless of prior temperature treatment. The best parameter values to describe C for the first flush for all plants were: $C_{f1}=0.73$, $t_{0.5}=10$, $a=4.77$. Mean canopy cover was the same as the maximum value observed for the first (and only) flush observed in the first refoliation. Large differences in the timing of the second flush were observed that appeared to be related to prior temperature treatments. The equation used to describe the first flush was inappropriate for describing the second flush. The simplest method to predict the final canopy cover, which was virtually complete at 65 d after defoliation for all treated plants, was to make the timing of the second flush a linear function of prior temperature treatment (Fig. 6). Although the linear model is a simplifying assumption for some of the observed changes in canopy cover, it provides a means of easily and accurately determining the value of canopy cover at the end of the second flush, the canopy cover attained before harvest (Table 2).

Leaf yield after second refoliation.

Plants subjected to the 17℃ treatment were able to recuperate, generating as much leaf dry weight in the more favorable temperature as plants that had been grown in a more favorable temperature previously. There were no significant differences in the mean of the two leaf harvests (Table 3) for the temperature treatments. The 17℃ and 18℃ treatments increased their leaf yields by 2.5 and 1.2 times compared with their previous harvests respectively. Their closest competitor, the 19℃ treatment, increased yields by 0.9 times from the previous harvest. The data support the interpretation that the optimum temperature for leaf growth is within the narrow range of 19–20℃. Plants given these temperature treatments generated 19% more leaf dry weight than any other treatment.

Table 3. Oven dry weights (70–75℃) of leaves (±s.e.) of *Erythroxylum coca* var. coca at the end of temperature treatments (second harvest) and after refoliation for 81 d in a greenhouse with a mean daily temperature for the period of 27.6±0.2℃ (third harvest). The difference between these two harvests and the mean of the two harvests are shown. Three plants (one each from the 17, 19, and 21℃ treatments) which showed a negative difference between the second and third harvests were eliminated from the comparisons. (maximum number of replications=4)

Temperature (℃)	Harvest Second	Third	Difference	Mean
	(g/plant)			
17	6.58±2.4	22.7±4.7	16.14±3.2	14.7±3.4
18	11.15±2.9	24.1±2.7	12.98±2.7	17.6±2.4
19	16.06±3.0	28.4±1.7	13.69±3.2	23.3±1.2
20	17.30±1.8	29.4±2.7	12.11±1.5	23.4±2.1
21	13.62±2.8	24.2±5.5	10.60±3.0	18.9±4.1
21.9	13.26±1.3	24.5±1.7	11.20±0.8	18.6±1.4

Conclusions.

Seasonal variations in leaf yield warn of the importance of not using a single harvest to extrapolate to an annual yield figure. Small differences in temperature around 19℃ can make a big difference in leaf yield. On the other hand, the ability of plants to regenerate leaves does not appear to be seriously affected by a long period of sub-optimal temperatures once the plants are placed in optimal temperatures. Whether coca plants have the ability to regenerate leaves after experiencing long periods of supra-optimal temperatures is less certain, and has not been fully investigated.

The lack of any after effect of temperature on leaf yield makes the attempt to model coca leaf growth over time much easier because just the current weather conditions must be considered along with the age, size or vigor of the plant. The previous harvest is not a good indicator of the next harvest if leaf yield has been limited by temperature. Results argue for a relatively stable annual leaf yield because the coca plant shows immediate recovery from the consequences of reduced leaf growth caused by sub-optimal temperatures.

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