THE PHYSIOLOGY OF SUGAR-CANE

VI. EFFECTS OF TEMPERATURE, LIGHT, AND WATER ON SET GERMINATION AND EARLY GROWTH OF SACCHARUM SPP.

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Summary

Freshly cut sets from irrigated cane gave 100% germination without an external water supply. Pre-soaking did not accelerate germination or subsequent growth.

Optimum temperature for germination in darkness or in daylight for cv. Pindar was in the vicinity of 30°C, with severe growth depression below 22°C and virtually no growth in the range 10–16°C. Bimodal temperature–growth curves were found for set root production. Diurnal temperature changes of 4 and 6 degC at 12-hourly intervals did not increase growth above that expected for the mean temperature. At temperatures between 30 and 34°C but not at 18°C, constant light was deleterious for dry matter production. Short days (8 hr) increased the shoot to root ratio and the leafiness (leaf area per unit dry weight of plant).

Saccharum spontaneum, *S. robustum*, and *S. officinarum* varieties differed in their response to temperature for germination. Genetic variability and tolerance to low temperature were greatest in *S. spontaneum*.

I. Introduction

Literature on the effect of temperature on the germination and subsequent shoot growth of sugar-cane cuttings (sets, setts) has been reviewed by Van Dillewijn (1952). Although varietal differences are evident, Mathur (1941) found that germination was adversely affected by temperature below 19°C and Rege and Wagle (1939) found that temperatures below 10°C were injurious. Sartoris (1929) observed some sprouting of buds and roots at temperatures as low as 6°C. The upper critical temperature range appears to be less well defined. Verret (1927) noted that 44°C was too high to allow good germination, but some growth did take place.

Van Dillewijn (1952) believes that differences in temperature optima for germination can be related to the origin of the variety. Canes of subtropical origin have a lower temperature optimum, in general between 26 and 33°C, than tropical canes for which Verret (1927) reports an optimum of 34–38°C.

We have examined the effects on germination of sets of varying components of the environment, singly and in combination. We define germination as the growth phase preceding the formation of adventitious roots (shoot roots) by the growing shoot. Included in our studies are effects of diurnal periodicity for temperature and light–dark cycles on a commercial cane variety (Pindar) and a comparison of temperature effects on varieties from *Saccharum spontaneum*, *S. robustum*, and *S. officinarum*.

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II. Materials and Methods

General experimental procedures adopted are outlined in this section. Specific environmental conditions are described at the beginning of each set of experimental results.

Except for the comparison of species (Section III(*f*)) all experiments were conducted with cv. Pindar.

(*a*) *Planting Material*

Sets were selected from uniform stalks of field-grown cane, usually from nodes 5, 6, and 7 (the node to which is attached the top visible dewlap leaf is counted as node 1), and cut with approximately 2 in. of internode on either side of the node. Excepting experiments on water requirements, sets were dipped in a 0·5% (w/v) organo-mercurial fungicide ("Aretan") prior to planting.

(*b*) *Growth Medium*

Plants were grown in vermiculite contained in 6-in. diameter cans, or 18-in. square germinating flats. Plants were watered once daily with a complete nutrient solution developed at the Hawaiian Sugar Planters' Experiment Station, Hawaii (Burr, personal communication), and once with water.

(*c*) *Statistical Methods*

The least significant difference of means (L.S.D.) was calculated from data for analysis of variance as:

$$\text{L.S.D.} = \sqrt{\frac{2\times\text{error mean square}}{\text{No. of observations in means}}}\times t,$$

with the t value for the number of degrees of freedom in the error term and $P = 0{\cdot}01$.

(*d*) *Artificial Lighting*

Artificial illumination was provided by an overhead bank of six Philips 400-W high-pressure mercury fluorescent lamps and two 200-W incandescent lamps in each controlled-temperature light chamber (dimensions 4 ft 6 in. by 4 ft by 20 ft high). Light intensity was controlled by moving the light bank up or down as required.

III. Results and Conclusions

(*a*) *Water Requirements for Germination*

Experimental conditions were:

Temperature: 30°C, constant.

Harvest: 14 days.

Measurements: percentage germination; dry weights and moisture contents of shoots and set roots.

Paraffin wax was applied to the cut ends of the sets before planting in the vermiculite medium to prevent excessive water loss. The following treatments were used:

(1) No external water, no pre-soaking.
(2) No external water, pre-soaked 3 hr.
(3) External water, no pre-soaking.
(4) External water, pre-soaked for 3 hr.

Germination was 100% for all treatments. No differences were evident in growth within treatments (1) and (2) or (3) and (4) due to pre-soaking hence the data for these pairs of treatments are combined in Table 1. The survival and

TABLE 1

EFFECT OF WATER REGIME ON GERMINATION OF CV. PINDAR SETS

Treatment	Germination (%)	Dry Weight (g)		Moisture Content (%)	
		Shoot	Set Roots	Shoot	Set Roots
No external water	100	0·093	0·112	79	32
Plus external water	100	0·840	0·086	89	90

regrowth ability of sets after germinating and remaining dry for 14, 24, and 29 days, are presented in Table 2. The following general conclusions are indicated:

TABLE 2

SURVIVAL OF GERMINATED SETS AFTER PERIODS WITHOUT WATER

Days without Water	Survival (%)	Observations
14	80	Most set roots dead, some resumed growth by secondary branching. New set roots produced
24	80	All set roots dead. Few (4–5 per set) new set roots produced
29	0	Shoots and set roots dead

(i) Diffusion pressure deficits of the shoot and root initials were greater than for the set and permitted sufficient water for germination to move from the set to the growing parts.

(ii) Growth of set roots was less affected than that of shoots by the lack of external water.

(iii) After 14 days without water, recovery of set roots was small. Shoots remained viable for 24 but not 29 days without water.

(b) Effects of Constant and Alternating Temperature on Germination of Sets in Darkness

Experimental conditions were:

Temperatures (°C): 40,40; 40,34; 34,34; 34,28; 28,28; 28,22; 22,22; 22,16; 16,16; 16,10; 10,10.

Temperature cycles: 12 hr/12 hr.

Harvest: 19 days.

Measurements: height of plants; fresh and dry weight of shoots and set roots.

In this series of experiments darkness was maintained to obviate the complicating effects of temperature during the photoperiod. Hence growth of roots and shoots was sustained by mobilization of food reserves in the bud and attached cutting.

Heights of shoots at 8- and 17-day intervals from planting are shown in Figure 1(*a*). The average temperature is plotted for alternating temperature regimes. Results of dry weight measurements after 19 days growth are given in Figures 1(*b*) and 1(*c*).

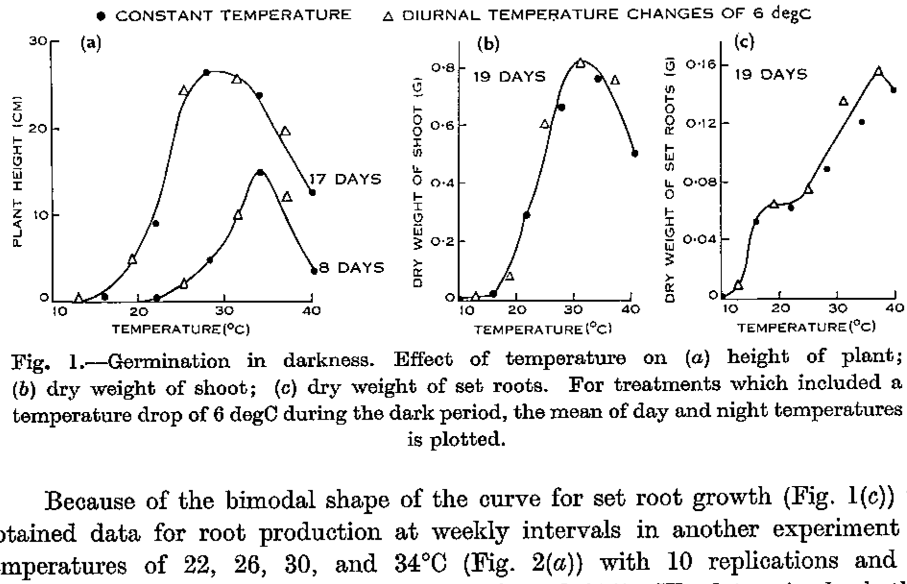

Fig. 1.—Germination in darkness. Effect of temperature on (*a*) height of plant; (*b*) dry weight of shoot; (*c*) dry weight of set roots. For treatments which included a temperature drop of 6 degC during the dark period, the mean of day and night temperatures is plotted.

Because of the bimodal shape of the curve for set root growth (Fig. 1(*c*)) we obtained data for root production at weekly intervals in another experiment at temperatures of 22, 26, 30, and 34°C (Fig. 2(*a*)) with 10 replications and at harvest intervals of 7 and 14 days (Figs. 2(*b*) and 2(*c*)). We determined whether the growth of shoots affected the growth of set roots, by excising the buds prior to planting (Fig. 2(*d*)). The inferences to be drawn are:

(1) At temperatures below 26°C, growth of shoots is severely curtailed.

(2) Optimum temperature for shoot germination and growth in terms of height of plant and fresh or dry weight production was about 30°C.

(3) Diurnal rhythm in temperature (6 degC rise and fall at 12-hourly intervals) had little effect on height of plants or dry weight production.

(4) Optimum temperature for growth of set roots shifts with age.

(5) A bimodal growth curve was obtained for set root growth over the temperature range 18–34°C. Weight of set roots produced at each temperature by intact sets and sets with buds excised was not significantly different.

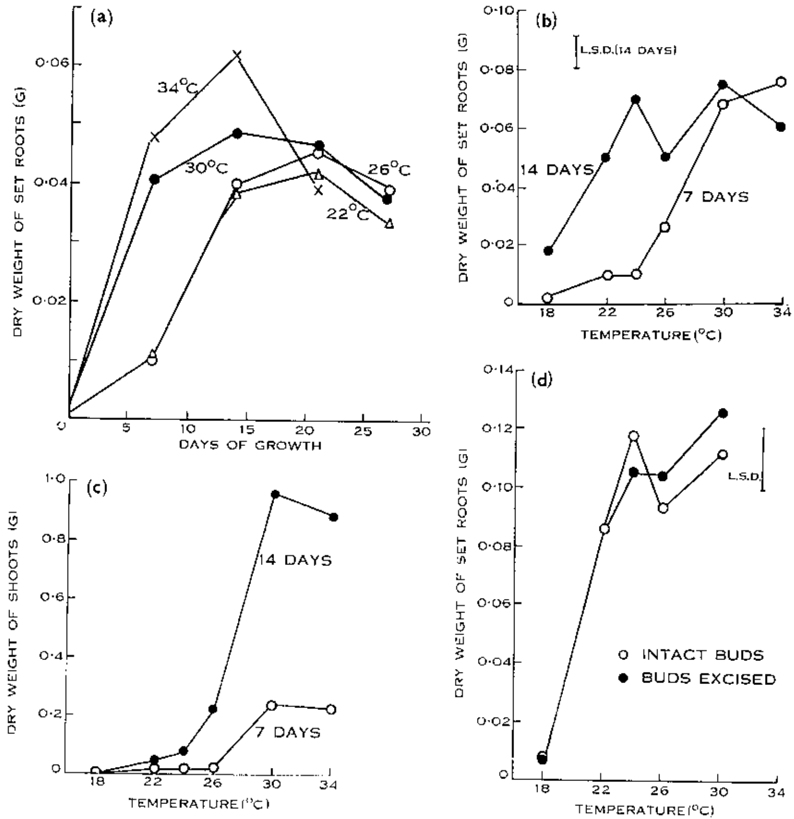

Fig. 2.—Germination in darkness. Bimodal effects of temperature on set root growth: (*a*) time course of development of set roots; (*b*) dry weight of set roots; (*c*) dry weight of shoots; (*d*) dry weight of set roots for intact plants and plants with buds excised prior to germination. L.S.D., least significant difference between means at 1% level.

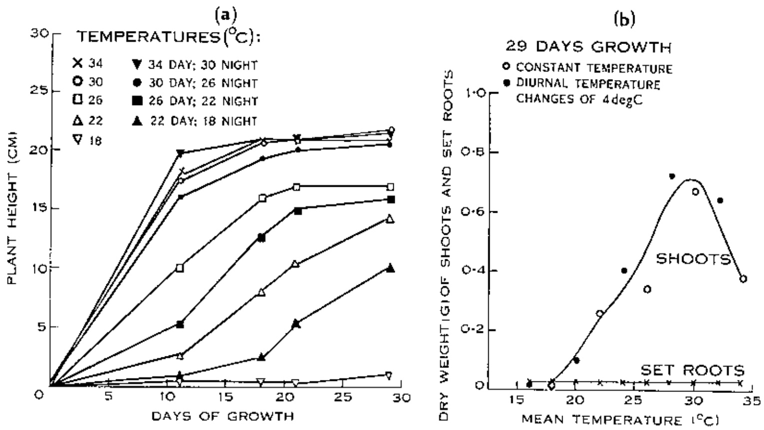

Fig. 3.—Germination in daylight. Effects of constant and diurnal temperature changes on (*a*) height of plants; (*b*) dry weight of shoots and set roots at 29 days from planting. For treatments which included a drop in temperature of 4 degC during the dark period, the mean of day and night temperatures is plotted.

(c) Effects of Constant and Alternating Temperature on Germination of Sets in Daylight

Experimental conditions were:

Light–dark cycles: 12 hr/12 hr.

Temperatures (°C): 34,34; 34,30; 30,30; 30,26; 26,26; 26,22; 22,22; 22,18; 18,18; 18,14.

Temperature cycles: 12 hr/12 hr.

Harvest: 29 days.

Measurements: height of plants; dry weights of shoots and set roots.

Results for measurements of plant heights (to top visible dewlap) at 11-, 18-, 21-, and 29-day intervals are presented in Figure 3(*a*). Dry weights of shoots and set roots (Fig. 3(*b*)) were determined at the 29-day interval. We conclude that:

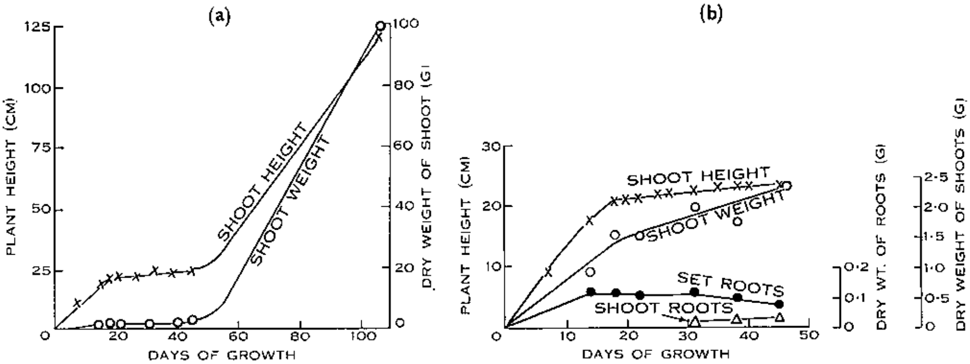

Fig. 4.—Germination and subsequent growth at 30°C in daylight: (*a*) shoot height and weight during development; (*b*) development of shoots and roots during the first 45 days.

(1) Rapid germination and high early growth rates in terms of height of plants occurred at elevated temperatures. A lag period followed during which plants growing at lower temperatures tended to catch up.

(2) Optimum temperature for production of dry weight for shoots was in the vicinity of 30°C. Significant effects of diurnal changes in temperature were not detectable.

(3) No significant effects of temperature were present on set root production at time of harvest.

(d) Time Course for Development at 30°C in Daylight

Experimental conditions were:

Light–dark cycles: 12 hr/12 hr.

Temperature: 30°C, constant.

Measurements: plant height was measured every 3 days and samples taken every 7 days for weight determinations. Dry weights of shoots, set roots, and shoot roots were recorded.

The results are presented in Figure 4. Three phases of growth were demonstrated:

(1) Rapid early growth for about 20 days for both height and weight.

(2) Virtual cessation of height growth, but continued increase in shoot weight.

(3) Resumption of a rapid growth rate after about 50 days.

Set root weight remained constant after 7 days, and began to decline after about 30 days. Shoot root growth was initiated at approximately 30 days.

TABLE 3

ANALYSIS OF VARIANCE OF EFFECTS OF TEMPERATURE AND DAY LENGTH ON TOTAL DRY WEIGHT PER PLANT

Source of Variance	Degrees of Freedom	Sum of Squares	Mean Square	F
Temperature	2	2210·87	1105·4	20·6**
Day length	2	3310·80	1655·4	30·8**
Replicates	7	829·71	118·5	2·2*
Interaction				
Temp. × day length	4	887·99	221·9	4·1**
Error	56	3009·0	53·7	
Total	71	10248·0		

* $P<0·05$. ** $P<0·01$.

(e) *Effect of Temperature and Duration of Photoperiod on Germination and Early Growth*

Experiment 1

Experimental conditions were:

Light–dark cycles: 8 hr/16 hr; 16 hr/8 hr; 24 hr/0 hr.

Temperatures (°C): 34,34; 34,30; 30,30.

Temperature cycles: 12 hr/12 hr.

Light source: artificial.

Average light intensity: $2·0 \times 10^5$ ergs/cm²/sec.

Harvests: 68 days.

Measurements: dry weight of leaves, shoots, roots; leaf area; total and reducing sugar content.

Table 3 shows analysis of variance for effects of temperature and duration of the light period on total dry matter production. Main and first-order interaction effects from the analysis of variance are presented graphically in Figure 5. Total dry matter production decreased as the temperature was raised from 30 to 34°C (Fig. 5(*a*)). Plants on a 34/30°C diurnal temperature cycle and 8, 16, or 24 hr of light produced dry matter as if they received 32°C constant temperature. Plants receiving 16 or 24 hr of light gave enhanced dry matter production compared to 8 hr of light (Fig. 5(*b*)). Maximum dry weight production was obtained with a 16-hr photoperiod and constant temperature of 30°C (Fig. 5(*c*)).

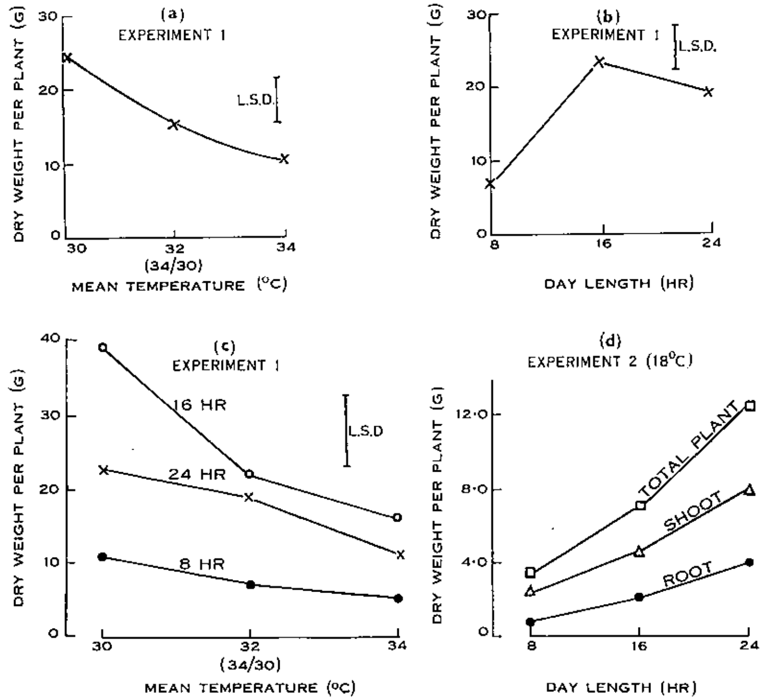

Fig. 5.—Germination under artificial light. Effects of temperature and day length on dry weight production. Charts for analysis of variance (expt. 1) of (*a*) main effects of temperature; (*b*) main effects of day length; (*c*) temperature–day length interaction; (*d*) main effects of day length at 18°C (expt. 2). L.S.D., least significant difference between means at the 1% level.

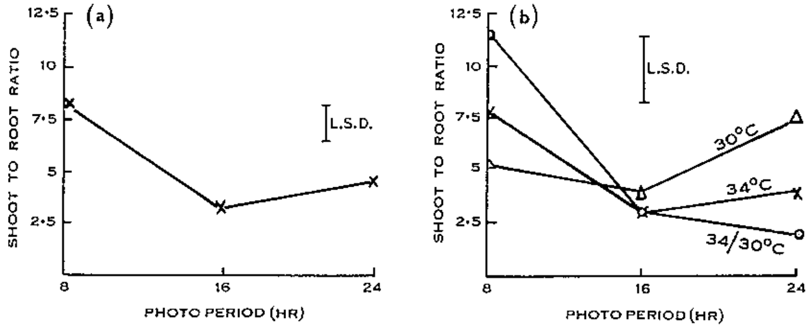

Fig. 6.—Germination under artificial light. Effects of temperature and day length on shoot to root ratios. Charts for analysis of variance on (*a*) main effects of day length; (*b*) temperature–day length interaction. The main effects of temperature were not significant. L.S.D., least significant difference between means at the 1% level.

The shoot : root ratio (dry weight) was enhanced on 8-hr photoperiods (Fig. 6(*a*)). The main effects of temperature were not significant but interaction of temperature and duration of photoperiod was observed on 8- and 24-hr photoperiods (Fig. 6(*b*)).

An index of temperature and day-length effects on the "leafiness" of the plants was obtained from the leaf area ratio (leaf area per unit plant dry weight). Temperatures between 30 and 34°C had only a minor affect on the leaf area ratio (Table 4—data from analysis of variance). Shortening the photoperiod to 8 hr gave a marked increase in the leafiness of the plants.

TABLE 4

EFFECT OF TEMPERATURE AND DURATION OF PHOTOPERIOD ON LEAF AREA

Main Effects	Leaf Area (cm)	Leaf Area Ratio*
Photoperiod (hr)		
24	1110	64·1
16	1438	56·4
8	866	118·4
Temperature (°C)		
34	742	70·0
34/30	1511	72·7
30	1136	63·3

* Leaf area per unit plant dry weight.

Analyses were made for total and reducing sugar content of the plants grown at 30°C (Table 5). Sugar content of stems and leaves (but not roots or leaf sheaths)

TABLE 5

EFFECT OF DURATION OF PHOTOPERIOD AT 30°C ON THE PRODUCTION OF REDUCING AND TOTAL SUGARS IN VARIOUS TISSUES

Duration of Photoperiod (hr)	Reducing Sugars (mg/g dry wt.)				Total Sugars (mg/g dry wt.)				Efficiency of Production*
	Stem	Leaves	Sheath	Root	Stem	Leaves	Sheath	Root	
24	52·3	3·0	7·5	5·0	119	30	30	5·0	0·038
16	210	4·6	15	7·0	336	45	60	7·0	0·10
8	46·5	1·5	7·5	5·0	105	15	30	5·0	0·003

* Ratio of total sugar to total dry weight of plant.

was affected by the duration of the photoperiod. Most sugar was obtained on a 16-hr day. This treatment also gave the highest efficiency of sugar production (total sugar/total dry weight of plant). Roots contained low levels of reducing sugars. No sucrose was detected by the analytical method.

Experiment 2

The same conditions were used as in the first experiment, but the plants were grown at 18°C. Plants were harvested after 70 days. Sugars were not determined.

In contrast to the first experiment, highest dry weight production was attained under constant light (Fig. 5(*d*)). Dry matter production increased linearly with day length from 8 to 24 hr. The maximum dry weight at 18°C was only 30% of that produced at 16 hr and 30°C in experiment 1. The effect of day length on the shoot to root ratio was not as marked as in the first experiment, the ratio being 2·0 for 16- and 24-hr photoperiods and 3·0 for an 8-hr photoperiod.

(*f*) *Effects of Temperature on Germination of* Saccharum *spp. in Darkness*

Experimental conditions were:

Temperatures (°C): 10, 16, 22, 28, 34, 40.

Harvest: 14 days.

Measurements: dry weights of shoots and roots.

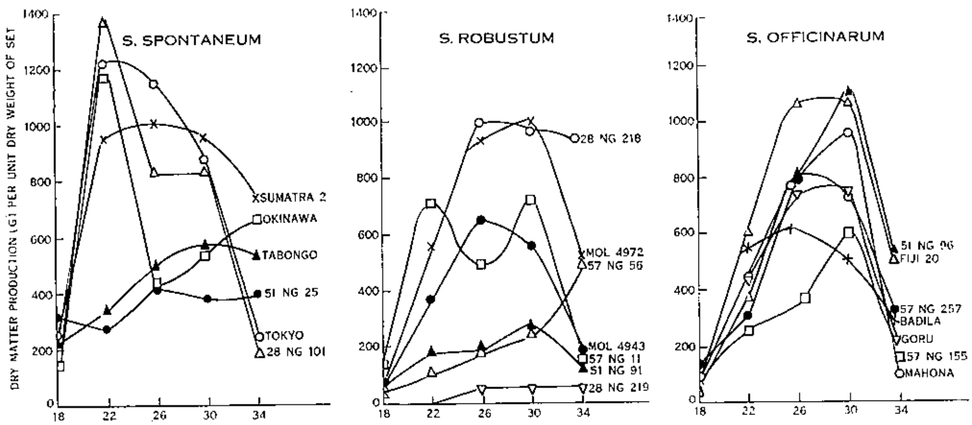

Fig. 7.—Effects of temperature on germination in darkness of varieties of *Saccharum* spp.

Seven varieties from each of the species *S. spontaneum*, *S. robustum*, and *S. officinarum* were compared. Six replicates for each variety were used. *S. spontaneum* varieties used included four collected in the tropics and subtropics and two from the temperate zone. *S. robustum* varieties were from New Guinea and *S. officinarum* from New Guinea and Fiji.

An analysis of our data revealed the yield of dry matter was linearly related to the initial weight of the cutting. To remove the effect of differences in stalk diameter the results have been expressed as dry matter per unit weight of cutting. Results for individual varieties are shown in Figure 7 and pooled data of varieties within species are given in Figure 8.

The pooled data for each species indicate a wider temperature tolerance in *S. spontaneum* than *S. robustum* or *S. officinarum*. No germination occurred in any variety at 10°C. The highest temperature used (40°C) was deleterious for all varieties. Genetic variability for temperature effects on germination was greatest for *S. spontaneum* and least for *S. officinarum*, with *S. robustum* occupying an intermediate position.

IV. Discussion

(a) *Water Requirement for Germination*

King (1934) and Van Dillewijn (1952) showed that pre-soaking of sets gave variable response but was generally beneficial. Glasziou (1958) divided stalks into single bud sets and placed them in an atmosphere saturated with water vapour. Buds and set roots developed in some sets but not others, there being no apparent relationship with the position the set occupied in the original stalk.

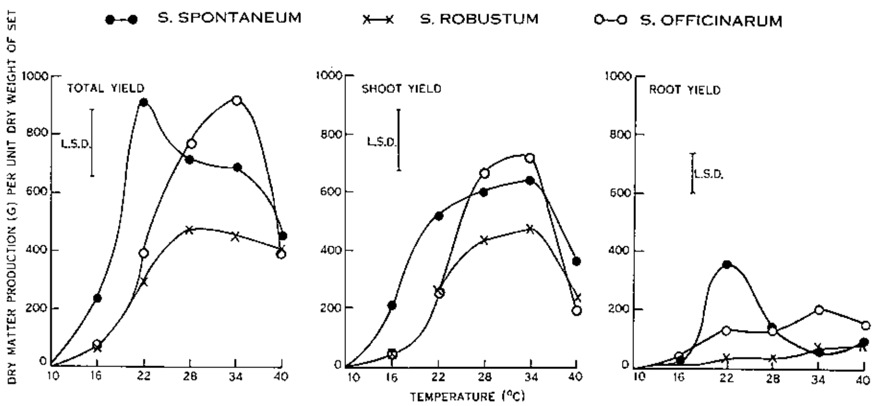

Fig. 8.—Effects of temperature on germination in darkness on *Saccharum* spp.—pooled data from Figure 7. Analysis of variance showed that species differences were significant at the 1% level. L.S.D., least significant difference of means at 1% level.

In our experiments all sets cut from irrigated cane stalks and planted immediately germinated without an external water supply. Water and metabolites within the set were sufficient for development of set roots, but growth of shoots was retarded. External water is, of course, required for further development. The set roots desiccate beyond recovery within 14 days. Pre-soaking of sets had no effect on germination or subsequent growth. We conclude that the water status of the plant prior to cutting for new planting material is a major factor in subsequent germination.

(b) *Temperature Effects on Germination*

The general patterns of development for shoots and set roots from newly planted cuttings show that each has an inherent but limited potential for development. The effect of temperature is on the rate of attainment of that potential. After fulfilling their inherent potential the set roots senesce. However, shoots produce adventitious roots which confer independence from the set and reprieve from a similar fate to the set roots.

Using seven varieties of canes from each of three species of *Saccharum*, we obtained a linear relationship ($r = 0 \cdot 67$) between initial set weight and dry weight of shoots and roots 14 days from planting. After 5 weeks (when shoot roots had developed) this relationship had broken down. Hence the potential for development of set roots prior to senescence and shoots prior to attainment of independence is a function of the nutrient available from the set.

A peculiar bimodal effect of temperature on the production of set roots was observed on the hybrid variety Pindar. Two optima are sometimes observed, one at 20–25°C and a second at 28–32°C. At other times a plateau rather than an optimum

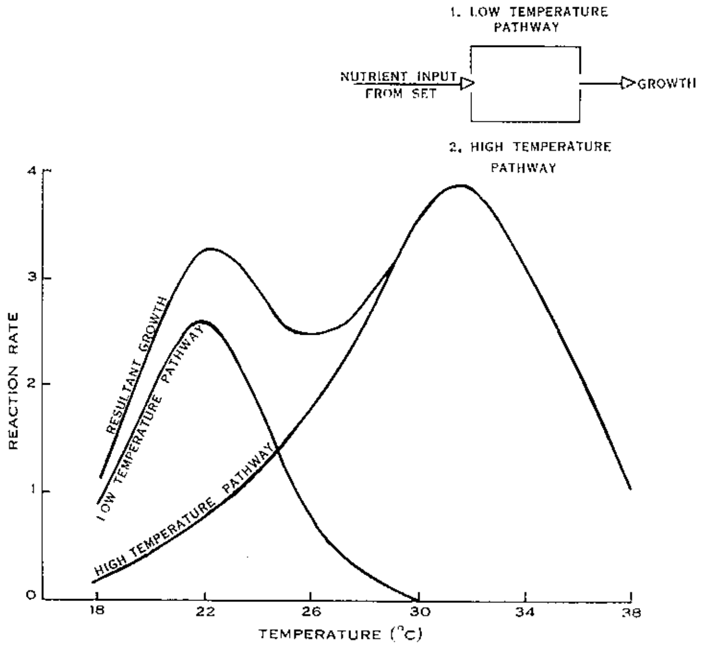

Fig. 9.—Diagram illustrating temperature effects on growth which is limited by the supply of an essential metabolite. Parallel pathways for synthesis of the metabolite have different temperature optima.

is seen at the lower temperature range. Our results indicated that competition by shoots and set roots for a common pool of metabolites did not account for this effect. A model system which assumes parallel pathways for synthesis of a metabolite essential for growth is illustrated in Figure 9. One pathway has a temperature optimum at about 20°C and the second at about 30°C. We assume that the low-temperature pathway predominates for set root growth in the *S. spontaneum* varieties we have examined, and that the high temperature pathway predominates for *S. officinarum* so that hybrids of these species such as Pindar exhibit a composite response pattern. We think it possible that similar effects of temperature on the normal root system may account for the marked repression of growth of *S. officinarum*-type canes when root temperatures are lowered to 17°C. Air temperatures have very much less effect than root temperatures (cf. Reports of Hawaiian Sugar Planters' Experiment Station for 1959 and 1960). In contrast all *S. spontaneum* varieties in our collection grow well at root temperatures in the range 15–20°C.

No significant changes in growth rates have been observed in treatments involving diurnal temperature fluctuations. Germination and growth approximated that expected for the mean temperature. Constant light was deleterious for dry weight production at a temperature of 30°C. However, at 18°C constant light gave the largest amount of dry matter. Hence we have no evidence to indicate that growth processes in cane are coupled to endogenous circadian rhythm.

V. Acknowledgment

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VI. References

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