PHYSIOLOGY OF SUGAR-CANE

VII. EFFECTS OF TEMPERATURE, PHOTOPERIOD DURATION, AND DIURNAL AND SEASONAL TEMPERATURE CHANGES ON GROWTH AND RIPENING

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Summary

Independent and interaction effects of day and night temperature, photoperiod duration, and diurnal thermoperiodicity were studied on sugar-cane grown under controlled environments. During the first 3 months of growth, day and night temperature effects were mainly additive, but at 6 months the interaction effects of all variables were numerous and complex. Many of the interaction effects could be attributed to increased responses to constant-temperature regimes with a 12-hr photoperiod. No evidence for thermoperiodicity requirements was found.

Sugar production per plant and sugar concentration in the stalk were highest at the optimum temperature (30°C) for dry matter production. Sugar concentration did not exceed 12% fresh weight when temperatures were maintained constant or when diurnal variations were given. However, when the temperature was varied on a relatively long-term basis, high sugar levels (17% of fresh weight) were attained by moving plants from high to low temperature. Sugar loss was incurred for the reverse situation. The results are discussed in relation to the ripening process in sugar-cane.

I. Introduction

Studies of temperature effects on growth and ripening of sugar-cane have given rise to the concept that growth at high average temperatures is conducive to development of a crop yielding a high weight of cane per acre but with low sugar content (van Dillewijn 1952). However, conflicting results obtained by different workers leave some doubt as to the validity of this generalization.

Field data from Taiwan (Sun and Chow 1949) and Hawaii (Clements, Shigeura, and Akamine 1952) show a positive correlation between the rate of stem elongation and both mean monthly minimum and maximum temperatures. For the Taiwan data the first and second orders of partial correlation coefficients for response to mean monthly minimum temperature were much larger than for mean monthly maximum temperature, which could be taken to indicate that temperature during the dark period is more important in controlling stem elongation. A negative correlation was obtained between sugar content and mean monthly minimum temperature.

Interpretation of field results is complicated in that high average temperatures are experienced when the day lengths are longest, and, for many areas, when the rainfall is greatest. The stage of development of the crop also affects results as the response of the plant to external factors decreases with age (Borden 1945). Shaw (1953) analysed data from a large number of cane-growing areas and found little

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correlation between the sucrose concentration in cane juice and the ratio of summer to winter temperature when the ratio was between 1·0 and 1·3, while above 1·3 the

TABLE 1

ANALYSIS OF VARIANCE FOR DAY AND NIGHT TEMPERATURE EFFECTS ON DRY WEIGHT PRODUCTION, STALK LENGTH, NODE NUMBER, TILLER NUMBER AND WEIGHT, AND STALK DIAMETER AT 106-DAY HARVEST INTERVAL

Experiment 1

Source of Variation	Degrees of Freedom	*F* Ratios							
		Total Dry Weight	Stalk Length	Stalk Dry Weight	Leaf Dry Weight	Node No.	Tiller No.	Tiller Fresh Weight	Stalk Diameter
Day temperature (*T*)	4	22·9**	38·9**	48·1**	42**	17·1**	16·3**	6·1**	7·2**
Night temperature (*t*)	4	10·7**	12·6**	9·5**	8·6**	25·8**	n.s.	n.s.	8·8**
$T \times t$ interaction	16	n.s.†	2·83**	n.s.	n.s.	n.s.	n.s.	1·8*	n.s.
Error‡	75	0·033	0·035	0·116	0·018	1·28	1·33	336	0·056

* $P < 0·05$. ** $P < 0·01$. † n.s., not significant.
‡ Values in this line are error mean squares.

TABLE 2

ANALYSIS OF VARIANCE FOR DAY AND NIGHT TEMPERATURE EFFECTS ON DRY WEIGHT PRODUCTION, STALK LENGTH, NODE NUMBER, TILLER NUMBER AND WEIGHT, AND STALK DIAMETER AT 209-DAY HARVEST INTERVAL

Experiment 1

Source of Variation	Degrees of Freedom	*F* Ratios							
		Total Dry Weight	Stalk Length	Stalk Dry Weight	Leaf Dry Weight	Node No.	Tiller No.	Tiller Dry Weight	Stalk Diameter
Day temperature (*T*)	4	9·0**	16·4**	12·7**	12·6**	14·9**	n.s.†	3·8*	3·6**
Night temperature (*t*)	4	4·7*	6·1**	5·7**	8·2**	32·2**	2·8*	n.s.	n.s.
$T \times t$ interaction	16	9·1**	2·0*	6·0**	5·0**	4·5**	n.s.	4·0**	4·2**
Error‡	125	0·011	0·005	0·04	0·006	2·98	1·44	328	0·058

* $P < 0·05$. ** $P < 0·01$. † n.s., not significant.
‡ Values in this line are error mean squares.

sugar content fell. These results are contrary to the notion that low temperature promotes sucrose content. Furthermore there was no consistent relationship between

TABLE 3

ANALYSIS OF VARIANCE FOR DAY AND NIGHT TEMPERATURE EFFECTS ON SUGAR CONTENT OF STALKS AND LEAVES

Experiment 1

Source of Variation	Degrees of Freedom	*F* Ratios			
		Sugar in Stalks		Sugar in Leaves	
		106 Days	209 Days	106 Days	209 Days
Day temperature (T)	4	20·5**	26·3**	8·7**	33·3**
Night temperature (t)	4	4·7*	n.s.†	n.s.	4·2*
$T \times t$ interaction	16	3·1**	n.s.	8·9**	n.s.
Error‡	25	1·599	0·0015	38	0·0002

* $P < 0·05$. ** $P < 0·01$. † n.s., not significant.

‡ Values in this line are error mean squares.

TABLE 4

ANALYSIS OF VARIANCE FOR DAY AND NIGHT TEMPERATURE, PHOTOPERIOD DURATION, AND DIURNAL TEMPERATURE CYCLE EFFECTS ON DRY WEIGHT PRODUCTION, STALK LENGTH, NODE NUMBER, STALK DIAMETER, TOTAL SUGAR PER PLANT, AND SUGAR PER 100 G FRESH WEIGHT OF PRIMARY STALKS AT 200-DAY HARVEST INTERVAL

Experiment 2

Source of Variation	Degrees of Freedom	*F* Ratios					
		Total Dry Weight	Stalk Length	Node No.	Stalk Diameter	Sugar per Plant	Stalk Sugar Concentration
Day temperature (T)	2	n.s.†	n.s.	7·9**	n.s.	n.s.	n.s.
Night temperature (t)	1	n.s.	7·0*	32·9**	n.s.	n.s.	n.s.
Photoperiod duration (H)	2	33·3**	10·5*	4·9*	28·9**	16·4**	250**
Diurnal temperature cycle (h)	1	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Interactions‡							
$T \times t$	4	n.s.	n.s.	n.s.	n.s.	n.s.	7·3*
$t \times H \times h$	2	n.s.	n.s.	n.s.	n.s.	3·3*	n.s.
$T \times H \times t$	4	13·0**	9·0*	n.s.	7·7**	32·4**	n.s.
$T \times H \times h$	2	n.s.	n.s.	n.s.	n.s.	7·9**	n.s.
$T \times H \times t \times h$	4	n.s.	3·0*	n.s.	n.s.	n.s.	4·5**
Error§	105	1·946	34	11	0·04	233	0·274‖

* $P < 0·05$. ** $P < 0·01$. † n.s., not significant.

‡ Only interactions for which significant effects were obtained are shown.

§ Values in this line are mean squares.

‖ 36 degrees of freedom.

sucrose content and the altitude of the growing area ranging from sea level to 1300 ft for 53 areas in Mexico. Shaw concluded that sugar concentration is an inherent function of latitude, reaching peak values at 18° north and south latitudes, and suggested that the causal agency was the day length during the critical period of crop maturation rather than temperature *per se*.

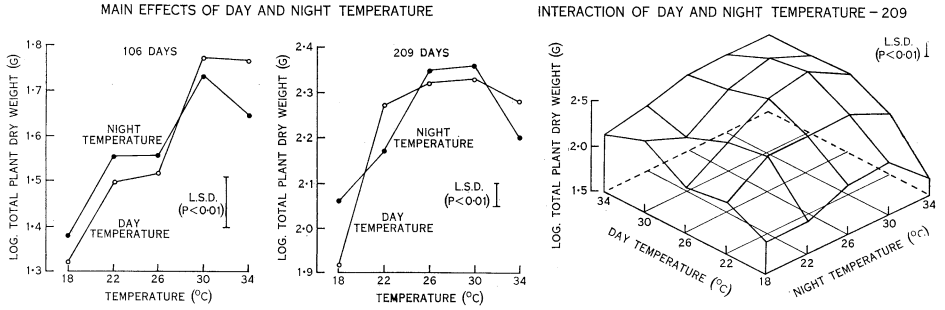

Fig. 1.—Effects of day and night temperature on dry weight production. Experiment 1.

Shading experiments at the Hawaiian Sugar Planters' Experiment Station (see Annual Report for 1961) have shown that growth of cane in the field increases as the light intensity is increased up to full sunlight. Compared with shaded plants, growth in full sunlight gave thicker but shorter stalks, broader and greener leaves, and a greater rate of tiller production (Martin and Eckart 1933). Day length effects have been demonstrated by Borden (1937) in that plants exposed all day to full

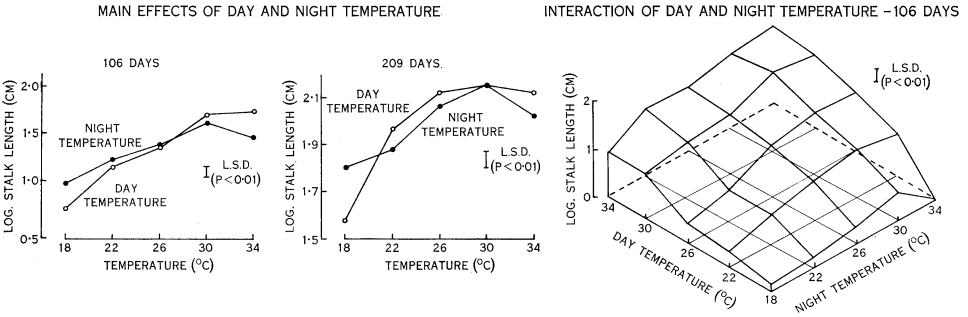

Fig. 2.—Effects of day and night temperature on stalk length. Experiment 1.

sunlight produced more dry matter than plants exposed until noon or from noon to sunset, the actual increase being affected by the amount of fertilizer applied. These results show that light intensity and duration of the photoperiod must also be considered when attempting to evaluate the effects of temperature on the plant.

The studies described in this paper were conducted under controlled environmental conditions to establish with greater certainty the independent and interaction effects of day and night temperatures and duration of photoperiod on growth, development, and ripening of the cane plant.

II. Materials and Methods

(a) *Growth Conditions*

Uniform one-bud sets from top internodes of cv. Pindar were germinated and grown in vermiculite in 2-gallon containers and watered daily, once with complete nutrient solution and once with de-ionized water. The containers were placed on trucks, four to each truck. Growth of all treatments, which commenced in March 1962,

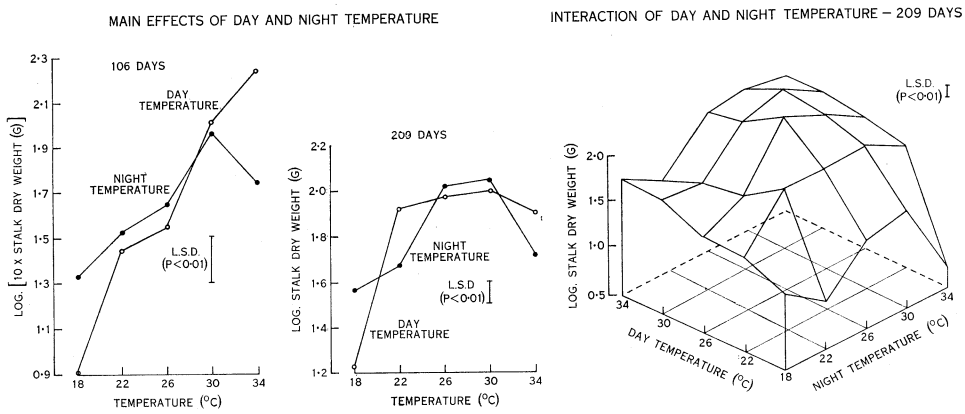

Fig. 3.—Effects of day and night temperature on stalk dry weight production. Experiment 1.

occurred under natural daylight in controlled environment greenhouses. All temperature and photoperiod changes were brought about by shifting trucks to the appropriate greenhouse or constant-temperature darkroom. Differences due to locations within a greenhouse were randomized by daily movements and rotation of trucks.

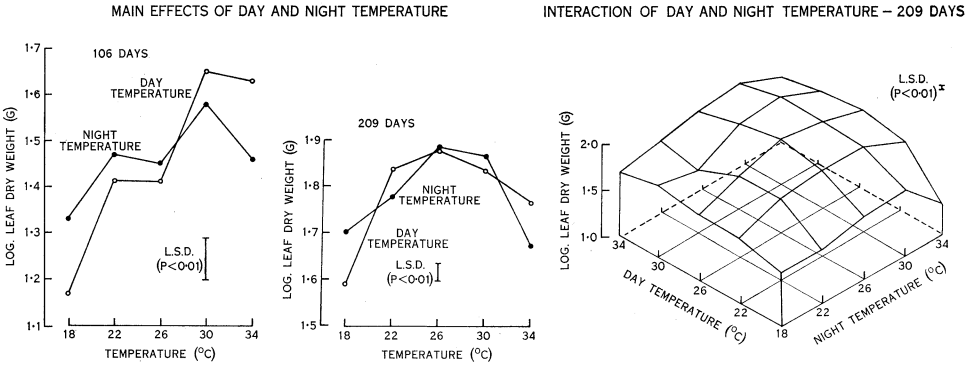

Fig. 4.—Effects of day and night temperature on leaf dry weight production. Experiment 1.

The phytotron system used is described in the 1964 Annual Report of this Institution and is essentially the same as in the Earheart Phytotron (Went 1957). The use of four single plant replications grown on the same truck was considered justified because of the high degree of environmental control, the randomization of position effects, and the lack of genetic variation in asexually propagated planting

material. Confirmation of this assumption was provided by the similarity of error mean square terms obtained at the 106- and 209-day harvests of experiment 1 as the latter harvest involved six replicate plants, three on each of two trucks. Lack of significance of the third-order interaction term in experiment 2 also supported the basic assumption as it provided an estimate of between-truck variation.

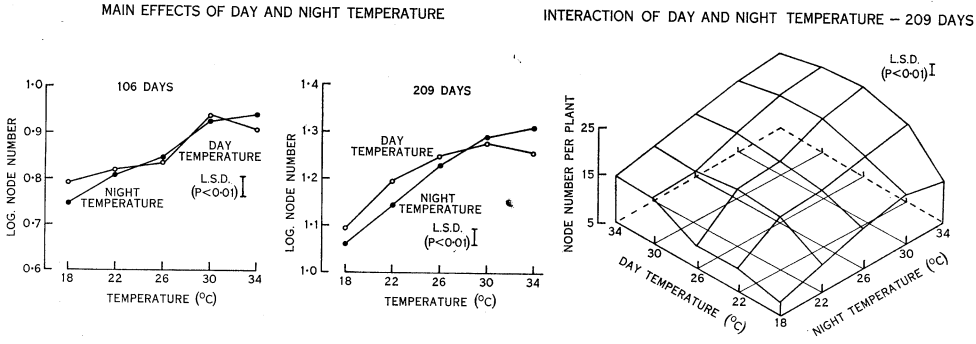

Fig. 5.—Effects of day and night temperature on number of nodes per stalk. Experiment 1.

(b) *Conditions for Experiment 1*

Five day and five night temperatures from 18°C to 34°C at 4-degree intervals were used in all combinations, temperature changes occurring at 12-hourly intervals. There were four replicates per treatment for the first harvest interval at 106 days, and six for the second at 209 days. A third harvest was made at 290 days on plants grown at constant temperature only, with four replicates per treatment.

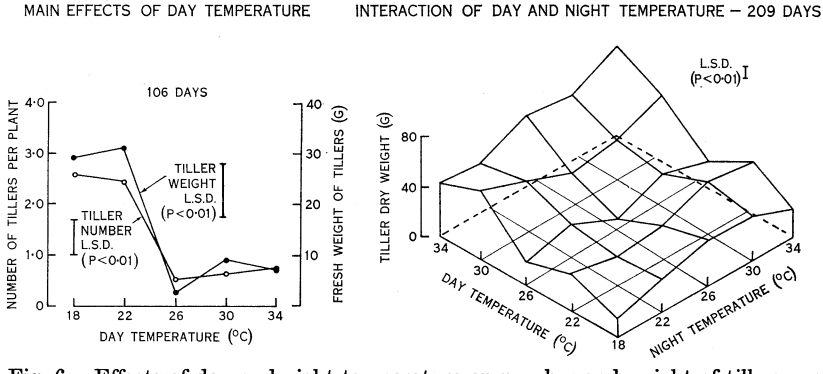

Fig. 6.—Effects of day and night temperature on number and weight of tillers per plant. Experiment 1.

(c) *Conditions for Experiment 2*

In this experiment plants were grown at all combinations of three day and night temperatures (22, 26, and 30°C) with either an 8- or 12-hr photoperiod given from 0800–1600 or 0600–1800 hr. Temperature changes were made on an 8/16 or 12/12 hourly cycle with changes at 0800 and 1600 hr or 0600 and 1800 hr, respectively. Each treatment contained four replicates and plants were harvested after 200 days.

(*d*) *Sampling Methods*

Fresh weight of the whole plant (including tillers but excluding roots) was recorded, and then, individually, fresh weight of tillers, stem, and leaves plus leaf

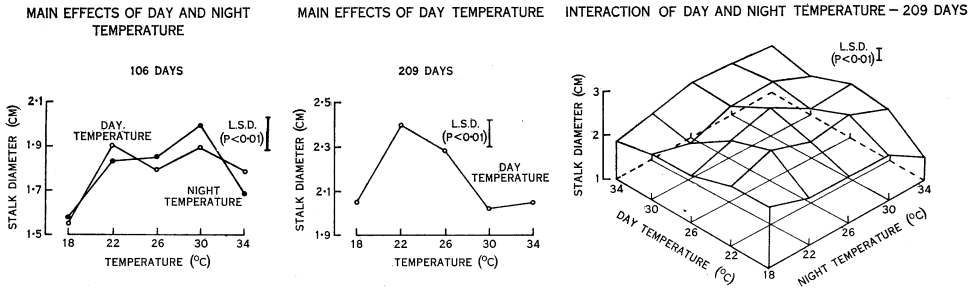

Fig. 7.—Effects of day and night temperature on diameter of stalks. Experiment 1.

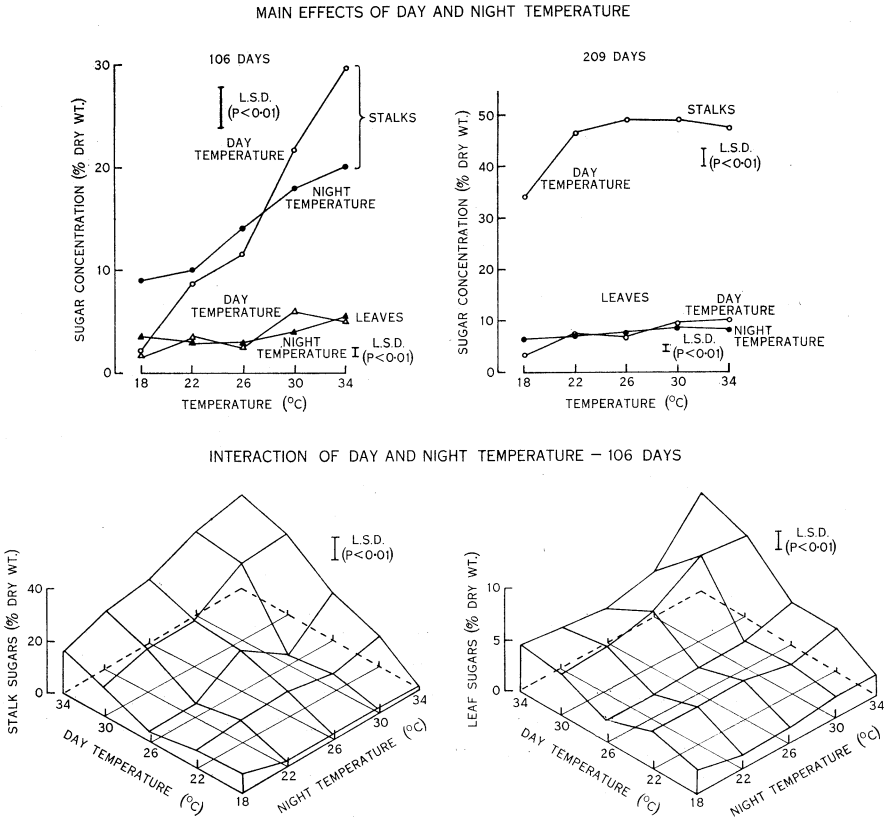

Fig. 8.—Effects of day and night temperature on sugar concentration in stalks and leaves. Experiment 1.

sheaths. Counting of nodes commenced with the pair encompassing an internode exceeding 0·5 cm in length. Stalk length was measured from base to apical meristem.

Mean internode length was calculated by dividing stalk length by node number minus 1. Mean stem diameter was also measured.

The plant parts were oven-dried at 70°C, reweighed, and immediately ground in a 5-in. laboratory mill. The ground samples were sealed in plastic bags and stored for sugar analysis.

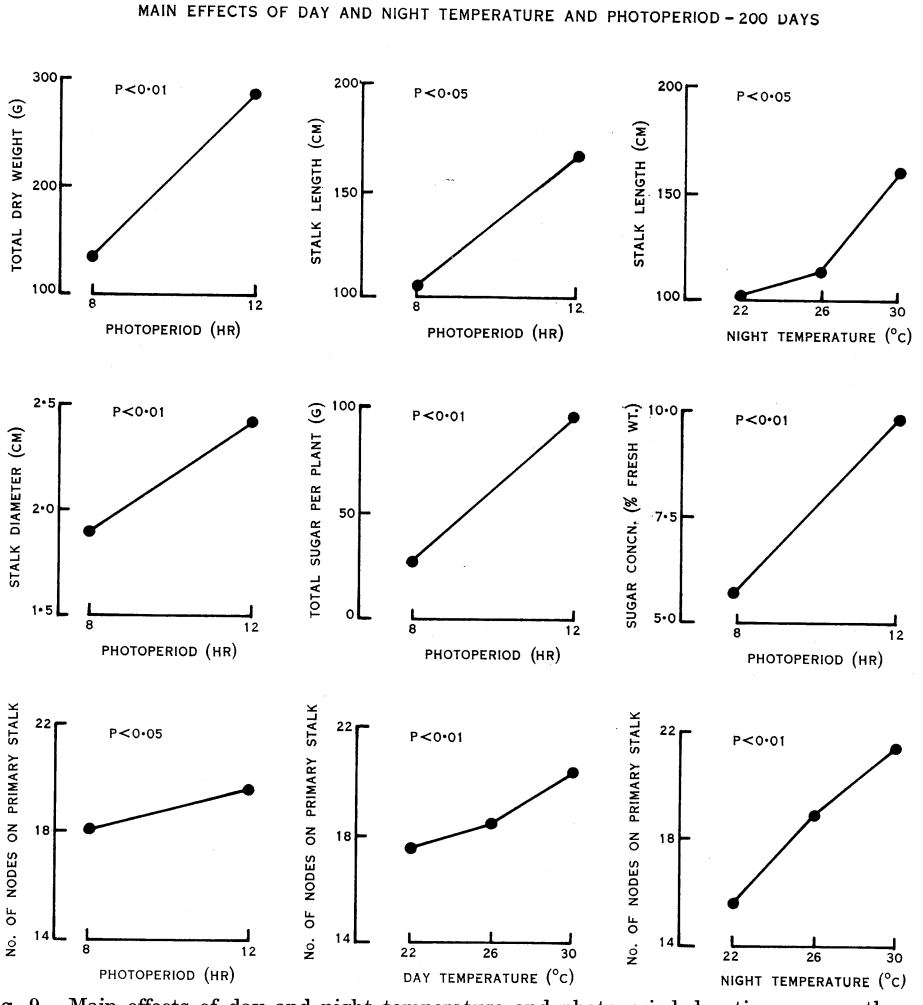

Fig. 9.—Main effects of day and night temperature and photoperiod duration on growth and development of cane. Diurnal temperature cycles did not attain significance as a main effect for any of the characters measured. Experiment 2.

(e) *Sugar Analysis*

The material from half of the replicates was bulked, prior to grinding, to give two samples per treatment. Total sugars were determined in stem and leaf tissue. The oven-dry material was extracted for 5 days with 70% ethanol, and the sugars in the ethanolic extract determined as previously (Hatch and Glasziou 1963).

(*f*) *Data Processing*

For experiment 1 at the first harvest interval at 106 days, transformation of some of the measurements to logarithms shows approximately linear responses to day and night temperatures from 18 to 30°C. Where applicable these transformations have been made and for continuity have also been used for the later harvest interval. All results were subjected to analysis of variance and the data presented are taken from these analyses. In general, first- and second-order interaction effects have been presented in graphical form only when these attained significance at the 1·0% level. Significance of main effects and interactions was determined by testing against significant higher-order interactions containing the variables in question. Analyses of variance on data are presented in Tables 1–3 for experiment 1, and in Table 4 for experiment 2.

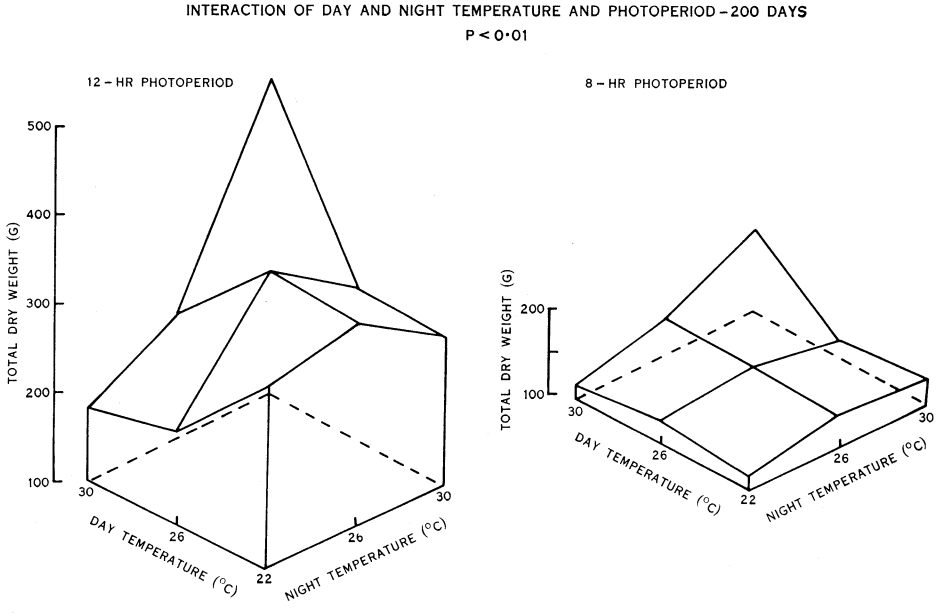

Fig. 10.—Interaction effects of day and night temperature and photoperiod duration on dry weight production. Experiment 2.

III. Results and Discussion

Sugar-cane is thought to have evolved on the flood plains and adjacent areas of the coastal rivers of New Guinea (Brandes 1958). In these areas the average maximum temperature is about 32°C and the minimum about 23°C. Temperatures rarely rise above 34°C or fall below 22°C. Seasonal variations are small between the cooler and warmer months, the range being about 3 degC, and there is only a difference of about 30 min between the extreme times of sunrise and sunset during the course of the year.

Our studies show that with a natural photoperiod, there are virtually no interaction effects of 12-hourly changes of day and night temperature on growth and development during the first 3 months (Table 1; Figs. 1–8). However, significant interaction effects were observed for the next 3-month period, much of which was attributable to the favourable responses obtained at constant temperatures, and

particularly at 22, 26, and 30°C. The constant-temperature effect was much reduced when the photoperiod was decreased to 8 hr [Figs. 9, 10, 11, 12(*a*)], and except for certain combinations for which no general pattern is evident [Figs. 12(*b*), 12(*c*)], there was almost no effect of varying the photoperiod and thermoperiod cycles in or out of phase with one another. In view of the constancy of the natural environment where sugar-cane evolved, it is perhaps not surprising that it grows well under controlled constant-temperature regimes. However, this is in sharp contrast with many other plants which show a requirement for thermoperiodicity (Went 1961).

The stalk is the storage organ for sugar in the sugar-cane plant. For illustrative purposes the time course of development of the stalk may be divided into four characteristic stages: germination, juvenile, and early and late adult stages, the latter being terminated either by onset of flowering or senescence.

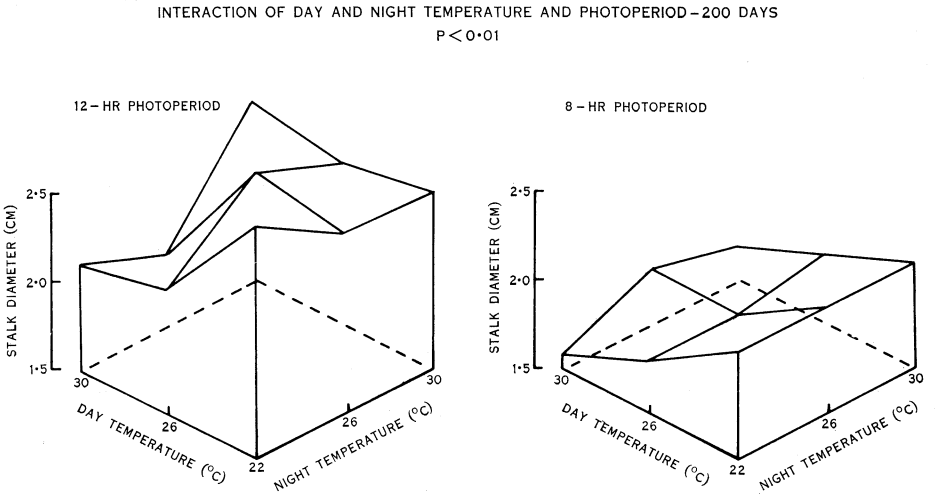

Fig. 11.—Interaction effects of day and night temperature and photoperiod duration on stalk diameter. Experiment 2.

Environmental effects on the germination stage have been described previously (Whiteman, Bull, and Glasziou 1963). Time courses for development of the primary stalk at temperatures from 18 to 30°C are shown in Figure 13. The shape of these curves is mainly determined by the effect of temperature on the rate of increase of leaf area and not on the rate of photosynthesis, since direct measurements made in full sunlight show that photosynthesis per unit leaf area is virtually independent of temperature over the range from 9 to 34°C (Waldron and Glasziou, unpublished data). During the juvenile stage the optimum temperature for plant and stalk growth is about 30°C (Figs. 1–3). As plants approach the early adult stage the leaf area per stalk tends to a constant value, the rate of production of new leaves being balanced by the senescence of old leaves. At this stage, the rate of stalk development also tends to a constant value which is independent of temperature, but as the stalk matures further the rate decreases. Thus stalks maintained at 22°C enter early adult stage at about 200 days, attaining a growth rate between 200 and 300 days which is approximately equal to the maximum rate attained at 30°C (Fig. 13). Direct

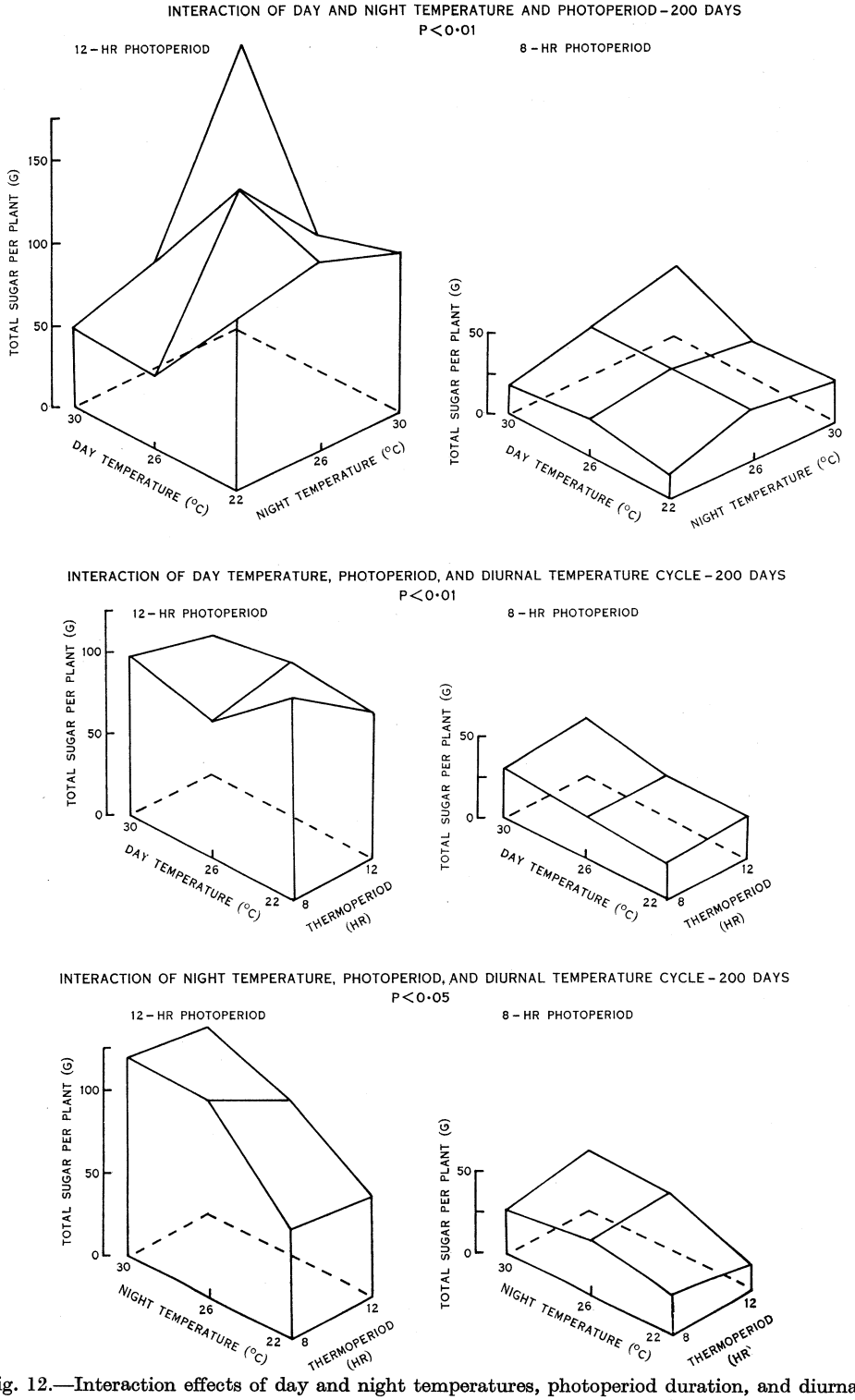

Fig. 12.—Interaction effects of day and night temperatures, photoperiod duration, and diurnal temperature cycle on total sugar per plant.

comparison of 106- and 209-day data show an apparent shift downwards in the optimum temperature for growth as the age of the plant increases (Figs. 1–3). This effect appears to be entirely due to the use of a chronological rather than a physiological time scale. For example stalk growth at 18°C constant temperature compared with 30°C gave a ratio of 0·034 during the first 106-day interval, 0·23 during the second 103 days, and 1·09 during the next 81 days. For the last period, plants at 18°C had just entered the early adult stage whereas those at 30°C were in the late adult stage.

For the two experiments so far reported the temperature and photoperiod regimes constituting each treatment were maintained throughout the whole growth period. Under such conditions, environments which gave the highest rate of dry

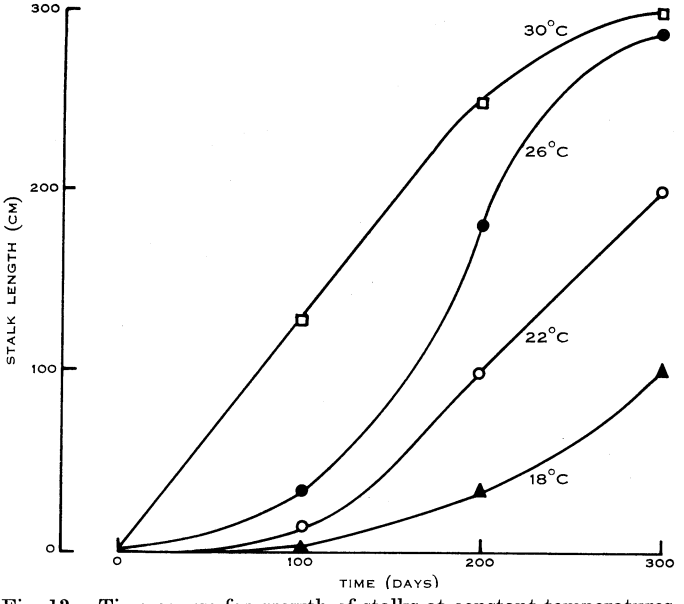

Fig. 13.—Time course for growth of stalks at constant temperatures.

matter production also gave the most sugar per plant and the highest sugar content on a dry weight basis (Figs. 1, 8, 9, 12). The sucrose content reached a maximum value in the stalk of about 12% fresh weight at 6 months of age and did not increase substantially over the next 3-month interval. Continuous growth at low temperature, or with diurnal changes including high day and low night temperature, or the reverse, did not result in higher sugar contents than obtained at 30°C constant temperature.

An explanation for sugar contents of 12–20% of fresh weight often observed in the field comes from studies in which plants raised in the field during the wet summer season (average temperature 26°C) were transferred to controlled environments and watered well. A negative correlation was obtained between the rate of stalk elongation and the rate of change of sugar content (Hatch and Glasziou 1963). In a similar experiment the sucrose content of plants placed at 17°C increased from 10 to 17% fresh weight during the first 90 days after which it declined slowly (Fig. 14).

Some of the plants which had attained high sucrose level were transferred to 30°C constant temperature, upon which an exceedingly high rate of stalk elongation was observed, accompanied by a rapid decline in sucrose content to 6·5% fresh weight after 35 days. When these plants were returned to 17°C constant temperature, stalk elongation virtually ceased and sugar storage was resumed. Hence we reject the notion that short-term (diurnal) variations in temperature are conducive to sugar storage except that they be accompanied by an overall long-term change in average temperature akin to the seasonal variations experienced under field conditions.

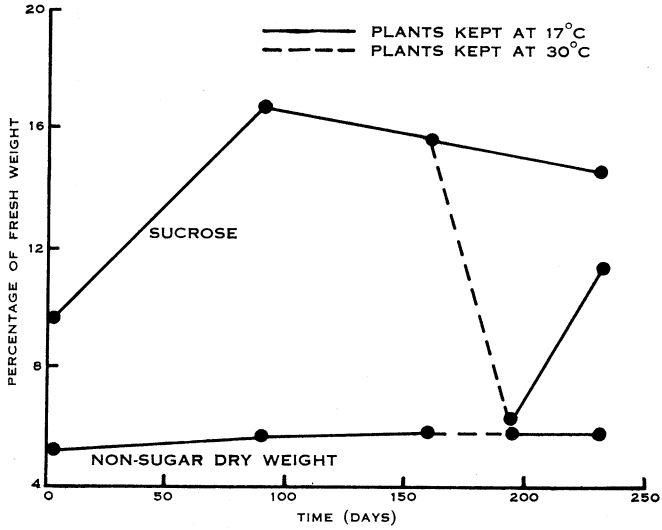

Fig. 14.—Changes in sugar contents of cane stalks in response to long-term changes in temperature for growth. Plants were raised under field conditions for 4 months at an average temperature of 26°C, then transferred to a constant-temperature greenhouse at 17°C. After 160 days of this treatment, some plants were treated for 35 days at 30°C, then returned to 17°C.

We suggest that the peak values for the sucrose concentration in cane juice at 18° north and south latitudes observed by Shaw (1953) are due to an optimum combination of seasonal temperature and day-length variations. At latitudes closer to the equator the temperature variation is too small, and at higher latitudes the day lengths during the winter period are too short.

IV. Acknowledgments

The authors are indebted to Dr. W. O. McCarthy, University of Queensland, and Mr. K. P. Haydock, Division of Tropical Pastures, CSIRO, for assistance with experiment design and statistical treatment of results.

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