

Natural Season-long and Diurnal Temperature Effects on Lettuce Seed Production and Quality

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Abstract. We investigated the effects of variation in ambient air temperature on seed production in the field during the reproductive development phase of ‘Salinas’ head-type lettuce (*Lactuca sativa* L.) in the central San Joaquin Valley of California where daytime maxima may exceed 38C for many consecutive days during reproduction. Florets were tagged daily for 41 days and harvested seeds were sampled to determine temperature-sensitive periods during seed development. The number of seeds per inflorescence (NOS), seed mass (SM), and seedling root length (SRL) were reduced and percentage germination (GERM) increased with increasing minimum (LT) and maximum (HT) temperatures. Daily HT > 35C greatly reduced NOS. Increasing LT reduced SM and SRL, but to a lesser extent than NOS ($r^2 = 0.23$ and 0.40 ; $P = 0.01$ and 0.001 , respectively). The advantage of increasing HT on GERM ($r^2 = 0.20$; $P = 0.01$) was overshadowed by the severe reduction in NOS and the vigor components SM and SRL. The periods of greatest sensitivity to high air temperature for NOS, SM, GERM, and SRL were - 1 to +1, - 4, +1, and - 4 to - 3 days from anthesis, respectively. The hours of peak sensitivity for these variables occurred during the same days at - 36, - 101, + 15, and - 83 hours from anthesis, respectively. Using Box-Jenkins time series analysis, diurnal periodicity in temperature sensitivity for the four variables was determined.

The lettuce inflorescence has a cymose cluster of flower heads with the oldest at the terminal end of the main axis (Hayward, 1938). Terminal buds on lateral branches flower first, but no other inflorescence positions are related to flowering time (Soffer and Smith, 1974a). The developmental biology of lettuce from the time of pollination through seed maturity has been investigated in detail” (Jones, 1927). Lettuce flowers open for no more than 2 h. Pollination and fertilization occurred in <6 h, with pollination beginning at 0800 HR and fertilization of the embryo sac beginning at 1100 HR and finishing by 1400 HR. Seeds were mature 12 days after pollination. The rate of flowering and rate of seed maturity through the flowering period are regulated by temperature (Gray et al., 1988; Jones, 1927). The effect of temperature on rate of flowering in the field is more pronounced during the early, than late period of flowering (Jones, 1927). The rate of inflorescence development increases as temperature increases (Gray et al., 1988).

Air temperatures to which the mother plant is exposed during the season-long period of flowering may vary and therefore have a differential effect on the quality of the sum amount of seed produced through the season. Under short daylength conditions, good seed set in lettuce occurs when nights are between 17 and 23C (Keller, 1962). In California, most lettuce seed is now grown in the central San Joaquin Valley (J. de Vries, personal communication, 1989), where daytime high temperatures may exceed 38C for many consecutive days during reproduction. The climatic conditions of this region are different from those in the cooler San Joaquin/Sacramento River delta and the Santa Clara Valley regions, where much of the lettuce seed was produced 60 years ago (Jones, 1927). Our study was undertaken to in-

vestigate the effects of a range of ambient air temperatures during the season-long reproductive phase of development on NOS, SM, GERM, and SRL. A novel technique was employed to identify the periods of sensitivity to temperature and the limiting day and night temperatures during seed development.

Materials and Methods

A 0.12-ha study area was established in 1988 on a Hanford sandy loam soil (coarse-loamy, mixed, thermic Typic Xerothent) at Fresno, Calif. Coated seeds of ‘Salinas’ lettuce of commercial quality were planted in late March, 2 cm apart in twin rows 20 cm apart on raised, shaped beds 1 m apart. Seedlings were thinned to 22 cm between plants for a final population of 91,000 plants/ha. A surface trickle irrigation system was installed with laterals placed on the center of each bed with in-line, turbulent-flow emitters every 50 cm along the lateral, which, when irrigating, discharged water at 2 liter·h⁻¹. The plants were watered about every 4 to 6 days, depending on weather conditions. When lettuce heads were ≈15 cm in diameter (mid-June), the top 5 to 6 cm each head was removed by hand to allow unrestricted bolting of the seed stalk.

Eight plants, chosen at random within the experimental area, were used for each sampling day. For 41 consecutive days, beginning 8 Aug. (day 220) and ending 17 Sept. 1988 (day 260), between 0800 and 0900 HR, 10 florets per plant, randomly chosen from florets that were pollinating that day (Jones, 1927), were marked with small paper tags. Seeds were harvested by hand when fully matured (≈15 to 20 days from pollination; stage G, Gray et al., 1988). The 10 florets from each of the eight replicate plants were bulked, threshed, and cleaned by hand so that all seeds were saved, and stored at 15C. When all sampling was complete, NOS and SM were determined. All seed samples were determined to be ≈9% moisture. Two rep-

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Abbreviations: ACF, autocorrelation function; AHT, average hourly temperature; GERM, percentage germination; HT, maximum temperature; NOS, number of seeds per inflorescence; LT, minimum temperature; nd, normal difference; PACF, partial autocorrelation function; sd, seasonal difference; SD, hourly temperature standard deviation; SM, seed mass; SRL, seedling root length.

licates of five seeds were chosen at random from plants 1, 3, 5, 7 and bulked and five from plants 2, 4, 6, and 8 and bulked. These were placed in a line on wetted blue blotter paper in 12 × 12-cm plastic germination boxes and maintained in a growth chamber at 15°C with continuous light at a 15° slant from vertical. Germination percent was evaluated after 7 days according to the rules of the Assn. of Official Seed Analysts (1981). Seedling radicle length was determined at this time. Examination of the coefficients of variation showed the two replications of 20 seeds to be an adequate sample size for estimating GERM and SRL.

A novel method was developed that used the seasonal variation in ambient air temperature to study the effects of temperature on seed production and yield. Hourly integrated ambient air temperature was measured at canopy height (1.5 m) and recorded with an electronic data logger. Temperatures were recorded from 2 weeks before until 2 weeks after inflorescence sampling. The average hourly temperature and the standard deviation for hourly temperature were calculated. After the sampling period, the temperature data were entered into two arrays. The first array consisted of the four dependent variables (NOS, SM, GERM, and SRL) for the 41 inflorescence sampling days with the daily HT and LT that bracketed each sampling by - 6 to + 8 days. The second array consisted of the 41 sampling days of seed data with the hourly temperatures that bracketed the time of anthesis (0800 HR; Jones, 1927) by - 123 to +49 h. This experimental method allowed observation of the effects of 41 natural daily temperature environments on lettuce seed production (NOS) and quality (SM, GERM, and SRL). Average daily temperature effects were also analyzed.

Regression analysis was used to determine the effect of daily HT and LT and hourly ambient air temperature on the four dependent seed variables. Sensitive periods of reproductive development to ambient air temperature were determined by the magnitude of the simple or multiple coefficients of determination (r^2 or R^2 , respectively), depending on whether linear or quadratic polynomial functions best described the relationships. Relationships among the four independent variables were also examined. All four dependent variables were examined for correlation with time of sampling. Periodicity of time-series data was examined with ACF and PACF function plots (Box and Jenkins, 1976). Examination of untransformed ACF and PACF plots indicated that the time-series for the four variables were not stationary; therefore, they were transformed using one nd ($Z_t = Y_t - Y_{t-1}$) and two sd ($Z_t = Y_t - Y_{t-24}$ and $Z_t = Y_t - Y_{t-12}$) functions, where Z_t and Y_t are the transformed and untransformed values for each period, respectively, and t is the time of the observed value of the parameter in the series (Hoff, 1983). AHT for the 41 sampling dates and the standard deviation (SD) of the AHT were also subjected to ACF and PACF analysis after being made stationary by two sd ($Y_t - Y_{t-24}$) and one nd ($Y_t - Y_{t-1}$) transformations for AHT and two sd ($Y_t - Y_{t-24}$ and $Y_t - Y_{t-12}$) and one nd ($Y_t - Y_{t-1}$) transformations for SD (Hoff, 1983). These were then compared with the results of the analyses for the seed variables to identify sources of periodicity. All statistical differences reported are significant at $P < 0.001$ unless otherwise indicated.

Results and Discussion

Season-long temperature conditions and effects. The lettuce seed mother plants were exposed to a wide range of temperatures during the flowering period (Fig. 1). Daily minimum temperatures ranged from 11.1 to 22.8°C and maximum temperatures

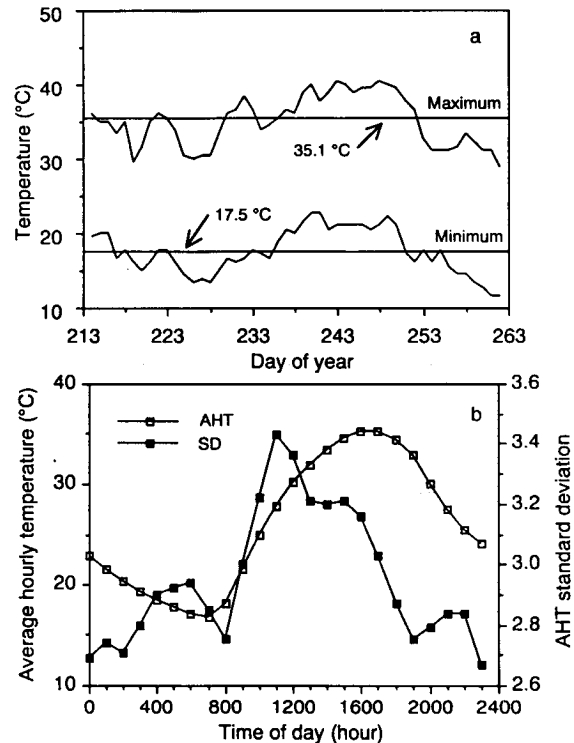


Fig. 1. (a) Daily HT and LT at inflorescence height during the reproductive development of 'Salinas' lettuce. Horizontal lines indicate season average LT and HT and (b) AHT and standard deviation (SD) of hourly temperature for the period from 0000 to 2300 HR the day of anthesis for 41 sampling dates in 1988 at Fresno, Calif.

Table 1. Simple correlation coefficients (r) between number of seeds per inflorescence, seed mass, percent germination, and seedling root length of 'Salinas' lettuce seed produced over 41 consecutive days in 1988 at Fresno, Calif.^a

Characteristic	SM	GERM	SRL
NOS	0.052 (0.746)	-0.083 (0.606)	0.413 (0.007)
SM		0.067 (0.676)	0.527 (0.0004)
GERM			-0.231 (0.147)

^aValue in parentheses indicates probability level, $df = 39$.

ranged from 30.0 to 40.6°C. Daily maximum temperature occurred at 1600 HR (+ 8 h from anthesis) and daily minimum at 0700 HR (- 1 h from anthesis; Fig. 1b). The greatest amount of variation (SD) in maximum temperature throughout the reproductive period occurred between 0900 to 1700 HR with a peak at 1100 HR; the least variation occurred at 2300 HR. Daily minimum and maximum temperatures were correlated ($r = 0.848$, $P = 0.0001$).

SM, GERM, and SRL decreased slightly with increasing day of year (Fig. 2). The decrease in SM with time agrees with the results of Soffer and Smith (1974a), who found that seed produced early in the season were heavier than those produced later. SRL was positively correlated with SM and NOS (Table 1). Increasing seedling vigor and subsequent crop performance have been shown to be positively related to SRL (Wurr and Fellows, 1984) and SM (Smith et al., 1973a, 1973b; Soffer and Smith, 1974b). Thus, seed produced late in the season may reduce the quality of the crop that is produced from this seed. The absence of a correlation between SM and NOS agrees with the findings of Soffer and Smith (1974a). The increase in SRL with increasing SM agrees with results of Gray et al. (1988).

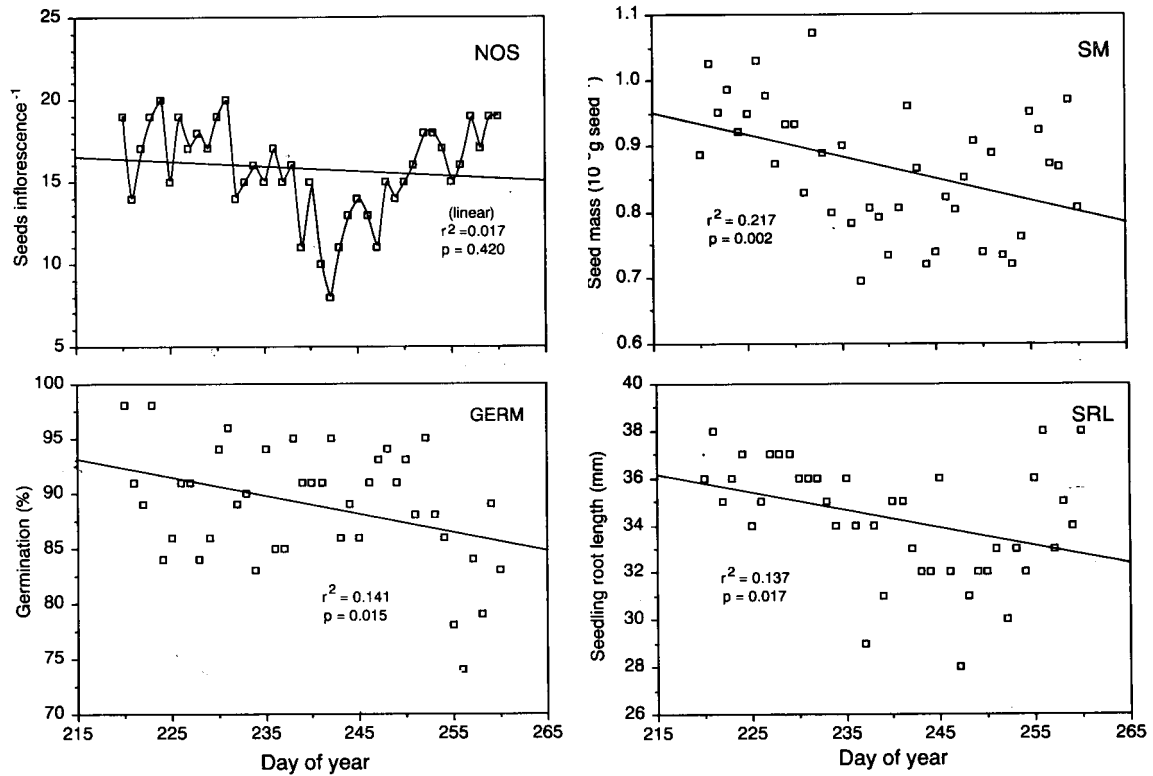


Fig. 2. Effect of day of sampling on NOS, SM, GERM, and SRL for 'Salinas' lettuce grown at Fresno, Calif., in 1988.

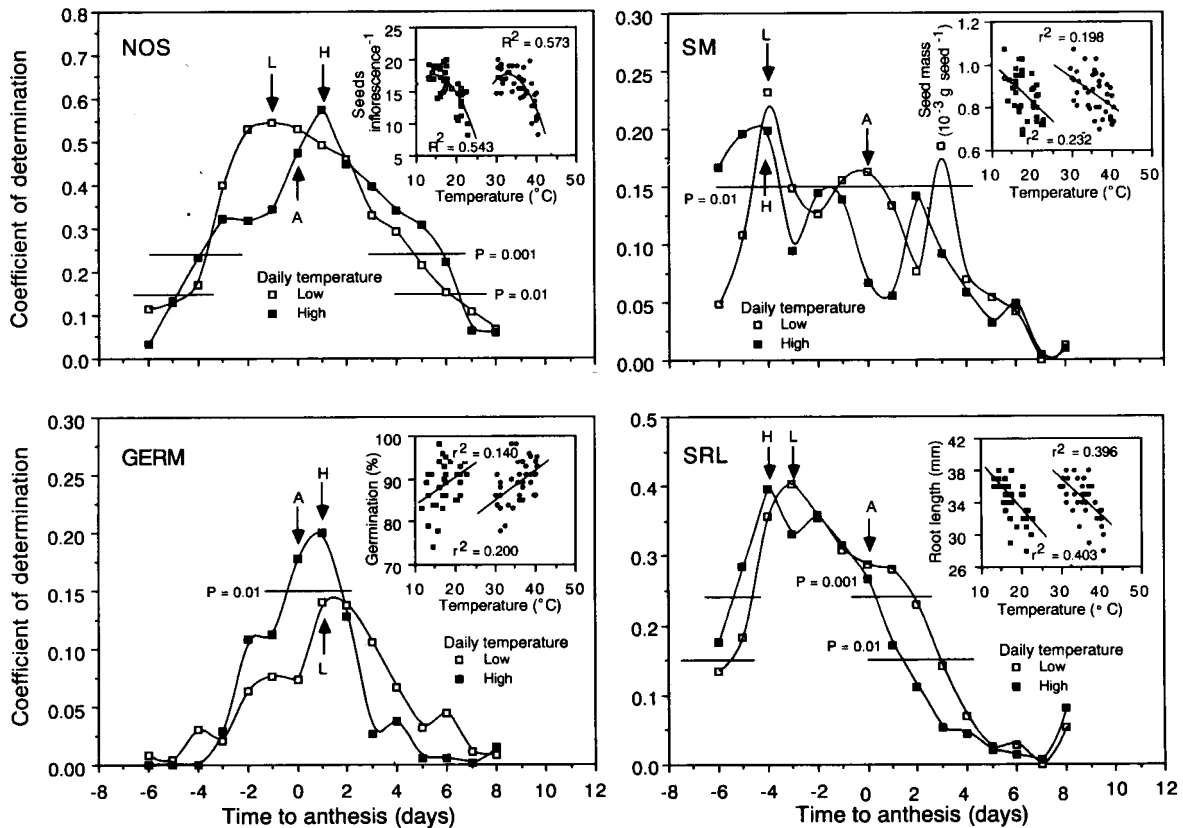


Fig. 3. Effect of daily HT and LT from -6 to +8 days from anthesis on NOS, SM, GERM, and SRL of 'Salinas' lettuce as measured by the quadratic or linear coefficient of determination (R^2 or r^2 , respectively). Arrows labeled A, L, H indicate the time of anthesis, and the day of greatest association with Land HT, respectively. Inset graphs show the relationship between the variables and temperature at the day most critical to development.

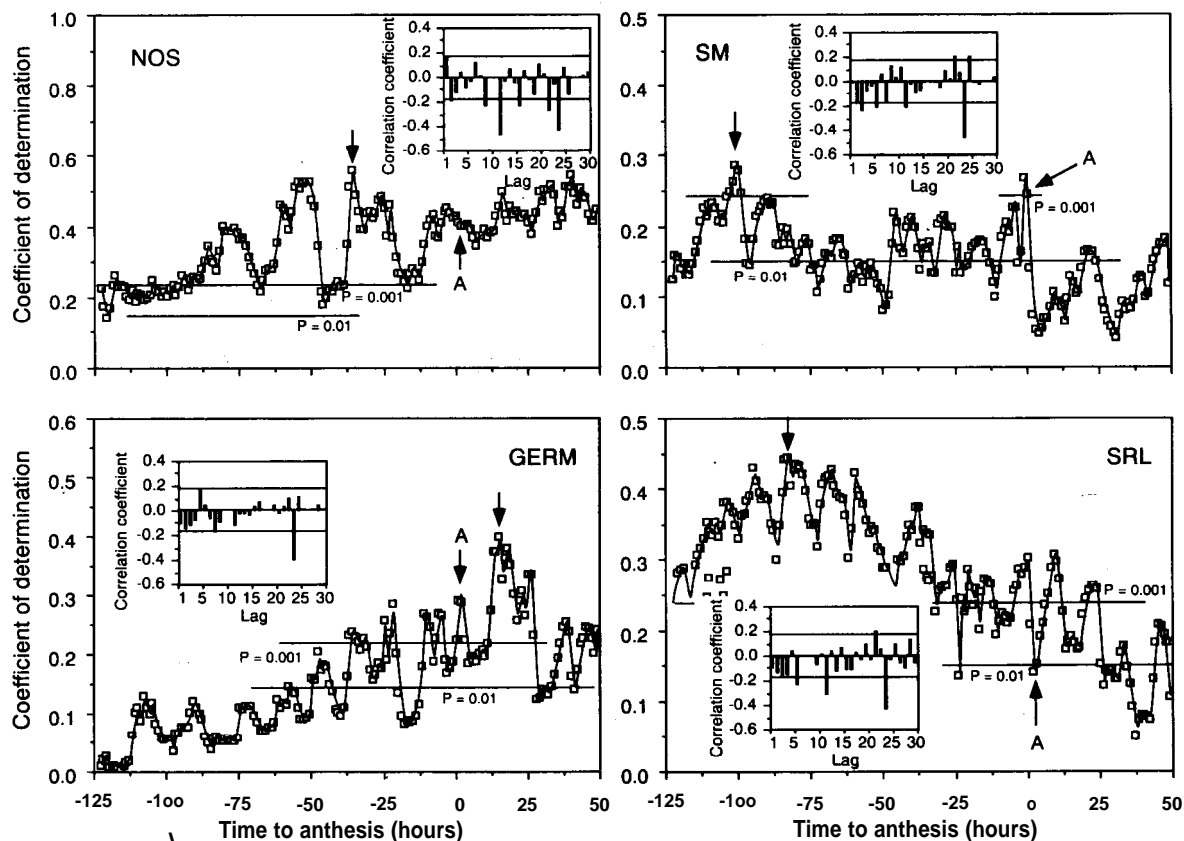


Fig. 4. Effect of air temperature - 124 to +48 h from the time of anthesis (0800 HR) on NOS, SM, GERM, and SRL of 'Salinas' lettuce as measured by the quadratic or linear coefficient of determination (R^2 or r^2 , respectively). Unlabeled arrows and arrows labeled (A) indicate the hour of greatest association with air temperature and time of anthesis, respectively. Insert graphs are the PACF plots. Vertical lines in each insert indicate the confidence limits of the PACF ($2 \times$ standard deviation).

Seed production, measured as NOS, was related to factors other than day of year, indicated by the varying trend throughout the sampling period and lack of a correlation with time (Fig. 2).

Daily temperature sensitivity near anthesis. Periods of sensitivity during inflorescence development based on daily HT and LT were identified for all four seed characteristics (Fig. 3). All four were more significantly related to actual hourly HT or LT than average daily HT or LT (data not shown). NOS was most sensitive to the daily HT + 1 days after pollination (Fig. 3). Sensitivity to LT reached a maximum between - 2 and 0 days from anthesis, and then decreased slowly. There were no relationships between NOS and HT and LT before - 3 or after + 6 days from anthesis. Daily LT and HT >17 and 35C, respectively, greatly reduced NOS and HT explaining more variation than LT (Fig. 3, NOS insert). These results generally agree with growth chamber studies of Keller (1962) and Gray et al. (1988) and the field studies of Soffer and Smith (1974b), showing that seed production is reduced at higher temperatures. Since NOS was affected by LT during the nights before anthesis and HT during the day of anthesis, it maybe that the number of ovules capable of successful syngamy is either predetermined at this time or the effectiveness of pollination or syngamy is affected after anthesis.

Both measures of vigor (SM and SRL) were adversely affected by increasing temperature (see Fig. 3 inserts). SM was more sensitive to LT than HT, as indicated by the size of the coefficients of determination ($r^2 = 0.232$ and 0.198 , respectively). SM was less affected by high temperature than SRL. The period of SM sensitivity to temperature was not as clearly

defined as with the other three variables. SRL was sensitive to both HT and LT at - 4 and - 3 days to anthesis, respectively (Fig. 3); sensitivity decreased after this time with no sensitivity to temperature after + 2 days from anthesis. This sensitive period coincides with megaspore development (Jones, 1927).

Since NOS and GERM were influenced by temperature near the time of anthesis (Fig. 4), high temperatures appear to affect the processes of pollination, syngamy, or initial seed development. Fusion of the polar nuclei occurs at the time of fertilization, and by 6 h after anthesis, fertilization is complete and zygotes begin embryo development (Jones, 1927).

Percentage germination was enhanced by increasing temperature during initial seed development (Fig. 3). This is a minor effect because a low amount of variation for GERM was explained by temperature ($r^2 = 0.14$ and 0.20 for LT and HT, respectively). The positive relationship between GERM and increasing temperature during seed development is in agreement with the findings of Barrington and Thompson (1952) and Keller (1962). Rate of germination has also been shown to increase with increasing temperature (Gray et al., 1988). The small advantage of increased GERM from increased daily HT and LT is greatly overshadowed by the severe reduction in NOS and the vigor components SM and SRL.

Hourly temperature sensitivity near the time of anthesis. The time of greatest high temperature sensitivity for NOS, SM, GERM, and SRL occurred at - 36, - 101, + 15, and - 83 h from pollination, respectively (unlabeled arrows, Fig. 4). Periodic responses by the coefficients of determination for NOS, SM, GERM, and SRL (Fig. 4) were also observed. These were

determined from transformed stationary time-series using Box-Jenkins analysis (Hoff, 1983). NOS and SRL had strong periodic correlations (lags) at 12 and 24 h. SM also had lags at these times, but the 12-h lag was not as significant as those for NOS and SRL. GERM percentage had only a 24-h lag, indicating that the lags were due to the autocorrelation between daily temperature cycles. ACF and PACF plots from transformed, stationary AHT and SD series produced lags at 24, and 12 and 24 h respectively (results not shown). The presence of very significant 12- and 24-h lags for NOS and SRL may indicate a relationship between these variables with the 12- and 24-h lags for SD. The interpretation and biological significance of these fluctuations are not clear and require further study.

The results from this study indicate that high ambient air temperature shortly before and after anthesis may adversely influence the productivity and quality of 'Salinas' lettuce grown for seed. The results also confirm and specifically quantify the effect of temperature on the components of seed quality. Daily maximum > 35C greatly reduced NOS. Similar high temperatures also reduced SM and SRL, but to much less of an extent. This study provides a new method for investigating effects of ambient temperature on lettuce seed production under field conditions. Further study is needed to determine the effect of high temperature on seed production in other lettuce genotypes. Information from such studies could be used for selecting environments that optimize the yield and quality of lettuce seeds. This method may also have application for studying other crops in which seed production and vigor have been reported to be adversely affected by elevated temperature (Thomas and O'Toole 1980).

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