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Modeling the Effects of Light, Carbon Dioxide, and Temperature on the Growth of Potato

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ABSTRACT

This study examined the effects of light, temperature and carbon dioxide on the growth of potato (*Solanum tuberosum* L.) in a controlled environment in order to ascertain the best growing conditions for potato in life support systems in space. 'Norland' and 'Russet Burbank' were grown in 6-L pots of peat-vermiculite for 56 d in growth chambers at the University of Wisconsin Biotron. Environmental factor levels included continuous light (24-h photoperiod) at 250, 400, and 550 μmol m^{-2} s^{-1} PPF; constant temperature at 16, 20, and 24 °C; and CO$_2$ at approximately 400, 1000 and 1600 μL L^{-1}. *Separate effects analysis* and *ridge analysis* provided a means to examine the effects of individual environmental factors and to determine combinations of factors that are expected to give the best increases in yields over the central design point. The response surface of Norland indicated that tuber yields were highest with moderately low temperature (18.7 °C), low CO$_2$ (400 μL L^{-1}) and high light (550 μmol m^{-2} s^{-1} PPF). These conditions also favored shorter stem growth. Russet Burbank tuber yields were highest at moderately low temperature (17.5 °C), high CO$_2$ (1600 μL L^{-1}) and medium light (455 μmol m^{-2} s^{-1} PPF). Models generated from these analyses will be used to project the most efficient conditions for growth of potatoes in closed ecological life support systems (CELSS) in space colonies.

THE INTERACTING INFLUENCE of environmental factors on the growth of potato is being studied to provide needed information on how to grow this crop in controlled environments for use in life support systems in space. The primary goal of this study was to identify and model the interrelationships between the yield of potato and the environmental effects of light, CO$_2$ and temperature at levels that can likely be achieved in a space system. We chose to use response surface methodology and separate effects analysis as aids in modeling these relationships. Specifically, we sought to check the sensitivity of the response over a range of experimental conditions so that the most useful conditions can be determined for food production in space systems.

The response surface methodology uses an estimated regression equation to approximate the response surface of potato growth to environmental factors. This methodology has been used by others to describe the effects of climatic factors on plant growth. Backer and Bargmann (1985) evaluated environmental studies performed in the field where the controlled factors were temperature and rainfall. In spite of the

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unstable environmental conditions, the fitted cubic model gave a good approximation of the effect of the local environmental factors of interest. Ormrod et al. (1984) used response surface methods with quadratic models to examine the effect of differing ozone and SO_2 mixtures on lettuce (*Lactuca sativa* L.), radish (*Raphanus sativus* L.), and pea (*Pisum sativum* L.) in a controlled environment. Here we have demonstrated its use with three environmental factors, indicating some of the complications that can arise.

MATERIALS AND METHODS

Experimental Procedures

The experiments on potato plants were conducted in five controlled environment chambers at the University of Wisconsin Biotron. Four plants of each of two potato cultivars (Norland and Russet Burbank) were grown in a chamber with carefully maintained and monitored light, temperature and carbon dioxide. All plants were started from sterile cultured plantlets grown on a modified MS medium. After approximately 20 d in sterile culture, plantlets were transplanted to 6-L plastic pots containing peat-vermiculite (1:1 by volume). Pots were watered to excess four times daily using a complete nutrient solution (Wheeler et al., 1986). To ensure good stolon and tuber development, stems were buried an additional 4 to 5 cm by adding extra peat-vermiculite to the pots 14 d after planting. Carbon dioxide levels were elevated by adding pure CO_2 to the incoming air stream of the chambers. Continuous lighting, i.e., a 24-h photoperiod, was chosen in order to obtain maximum productivity (i.e., g m^{-2} day^{-1}). Previous research has shown that Russet Burbank and Norland respond well to continuous light (Wheeler and Tibbitts, 1986). At 4 wk, two uniform plants for each cultivar in each chamber were retained and the others discarded. At harvest 8 wk after planting, tubers, leaves, stems, roots, and stolons were separated, dried and weighed. The length of the longest stem was also determined.

Three levels of each environmental factor—light, temperature and CO_2—were chosen evenly over a range that was thought to be large enough to detect significant effects (Table 1). The levels of CO_2 and temperature were selected to bracket the assumed optimum levels for tuber production, while the three levels of light were selected up to the maximum level attainable in the growth chambers. The three selected levels of each environmental factor were coded as −1, 0, and 1 for ease of discussion.

In order to make efficient use of resources and to investigate second-order effects, a modified central composite design (Box and Wilson, 1951) with blocking was employed, consisting of (i) a 2^3 factorial component using the three environmental factors at the two extreme levels, (ii) central points with all factors at intermediate levels, and (iii) six axial points with two factors at medium levels and the third at the highest or lowest level. The study was divided into four runs, or blocks, since only five chambers were available. The central point was included in each run. The factorial points were split among the first two runs and the axial points were in runs three and four. Two additional points were included in run four, for a total of 20 experimental units (Table 2).

The blocking introduced by running only five chambers at a time had the potential to create substantial differences due to uncontrolled changes in the chambers or in the plant material from run to run. The optimal fractional design protocol (Box et al., 1978) could not be followed due to a requirement to provide data from particular combinations of conditions to NASA early in the study. It was still possible to extract information on the effects of environmental factors using the extra central design points to estimate block differences, although some effects of environmental factors could be confounded with run-to-run differences if the latter are not strictly additive.

Statistical Procedures

It was assumed that potato plants respond to the levels of light, CO_2, or temperature in approximately a quadratic manner over the range of conditions commonly used for plant growth. Extreme levels of conditions will produce deviations from the quadratic response. For instance, plants respond with nearly linear growth to a moderate range of temperature but have reduced growth at both lower levels and higher levels providing a quadratic type response (Salisbury and Ross, 1978). The simplest mathematical model that shows this behavior is a second-order model (Box and Draper, 1987, sec. 5.6).

This approach of using an empirical model was preferred to using physiological information to develop a mechanistic model, because adequate knowledge of the underlying mechanisms that control potato growth and tuber development in controlled environments is not available. The model chosen for each potato cultivar was second-order with an added third-order factor (Box and Draper, 1987, sec. 7.4),

$$\textit{Response} = \textit{block} + \textit{main effects} + \textit{interactions} + \textit{error}\,, \qquad [1]$$

or

$$\textit{Response} = \textit{block} + \sum_{k=1}^{3} (b_k X_k + b_{kk} X_k^2) + \sum_{k=1}^{3} \sum_{j=1}^{k-1} b_{jk} X_j X_k + b_{123} X_1 X_2 X_3 + \textit{error}\,.$$

The *response* is the plant response, e.g., shoot dry weight, and is actually the average of the two plants of one cultivar in a chamber, using the chamber as the experimental unit

Table 1. Experimental and coded levels for light, carbon dioxide and temperature.

Light (μmol m^{-2} s^{-1})	250	400	550
Carbon dioxide (μL L^{-1})	400	1000	1600
Temperature (°C)	16	20	24
Coded levels	−1	0	1

Table 2. Modified central composite design of environmental levels in each chamber expressed as coded values for levels maintained.†

	Block	Chamber	Light	Temp.	CO_2
Central points	1, 2, 3, 4	102	0	0	0
Factorial points	1	106	+1	+1	+1
	1	108	+1	−1	+1
	1	110	+1	−1	−1
	1	112	−1	−1	+1
	2	106	+1	+1	−1
	2	108	−1	+1	+1
	2	110	−1	+1	−1
	2	112	−1	−1	−1
Axial points	3	106	0	0	−1
	3	108	0	0	+1
	3	110	0	−1	0
	3	112	0	+1	0
	4	106	−1	0	+1
	4	108	−1	0	−1
	4	110	+1	0	0
	4	112	−1	0	0

† Coded levels (−1, 0, 1).

for studying the environmental factors. Responses were standardized to have mean value of 1 at the center point. *Block* is the mean for the block of five chambers run at once. The X_k, or X_j, are the coded values of light ($j,k=1$), carbon dioxide ($j,k=2$) and temperature ($j,k=3$) in the chamber. The coefficients b_k, b_{kk}, b_{jk} and b_{123} are measures of the relative strengths of the linear, quadratic and two way and three way interactions effects, respectively. The *error* is assumed to be normally distributed with a mean of 0 and some unknown variance σ^2. While one could combine models for the two cultivars, this was not done due to the marked difference in cultivar response to the environmental factors.

Estimates of model parameters were obtained by the least squares method (Draper and Smith, 1981). Using both backward and forward stepwise regression, all nonsignificant terms, i.e., model terms that did not contribute significantly at the 5% level to explaining part of the variability in the data, were removed from the model (Chatterjee and Price, 1977). The resulting parsimonious models for the plant responses were the simplest models that still adequately explained a significant portion of the observed variability in the data.

The response surface, estimated from the model in Eq. [1] over the continuous domain of the environmental factors (Box and Draper, 1987), was examined by two analytical methods, *separating effects* and *ridge analysis*, to visualize the combined effects of the environmental factors (Box, 1954; Box and Youle, 1955). Separating effects provided a general analysis of the effect of each factor and of the interaction among factors, allowing examination of the importance of each factor in explaining the plant response. Ridge analysis detailed the surface along the path of maximum response from the central point of the environmental factors, which can help in determining what direction to increase or decrease the environmental factor levels away from the center to increase plant response.

Separating effects analysis examines the contribution of each environmental factor to the regression equation, followed by a discussion of the interacting factors that modify the magnitude of the estimated response. The entire fitted equation is then examined and aspects of the fit are illustrated using graphs. We consider plant response relative to the central point and study the range of estimated response over the domain of the environmental factors to get an idea of sensitivity. When interactions are important, we may consider the range of response to one factor for different levels of a second factor.

Ridge analysis interprets the response surface from the viewpoint of moving from the central point toward maximum plant response. This can help determine which environmental factor, or combination of factors, is most important in predicting high plant response (Box and Draper, 1987; Draper, 1963). If one views the response surface as a contour map, ridge analysis uses an eigenvalue—eigenvector decomposition to rotate the environmental factor axes to align with the major (ridge) and minor axes of the contour ellipses. Ridge analysis documents the smallest change from the central point needed to achieve the greatest plant response. It can also guide design of follow up experiments when the maximum plant response is projected at environmental levels beyond the domain of the current experiment.

Confidence intervals at selected levels of the environmental factors can be used graphically to show the precision of the estimated plant response (*cf.* Box and Draper, 1987, sec. 3.12). The most accurate estimates of plant response will be at the central point. Note that statements about confidence intervals are predicated on the assumption that the second-order surface is appropriate. If one is interested in confidence regions for the levels of environmental factors needed to ensure a certain plant response, one can invert one-sided confidence intervals (Williams, 1959) and state that the plant response is no lower than an estimated lower confidence limit if environmental factors are set in a certain range.

RESULTS

Initial analysis of both cultivars together showed significant block × cultivar interaction, indicating that it was necessary to analyze the cultivars separately. The parsimonious regression equations for Russet Burbank and Norland based on the model of Eq. [1] are presented in Table 3 for dry weights of leaf, stem, and tuber portions of the plants and for the stem length. Regression equations were similar with and without the two additional design points in block four (Table 2), and only results for the full data are presented. The regression equations were adjusted to be 1.0 at the central point. Detailed discussion follows primarily for the Norland cultivar.

Block-to-block variability formed a substantial part

Table 4. Block means relative to central point.

	Experimental run (block)				
Plant response	1	2	3	4	R^2
		Norland			
Leaf (g)	1.214	1.073	0.828	0.885	56.2%
Stem (g)	1.083	1.252	0.805	0.860	44.2%
Tuber (g)	1.326	0.871	0.940	0.862	58.1%
Leaf (cm)	0.964	0.837	0.973	1.227	26.3%
		Russet Burbank			
Leaf (g)	1.202	0.967	0.834	0.997	53.0%
Stem (g)	1.107	1.025	0.801	1.068	10.8%
Tuber (g)	1.220	0.973	0.916	0.892	38.2%
Leaf (cm)	0.901	0.904	0.945	1.250	34.7%

Table 3. Potato growth equations in response to environmental variables.

Regression equation†	SD	R^2‡
Norland		
Leaf (g) $= 1 + 0.047C + 0.120T + 0.034LC + 0.043LT - 0.101T^2$	0.045	90.3%
Stem (g) $= 1 - 0.200L + 0.332T + 0.107LC - 0.171LT - 0.107CT$	0.131	89.0%
Tuber (g) $= 1 + 0.081L - 0.208T - 0.086LC - 0.322T^2$	0.098	86.4%
Stem (cm)* $= 1 - 0.394L - 0.140C + 0.391T + 0.137LC - 0.101LT + 0.383L^2$	0.143	93.5%
Russet Burbank		
Leaf (g) $= 1 + 0.117T$	0.087	50.8%
Stem (g) $= 1 + 0.088C + 0.499T + 0.104LC + 0.106LCT$	0.105	95.1%
Tuber (g) $= 1 + 0.112L + 0.096C - 0.276T - 0.052LT - 0.051CT - 0.251L^2 - 0.299T^2 - 0.063LCT$	0.063	97.9%
Stem (cm) $= 1 - 0.276L + 0.204T + 0.111LC - 0.092LT + 0.183C^2$	0.129	88.1%

* Equations significant at 0.05, except for Norland stem length which is at 0.08.

† Light (L), carbon dioxide (C) and temperature (T) are expressed in coded values.

‡ Blocks are removed from explained variation (R^2) and equations.

of the total variation and was removed for the presentation of Table 3. The block means and the percent explained variation (R^2) are shown in Table 4. Since the environmental combinations in the first block were chosen with the expectation of high yields, the larger block means are not surprising and may reflect the confounding mentioned in the Materials and Methods. Regression equations, using only the central points to estimate block effects, were developed to try to separate blocks and main effects (not presented). These were not significantly different from those shown in Table 3, indicating that the confounding may not be that important.

Separating Effects Analysis

The regression equations for the plant responses of Norland (Table 3) show differing degrees of complexity. Most response equations involved some interaction of factors. We used separating effects to isolate the effects of light, carbon dioxide, and temperature on the dry weight measurements for Norland potato. Throughout, low, medium, and high levels of the environmental factors refer to Table 1. Note that statements concerning confidence intervals are only appropriate if the second order model is assumed to be correct and if responses are normally distributed.

The equation for tuber weight can be decomposed into a quadratic part involving temperature and a light × CO_2 interaction (Table 3). With light and carbon dioxide fixed at the medium levels, tuber weight ranged from 0.886 relative to the central point at low temperature up to 1.034 at 18.7 °C and back down to 0.470 at high temperature (Fig. 1a). This estimated quadratic response was modulated up or down by light and CO_2 levels: if both are high (or both low), estimated tuber weight would be 0.086 lower, while if one was high and the other low, the weight would be 0.086 higher (Fig. 1b). Thus, the range of tuber weight relative to the central point was from 0.384 (at high temperature with light and CO_2 both high or both low) to 1.120 (at 18.7 °C with light and CO_2 at opposite extremes).

Leaf weight was also shown to have a quadratic response to the temperature, but the form of this response was affected by light level. At low light and medium CO_2, leaf weight relative to the central point ranged from 0.822 (low temperature) to 1.0 (medium) to 0.976 (high) (Fig. 2a). At high light, the range was from 0.736 to 1.0 to 1.062 (Fig. 2c), with an intermediate range at the medium light level (Fig. 2b). Note that temperature had a more marked effect on leaf weight from the low to medium levels than from the medium to high levels. The 95% pointwise confidence intervals in these figures show the precision of the estimated regression line over the temperature domain when light was at low, medium, and high levels and CO_2 was at the medium level. Carbon dioxide had a linear effect on relative leaf weight, which was enhanced as light level was increased. The range of leaf weight response to CO_2 was from 0.987 to 1.013 at low light and from 0.919 to 1.081 at high light. The effect of light was in turn modulated by both temperature and CO_2. The greatest effect occurred with both CO_2 and temperature at high or low levels, with a range of response from 0.923 to 1.077. No effect of light on mean leaf weight was found at medium temperature and CO_2 levels.

Norland stem weight presented a somewhat more complicated equation, since all three two-way interactions were present (Table 3). Increased temperature

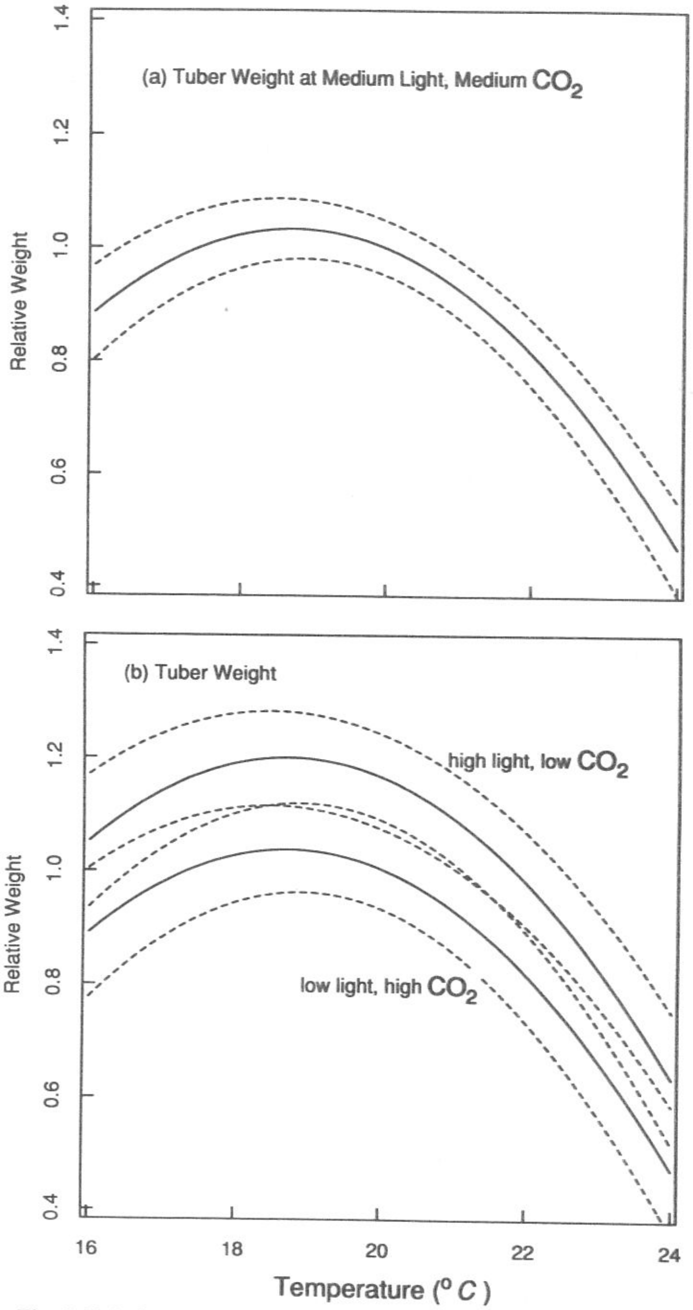

Fig. 1. Relative tuber weight of Norland potato vs. temperature (a) with medium levels of CO_2 (1000 μL L^{-1}) and light (400 μmol m^{-2} s^{-1} PPF); (b) with light and CO_2 at opposite extremes for lowest and highest relative response. Solid lines are estimated leaf weight; dotted lines are two-sided 95% confidence intervals [shrunken by $\sqrt{2}$ in (b)].

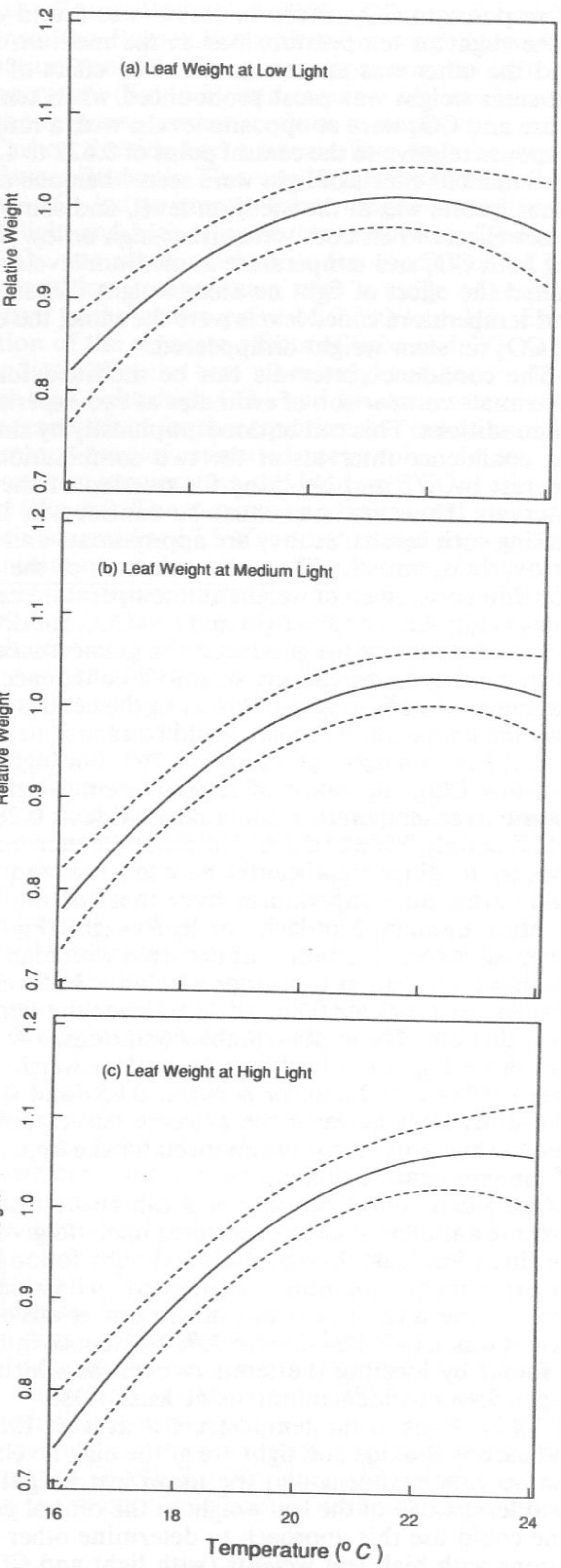

Fig. 2. Relative leaf weight of Norland potato *vs.* temperature with medium level of carbon dioxide (1000 μL L^{-1}) at three levels of light: (a) low (250 μmol m^{-2} s^{-1} PPF), (b) medium (400 μmol m^{-2} s^{-1} PPF) and (c) high (550 μmol m^{-2} s^{-1} PPF). Solid lines are estimated leaf weight; dotted lines are two-sided 95% confidence intervals.

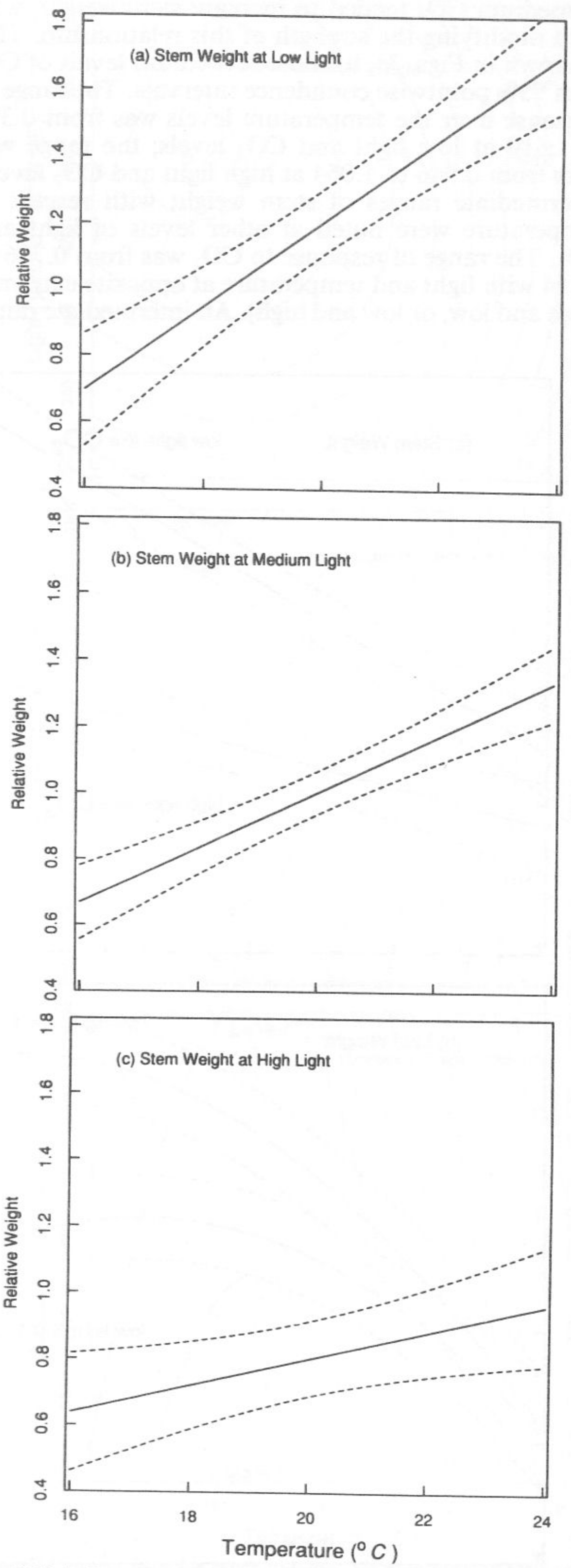

Fig. 3. Relative stem weight of Norland potato *vs.* temperature with medium level of CO_2 at three levels of light. See Fig. 2 for details. Solid lines are estimated stem weight; dotted lines are two-sided 95% confidence intervals.

at medium CO_2 tended to increase stem weight, with light modifying the strength of this relationship. This is shown in Figs. 3a, b, and c at medium levels of CO_2 with 95% pointwise confidence intervals. The range of response over the temperature levels was from 0.390 to 1.610 at low light and CO_2 levels; the range was only from 0.946 to 1.054 at high light and CO_2 levels. Intermediate ranges of stem weight with respect to temperature were noted at other levels of light and CO_2. The range of response to CO_2 was from 0.786 to 1.214 with light and temperature at opposite extremes (high and low, or low and high). An intermediate range of response to CO_2—0.786 to 1.214—was found when either light or temperature was at the medium level and the other was at an extreme. The effect of light on stem weight was most pronounced when temperature and CO_2 were at opposite levels, with a range of response relative to the central point of 0.622 to 1.278. Less marked effects of light were seen when one of the other factors was at the medium level, and somewhat lesser effects when both were either high or low. Having both CO_2 and temperature at medium levels eliminated the effect of light on stem weight. When light and temperature coded levels were the same, the effect of CO_2 on stem weight disappeared.

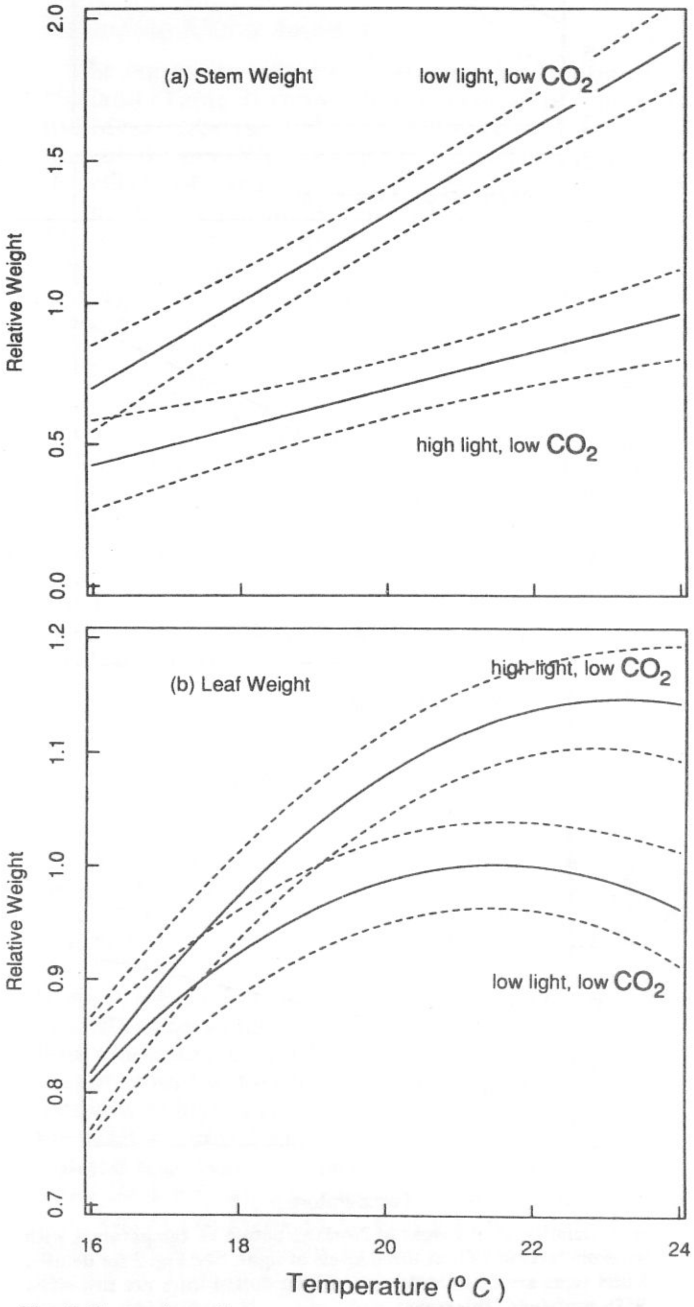

Fig. 4. Comparison of response curves with Norland potato for light and CO_2 levels that lead to lowest and highest relative response for (a) stem weight *vs.* temperature and (b) leaf weight *vs.* temperature. Solid lines indicate estimated weight; dotted lines are two-sided 95% confidence intervals shrunken by $\sqrt{2}$. Shaded region corresponds to temperatures with significantly different plant response between light levels.

The confidence intervals can be modified for approximate comparison of estimates at two experimental conditions. This can be done graphically by shrinking confidence intervals at the two combinations of interest by $\sqrt{2}$ and checking for overlap of the two intervals. However, one must be cautious in interpreting such results, as they are approximate and may be overly optimistic. Thus, the extremes of the relationship between stem weight and temperature can be shown (Fig. 4a). For low light and low CO_2, conditions for which temperature produced the greatest increase in stem weight, one can say with 95% confidence that the range of stem weights relative to the central point over the temperature domain could be as wide as 0.543 to 2.071 or as narrow as 0.851 to 1.763. For high light and low CO_2, the range of relative stem weight response over temperature could be as wide as 0.267 to 1.119, or only 0.583 to 0.803. Note that the stem weight appears to differ significantly between low and high light levels for temperatures over most of the temperature domain. Similarly for leaf weight (Fig. 4b), the most favorable conditions occurred with high light and low CO_2, leading to a range of relative leaf weights of 0.767 to 1.193, or 0.867 to 1.105 over the temperature domain. The least favorable conditions, low light and low CO_2, could lead to relative leaf weights between 0.759 and 1.040, or between 0.859 and 0.964. The differences between the extreme curves for leaf weight (Fig. 4b) is most pronounced for the upper half of the temperature domain.

One sided confidence intervals can be used to determine an interval of temperatures likely to give leaf weights of at least 95% of the maximum found over the experimental conditions. Fixing carbon dioxide and light at the high levels, the maximum relative leaf weight was 1.147. The inverse 95% confidence interval is found by locating the temperatures for which the upper 95% confidence limit is at least $1.089 = 0.95 \times 1.147$. Thus, if the temperature is at least 19.3 °C and carbon dioxide and light are at the high levels, we can be 95% confident that the mean leaf weight will be at least 1.089 of the leaf weight at the central point. One could use this approach to determine other conditions with high leaf weights (with light and CO_2 at somewhat lower levels), or to examine experimental conditions for optimal growth of tubers or stems.

Ridge Analysis

While the Norland regression equations for dry weights were complicated by interactions, they led to fairly straightforward analysis using separating effects. The same could be said for Norland stem length and for the Russet Burbank equations, except for one response: the Russet Burbank tuber weight regression equation contains two quadratic terms, for light and temperature (Table 3), and requires and examination of the response surface in three dimensions.

Carbon dioxide had a linear effect on tuber weight of Russet Burbank. This was largely a positive effect—more CO_2 led to greater tuber weight—except under high light and high temperature conditions. The effect of CO_2 was most marked under conditions of high light and low temperature, with a range of response relative to the center point of 0.790 to 1.210. Examination of the separate effects of light and CO_2 seems to indicate that the best tuber weight response should be at high light, high CO_2, and low temperature. The response surface for this equation was examined using a contour map of estimated mean tuber weight, as it depends on temperature and light with CO_2 at the high level (Fig. 5a). The maximum relative yield was 1.217, which occurred at 17.5 °C and 455 μmol m^{-2} s^{-1} PPF. Examination of the *rising edge* from contour plots of CO_2 against temperature (Fig. 5b) indicated that higher tuber yields may be possible by increasing the CO_2 levels beyond those considered in this experiment. This figure is actually the projection of a four-dimensional surface; at every combination of CO_2 and temperature, the light level is set to yield the highest expected tuber weight. Along the rising ridge of Fig. 5b, light ranges from 440 to 460 μmol m^{-2} s^{-1} PPF as carbon dioxide ranges from the low to the high level. That is, as light increases with CO_2, the tuber yield increases when the temperature is near 18 °C.

Norland tuber weight also had a rising ridge (Table 3 and Fig. 5c), with rising tuber yield as CO_2 is decreased. The rising ridge is vertical (Fig. 5c), reflecting the fact that temperature appears to act independently of carbon dioxide and light. Along the rising ridge of Fig. 5b, light ranges from 390 to 680 μmol m^{-2} s^{-1} PPF as CO_2 ranges down from the high to the low level. That is, as light increases and CO_2 decreases, the tuber yield increases when the temperature is near 19 °C. The light levels along this rising ridge (Fig. 5c) that are beyond the experimental conditions were for carbon dioxide levels above 1000 μL L^{-1}. Within the experimental conditions, the maximum relative yield for Norland tubers of 1.201 occurred at low CO_2, high light, and 18.7 °C.

Ridge analysis permits selection of conditions at a given distance from the central design point that would lead to the greatest increase in mean tuber weight. The best conditions would lie along the *maximum ridge* through the central point. For Russet Burbank, the best return along the maximum ridge comes from first raising CO_2 levels. For Norland, one maximizes yield along the maximum ridge by dropping the temperature.

DISCUSSION

The response surface has been assumed to be second order for the purpose of this analysis, as is commonly done in a central composite design (Box and Draper, 1987, ch. 9). A second-order surface has a unique maximum with the surface gradually sloping away. Often the maximum is at a quadratic peak, but it may be on a rising ridge, as was the case for tuber

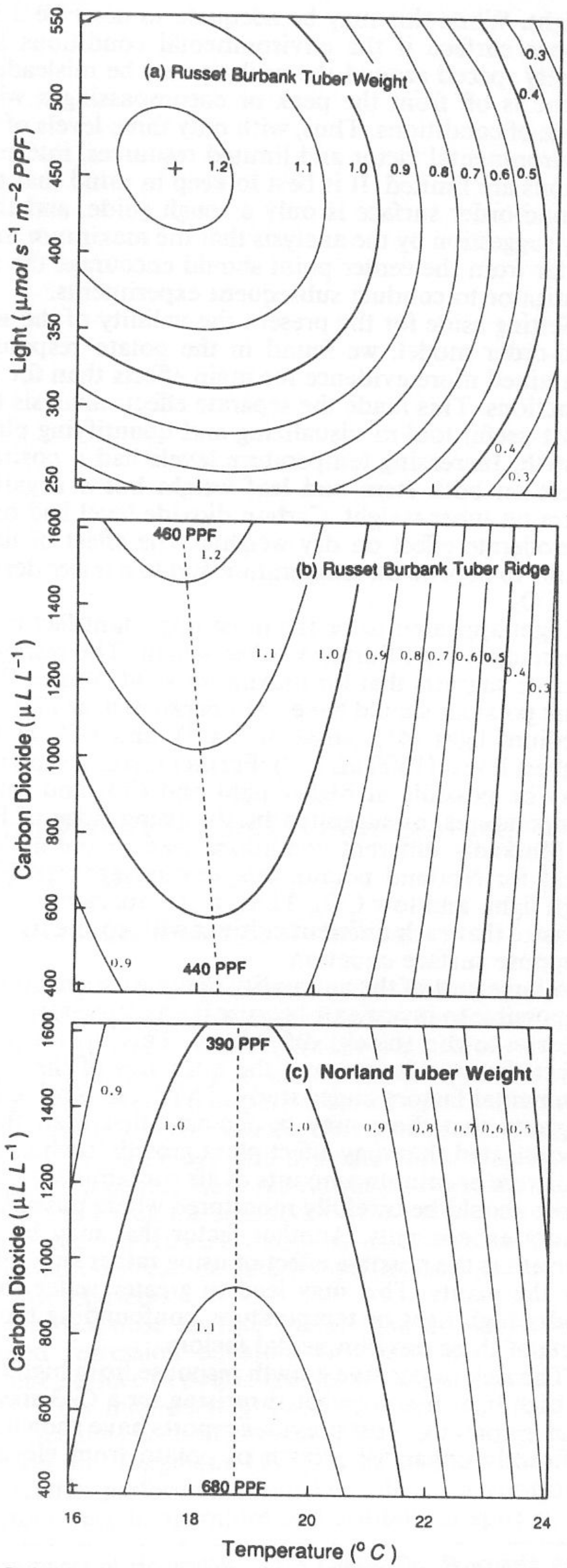

Fig. 5. Contour map for tuber weights. Thicker contour lines are at multiples of 0.5 × tuber weight at the central point; thinner contour lines occur at intervals of 0.1. (a) Russet Burbank tuber weight *vs.* temperature and light with CO_2 at the high level (1600 μL L^{-1}). Maximum relative yield of 1.217 (+) occurred at 17.5 °C and 455 μmol m^{-2} s^{-1} PPF. (b) Russet Burbank tuber weight *vs.* temperature and CO_2 along the rising ridge (dashed line). The range of light levels along the rising ridge is only 440 to 460 μmol m^{-2} s^{-1} PPF. (c) Norland tuber weight *vs.* temperature and CO_2 along the rising ridge (dashed line). The range of light levels along the rising ridge is 680 down to 390 μmol m^{-2} s^{-1} PPF.

weight. While this may be adequate to describe a response surface if the environmental conditions are closely spaced around the peak, it may be misleading if one is off from the peak or encompassing a wide range of conditions. Thus, with only three levels of an environmental factor and limited resources, interpretations are limited. It is best to keep in mind that the second-order surface is only a rough guide, and that any suggestion by the analysis that the maximum may be far from the center point should encourage the investigator to conduct subsequent experiments.

Setting aside for the present the validity of the second-order model, we found in the potato responses examined more evidence for main effects than for interactions. This made the separate effects analysis the most useful tool in visualizing and quantifying plant growth. Increasing temperature levels had a positive effect on both stem and leaf weight but a negative effect on tuber weight. Carbon dioxide level had only a moderate effect on dry weights. The effect of light seems to depend on temperature and to a lesser degree on CO_2.

Light appeared to be the most important factor influencing Russet Burbank tuber weight. The response surface suggests that for maximum yield, Russet Burbank potatoes should have a temperature near 17.5 °C, medium light (455 μmol m^{-2} s^{-1}), and CO_2 at the highest levels (1600 μL L^{-1}). Further increases in yield may be possible at higher light and CO_2 and lower temperatures, as suggested by the rising ridge of Fig. 4. Markedly different conditions lead to the highest yield for Norland potato: temperature near 18.7 °C, high light, and low CO_2. Thus, it is important to emphasize that each different cultivar will require its own response surface equation.

A large part of the variability in our experiment was impossible to investigate because it was associated with the run-to-run (block) differences. This in turn may affect the significance and the estimates of the environmental factors under study. This large block effect suggests that there may be factors other than those investigated that may affect plant growth, such as soil moisture or minute amounts of air contaminants, and those should be carefully monitored where possible in future experiments. Another factor that may be important is the possible effect of using rather small pots for the plants. This may lead to greater water stress under high light or temperature, confounding the effects of these environmental factors.

The lack of positive growth response from high CO_2 at high light is somewhat surprising for a C-3 species such as potato. Most previous reports have shown significantly enhanced growth of potato from elevated CO_2 (Arthur et al., 1930; Collins, 1976), although Goudriaan and de Ruiter (1983) did note a slight negative response of potato to elevated CO_2. Our choice of continuous lighting may have affected the plants' ability to respond to CO_2 since some potato cultivars (other than Norland and Russet Burbank) have been shown to injure under continuous light (Wheeler and Tibbits, 1986). Thus, these results should be interpreted only for continuous light situations. Use of shorter photoperiods may cause shifts in plant response or different interactions among the environmental factors included in this study.

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