THESIS

RELATION OF ELEVATION TO POTATO GROWTH AND PROPAGULE PRODUCTIVITY

Submitted by

Timothy K. Hartz

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WE HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER OUR SUPERVISION BY TIMOTHY K. HARTZ ENTITLED RELATION OF ELEVATION TO POTATO GROWTH AND PROPAGULE PRODUCTIVITY BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE.

Committee on Graduate Work

Adviser

Head of Department

ABSTRACT OF THESIS

RELATION OF ELEVATION OF POTATO GROWTH AND PROPAGULE PRODUCTIVITY

To document the effects of the high altitude environment on the growth and development of the potato (S. tuberosum), plants of cv. Kennebec were grown at sites ranging from 1533 to 3213 m. Temperature and light were the environmental parameters of primary interest and the experiment was designed to eliminate other influences. Since insolation was high at all sites, shade structures were installed to provide a wider range for this factor.

Maximum vegetative growth occurred at 2372 m. This site had a mean temperature of 17° C with a wide diurnal range. Above 2800 m, unshaded leaves exhibited a pronounced folding considered to be a response to high light intensity. Tuber fresh weight per plant decreased only slightly with increasing elevation. Shading increased vegetative growth and reduced tuber yield and specific gravity at all elevations. Shading also retarded maturity as evidenced by the consistently higher nitrate content of leaves from shaded plants. Regression analysis indicated that maturity, as measured by tuber specific gravity, was highly correlated with accumulated heat input. Net assimilation and tuber yield were positively correlated with total insolation and a revised measure of heat input designed to compensate for increasing respiratory losses with increasing night temperature. A comparison of site potential is presented.

Tubers produced at the various sites were grown in a greenhouse under controlled conditions to determine the effect of the parents' environment on the yield potential of the succeeding generation. Rate of emergence of the progeny increased with increasing elevation of the parent. This earlier emergence was reflected in earlier vegetative growth and tuber initiaion which resulted in higher tuber yield early in the season. However, when grown to completion, there was no significant difference in vegetative growth or tuber yield among groups. Photosynthetic rates were determined. The environment of the parent had no influence on the photosynthetic activity of the progeny.

Timothy K. Hartz
Horticulture Department
Colorado State University
Fort Collins, Colorado 80523
Summer, 1977

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INTRODUCTION

The San Luis Valley of Colorado is one of the largest high altitude agricultural areas in the United States. By virtue of its altitude it possesses a unique combination of climatic characteristics. It is of economic as well as academic interest to understand the effects of this climate on the crops produced.

The potato (S. tuberosum), an important crop in the San Luis Valley ($30 million in 1976), presents an interesting challenge. The relationship of potato growth and development to environmental conditions is very complex. In addition, since the potato is vegetatively propagated, the environment under which a tuber is produced can influence its performance when used as a propagule. There is a considerable body of information pertaining to this phenomenon; of interest here are the observations of commerical potato growers in California that seed tubers produced in the San Luis Valley exhibit faster, more uniform emergence and earlier yield than seed produced in other areas.

This study had two objectives: first, to quantify the effects of the high altitude environment on potato plant growth and second, to document the effects of this seed production environment on the performance of the succeeding generation.

LITERATURE REVIEW

High Altitude Environment

The characteristics of the high altitude environment of primary interest to this study are temperature and solar radiation. As a general rule average air temperature decreases at the rate of 0.5^{o} C per 100 m. This rule breaks down at night in the mountains as katabatic air flow cools the valleys below the expected. The most pronounced effect of the temperature decrease is the shortened frost-free period. In general total insolation increases with increasing elevation (App. Fig. 1); however, localized climatic conditions strongly affect the insolation received (14). Although longwave radiation is nearly independent of elevation (64), the amount of biologically effective ultraviolet-B radiation increases with elevation (14). Very high light intensities have been shown to cause destruction of chlorophyll and reduce photosynthesis, a phenomenon called solarization (53). These high levels of insolation, in conjunction with the increases UVB restricts vegetative growth and cell elongation. For a review of plant response to the high altitude environment, see Tranquillini (64).

The effects of temperature and insolation will be considered in discussing several aspects of potato growth and development: growth of the vine, tuber initiation, tuber bulking[z] and final yield. The interaction of light and temperature is complex and not well documented so, for the most part, they will be considered separately.

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[z] tuber bulking refers to the rate of tuber growth as a whole.

Vegetative Growth

Stems and leaves show different response to temperature. Maximum leaf weight is reached at 12-14° C, maximum stem weight and elongation at 18° C (5). Other investigators (6, 48) have found slightly higher optimum values. It should be noted that much of this work has been done in greenhouses at relatively constant temperature or at small diurnal fluctuations; consequently, field response might be expected to be somewhat different.

At relatively low light intensities Borah and Milthorpe (6) found leaf area to increase with increasing radiation. At intensities normally encountered in the field, leaf area decreases and specific leaf weight increases with increasing insolation (5, 55). Pohjakallio (49) found that the ratio of top to tuber weight was increased by shading the plants. Stem length decreases with increasing insolation (5). Ultraviolet radiation has a pronounced shortening effect on stems. Selective screening of UV increased potato stem length dramatically (42, 45). Effects of daylength will not be considered here as daylength differences among sites were minimal.

Tuber Growth

In any discussion of tuber initiation, there is a total agreement on only one fact: cool temperature hastens and high temperature inhibits initiation (7, 13, 24, 57, 70, 71, 72). Werner (72) found that tuberization occurred at low temperatures or with large diurnal temperature fluctuations. Burt (7) took plants growing at 20° C/15° C day/night and exposed then to 3-9° C for one week. In all cases, tuberization was

induced. Slater (57) found that reduction of night temperature alone hastened initiation; furthermore, by lowering the night temperature of only the shoot, tuberization was encouraged. The stimulus for initiation is unclear. Gregory (24) was able to show that potato plants grown under 'inducing' conditions (8 hr photoperiod, 20^{o} C day, 14^{o} C night) were capable of inducing tuberization when grafted on plants growing in non-inducing conditions. He concluded that a hormone-like substance was produced in the vine under inducing conditions which was translocated to the non-induced portion. An alternative explanation is held by Burt (7), Slater (57) and Borah and Milthorpe (6). A smaller proportion of assimilates is used by the vine at low temperatures and high light intensities. They suggest that there would be surplus assimilate which would provide the stimulus for tuber formation. In support, Burt and Slater found that tuber initiation was associated with an increase in the concentration of soluble sugars in the stolon tip. For a review of tuber initiation, see Madec (35).

The number of tubers increases with decreasing temperature, especially night temperature (5). In general, tuber number is positively correlated with daily insolation (6, 23). Sale (55) found that while the number of stolons was not significantly affected by solar input, the number of tubers greater than 1 cm in diameter was. One explanation is that high light intensities increase photosynthesis while restricting vegetation growth, creating a surplus of assimilate.

There is apparent disagreement about the period during which tuber initiation takes place. The more widely accepted theory is that all tubers are initiated over a period of about two weeks (21, 33, 58). More recent work (6) suggests that tubers are initiated throughout the period

of tuber bulking. In work by Sale (55) the number of tubers increased until maximum leaf area was attained. It seems likely that tubers are being initiated and resorbed throughout the season but that only those tubers set early contribute significantly to the final yield (41). Tuberization is traditionally considered to be photoperiod sensitive. Although tuberization is hastened by short days, most commercial varieties tuberize even under long day conditions.

After a short initial exponential phase the rate of bulking is linear over most of the season (40, 41). The maximum bulking rate was found to be negatively correlated with time of initiation of tubers (6, 9, 22). Sale (55) showed that shading delayed the attainment of maximum bulking rate but had little effect on the rate itself. In general, high bulking rates are associated with conditions which encourage early emergence, high tuber number and late initiation (22).

Photosynthesis, Respiration and Net Assimilation

Chapman and Loomis (16) determined photosynthetic rates for attached single potato leaves. They found that light saturation at atmospheric concentration of CO_2 was approximately 3000 foot candles. There was no detrimental effect on the rate at higher intensities, at least to 10,000 f.c. (approximately 100,00 lux). Curiously the Q_{10} of photosynthesis was near unity over the range 18-40^{o} C. While he found a higher value of light saturation, Winkler (73), working with single potato leaves, also determined that temperature had little effect on net (apparent) photosynthesis over the range 10-27^{o} C. Thomas and Hill (62) observed this same relationship with alfalfa between 16-27^{o} C. Stoy's work (60), with spring what is in agreement; the Q_{10} of photosynthesis

between 15-35^{o} C is near unity. Working with potato and spring wheat respectively, Winkler (73) and Stoy (60) both found respiration to increase much faster than photosynthesis, with the average Q_{10} for respiration near 2 over the normal field temperature range, although the magnitude of respiration is small in comparison. It should be remembered that the rates referred to here are for dark respiration. There is evidence that photorespiration of C_3 plants like the potato may be much higher (18). Winkler (73) and Borah and Milthorpe (6) agree the optimum mean temperature for dry matter production and tuber growth is 17-18^{o} C.

With all the problems inherent in measuring photosynthesis, the more widely studied parameter is net assimilation rate (increase in total dry matter leaf area^{-1}time^{-1}). An added advantage of NAR is that it reflects the plant's performance over time. Numerous attempts have been made to correlate NAR with environmental conditions. With potato, as with some other crops, these attempts have mainly produced inconsistent results and unsatisfactory correlations. It appears that NAR is positively correlated with temperature, insolation and daily temperature range and negatively correlated with night temperature (69). Relative growth rate of potato was found to be positively correlated with total insolation (59). However, the growth of the potato over the season cannot be adequately explained by environmental factors alone.

Moorby (40) found that NAR decreased until the maximum leaf area was attained, then increased while leaf area was declining late in the season. He attributed the initial decrease on the increasing mean age of the leaves, reduced insolation as the season progressed and a greater respiratory load due to the increasing proportion of non-photosynthetic

tissue. The subsequent rise is more difficult to explain. It could not be caused by environmental factors and Winkler (73) showed that, under test conditions, photosynthetic rate declined with age after senescence. One explanation is that the developing tubers exert an influence on the vine; the rate of assimilation is controlled by the ability of the tubers to store the assimilate. The implication is that the leaves do not always function directly in relation to the environmental conditions. There are two basic ways to test this hypothesis. The first is to alter the 'sink' provided by the storage organs. Burt (8) removed tubers from plants 21 days after initiation. This reduced the net assimilation rate of the plants and caused an accumulation of photosynthate in the leaves. Plants with tubers removed showed increased top growth and top dry weight but not enough to offset the loss of the tubers (46). The same phenomenon has been observed in apples (36), tomatoes (43) and wheat (30). Burt (10) found that lowering the temperature around the developing tubers, presumably slowing tuber growth, also reduce NAR. The second method to test the sink theory is to partially defoliate the plant and test the photosynthetic rate of the remaining leaves. Work on maize (29) and apple (27, 28) show that partial defoliation led to increased photosynthetic rates in the remaining leaves.

All of these studies point to a 'feed back' system in which the demand for assimilates regulates the rate of photosynthesis. For possible mechanisms of this system, see King et al. (30). An alternative explanation for this reponse in defoliation experiments is given by Wareing et al. (68). They suggest that under field conditions photosynthetic rates are limited by levels of carboxylating enzymes. They found that partial defoliation caused a significant rise in carboxylating

enzyme activity and photosynthetic rate in the remaining leaves (bean and maize were tested, among others). The rise in enzyme activity, plus decreased competition among leaves for mineral nutrients and possibly hormonal substances supplied by the roots, could account for the rise in NAR of a potato plant as leaf area is declining due to senescence.

With this information in mind, it would be easy to underestimate the role of temperature and light on final yield. These two factors heavily influence vine growth, time of tuber initiation, number of tubers initiated and the growth potential of each tuber (6, 41).

Effect of Environment on Yield Potential of Propagules

There is a considerable body of evidence that suggest that environment under which a tuber is produced affects its subsequent performance as seed. It has long been common practice for southern growers to import northern seed. The northern seed appeared to be more vigorous and exhibited a lower level of virus infection (28, 70, 71). Went (71) undertook a series of experiments to test the effect of temperature on vigor of the seed. Using a virus-free clone, he showed that tubers grown at low temperatures, especially low night temperatures, produced higher yields when used as seed than those grown at higher temperatures. This effect was apparent to the fourth clonal generation no matter what the environment of the succeeding generations. Since it is difficult to imagine the transfer of a specific tuber-forming hormone through four generations, Went concluded that only the tendency toward tuber formation is transmitted.

It is known that conditions under which a tuber is grown and the time of lifting (maturity) affects dormancy and sprout development which in turn influence subsequent yield. Krijthe (34) showed that very immature tubers have a shorter dormant period and more rapid sprout growth than mature tubers. However, as a general rule, the more mature the tuber, the shorter the dormant period and the faster the sprout development (12). According to Toosey (63) any factor which hastens tuber initiation on the parent plant accelerates the rate of physiological aging of the tuber and results in larger and more highly developed sprouts. However, Goodwin et al. (22) state that environmental and cultural influences on sprout development are small compared with the effect of storage conditions.

The effect of sprout development of the seed tuber on subsequent field performance is in question. Some argue that increased sprout development at planting hastens emergence, tuber initiation and senescence, resulting in lower yield at maturity (17, 25); in effect, it displaces part of the vegetative cycle (63). Others (11, 39) contend the phases of growth are not changed, only advanced. Yield potentials would be the same, the only factor that would influence yield would be the different climatic conditions under which the performance of the seed is observed. The only point of agreement is that advanced sprouting will produce earlier emergence and therefore earlier marketable yield.

A distinction should be made between the maturing or 'aging' that occurs as the plant develops in the field and physiological changes or 'aging' that occurs in storage. They would undoubtedly not be the same; unfortunately, in much of the literature, the distinction is not

made. When on encounters terms like maturity and physiological age their meaning is frequently unclear.

Influence of Altitude on Potato Plant Growth

The effects of altitude on growth and productivity of the potato have been explored by several workers. Kozlowska (31, 32) and Ronsen (54) agree that size of the vine and tuber yield both decrease with increasing elevation, probably due to suboptimal temperatures and shortened frost-free period; Kozlowska also considers changing soil conditions. Due to the combination of high latitudes and low elevations in the studies of Kozlowska and Ronsen, the primary influence of light would have been one of daylength. In the present study the influence of light was primarily one of intensity and total insolation.

There is apparent disagreement on the effects of altitude at which 'seed' is produced upon its yield potential. Kozlowska found that, when transferred to the lowlands, seed produced from 400 to 1200 m gave higher yields than lowland produced seed. Ronsen showed a decrease in yield potential with increasing elevation of production. Iritani (26) found no significiant difference in yield with tubers produced at different elevations (1430-2000 m). These results are not necessarily contradictory. Since the site characteristics, storage conditions and cultural practices are not adequately discussed, these studies cannot be directly compared and therefore are of little value to the present study.

There are several possible ways in which the elevation of production of the parent plant could influence the yield potential of the seed tubers. As previously discussed, Went (71) concluded that the tendency

to tuberize, influenced by the temperature regime, can be passed on to succeeding generations. Another possibility is that the set of environmental conditions at higher elevations inhibits virus multiplication within parent plants, producing healthier, more vigorous seed (31, 32).

MATERIALS AND METHODS

Field Experiment

Six sites, ranging in elevation from 1533 to 3213 m were used. The 1533 m site was in Fort Collins, Colorado (41°N, 105°W). The remaining five were located in the mountains near Aspen, Colorado (39°N, 107°W), approximately 43 km west of the Continental Divide. In the mountains, aspect was considered an important factor; therefore, at 2800 and 3200 m, sites of both north and south aspect were selected. The maximum daylength difference among sites was <20 minutes so photoperiod was considered to have no influence on the experiment. At the mountain sites maximum and minimum thermometers measured daily air temperature extremes at one meter above the soil surface in U.S. Weather Bureau shelters. Solar radiation was recorded by a Matrix MK14E pyranometers. Data for the Fort Collins site were obtained from the USWB station on the Colorado State University campus.

Large differences in temperature among sites were anticipated. However, insolation was expected to be high at all sites. In order to determine the importance of this parameter shade structures were erected at each site. These structures consisted of an 'A' frame with two 3.7 m lengths of 1.2 m high snow fence hung on metal posts (Fig. 1). The snow fence slats were 3.8 by 1.3 cm separated by 6.4 cm spaces. This type of shading was chosen because it would not significantly change either the temperature regime or the spectral composition of sunlight. By measuring the insolation and temperature under these structures it

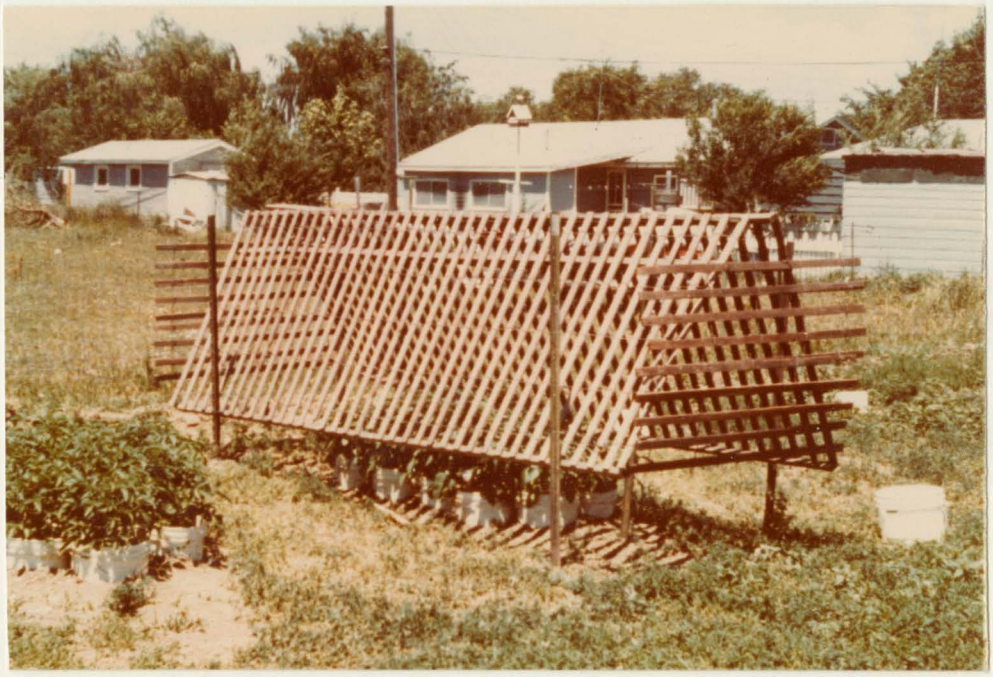

Figure 1. Shade structure (3.7 x 1.2 m).

was determined that 48% reduction in light was achieved with only an average 0.5° C decrease in day air temperature and a 0.5° C increase at night. All shade structures were erected along an east-west axis. Hereafter, the term treatment will refer to the shade or no shade condition.

Whole tubers (cv. Kennebec) from a clone grown in the San Luis Valley of Colorado were used. Whole tubers weighing 55 ± 5 g were grown in 13 l plastic pails containing approximately 9 l of an artificial soil mix. A single tuber was planted at a depth of 10 cm in each container. The mix was 40% peat, 30% vermiculite and 30% sand by volume. Fifteen g of triple superphosphate, 10 g KNO_3 and 5 g $(NH_4)_2SO_4$ were incorporated per 28 l of mix. Micronutrients were added in solution, 45 mg/l, 0.5 l per container. For analyses of the soil mix and micronutrients, see appendix tables 1 and 2. Tensiometers were used to monitor soil matric potential. Pre-irrigation soil water tension was -20 centibars, near the breakpoint of the soil moisture curve for this type of mix (44). Holes were drilled in the containers for drainage. Black paper covers were placed on the soil surface to reduce evaporation.

On May 29, 1976 containers designated for the six sites were planted at the 2372 m site. This was done to minimize environmentally induced differences in rate of emergence. Several frosts in June killed the earliest growth but no plants were lost. On June 19, 24 plants were transferred to the 1533 m site. On June 27, the remainder of the plants were distributed, 24 per site. Those destined for the two highest sites spent a day at 2827 m to acclimate. On June 29 one-half the plants at each site were placed under the shade structures. In all cases the containers were placed in three rows of four along an east-west axis.

Epstein and Robinson (20) found a high correlation between the length of Kennebec potato leaves and their area. On July 14 three leaves per plant were tagged, a total of 36 leaves per treatment per site. The leaves chosen were the third leaf from the terminal cluster on a stem. At weekly intervals beginning July 14 and ending August 11 the length of these tagged leaves, from the base of the petiole to the apex of the apical leaflet, was measured.

A reflectance meter described by Riggert (51) was used to determine leaf color in a non-destructive manner. Two fully expanded leaves judged to be representative were selected from each plant, a total of 24 per treatment per site. The measurement was taken in the middle of the lamina of the apical leaflet. A blank white index card was used for the zero reading. The zero reading was checked after each twelve measurements. Measurements were taken on August 12 and 13.

Canopy temperature was measured with a Barnes PRT-5 radiation thermometer. Measurements were taken on August 20-21. The instrument sensing unit has a 2^{o} field of view. Measurements were taken at a distance of 3 m, making the field approximatley 10 cm in diameter. Air temperature and insolation (measured by the instruments previously described), as well as time of day, wind and cloud conditions, were recorded for each canopy temperature measurement.

Early in August symptoms of possible nitrogen deficiency began to appear. On August 5 three g NH_4NO_3 was added in solution to each container.

Two harvests were taken at each site, one-half of each treatment population each time. The 1533 m site was harvested on August 11 and 17, the others on August 17 and 25. The reason for this will be discussed

later. Data obtained for each plant were:

1. Stem number and length
2. Number and length of internodes on the longest stem
3. Fresh and dry weight of the vine
4. Number of tubers greater than 1 cm in diameter
5. Weight of tubers greater than 1 cm in diameter
6. Specific gravity of the tubers[z]

Dry matter content of the tubers was calculated from specific gravity using the prediction of Schippers (56). Vine dry weight was obtained by drying the tissue in a forced draft oven at 70° C for 48 hours. The third and fourth leaves from the terminal leaf cluster on each stem of a plant (an average of 14 leaves per plant) were removed and dried separately by the same procedure.

This selected leaf tissue was analyzed for nitrate content. The dried tissue was ground with a Wiley mill through a 40-mesh stainless steel screen. The analysis performed was essentially that of Cantliffe et al. (15); however, resin was not used. Nitrate ion activity was measured in 0.025 M $Al_2(SO_4)_3 \cdot 16\ H_2O$ + 10 mg/ml NO_3-N extracting solution with an Orion 92-07 nitrate ion activity electrode and a Corning Ag/AgCl reference electrode with a ceramic junction together with an Orion 801 Digital Millivolt Meter. Aliquots containing 400 mg of tissue were used. Five samples from each treatment at each site were tested; the small amount of tissue per plant necessitated the combining of two plants for each sample. The remaining leaf tissue was sent to

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[z] Specific gravity was measured using a combination of tubers from six plants. Six to eight tubers weighing approximatley 300 g total were used for each measurement. Specific gravity was determined by the weight in air-weight in water method.

Agricultural Consultants Laboratory in Brighton, Colorado for determination of nitrogen (excluding NO_3-N) and carbon content. These analyses were performed using the methods described in the AOAC Methods of Analysis (2).

A split plot statistical design was employed with elevation being the main plot and light intensity (shade or no shade) the split plot. Each of the individual plants within the split plot was assigned a number and considered a replication. A two-way analysis of variance was performed.

The tubers were stored at 4^{o} C from harvest until October 29 when they were transferred to 8^{o} C and held for the remainder of the storage period.

Greenhouse Experiment I

Tubers produced at the 1533, 2372, and 3198 m sites were used for this experiment. On November 30, 1976 the tubers were removed from 8^{o} C storage and placed in a dark room at 24^{o} C. On December 11 whole tubers 35 $\pm$ 5 g were selected. All showed sprout development, averaging 0.5 cm. There was no apparent difference in sprout development between treatments or among sites. Ten tubers from each treatment at each site were planted in the containers used in the field experiment previously described, one per container. The soil mix and fertilization were essentially the same as the field experiment, with several modifications. Analysis of the mix (appendix table 1) indicated that the addition of micronutrients was not necessary. Also, the pH of this mix was 4.1, compared to 5.2 for the field experiment. The discrepancy was apparently the result of using different sources of peat. The addition of 0.2% $Ca(OH)_2$ by weight of dry mix brought the pH into the range of the field experiment. To reduce possible pathogen infection the containers were soaked in a 1000 PPM available chlorine solution (diluted household bleach) and the sand for the soil mix was steam sterilized. All tubers were planted at a depth of 10 cm.

To minimize shading in the limited space available, a platform was constructed on the north half of both benches and the plants were tipped slightly to the south. Plants were set out in five randomized complete blocks with two plants from each treatment at each site per block, one replicate on the bench, one on the platform (Fig. 2).

Again, pre-irrigation soil water tension was -20 centibars as measured by tensiometer. The plants were grown in the Plant Science Greenhouse on the CSU campus. The section was maintained at an average

Figure 2. Design of one complete block for greenhouse experiment I. Each row has one replicate of each group.

daily maximum and minimum of 29° C and 10° C, respectively. During the growth period the highest temperature recorded was 32° C, the lowest 8° C. The average daily insolation was 180 cal cm^{-2} during the experimental period. Aphids were controlled by periodic spraying with Isotox.

Date of emergence was recorded. Plant height, from the surface of the medium to the tip of the highest leaf, was measured on January 22 and February 11, 1977. Beginning February 14 the plants were harvested at weekly intervals, one block per week until March 14. Measurements taken were number of tubers greater than 1 cm in diameter and their total weight per plant. On the last block harvested fresh and dry weight of the vines was also recorded. Hereafter the term group will refer to plants grown from tubers produced at a particular elevation and treatment.

Greenhouse Experiment II

For this experiment, the soil mix used was identical to that used in the greenhouse work previously described. On January 4, 1977 whole tubers 35 $\pm$ 5 g, grown at the 1533, 2372, and 3198 m sites were removed from 8^{o} C storage and placed in a dark room at 24^{o} C. On January 12 twelve tubers from each treatment at each site were planted at a depth of 10 cm in 2.4 l cans, one per can. Each can contained 1000 g dry weight of soil mix. Plastic liners (6 mil) were used to eliminate rusting and reduce the chance of pathogen infection. Water content of the soil mix was maintained between 38-41% by weight. Again, date of emergence was recorded. At the time of planting, sprout length was noticeably different among sites (Fig. 3) but not between treatments.

Photosynthetic rates were measured in the CO_2 exchange system described by Ronco (52). The essential elements of the system are an airtight chamber illuminated by a bank of lights and connected to an infrared gas analyzed (IRGA). The plant is placed inside the chamber; a pump circulates air in the closed system from the chamber to the IRGA which monitors CO_2 concentration. The decrease in CO_2 with time is recorded by a strip chart recorder. Measurements were made between February 15 and February 28. For the tests the chamber air temperature was 27 $\pm$ 1^{0} C and plant illumination was 2500 foot candles as measured by a Weston 756 light meter. To prevent CO_2 evolution from root respiration or soil microorganisms, a warm mixture of 50% paraffin and 50% mineral oil was poured over the soil surface and allowed to form an airtight seal. A container with no plant was tested in the chamber to confirm the integrity of the seal. Measurements were made in sets of

Figure 3. Sprout development at planting (greenhouse experiment II) for tubers produced at different elevations.

six, one plant for each treatment at each site. All measurements were made at -10 centibar soil moisture deficit (41% H_2O by weight). All leaves were removed and leaf area for each plant was determined by a Hayashi Denko AAM-5 Automatic Area Meter. The leaf tissue was then dried in a forced draft oven at 70^{o} C for 48 hours and weighed.

Photosynthetic rate was calculated between CO_2 concentrations of 335 and 215 PPM, an activity period of 10-15 minutes. The rates were computed by the equation:

$$P_n = (MVT_1P/LTP_1)(\Delta PPM/hr \times 10^{-6}) \; / \; DWL \text{ or } LA$$

where:

M = mole weight of CO_2 (44.10 mg)
V = volume of closed system (34.48 liters)
$T_1 = 273^{o}$ K
P = average barometric pressure in Ft. Collins (635 mm Hg)
L = mole volume of CO_2 (22.414 liters)
T = chamber temperature (300^{o} K)
P_1 = standard barometric pressure (760 mm Hg)
ΔPPM/hr = CO_2 exchange rate (120 ppm/fraction of hour)
DWL = dry weight of leaves (g)
LA = leaf weight (dm^2)
P_n = net photosynthesis (mg CO_2 $g^{-1}hr^{-1}$) on dry weight basis or (mg CO_2 $dm^{-2}hr^{-1}$) on leaf area basis.

RESULTS

Site Characteristics

Table 1 details the site characteristics. It can be seen that mean and daily maximum temperature decreased while total insolation increased with increasing elevation. Minimum temperature shows a different trend. The low night average at 2372 m is the result of katabatic air flow into the valley. Total insolation increased 13% between 1533 and 3198 m. The increase is not constant however, as the insolation received at each site is influenced by localized climatic conditions (14). It is likely that intensities greater than the solar constant [1.94 cal $cm^{-2}min^{-1}$ (1)] occurred as Tranquillini (64) reported intensities of this magnitude have been observed at 2000 m. Intensities greater than the solar constant occur when scattered high cumulus clouds focus sky radiation. Even under the shade structures the intensity would probably exceed saturation for a single leaf much of the time. However, with a high degree of mutual shading, the higher intensities would allow more leaves to operate at maximum capacity for a longer period each day.

The low average insolation for the 2817 m site is not only the result of its north exposure but the high degree of shading by the forest canopy in early morning and late afternoon. Due to the unusual conditions at this site and a problem with rodents defoliating the plants at 3213 m, the data presented will be from the four remaining sites unless otherwise stated.

Table 1. Site climatic characteristics for the period June 29 to August 17, 1976.

Elevation and exposure m	Air Temperature max °C	Air Temperature min °C	Air Temperature mean °C	Insolation cal $cm^{-2} day^{-1}$
1533[z]	29	14	22	472
2372	27	7	17	505
2817 north	22	9	16	380
2827 south	24	8	16	496
3198 south	21	9	15	530
3213 north	19	6	13	505

[z] The 1533 m and 2372 m sites were approximately level but the higher sites were on mountain slopes.

Field Experiment

Field Observations:

a) Plant morphology

Plant size decreased with increasing elevation as shown in Fig. 4. A striking morphological difference between treatments is the pronounced folding of the leaves of the unshaded plants (Fig. 5). In contrast, the leaves of the shaded plants are completely open, in fact convex. This phenomenon was noticed at the four highest sites with the severity of the folding increasing with increasing elevation. The plants pictured are from 3198 m.

b) Canopy temperature

Five canopy temperature measurements were made with an infrared radiation thermometer. Although the canopy temperature varied considerably with insolation, wind and ambient air temperature, in all cases the unshaded plants were warmer than the shaded. This difference averaged 2-3^{o} C.

c) Leaf color

At all sites shaded leaves gave higher absorption readings than unshaded leaves, indicating a darker green color (Fig. 6). This corresponds to visual observations made throughout the season. This is a strong indication that the shaded leaves had a higher concentration of chlorophyll per unit area (67). The difference between treatments was significant at the 5% level (appendix table 3). The trend with altitude is less clear. In general, absorption decreased with increasing elevation.

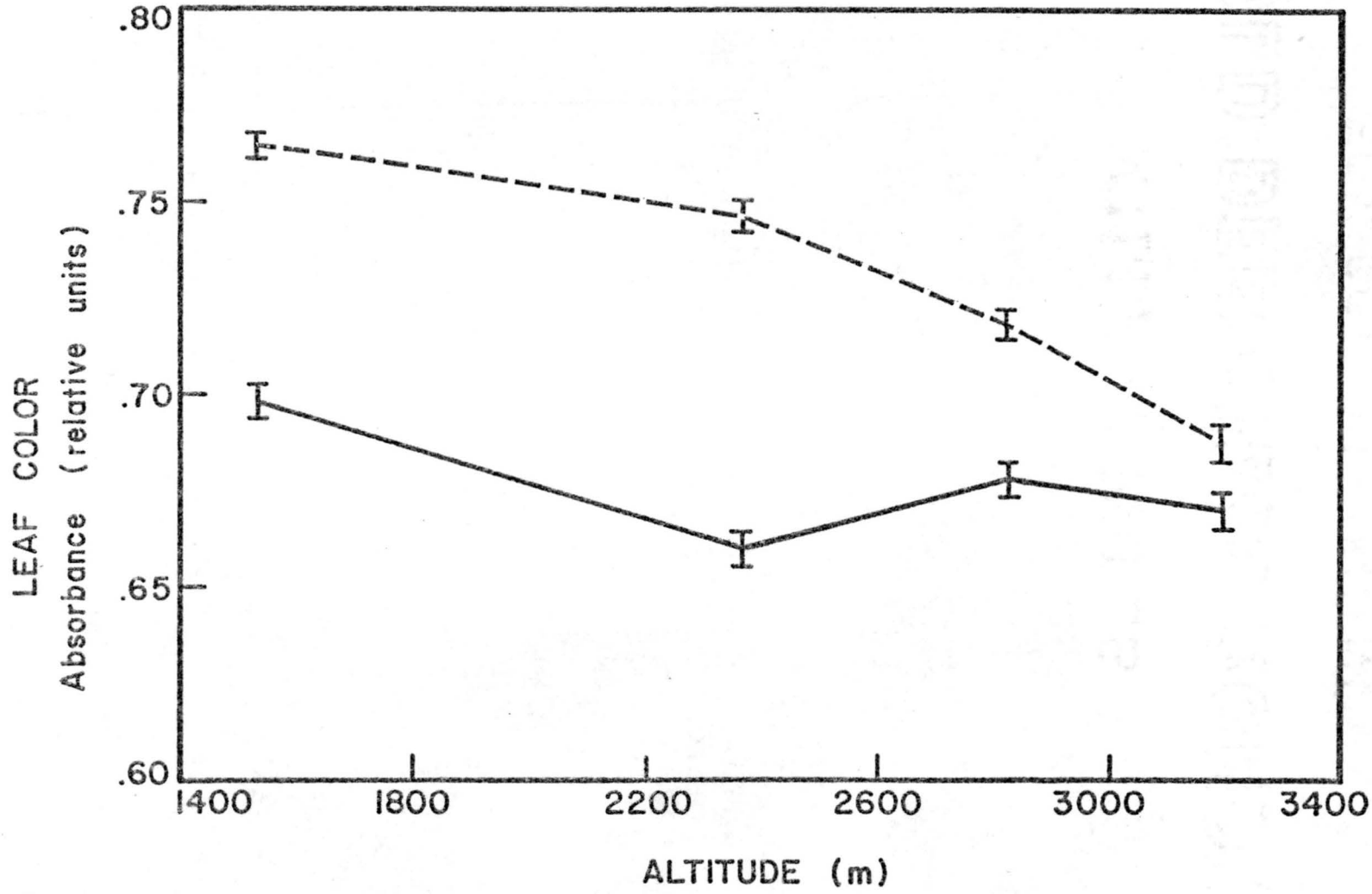
Figure 4. Comparison of plants produced at different elevations, increasing elevation from left to right. Signs designate thousands of feet. Unshaded plants in front row, shaded plants in back.

(a)

(b)

Figure 5. Unshaded leaf (a) and shaded leaf (b) from 3198 m.

Fig. 6. Potato leaf color as a function of reduced insolation (dashed line) and altitude. Each point is the mean of 24 measurements taken on August 12-13, 1976. Vertical bars indicate standard errors.


.80
.75
.70
.65
.60
LEAF COLOR
Absorbance (relative units)
1400
1800
2200
2600
3000
3400
ALTITUDE (m)

Vegetative Growth:

a) Stem number

Stem number averaged seven per plant but was highly variable. There was no clear trend between treatments or among elevations.

b) Stem length

Several trends are apparent. Stem length was greatly influenced by insolation as evidenced by the increased length of the shaded plants at all elevations (Fig. 7). Stem length also decreased with elevation above 2372 m. This seems to be at least partially a response to temperature, 17° C being suboptimal for stem growth. The confounding factor is the increasing ultraviolet radiation with elevation (14) which exerts a strong influence on stem elongation.

c) Leaf length

Due to the morphological differences among sites and treatments, the prediction equation (20) for determining leaf area from leaf length could not be used with any degree of accuracy; consequently, leaf length will be the parameter discussed. Figure 8 shows an increase in leaf length through time. Relatively little leaf extension occurred after July 28. At all elevations the leaves of shaded plants were significantly longer than those of unshaded. From Fig. 8 it is clear that leaf length reached its maximum at 2372-2827 m (16-17° C mean temperature).

d) Internodes

The number of internodes on the longest stem decreased with increasing elevation (Fig. 9). This would indicate more leaves per stem at 1533 m but not enough more to offset the larger leaf size at the

Fig. 7. Potato stem length as a function of reduced insolation (dashed line) and altitude. Each point is the mean of 24 measurements taken on August 17, 1976. Vertical bars indicate standard errors.

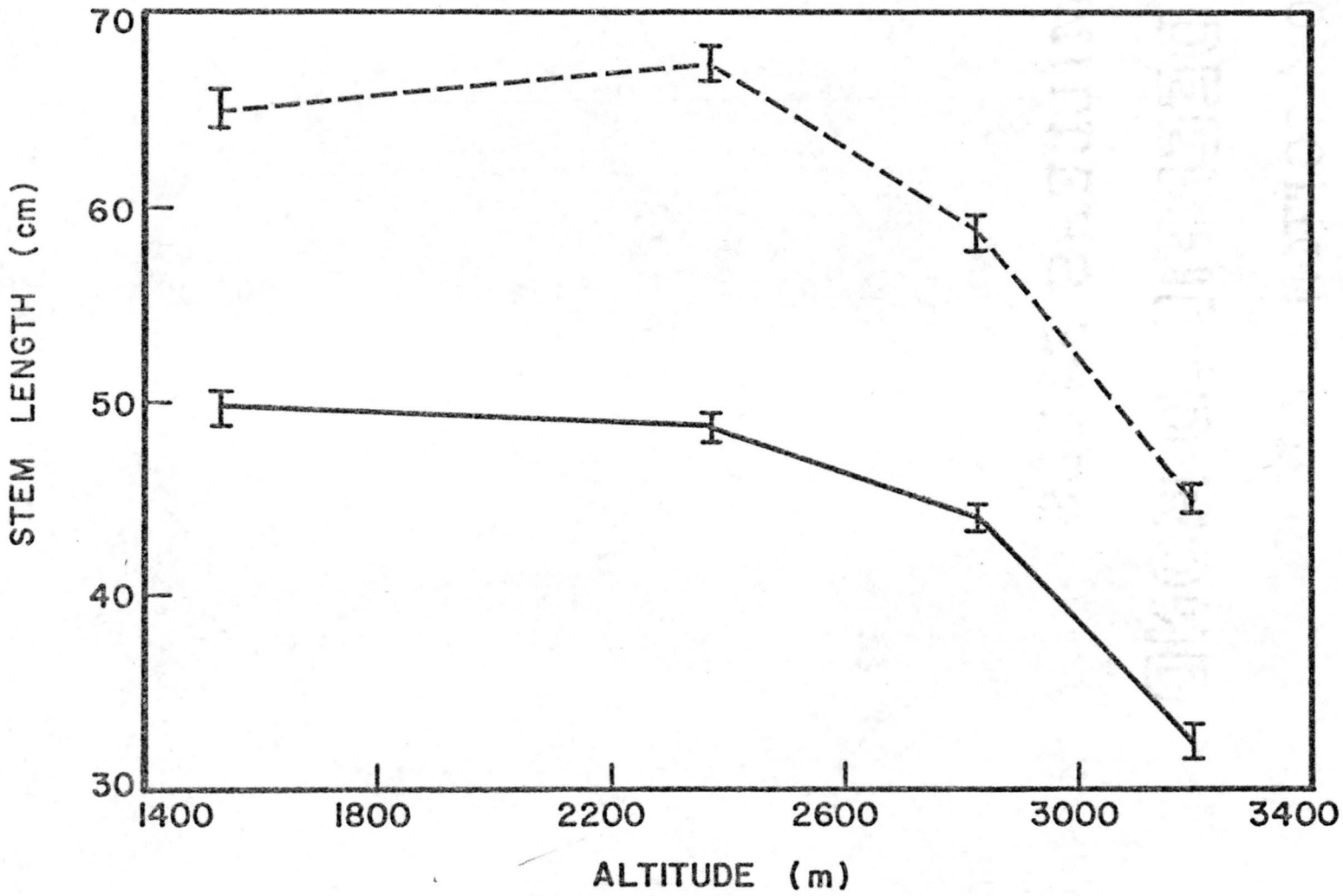

70
60
50
40
30
STEM LENGTH (cm)
1400
1800
2200
2600
3000
3400
ALTITUDE (m)

Fig. 8. Potato leaf length as a function of insolation and altitude. Each point is the mean of 36 measurements.

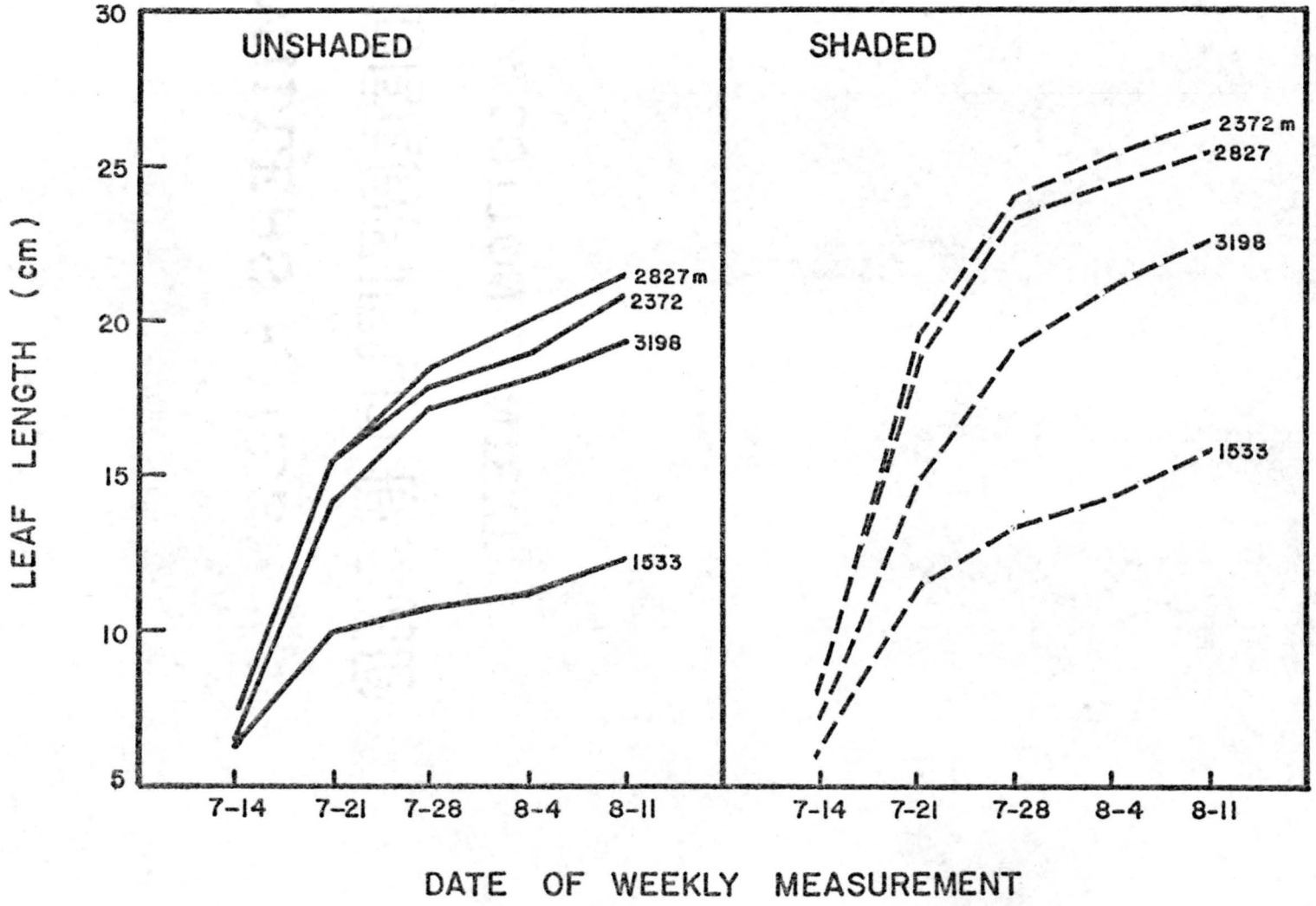
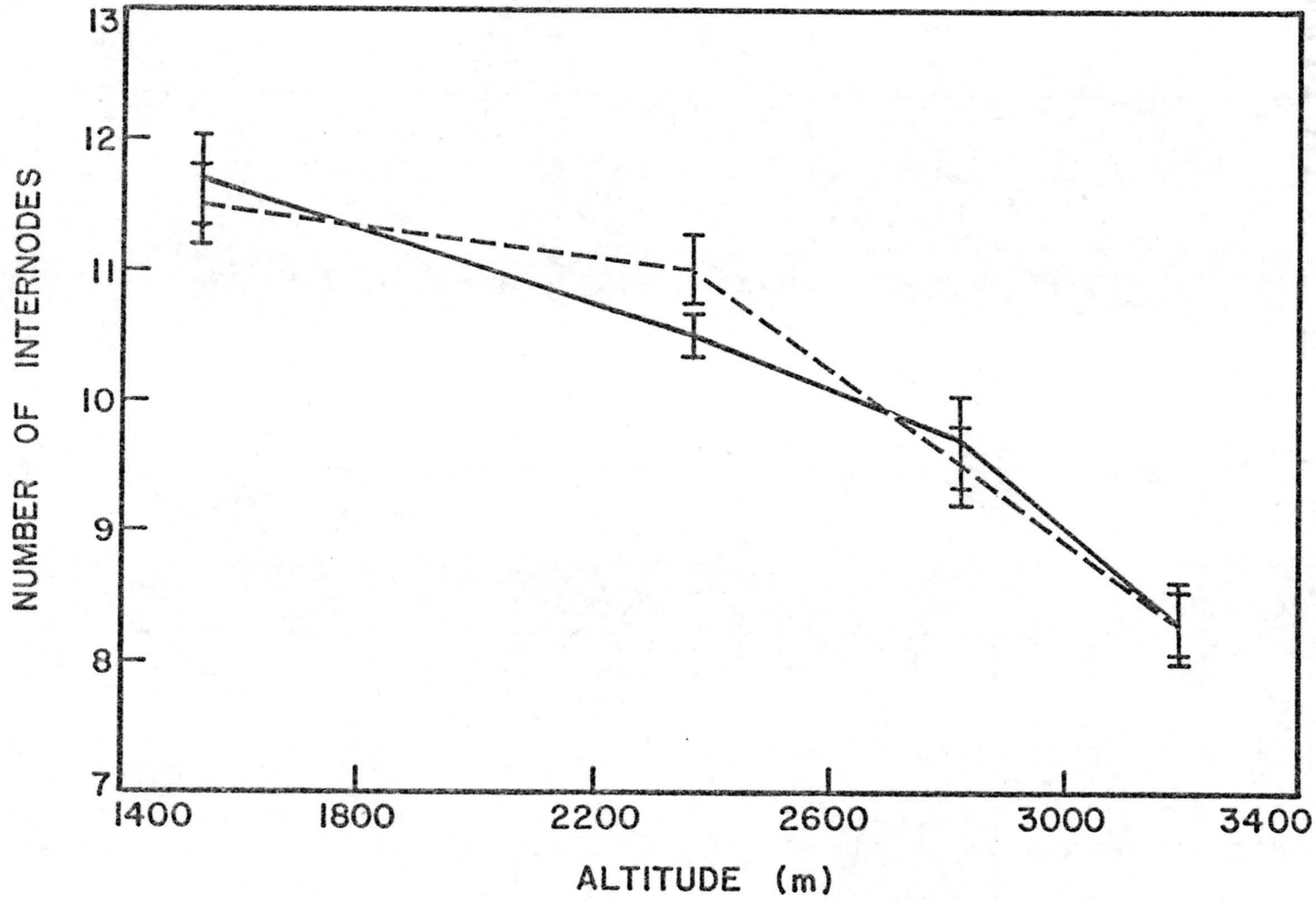

UNSHADED
SHADED
LEAF LENGTH (cm)
30
25
20
15
10
5
2827m
2372
3198
1533
2372 m
2827
3198
1533
7-14
7-21
7-28
8-4
8-11
DATE OF WEEKLY MEASUREMENT

Fig. 9. Number of internodes on the longest stem of potato plants as a function of reduced insolation (dashed line) and altitude. Each point is the mean of 6 plants harvested August 17, 1976. Vertical bars indicate standard errors.


NUMBER OF INTERNODES
13
12
11
10
9
8
7
1400
1800
2200
2600
3000
3400
ALTITUDE (m)

higher, cooler sites. Shading clearly lengthed internodes but did not increase their number.

e) Vine dry weight

Vine dry weight reaches a maximum at 2372 m (17^{o} C mean temperature) (Fig. 10). At 1533 and 2372 m vine dry weight was greater for shaded than unshaded plants; however, this difference was not statistically significant. At the higher elevations, there was little difference between treatments. It should be pointed out that the dry weight of the vine is only a small portion of total plant dry weight at harvest.

f) Leaf tissue carbon and nitrogen

Nitrate content of the leaves increased with increasing elevation (Fig. 11). In all cases shaded plants showed higher nitrate concentrations than their unshaded counterparts. The reason for the low value for the 2372 m shaded plants is unknown. Table 2 indicates that while total nitrogen is relatively constant at all elevations, the percent carbon in the leaf tissue is much higher at 2372 m than either remaining site. This results in a larger carbon to nitrogen ratio at 2372 m. The 1533 m plants have the lowest carbon content. The C/N ratio was consistently higher in unshaded plants. Analysis of variance for carbon and nitrogen content is presented in appendix tables 7 and 8.

Tuber Growth:

a) Tuber number

Tuber number was highly variable. The trend toward higher number for shaded than unshaded plants is not significant at any one elevation

Fig. 10. Potato vine dry weight as a function of reduced insolation (dashed line) and altitude. Each point is the mean of 6 plants harvested August 17, 1976. Vertical bars indicate standard errors.

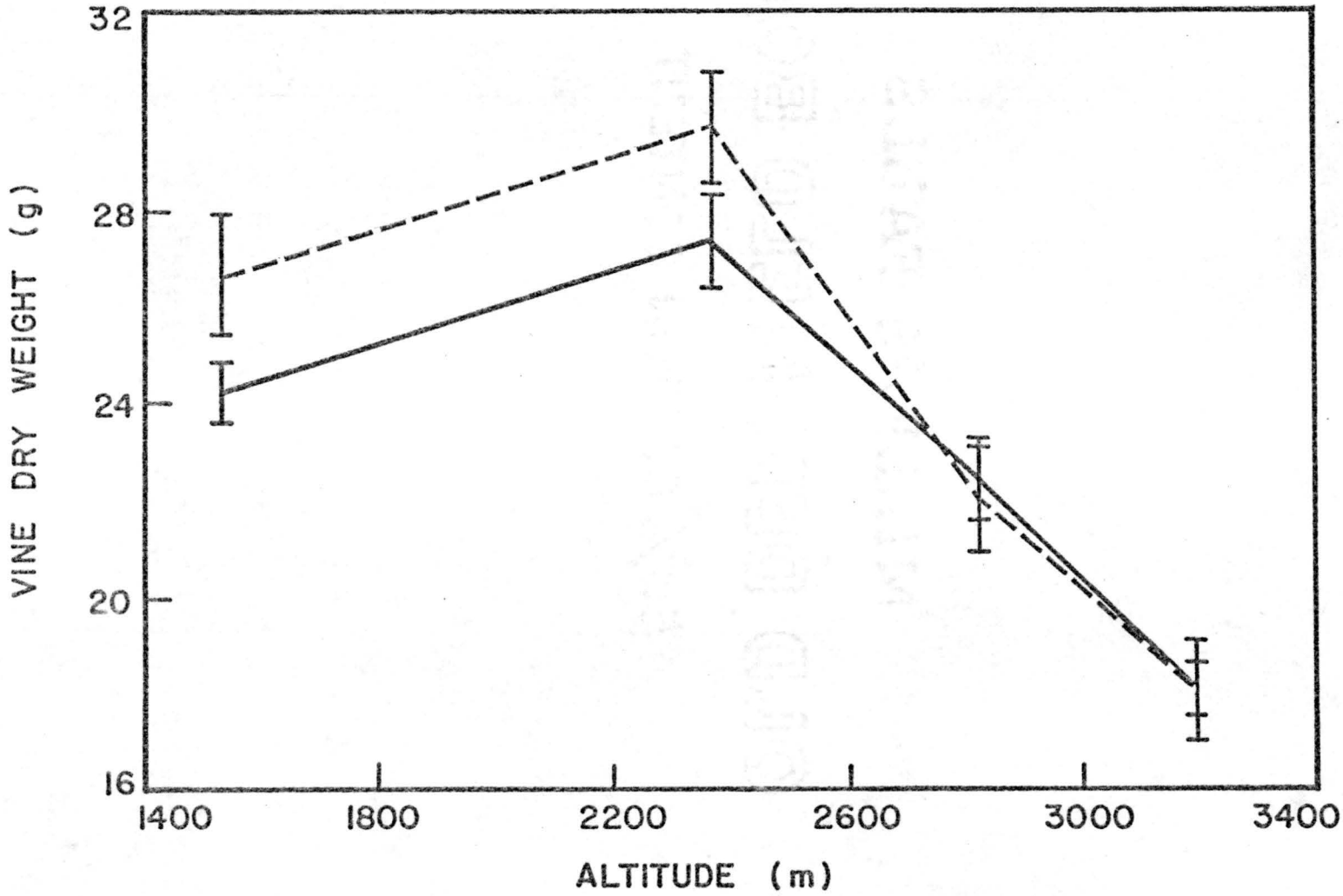

VINE DRY WEIGHT (g)
32
28
24
20
16
1400
1800
2200
2600
3000
3400
ALTITUDE (m)

Fig. 11. Nitrate content of potato leaf tissue as a function of reduced insolation (dashed line) and altitude. Each point is the mean of 5 measurements. Vertical bars indicate standard errors.

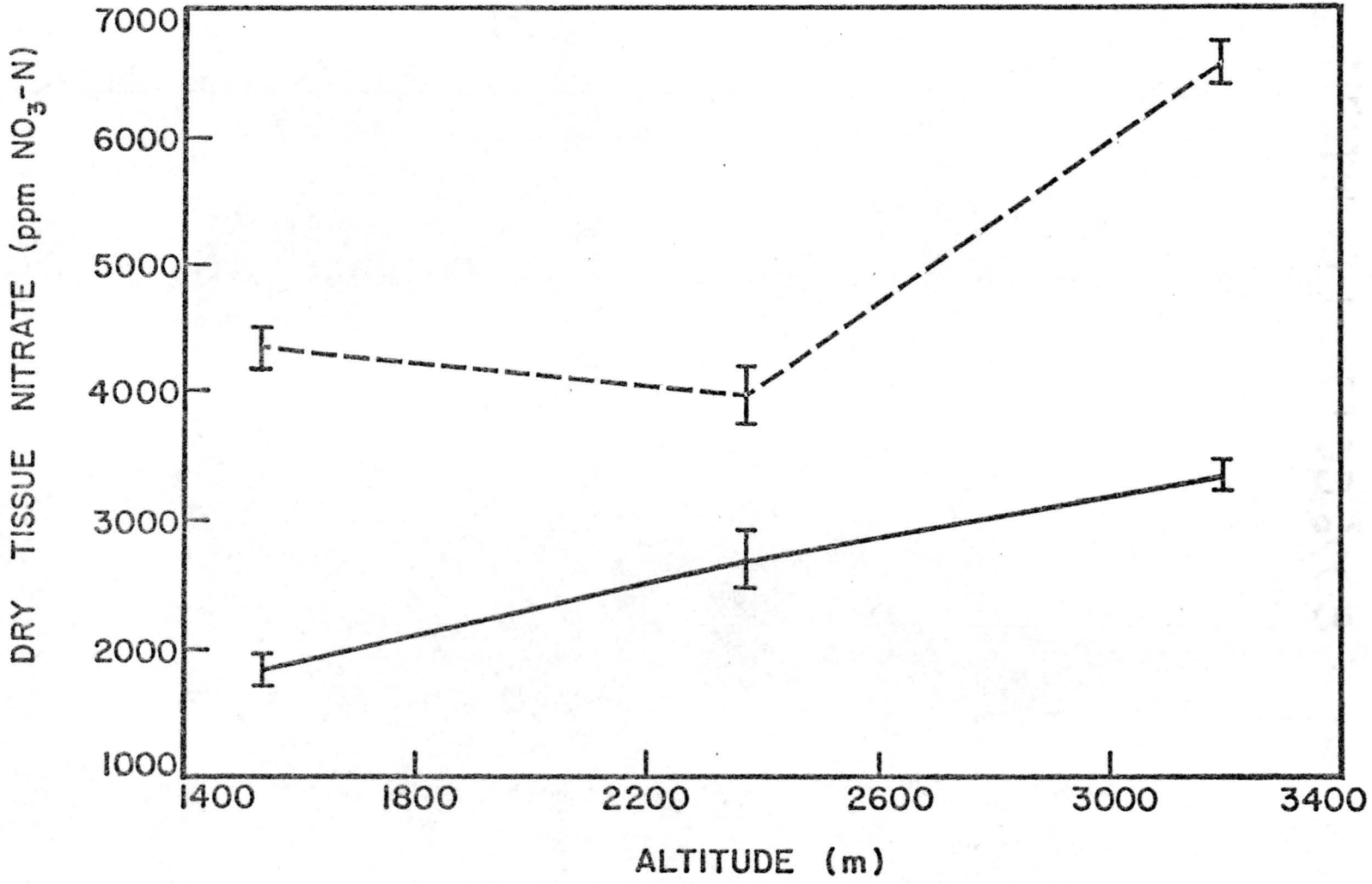

DRY TISSUE NITRATE (ppm NO_3-N)
7000
6000
5000
4000
3000
2000
1000
1400
1800
2200
2600
3000
3400
ALTITUDE (m)

Table 2. Carbon and nitrogen content of potato leaf tissue as percentage of dry weight.

Elevation (m)	Unshaded			Shaded		
	% carbon	% nitrogen[z]	ratio C/N	% carbon	% nitrogen[z]	ratio C/N
1533	29.9	4.3	7.0	27.2	4.9	5.6
2372	41.7	3.8	11.0	29.3	4.4	6.7
3198	33.9	4.2	8.1	28.9	4.7	6.1

[z] includes NO_3-N

but is significant overall (appendix table 9). The more pronounced trend is increasing tuber number with elevation (Fig. 12). The dramatic increase in tuber number at 3198 m can not be attributed to any one factor. In all groups there were undifferentiated stolons and stolons bearing tubers less than 1 cm in diameter.

b) Tuber fresh weight

From Table 3 it is clear that shading significantly reduced tuber weight per plant at all elevations. The effect of elevation is less clear. Yield decreased with elevation, but very slowly. There is virtually no difference between 1533 and 2372 m on August 17. With one more week's growth all mountain sites approached or surpassed the yield obtained at 1533 m. As expected, mean tuber weight decreased with increasing elevation.

Field Growth Analysis:

An attempt was made to correlate several aspects of field growth to environmental conditions. Data from both treatments at all sites and harvests were used. Each value is the mean of six plants.

a) Maturity

Dobbins (19) found the rate of development of many field crops to be a function of temperature. The time to certain phenological events such as flowering, crop maturity or senescence can be predicted by a measure of accumulated heat input. High correlations have been found between accumulated heat and maturity in many crops, including cabbage (27), corn (50), and grape (4). This type of prediction system is used commercially for peas and sweet corn.

Fig. 12. Number of tubers per plant as a function of reduced insolation (dashed line) and altitude. Each point is the mean of 6 plants harvested August 17, 1976. Vertical bars indicate standard errors.

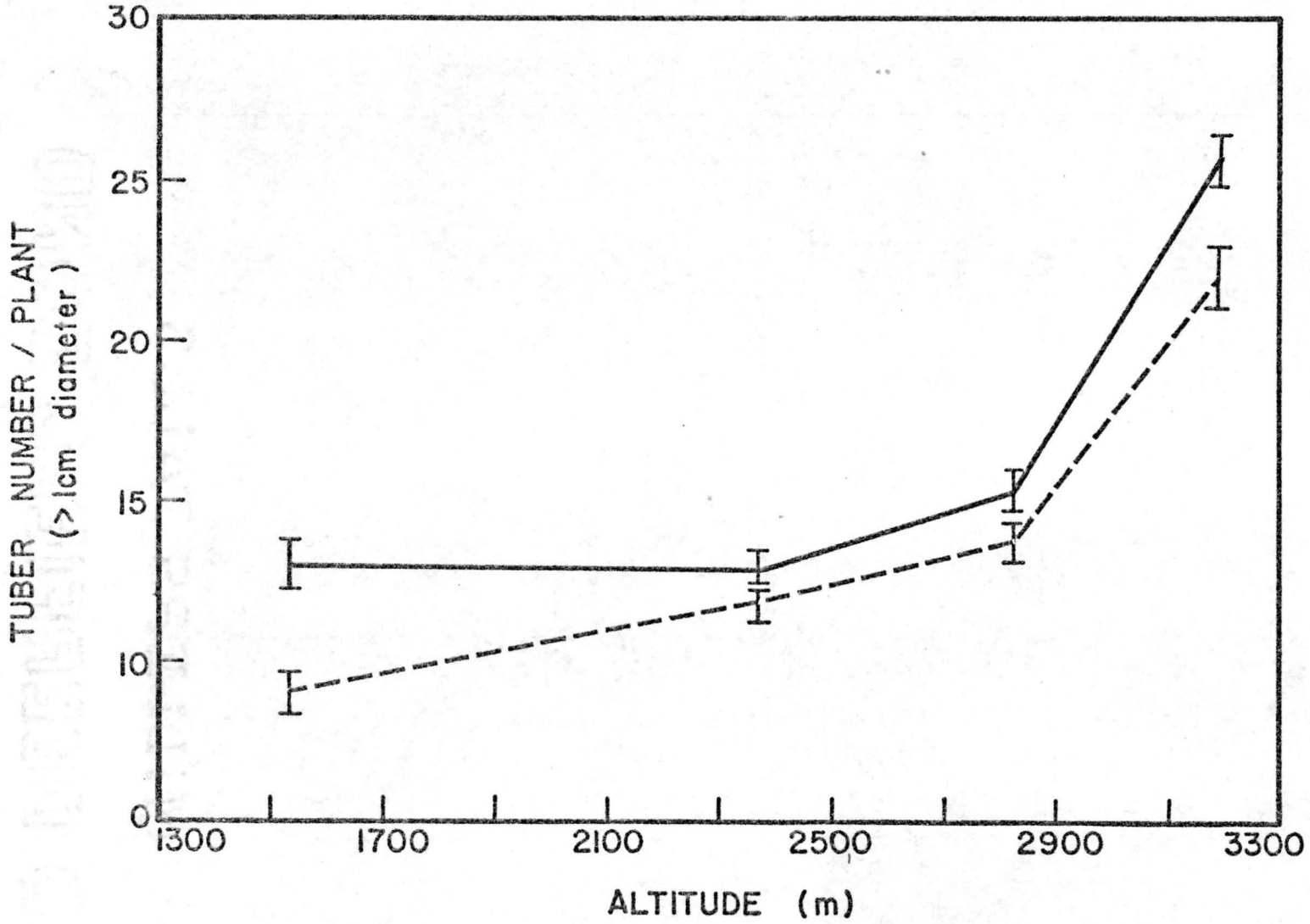

TUBER NUMBER / PLANT
(> 1cm diameter)
30
25
20
15
10
0
1300
1700
2100
2500
2900
3300
ALTITUDE (m)

Table 3. Tuber fresh weight in grams per plant. Standard error indicated by parentheses.

	Elevation (m)	August 11	Harvest Date August 17	August 25
Unshaded	1533	398 (11)	470 (20)	
	2372		454 (16)	582 (27)
	2827		388 (27)	480 (44)
	3198		378 (14)	464 (18)
Shaded	1533	233 (7)	334 (24)	
	2372		305 (13)	432 (12)
	2827		279 (19)	382 (12)
	3198		275 (23)	349 (10)

There are several methods of calculating heat input. For this study, a modified version of the USDA (66) Growing Degree Day (GDD) system was utilized. GDD is calculated daily by the formula:

$$\frac{\text{max temp } (\leq 86^{o}\text{ F}) + \text{min temp } (\geq 50^{o}\text{ F})}{2} - 50^{o}\text{ F}$$

and is summed through the season. In my work, a base of 40, rather than 50, was used since a cool season crop like potato would be expected to show considerable physiological activity below 50^{o} F; also, a base of 50 would obscure the low night temperatures at the mountain sites.

The best measure of maturity available for potatoes was considered to be specific gravity of the tubers. Accumulated heat, as measured by GDD, was highly correlated with specific gravity ($r = 0.92$). The small effect of insolation (Table 4) reinforces the concept that maturity is a function of temperature (heat energy).

Net assimilation (total plant dry matter) is the difference between photosynthesis and respiration; as such it would be dependent on day and night temperature and insolation. To avoid a complex regression model, the effect of day and night temperature were combined into a single factor, based on the GDD principle. This factor was calculated, using fahrenheit notation:

$$\text{Revised GDD} = \text{GDD} - \tfrac{1}{2}(\text{min temp} - 40)$$

The correction was added to weight the effect of increasing respiratory losses with increasing night temperature. This variable was a more effective predictor of net assimilation than the standard GDD or any combination of temperature related variables listed in appendix table 10.

Table 4. Regression analyses of selected growth characteristics. Independent variables shown are the best predictors of those listed in appendix table 11 and are significant at 5% level.

Dependent Variable	Independent Variable	Multiple Linear		Increase in R^2
		R	R^2	
Specific gravity	GDD	0.918[z]	0.843[z]	
	+Total insolation	0.949	0.900	0.058
Net assimilation (total dry matter)	Revised GDD	0.903[z]	0.816[z]	
	+Total insolation	0.928	0.862	0.054
Tuber fresh weight	Revised GDD	0.762[z]	0.581[z]	
	+Total insolation	0.928	0.861	0.280
	+Daily temperature range	0.965	0.932	0.071

[z] Simple linear correlation coefficient, r; and coefficient of determination, r^2.

When total insolation was added to the regression model with revised GDD, a multiple correlation coefficient of 0.93 was achieved.

Final yield is the end product of many factors; as such it can not be easily explained or predicted. In this study, the best predictors of yield appear to be revised GDD, total insolation and mean daily temperature range. Table 4 summarizes the regression analysis of the field data. Prediction equations are given in appendix table 12.

Fig. 13. Greenhouse experiment I. Cumulative emergence of progeny grown from tubers produced at various elevations and levels of insolation. Solid lines represent unshaded parents, dashed lines represent shaded parents.

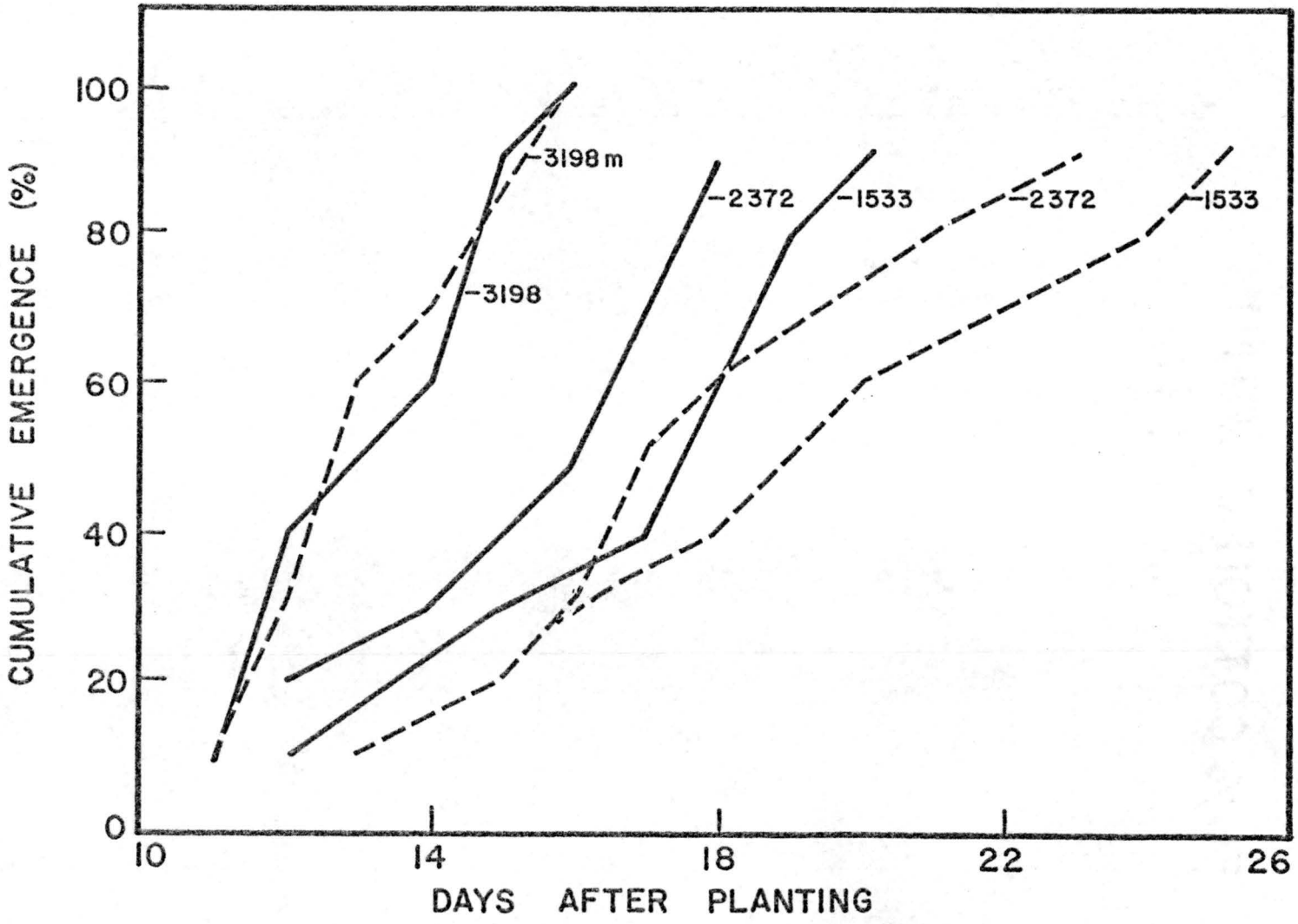
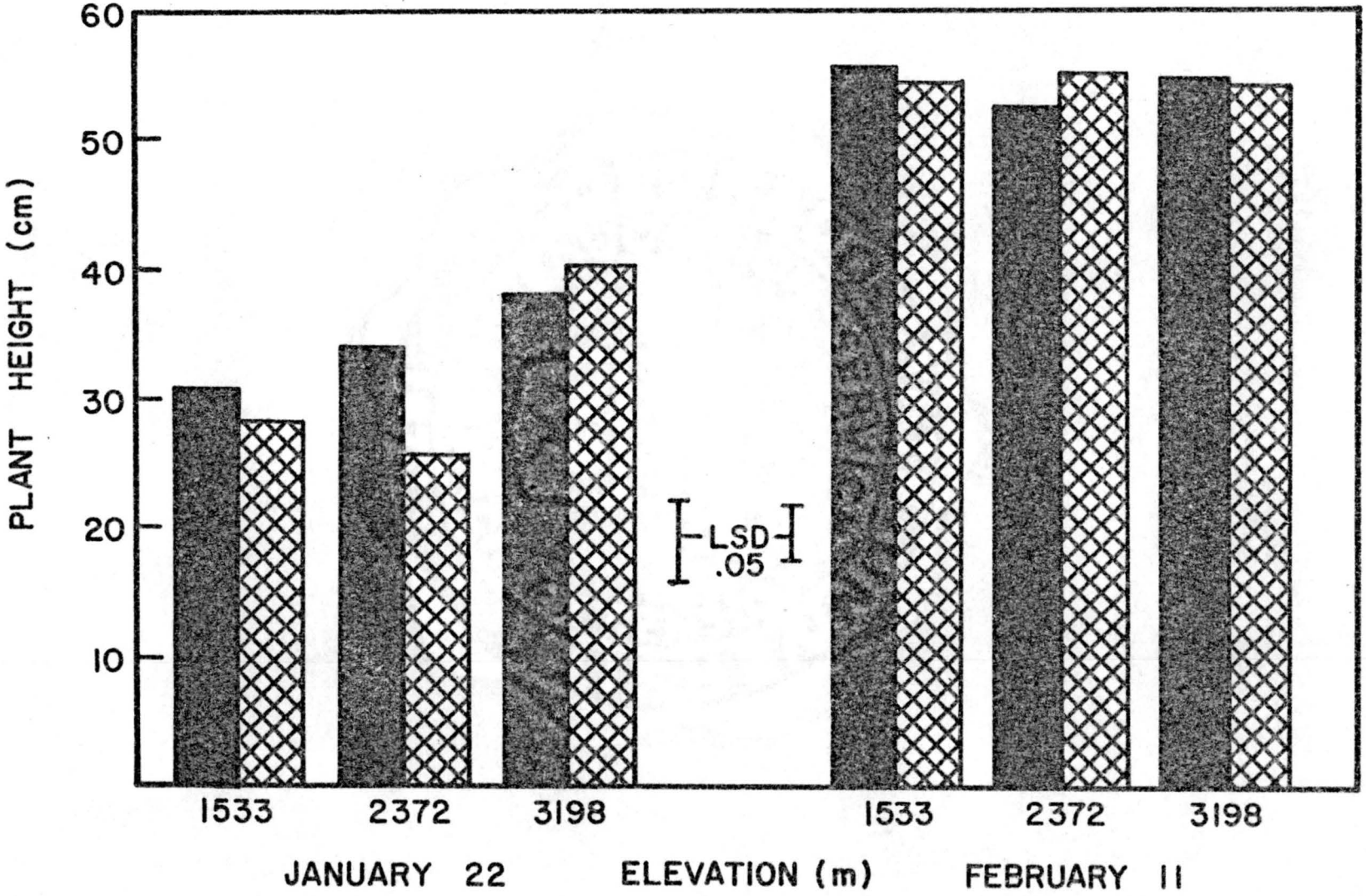

CUMULATIVE EMERGENCE (%)
100
80
60
40
20
0
10
14
18
22
26
DAYS AFTER PLANTING
3198 m
3198
2372
1533
2372
1533

Fig. 14. Greenhouse experiment I. Plant height of progeny grown from tubers produced at various elevations and levels of insolation. Each bar represents the mean of 10 plants. Solid bars represent unshaded parents, checkered bars represent shaded parents.

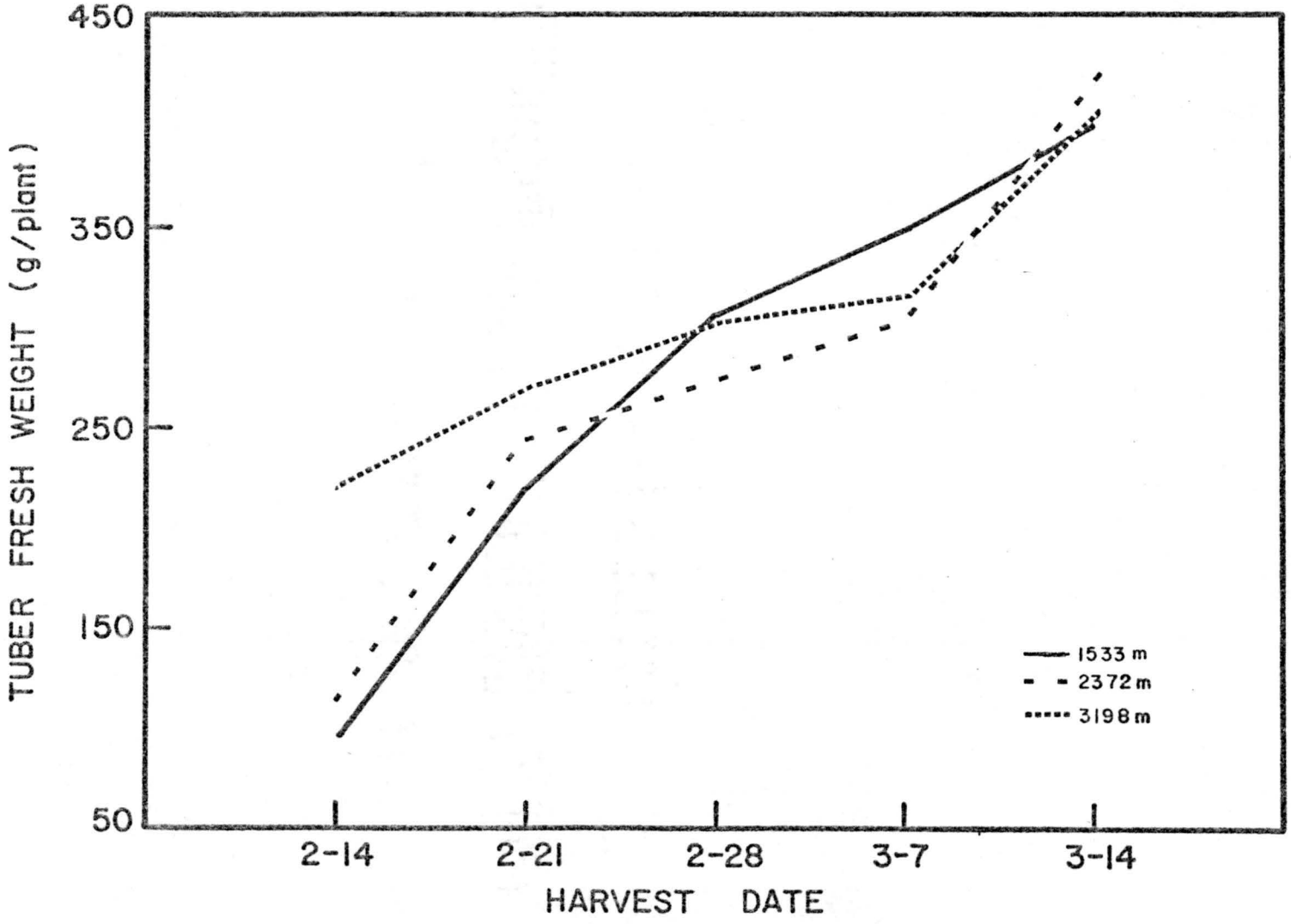

60
50
40
30
20
10
PLANT HEIGHT (cm)
LSD .05
1533
2372
3198
1533
2372
3198
JANUARY 22
ELEVATION (m)
FEBRUARY 11

Tuber Growth:

The small number of plants used in this experiment make statistical analysis difficult, if not impossible; therefore, these data are not conclusive and should be viewed only as trends. Tuber number was highly variable; no clear trend was apparent. The differences in tuber weight per plant between groups from shaded or unshaded parents were small, so the data will be combined for clarity. Figure 15 shows the mean yield through the season for seed grown at the different elevations. The most striking feature is the greater early (February 14) yield of the 3198 m group. Overall harvests the 3198 m group showed significantly greater yield by virtue of this early advantage (appendix table 10). The difference disappears at later harvests. At the last harvest, the mean yield for all groups is virtually the same. Judging by the condition of the vines (Fig. 16) it is assumed that tuber bulking was nearly complete by the last harvest.

Figure 16. Vines (greenhouse experiment I) at last harvest March 14, 1977.

Fig. 15. Greenhouse experiment I. Tuber yield of progeny as a function of production elevation of parent plant. Each point is the mean of 4 plants.


450
350
250
150
50
TUBER FRESH WEIGHT (g/plant)
2-14
2-21
2-28
3-7
3-14
HARVEST DATE
1533 m
2372 m
3198 m

Greenhouse Experiment II

As a group the plants grown from 3198 m seed in the greenhouse were larger than the other groups when tested, presumably due to earlier emergence associated with advanced sprout development at planting (Fig. 3). There was a clear relationship between plant size, as leaf area or dry weight, and photosynthetic rate (Fig. 17). This is to be expected as mutual shading of leaves would increase with plant size. Also, the apparatus provided direct overhead illumination and the structure of the assimilation chamber allowed only minimal reflection. Beyond this relationship there was still considerable variation in the data. The coefficient of variation in photosynthetic rate for the 20 plants between 1.25 and 1.45 g leaf dry weight was 11.0. To determine if the groups were performing differently, analysis of covariance was done using both leaf area and leaf dry weight as the covariate. This analysis was performed using the BMD09V computer program.

Table 5 shows the adjusted group mean photosynthetic rates are very similar; from the t-test comparisons of these adjusted means it is clear that no significant difference in rate exists among groups.

Fig. 17(a). Greenhouse experiment II. Photosynthetic rate of progeny as a function of leaf area. Symbols indicate altitude of parent.
o = 1533, Δ = 2372, □ = 3198 m.

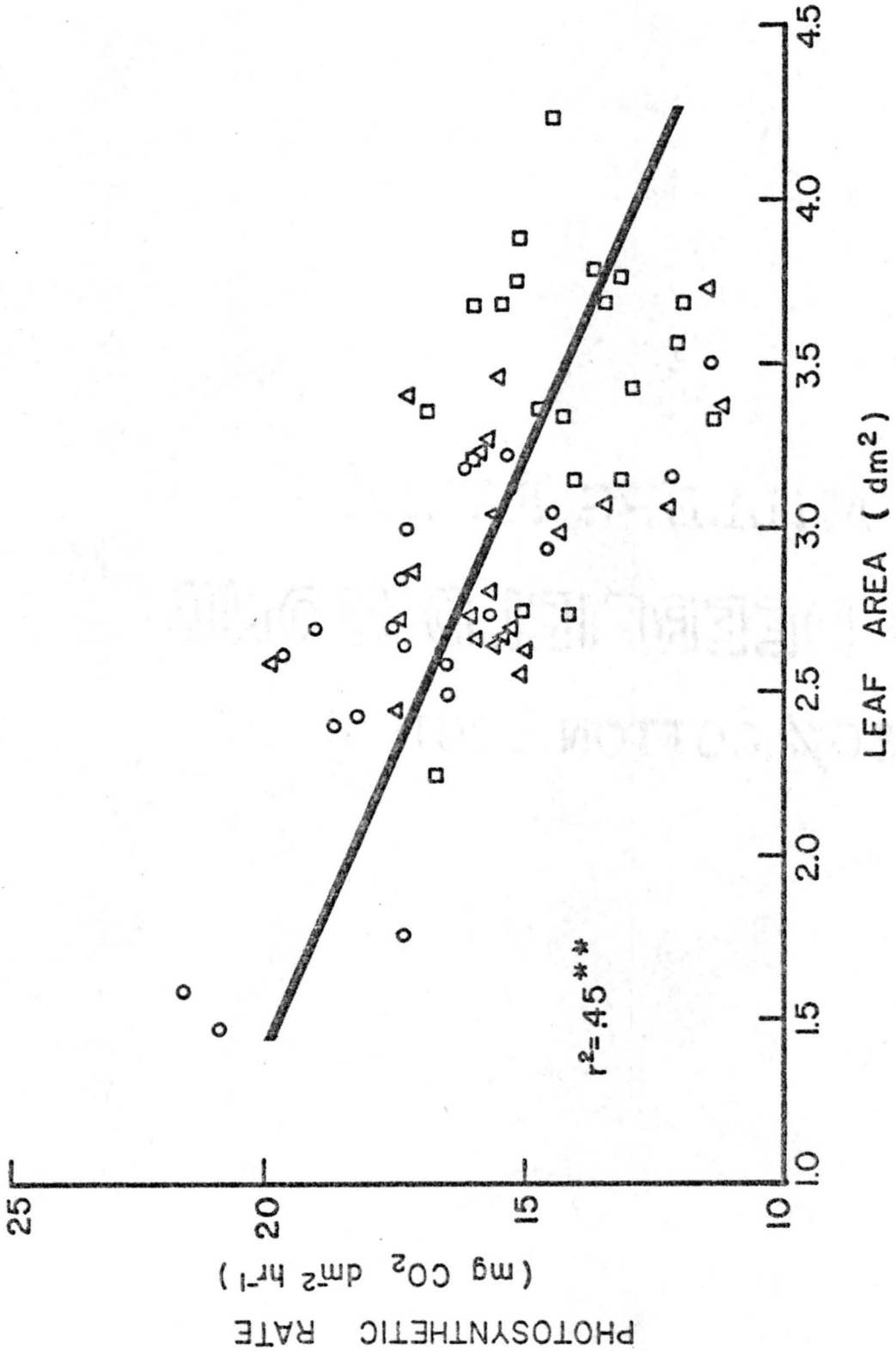

PHOTOSYNTHETIC RATE
(mg CO_2 dm^{-2} hr^{-1})
25
20
15
10
1.0
1.5
2.0
2.5
3.0
3.5
4.0
4.5
LEAF AREA (dm^2)
r^2= .45**

Fig. 17(b). Greenhouse experiment II. Photosynthetic rate of progeny as a function of leaf dry weight. Symbols indicate altitude of parent. o = 1533, Δ = 2372, □ = 3198 m.

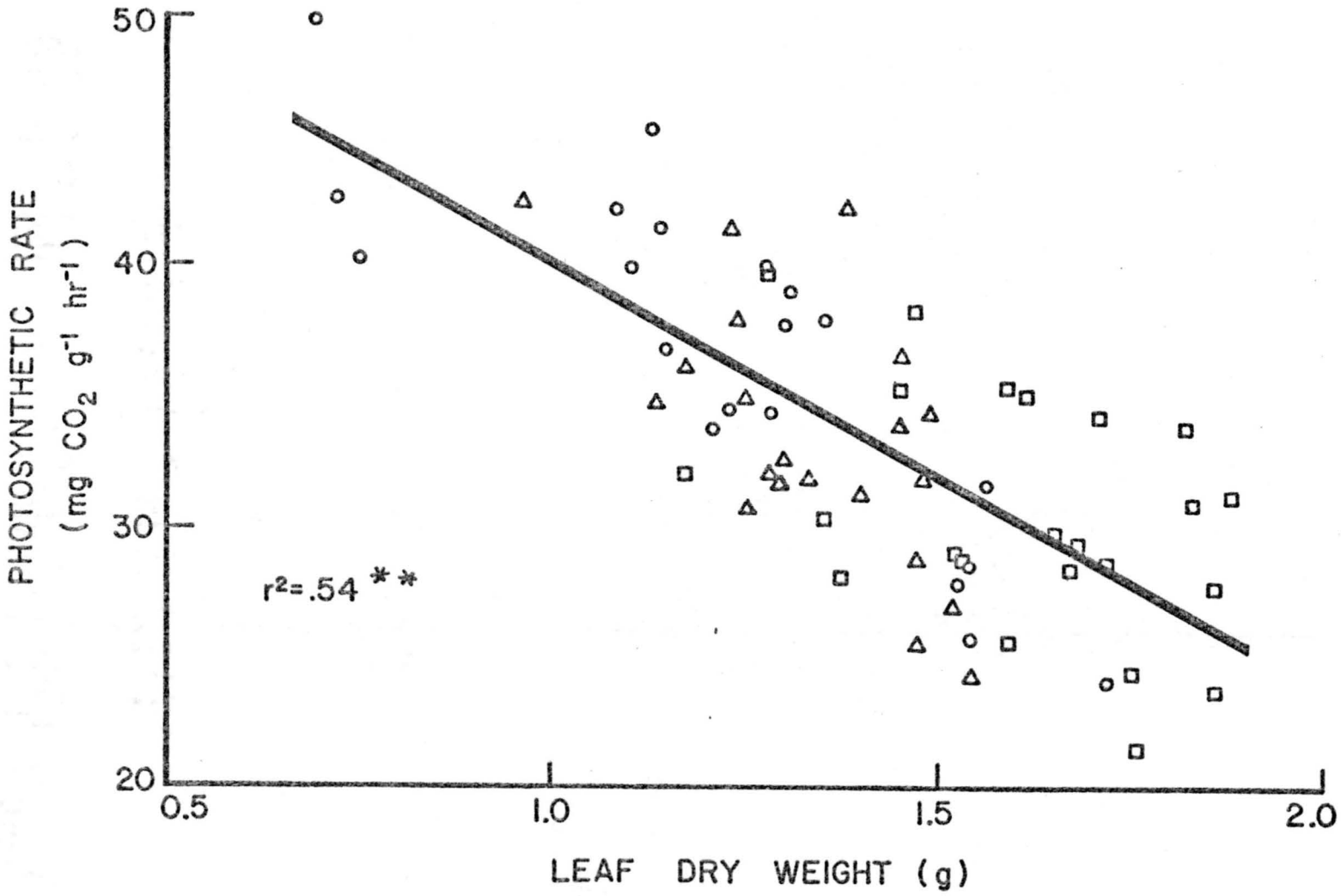

50
40
30
20
0.5
1.0
1.5
2.0
PHOTOSYNTHETIC RATE
(mg CO_2 g^{-1} hr^{-1})
r^2=.54 **
LEAF DRY WEIGHT (g)

Table 5. Greenhouse experiment II. Comparison of photosynthetic rate of progeny. Data is from analysis of covariance (BMD09V computer program); covariate is leaf dry weight per plant. Group indicates altitude of parent. Each group contained 11 plants.

Group	Group Mean Photosynthetic Rate (mg CO_2 $g^{-1}hr^{-1}$)	Adjusted Group Mean Photosynthetic Rate (mg CO_2 $g^{-1}hr^{-1}$)
1533	34.85	33.88
1533[z]	39.35	34.15
2372	34.36	33.61
2372[z]	33.62	32.00
3198	30.67	33.11
3198[z]	29.65	35.27

t-Test Matrix for Adjusted Group Means

	1533	1533[z]	2372	2372[z]	3198	3198[z]
1533	0.00					
1533[z]	-0.14	0.00				
2372	0.15	0.28	0.00			
2372[z]	1.06	1.13	0.91	0.00		
3198	0.41	0.48	0.27	-0.59	0.00	
3198[z]	-0.68	-0.45	-0.82	-1.55	-1.17	0.00

[z] Shaded parents.

DISCUSSION

Field Experiment

The effects of temperature and light on vegetative growth are rather neatly separated by the structure of this experiment. Temperature effects can be determined by comparing elevations, responses to light by comparing treatments. There remains some interaction as differences in light intensity and quality exist among sites.

The response of vegetative growth to temperature and light in this study corresponds closely to that in the literature. Stem length reached a maximum at 2372 m, mean temperature 17^{o} C; leaf length peaked at 2372-2827 m, mean temperature 16-17^{o} C. Bodlaender (5) and Petri (48) found essentially the same results. Vine dry weight was highest at 2372 m. Considering these responses together, it is clear the largest amount of photosynthetic surface was produced at 2372 m.

As expected, shading significantly increased top growth. The most dramatic increase was in stem length. Since the number of internodes is basically the same in both treatments, the increased length is the result of elongation of nodes; leaves also show this elongation. The reduction in ultraviolet radiation with shading is probably responsible. As UVB radiation increases with altitude [8% between sea level and 3200 m (14)], this also helps to account for the great difference in plant size between 2372 and 3198 m where the mean temperature differential is only 2^{o} C. The higher absorbance readings of the shaded plants indicate a higher chlorophyll content per unit area (67).

Presumably shading reduced the destruction of chlorophyll by the very high light intensities prevalent. The leaf curling exhibited by the unshaded plants (Fig. 5) is probably also a response to light. In this position the amount of light striking the leaf surface would be reduced. In contrast, the convex configuration of the shaded leaves would allow the maximum amount of light possible to reach the leaf.

The increased tuber number per plant of unshaded over shaded plants corresponds to the observations of Sale (55) whose study was also in an area of high solar input (but low altitude). Presumably the unshaded plants have more assimilate available for translocation, providing the impetus for more tubers to be initiated. The tremendous increase in tuber number at 3198 m can only be explained as a combination of factors. This site exhibits the conditions traditionally associated with tuberization: very high insolation and low day and night temperature. Additionally, if some tubers are indeed resorbed later in the season, as suggested by Krijthe (33), the lower, warmer sites may have already resorbed some tubers.

The relationship of tuber number, tuber bulking rate and final yield is unclear. There never appears to be a shortage of potential sites for tuber formation (41). That was the case in this study as all groups had undifferentiated stolons and tubers less than 1 cm in diameter. There is no satisfactory explanation for the different growth rates of tubers on the same plant (41). High tuber number had been associated with increased net assimilation and tuber yield (6, 55). The question is, which is the cause, which the effect?

When harvested the same day, tuber fresh weight per plant decreased with increasing altitude (and decreasing mean temperature). This is

expected from the work of Kozlowska (31, 32) and Ronsen (54); it is the small magnitude of the change that is surprising. Yield on August 17 was reduced less than 20% from 1533 to 3198 m and virtually not at all between 1533 and 2372 m. The decrease in yield with shading is more dramatic. Higher insolation resulted in greater assimilation and a more favorable distribution of assimilate. Also, Sale (55) found that shading, while it did not affect the maximum bulking rate significantly, delayed the attainment of this rate.

For the most part the potato has defied conventional growth analysis (59). The myriad conflicting and compounding influences on potato growth are roadblocks to understanding the true effects of the environment. As a result, the effects of certain environmental parameters have usually been considered on particular aspects of growth and their relation to growth and development as a whole has been described in abstract terms. This study has been designed to remove or reduce all factors which influence potato growth and development except light and temperature. For this reason the relationship of light and temperature to potato growth was expressed with more clarity and it enables one to view this relationship in a new way.

It is now a widely accepted principle that plant development is a function of temperature. Certain phenological events (flowering, crop maturity, senescence, etc.) occur at a given level of accumulated heat input (4, 19, 27, 50). As far as could be determined this concept has not been applied to the potato. To test this concept a valid measure of physiological development, or maturity, was needed. Vine senescence would have been ideal, but the growing season at the mountain sites was too short to reach that stage. Also, flowering did not occur.

Consequently, specific gravity of the tubers was chosen as an alternative. Since all plants emerged under the same conditions and all sites exhibited tuber inducing environmental conditions (70), it is assumed there was little difference in time of tuber initiation among sites. Also, all sites received high insolation. For these reasons specific gravity should be a valid measure of maturity. The close correlation of specific gravity with Growing Degree Days is a clear indication that the rate of development in potato is indeed strongly influenced by temperature regime.

It has been recognized (27) that insolation is a modifying influence in the rate of development. There are several ways the level of insolation would affect specific gravity: higher insolation would result in increased assimilation and would raise plant and soil temperature. The small effect of insolation in this case is attributable to the fact that even the shaded plants received intensities greater than saturation much of the time.

For added evidence that temperature regime governs the rate of development, consider the nitrate concentration of the leaf tissue. Nitrate content would be expected to decrease with vine maturity. In fact, it did decrease with increasing mean temperature, supporting the connection between maturity and temperature. Further, by reducing canopy temperature, shading retarded maturity as evidenced by the consistently higher nitrate content of leaves from shaded plants.

The high correlation between net assimilation and the revised GDD is not intended as a measure of maturity but rather as a measure of how temperature affects photosynthesis and respiration. As such it proved more effective than any combination of raw temperature variables. It

has the added advantage that, since it is calculated daily, it inherently carries a chronological factor the other temperature variables do not. The addition to the normal GDD of the correction term to compensate for higher night temperatures dramatically increased the correlation with net assimilation. The success of this correction term indicates that respiratory losses are significant even at the relatively cool night temperatures encountered in this study. The relatively small influence of total radiation is again due in part to the fact that light is seldom limiting, even under the shades.

The high carbon content of the leaf tissue of the 2372 m plants could be due in part to the conservation of assimilate by the low night temperature. An alternative explanation is that the lower night temperature slows the rate of translocation, causing a buildup of assimilate in the leaves. This is unlikely, however, as Swanson and Geiger (61) found that translocation rate in sugarbeet was only temporarily reduced when the temperature was lowered to 1^{o} C.

On the surface the relationship of net assimilation with temperature and light is in apparent disagreement with proponents of the sink theory who argue that net assimilation rate is insensitive to light and temperature fluctuations during tuber bulking (41). This is not the case. Previous workers (40, 69) were unsuccessful in correlating net assimilation rate with environmental conditions. In the present study assimilation *rate* was not considered. Furthermore, the fact that all groups show similar response to environmental conditions despite vast differences in plant size suggest that photosynthetic rates are not directly in response to those conditions. Clearly, a sink system could be operating.

The same parameters effective in predicting net assimilation are naturally the most useful in predicting tuber yield. The increased effectiveness of total insolation in the yield model must be due to its influence on the distribution of assimilates. Temperature range is positively correlated with yield. Large diurnal fluctuations would tend to maximize photosynthesis and minimize respiration.

Some might question the applicability of this type of growth analysis to normal field situations. Granted, nutrient levels, soil moisture relations, planting densities, etc. would strongly influence plant response and the prediction models would have to be adjusted accordingly. Plant response to climatic conditions outside the range of this experiment would have to be investigated. Also, to increase reliability the environmental parameters should be considered from the date of emergence rather than the date of planting. From the strength of the correlations obtained in this study it seems likely that, with these modifications, reasonable predictions of plant performance could be obtained.

Using the concepts supported by this growth analysis it is possible to compare the production potential of the different sites. The concept of maturity as a function of temperature suggests that vine senescence and the end of tuber bulking could be predicted by a measure of accumulated heat input. This is at odds with the traditional view that vine senescence is brought on by the influence of the tubers (41). Production potential should be compared at an equivalent stage of maturity (i.e. equal GDD) rather than on the same day. Using this criterion, the 1533 and 2372 m sites can be compared. When harvested on August 17 there is virtually no difference in yield. However, in terms of accumulated heat, 2372 m on August 25 is equivalent to 1533 on August 17.

Using this criterion, the 2372 m site has the distinct advantage. Clearly, the low night temperature at 2372 m conserves assimilate and slows the rate of development, resulting in more days of photosynthesis to a given stage of maturity. In fact, the 2372 m site appears to be ideal for potato production. The 17^{o} C mean tempearture is optimum for the production of dry matter (73) and provides the most advantageous balance of vine to tuber growth, allowing the greatest amount of assimilate to be diverted into the tubers (6). This potential advantage is usually not realized as the average frost-free period at this elevation [73 days (47)] is not long enough to allow the crop to reach senescence.

In much of the previous work, the response of the potato to temperature and light has been masked by a plethora of influences: seed source, sprout development, time of planting and emergence, time of tuber initiation, soil factors, moisture relations, nutrient supply, disease, etc. This study was structured to eliminate or reduce these compounding influences. That is the source of its value and its limitations. The results obtained are not directly applicable outside the range of this experiment and certainly not to normal field situations. Rather it is hoped that tradition concepts of the effects of temperature and light on potato growth and development will be reconsidered.

Greenhouse Experiments

In the first greenhouse experiment there was no visual difference in sprout development at planting among groups, yet there was a clear difference in the rate of emergence. This implies different levels of physiological activity. This idea is supported by the dramatic acceleration of sprout development one month later shown by the tubers from 3198 m used in the photosynthesis work (Fig. 3). The reason for the increased activity of the 3198 m group is unclear but the pattern follows that found by Krijthe (34); very immature tubers show faster sprout development than mature. The 3198 m tubers were very immature in comparison with those produced at 1533 m (specific gravity 1.054 compared to 1.077). The general rule, however, is that rate of sprout growth increases with maturity of the tuber (63). Shaded tubers were less mature (lower specific gravity) than unshaded tubers. This helps to explain the slower rate of emergence of the plants grown from shaded tubers.

Accelerated emergence of the tubers from the highest site resulted in greater vegetative growth early in the season but all groups were roughly equivalent by February 11. This would be expected as the time difference in emergence was not great and all plants were exposed to similar environmental conditions throughout their growth.

The time of tuber initiation can be roughly estimated by extrapolating the tuber bulking curves (Fig. 15) to the baseline (22). Using this technique it is apparent that tuberization occurred first in the 3198 m group, undoubtedly associated with earlier emergence and possibly with earlier induction by the mother tuber. As all seed was

produced under 'inducing' environmental conditions (70) the influence of the mother tuber on initiation should be minimal. Due to the small number of plants grown and the variability inherent with the potato, tuber bulking rates show considerable variation from the expected linear relationship. It appears the rate of bulking is slightly lower in the 3198 m group but definite conclusions should not be drawn. The most obvious difference among groups was the earlier yield produced by the 3198 m group. All groups gave similar tuber yields on the last harvest date, when all vines showed advanced senescence. Clearly these results do not agree with Went (71) who found the air temperature of the parent plants to have a pronounced effect on the yield potential of succeeding generations, even when the progeny were grown to completion.

According to Headford (25) the vast majority (>90%) of the dry matter gain by a potato plant in the first 20 days from emergence is translocated from the mother tuber. Differences in reserves of nutrients and hormones among seed pieces could be expected to influence early field growth. This apparently manifested itself in the rate of emergence of the groups in the second greenhouse experiment, but did not affect photosynthetic capacity. All groups showed similar photosynthetic rates when adjusted for plant size. The rates are comparable with those obtained by Winkler (73). There are several possible explanations for the disturbing scatter of the data. Plant with multiple stems were tested along with single stem plants; the degree of shading would be different. Also, there was considerable difference among plants in the number of days from emergence to testing. Winkler (73) showed leaf age to be an important factor in photosynthetic rate.

Kozlowska (31, 32) found that mountain grown seed (400-1200 m) gave higher yields than lowland seed when both were grown in the lowland. How can this work be reconciled with the present study? First it must be recognized that all seed tested in this experiment was produced above 1500 m. If the high altitude environment imparts an intrinsic quality to seed tubers, this could have been overlooked. Also, Kozlowska found that the high altitude environment apparently suppressed virus multiplication in potato plants. This would obviously increase seed vigor and reduce field losses. Since viral expression in these experiments was very limited, this influence would not have been a significant factor.

What are the practical implications of this study? The rate and uniformity of emergence increased with increasing elevation of seed production. This is the same response observed by California growers comparing San Luis Valley seed to seed grown near Santa Maria, California. Santa Maria has cooler days, warmer nights and probably lower insolation (66) than the San Luis Valley. Apparently a combination of these climatic factors is responsible for this difference in performance as no one factor has been clearly implicated by this study. The mechanism involved is unknown and is beyond the scope of this study. When grown to completion there may or may not be a difference in yield, but the Colorado seed would give an earlier acceptable yield as demonstrated by the 3198 m group. This is important in areas with short growing seasons and in cases where an early crop is economically advantageous. This results in a higher production per 'in ground' day. If earlier emergence is the only benefit of San Luis Valley seed, it is likely that this advantage could be nullified by varying storage conditions (22).

SUMMARY

Optimum temperature for stem elongation was higher than for leaf expansion; maximum photosynthetic area was produced at a mean temperature of 17° C, which occurred at 2372 m. Shading significantly increased vegetative growth at all elevations. Tuber fresh weight per plant decreased with increasing elevation when harvested on the same day; with an extra week of growth, the yield of all the higher sites approached or surpassed that achieved at 1533 m. Shading dramatically reduced tuber yields at all elevations.

Regression analysis was performed on the field data. It was found that tuber specific gravity, used in this study as a measure of maturity, was highly correlated with accumulated heat input [the USDA Growing Degree Day system was used (65)]. This indicates that in potato, as in many other crops, rate of development is a function of temperature. Net assimilation and tuber yield were positively correlated with a modified GDD measurement designed to compensate for increasing respiratory losses with increasing night temperature. These parameters were also positively correlated with total insolation. It is suggested that the production potential of the 2372 m site is greater than at 1533 m by virtue of its lower respiratory losses and slower rate of development which results in more days of photosynthesis to a given stage of maturity. However, this potential is seldom realized as other factors, primarily the length of the frost-free period, are limiting. It appears that, under environmental conditions normally encountered

in potato producing areas, temperature regime is the most important environmental parameter affecting yield. The shade treatment used in this experiment significantly reduced yield, but the shade decreased insolation by nearly half, far below normal field conditions.

The effect of the elevation of production on the yield potential of seed tubers was then investigated. Seed tuber sprout development and rate of emergence increased with increasing elevation of the parent plant. This corresponds to observations made by commercial growers in California when comparing seed produced in the San Luis Valley of Colorado with seed from areas of lower elevation. When grown to completion, there was no significant difference in plant size or tuber yield. All groups tested showed similar photosynthetic rates.

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APPENDICES

Fig. A1. Increase in solar intensity with altitude [from Becker and Boyd (3)].

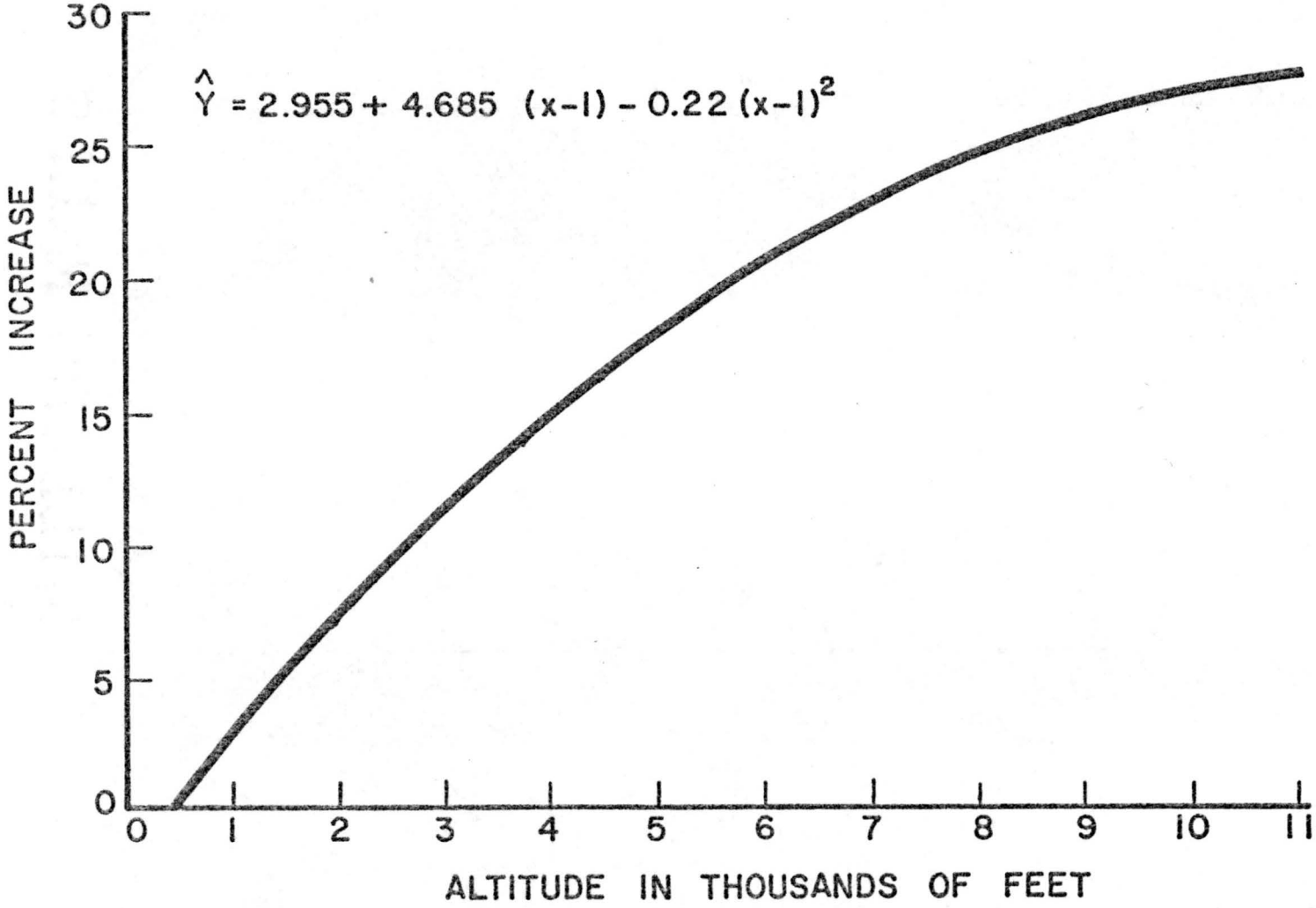
$\hat{Y} = 2.955 + 4.685\ (x-1) - 0.22\ (x-1)^2$
PERCENT INCREASE
30
25
20
15
10
5
0
0
1
2
3
4
5
6
7
8
9
10
11
ALTITUDE IN THOUSANDS OF FEET

Table A1. Analysis of soil mix[z].

pH	5.2
Texture	Loamy sand
Organic matter	5.4%
Conductivity	2.5 mmhos
NO_3-N nitrogen	158 ppm
Phosphorous	71 ppm
Potassium	345 ppm
Lime	Low
Iron	63.4 ppm
Zinc	8.7 ppm
Copper	0.46 ppm
Manganese	20.4 ppm

[z] This mix was used in greenhouse experiment I. The mix used in greenhouse experiment II was essentially the same; that used in the field experiment contained added micronutrients listed on the following page.

Table A2. Analysis of soluble trace elements used in the field experiment.

	(%)
Inert	60.15
Mn	8.15
Fe	7.5
Cu	3.2
Zn	4.5
B	1.45
Mo	0.046
S	15.0

Table A3. Leaf color of potato. Values are means of 24 measurements taken August 12-13, 1976. LSD at 5% level.

		Treatment		
		Shaded	Unshaded	Average
Altitude of Production (m)	1533	0.764	0.698	0.731
	2372	0.746	0.660	0.703
	2827	0.713	0.678	0.698
	3198	0.687	0.670	0.679
	Average	0.729	0.677	

altitude LSD = 0.009
interaction LSD = 0.012

ANALYSIS OF VARIANCE

Source	df	F value
Treatment	1	280.7**
Altitude	3	47.8**
Treatment x altitude	3	23.0**
Error	183	

Table A4. Stem length of potato. Values are means of six plants harvested August 17, 1976. LSD at the 5% level.

		Treatment		
		Shaded	Unshaded	Average
Altitude of Production (m)	1533	64.8 cm	50.5	57.6
	2372	67.6	48.2	57.9
	2827	59.4	43.6	51.5
	3198	46.0	32.4	39.2
	Average	59.7	43.7	

altitude LSD = 2.7

ANALYSIS OF VARIANCE

Source	df	F value
Treatment	1	247.36**
Altitude	3	75.55**
Treatment x altitude	3	1.66
Error	184	

Table A5. Vine dry weight of potato. Values are means of six plants harvested August 17, 1976. LSD at the 5% level.

		Treatment		
		Shaded	Unshaded	Average
Altitude of Production (m)	1533	26.6 g	24.2	25.4
	2372	29.6	27.3	28.5
	2827	22.0	22.4	22.2
	3198	18.0	18.1	18.0
	Average	24.1	23.0	

altitude LSD = 3.55

ANALYSIS OF VARIANCE

Source	df	F value
Treatment	1	0.74
Altitude	3	12.96**
Treatment x altitude	3	0.35
Error	40	

Table A6. Leaf dry tissue NO_3-N content of potato. Values are means of five samples. [a]LSD at the 5% level.

		Treatment		
		Shaded	Unshaded	Average
Altitude of Production (m)	1533	4369 ppm	1836	3103
	2372	3990	2689	3340
	3198	6583	3355	4972
	Average	4983	2627	

altitude LSD = 432

interaction LSD = 611

ANALYSIS OF VARIANCE

Source	df	F value
Treatment	1	189.9**
Altitude	2	47.2**
Treatment x altitude	2	10.9**
Error	24	

Table A7. Percent carbon in dried leaf tissue. Values are means of five measurements. LSD at the 5% level.

		Treatment		
		Shaded	Unshaded	Average
Altitude of Production (m)	1533	27.2	29.8	28.5
	2372	29.3	41.7	35.5
	3198	28.9	33.9	31.4
	Average	28.5	35.1	

altitude LSD = 0.86

interaction LSD = 1.22

ANALYSIS OF VARIANCE

Source	df	F value
Treatment	1	384.9**
Altitude	2	142.5**
Treatment x altitude	2	73.0**
Error	24	

Table A8. Percent nitrogen (including NO_3-N) in dried leaf tissue. Values are means of five measurements. LSD at the 5% level.

		Treatment		
		Shaded	Unshaded	Average
Altitude of Production (m)	1533	4.9	4.3	4.6
	2372	4.4	3.8	4.1
	3198	4.7	4.2	4.5
	Average	4.7	4.1	

altitude LSD = 0.14

ANALYSIS OF VARIANCE

Source	df	F value
Treatment	1	107.7**
Altitude	2	31.0**
Treatment x altitude	2	0.1
Error	24	

Tabel A9. Tuber number per plant (>1 cm in diameter). Values are means of six plants harvested August 17, 1976. LSD at the 5% level.

		Treatment		
		Shaded	Unshaded	Average
Altitude of Production (m)	1533	9.0	13.0	11.0
	2372	11.8	12.8	12.3
	2827	13.7	15.3	14.5
	3198	22.0	25.7	23.8
	Average	14.1	16.7	

altitude LSD = 2.8

ANALYSIS OF VARIANCE

Source	df	F value
Treatment	1	6.94**
Altitude	3	34.90**
Treatment x altitude	3	0.57
Error	40	

Table A10. Greenhouse experiment I. Tuber yield in grams per plant. Values are means of four plants. LSD at the 5% level.

Altitude of Parent	2/14	2/21	2/28	3/7	3/14	Average
1533	93.5	215.8	297.6	344.0	395.0	269.9
2372	113.3	240.3	271.0	301.0	417.3	268.6
3198	217.3	263.8	296.5	310.3	399.0	297.4
Average	141.3	239.9	289.6	318.4	403.8	

Harvest date LSD = 28.3
Altitude LSD = 21.9
Interaction LSD = 49.0

ANALYSIS OF VARIANCE

Source	df	F value
Harvest date	4	95.31**
Altitude	2	4.45*
Harvest date x altitude	8	3.87*
Error	45	

Table A11. Independent variables tested in the regression analysis of growth characteristics presented in text, table 4.

Altitude

Days to harvest

Mean maximum temperature - July

Mean maximum temperature - August

Mean maximum temperature - growing season

Mean minimum temperature - July

Mean minimum temperature - August

Mean minimum temperature - growing season

Mean daily temperature range

Mean daily insolation - July

Mean daily insolation - August

Mean daily insolation - growing season

Total insolation received

Growing Degree Day[z]

Growing Degree Day - revised[y]

[z] calculated $\frac{\text{max temp } (\leq 86) + \text{min temp } (\geq 40)}{2} - 40$

[y] calculated GDD - ½(min temp - 40)

Table A12. Regression equations for the selected growth characteristics presented in text, table 4.

Dependent variable: Specific gravity

$Y = 1.01269 + 0.00004\ GDD$

Dependent variable: Net assimilation

$Y = -77.869 + 0.144\ \text{Revised GDD} + 0.0007\ \text{Total insolation}$

Dependent variable: Tuber fresh weight

$Y = -247.89 + 0.6035\ \text{Revised GDD} + 0.0088\ \text{Total insolation} - 8.06\ \text{Mean daily temperature range}$