

Growth, Partitioning, and Harvest Index of Tuber-Bearing *Solanum* Genotypes Grown in Two Contrasting Peruvian Environments¹

Received for publication December 24, 1985 and in revised form May 9, 1986

REYNALDO G. VICTORIO², ULISES MORENO, AND CLANTON C. BLACK, JR.*³
Departamento de Biología, Universidad Nacional Agraria, La Molina, Lima, Peru

ABSTRACT

Ten *Solanum* potato genotypes, including four primitive species and six hybrids, were grown to maturity near 230 and 3273 meters in elevation at two sites, Coast and Sierra, in Peru. Growth data, with emphasis upon tubers and leaves, were collected periodically to analyze the plant components which differed in these contrasting environments. Nine of the *Solanum* species/cultivars effectively partitioned dry matter into tubers with values reaching 73 to 85% of the total plant at mature harvest in the Sierra but dropping to 33 to 75% on the Coast. These harvest index differences were, however, accompanied by no consistent changes in total leaf area, specific leaf area, nor number of tuber initiated. Consistent differences did occur in having shorter plants in the Sierra and an increased tuber dry matter percentage, 20 to 28%, in the Sierra compared to 14 to 21% on the Coast. Linear relationships exist between plant tuber harvest index versus tuber yield and versus total plant dry matter on both the Coast and in the Sierra.

Plants can exhibit a remarkable flexibility in the range of environments in which they grow well. Hence, much effort has and is being expended to learn the mechanisms of this flexibility and how to enhance or manipulate it either genetically, culturally, or chemically. The potato (primarily *Solanum tuberosum*) has long been grown, indeed many tuber-bearing species originated, in Peru under various environmental circumstances ranging from those in the Andean highlands up to near 4,000 m elevation down to near sea level in the coastal desert. In an effort to understand the growth of the potato plant and how to improve potato production, we have been investigating the physiological and biochemical mechanisms underlying the environmental adaptations of potatoes in Peruvian environments (9–11, 14). The work we present here is part of a continuing study on the growth of the potato plant with emphasis upon the partitioning of assimilates into tubers.

¹ Supported by a research project on Environmental Plant Physiology and Crop Productivity from the International Atomic Energy Agency, and the United Nations Development Program to U. M. and to the Universidad Nacional Agraria (UNA), La Molina, Lima, Peru. We also acknowledge support by the Physiology Department of both the International Potato Center (CIP) and UNA in providing the necessary operational facilities.

² Permanent address: Universidad Nacional San Antonio Abad, Agronomy Department, Cuzco, Peru.

³ Permanent address: University of Georgia, Department of Biochemistry, Athens, GA 30602.

Potato production in these contrasting environments has been the subject of much genetic, breeding, and selection work. Indeed, many of the *Solanum* genotypes in this study come from this plant improvement work at the Universidad Nacional Agraria or at CIP (9–11). From physiological work covering several decades of research both in controlled environment growth chambers and in natural environments we know that the lengths of both the day and the night period plus the diurnal temperature regimes strongly influence assimilate partitioning by the potato plant (9–11, 14). Much of this earlier physiological work was done with *S. tuberosum* L., but in Peru other species also are commonly grown which we wished to study. In addition, we wished to investigate a range of temperature and photoperiod adaptations known to exist within tuber-bearing *Solanum* species/cultivars.

In this physiological growth and partitioning study we selected 10 potato genotypes which either are endemic or were developed in the Peru potato breeding programs. Their tubers were planted in large woven nylon bags that contained the same soil media. Plants were grown in the coastal environment near 230 m elevation and in the Andean environment of near 3273 m in the Mantaro Valley. We applied good cultural practices such as fertilization or watering and followed growth, partitioning, and water status of the plants through each growing season in these two contrasting environments. In this report we pay special attention to tuber and leaf growth, as modulated by the two contrasting environments with the 10 potato genotypes, because of their ultimate relationship to understanding and enhancing potato production. This work largely comprises the thesis research of Victorio (15).

MATERIALS AND METHODS

Two experimental sites with naturally contrasting environments were selected because they represent major potato growing environments in Peru. One site was in La Molina at the National Agricultural University which is at an elevation of 230 m above sea level and in the coastal desert region where irrigated potatoes are grown; we will refer to this site as Coast. The second site was in the Mantaro Valley at the International Potato Center Station near Huancayo, which is at an elevation of 3273 m and is typical of Andean potato farming; we will refer to this site as Sierra.

The more exact location, air and soil temperature, and RH that generally prevailed at each experimental site were as follows for the Coast and Sierra, respectively: 12°05' and 12°07' latitude south; 76°57' and 75°02' longitude west; 23.1°C and 20.9°C average seasonal maximum; 16.3°C and 6.2°C average seasonal minimum; 22°C and 15.5°C average soil temperature at 20 cm depth; and 95:66% and 82.9:35.3% air RH maximum:minimum. The average temperatures were calculated using

Went's equations (16) as 20.5°C:17.8°C and 17.2°C:9.9°C for day:night in the Coast and Sierra, respectively. The photoperiod was nearly equal at the two sites with between 12 and 13 h of light.

For our work we selected the 10 potato genotypes listed in Table I. We have given each genotype a 'cultivar' code number for convenience which will be referred to in the presentation of data. Hence, on all graphs and tables the 'cultivar' numbers will refer to the numbered genotypes in Table I. More details on the genetic and breeding background of these genotypes are available elsewhere (9-11, 14, 15). Yungay and Mariva were originally selected for coastal potato production.

Tuber seeds of uniform sizes at the same tuber-sprouting age were selected and planted at both sites in three replications. Soil was obtained from the Mantaro Valley, homogenized, and about one-half was transported to La Molina near the coast. Two hundred kg of soil was placed in large woven nylon bags at each site and used to grow the plants. Therefore, the same soil type, soil volumes, watering, fertilizer, experimental design, and protocol were used at both sites to ensure that growth environment was the primary difference in our study. At each harvest date the entire plant material was obtained; care was taken throughout the study to collect any detached vegetative material.

Plants were harvested at 60, 90, and 120 d on the Coast and at 60, 90, and 150 d in the Sierra. It is critical to know that the plant maturity harvest date was near 120 d on the Coast and near 150 d in the Sierra. At both sites final harvesting was done when plants were physiologically mature and clearly declining as indicated by seed production, yellowing of leaves, lodging, and a general plant senescence. At each harvest date the following growth data were collected for entire plants: leaf area, number, fresh and dry weight; stem number, length, fresh and dry weight; tuber number, fresh and dry weight; root length, fresh and dry weight; and flower and seed numbers, fresh and dry weights. Data in this manuscript represent the average for the 3 replications combined with emphasis upon the final harvest data, particularly with regard to partitioning into leaves and tubers. A thesis giving data at each harvest date is available (15).

RESULTS

Good growth was obtained on both sites for all genotypes with the exception of *Solanum acaule*, which is a noncommercial wild potato in Peru. Vegetatively *S. acaule* grew slowly and only produced a small number of miniature (<0.5 cm diameter) tubers. Hence, *S. acaule* data often will be absent in this presen-

tation. Although *Solanum curtilobum* grew well, in our growth analysis it often responded independently of all other species. Hence, *S. curtilobum* growth data are somewhat unique relative to the other potatoes. Separately we plotted and analyzed the growth data for all harvest dates and found typical biological sigmoid growth curves. We chose to give examples here of detailed data related to partitioning into various plant parts for only 3 species and only at the final harvest dates. *Solanum stenotomum*, 'cultivar' 5, exhibited partitioning tendencies similar to 'cultivars' 2, 6, 8, and 9, whereas 'cultivar' 7, *Solanum chaucha*, was similar to hybrids 3 and 10 of Table I.

Polygonal diagrams of growth responses and partitioning of assimilates into leaves, stems, roots, and tubers are presented for Yungay, 'cultivar 10' (Fig. 1), *S. stenotomum* (Fig. 2) and *S. curtilobum* (Fig. 3). The eight axes in each figure present values for organ growth characteristics at the final harvest. The values are joined by a dotted line for Coast data and a solid line for Sierra data which result in the polygons. The upper portion of each polygon refers to aerial plant parts, and the shaded lower portion refers to the underground roots and tubers. Therefore, growth and partitioning into shoots and leaves versus roots and tubers can be directly visualized from the polygons for plants grown in the contrasting environments of the Sierra versus the Coast.

With all species tuber production on a dry weight basis was higher in the Sierra compared to the Coast (Figs. 1-3). From an agricultural viewpoint we wished to analyze how each genotype adjusted its size of source and assimilate partitioning to allocate matter into the tubers; so partitioning between leaf and tuber will be emphasized hereafter.

In 'cultivar' 10 the increased Sierra tuber allocation is offset by a decreased allocation into leaves and stems as can be visualized by the larger (above ground) Coast polygon in Figure 1. However, the number of tubers initiated was equal in both environments. Therefore, tuber dry matter allocation, not tuber number, is the component which determines tuber production in 'cultivar' 10.

In contrast 'cultivars' 5 (a diploid) and 1 (a pentaploid) (Table I) in Figures 2 and 3, respectively, both initiated more tubers (axis 7) in the Sierra and simultaneously partitioned more matter into tubers (axis 8). Otherwise, 'cultivar' 5 (Fig. 2) reduced its allocation into leaves and stems similar to cultivar 10 (Fig. 1). The unique features of *S. curtilobum* again are emphasized by the almost equal but small above ground growth allocation in both the Coast and the Sierra (Fig. 3). Thus, at least three types

Table I. *Solanum* Tuber-Bearing Genotypes Selected for This Study

'Cultivar' Code No.	Species	Name or No.	Ploidy and Chromosome No.
1	<i>Solanum curtilobum</i>	'Shiri'	2n = 5x = 60
2	<i>S. tuberosum</i> × <i>S. andigena</i> (Hybrid)	Hibrido (B) UNA 178-3-75	2n = 4x = 48
3	<i>S. tuberosum</i> × <i>S. andigena</i> (Hybrid)	Hibrido (12) UNA 35-5-79	2n = 4x = 48
4	<i>Solanum acaule</i> (wild)	'Acaule'	2n = 4x = 48
5	<i>Solanum stenotomum</i>	'Ishcupuro'	2n = 2x = 24
6	<i>S. tuberosum</i> × <i>S. andigena</i> (Hybrid)	Hibrido (15) UNA 35-3-79	2n = 4x = 48
7	<i>Solanum chaucha</i>	'Huayro'	2n = 3x = 36
8	<i>S. tuberosum</i> × <i>S. andigena</i> (Hybrid)	'Mariva'	2n = 4x = 48
9	<i>S. tuberosum</i> × <i>S. andigena</i> (Hybrid)	'Tomasa Condemayta'	2n = 4x = 48
10	<i>S. tuberosum</i> × <i>S. andigena</i> (Hybrid)	'Yungay'	2n = 4x = 48

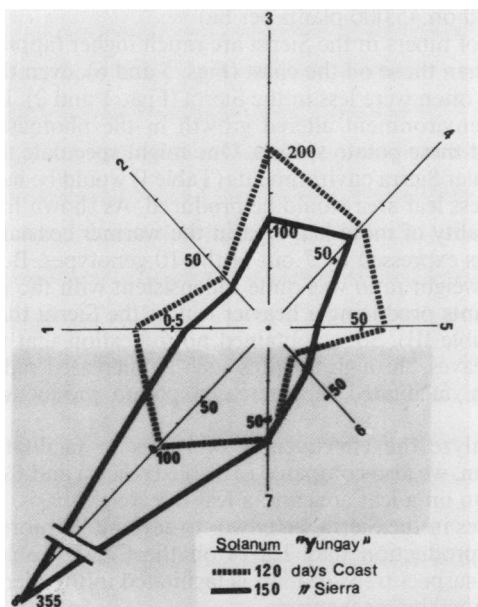


FIG. 1. Polygonal diagrams representing the growth responses and partitioning of assimilates for the harvest at maturity with *S. tuberosum* × *S. andigena*, Yungay, grown on the Coast and in the Sierra. Key to axes: 1, leaf area (m²); 2, total leaf dry wt (g); 3, total number of leaves; 4, longest stem (cm); 5, total dry wt of stems (g); 6, total dry wt of stolons and roots (g); 7, total number of tubers; and 8, dry weight of tubers (g).

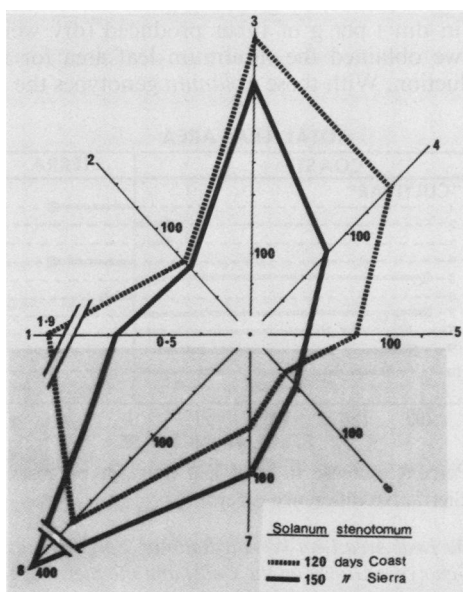


FIG. 2. Polygonal diagrams representing the growth responses and partitioning of assimilates of the mature crop for *S. stenotomum*. Key to axes same as Figure 1.

of allocation are present in tuber bearing *Solanum* species; all of which result in increased tuber production in the Sierra environment compared to the Coast environment (Figs. 1-3).

Seemingly, there is a direct relationship between subterranean growth and total production in potato plants. Such relationships are shown in Figure 4 for total subterranean dry weight as a function of total plant dry weight. Indeed, one can calculate that in the Sierra nearly 88% of the plant is below ground with all species (Fig. 4). On the Coast a direct relationship also is evident, although the maximum below ground is nearly 77% of the plant. But sets of the *Solanum* species seem to follow two linear lines (Fig. 4) for unknown reasons when grown in the Coast environ-

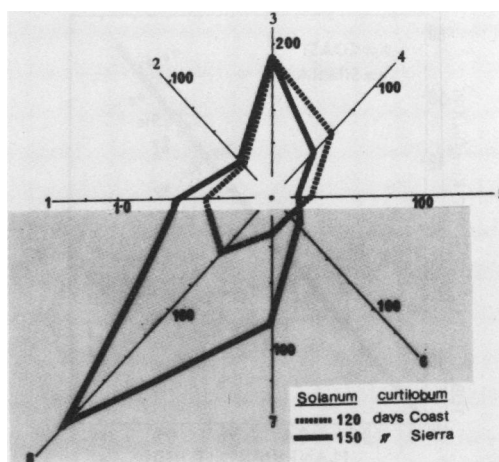


FIG. 3. Polygonal diagrams representing the growth responses and partitioning of assimilates by *S. curtilobum* at the final mature crop harvest. Key to axes same as Figure 1.

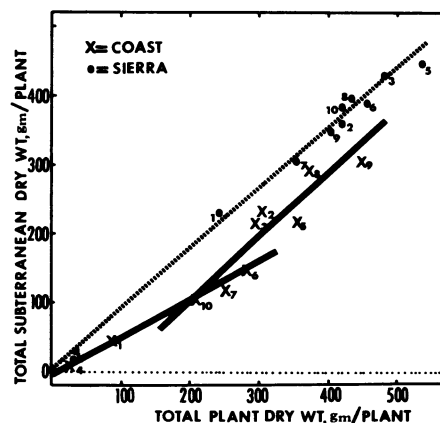


FIG. 4. Direct relationship between subterranean yield, including roots and tubers, and total plant dry matter for potatoes grown on the Coast and in the Sierra. The number by each symbol refer to 'cultivar' in Table I.

ment.

Certainly, the data in Figures 1 to 4 lead one to confirm that tubers are a major sink in the potato plant. By calculating the plant harvest index which is defined as the total tuber:total plant ration (on a common basis), a more quantitative analysis of tuber partitioning is obtained. Figure 5 shows a strong linear relationship between tuber fresh weight, calculated on a hectare basis, and plant harvest index. Note *S. acule* produced only a few tubers, therefore it is omitted, and that *S. curtilobum*, 'cultivar' 1, uniquely fails to fall along the line as already partially discussed regarding Figure 3. With these two species as exceptions, the coefficient of correlation for the data and line in Figure 5 is 0.88. The harvest index for each species was higher in the Sierra than in the Coast with values in the Mantaro Valley ranging from 0.73 to 0.85.

A similar linear response, which does not extrapolate through zero, also is obtained by graphing total tuber dry weight versus plant harvest index with a regression coefficient of 0.92 (Fig. 6). The slope of the regression line in Figure 6 is altered compared to Figure 5 because of another growth characteristic of potatoes clearly influenced by environment, namely the tuber dry matter content which is increased in the Sierra for all genotypes.

Table II presents three additional analyses of tuber growth either in the Coast or Sierra environments including percent dry matter. In the Sierra the potatoes are much denser. Indeed, this

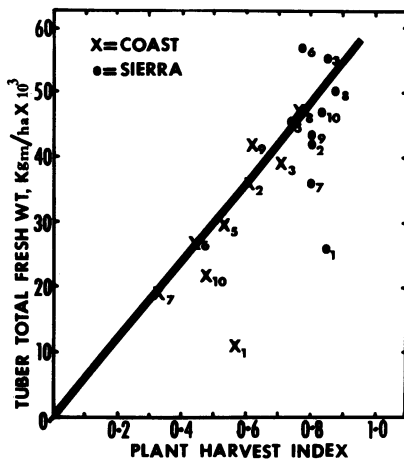


FIG. 5. Direct relationship between plant harvest index defined as total tuber dry wt:total plant dry weight and tuber production on a fresh weight basis.

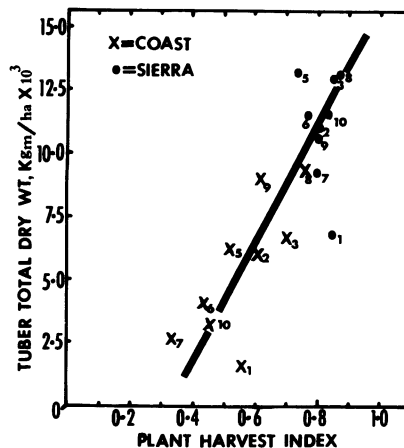


FIG. 6. Direct relationship between plant harvest index (see Fig. 5) and tuber production on a dry weight basis.

Table II. Effectiveness of Potato Genotypes in Tuber Production on the Coast and in the Sierra of Peru

'Cultivar' Code No	Tubers Dry Wt		Tubers Dry Wt		Tuber Dry Matter	
	Coast	Sierra	Coast	Sierra	Coast	Sierra
	g/dm ² of leaf area		g/g leaf dry wt		% of fresh wt	
1	46	107	2.8	11.3	14.6	26.2
2	85	188	5.5	13.8	16.5	26.3
3	88	210	4.5	14.3	17.4	24.3
4						
5	32	141	2.9	6.9	21.1	28.3
6	72	169	3.1	10.1	15.0	20.1
7	27	163	1.8	11.7	14.3	25.4
8	76	251	5.7	14.9	19.9	24.7
9	63	249	4.3	9.2	21.6	24.8
10	41	271	2.9	16.1	14.5	24.6

feature is well known to Peruvians who much prefer to consume Sierra potatoes and to export Coast potatoes. The lower dry matter values for Coast potatoes (Table II) alter the slope of the line in Figure 6, which is on a tuber dry weight basis. Also evident in Figures 5 and 6 is the high productivity of the potato plant reaching values of 50,000 kg fresh weight per ha in the Sierra

(calculated on 45,000 plants per ha).

Yields of tubers in the Sierra are much higher (approximately double) than those on the coast (Figs. 5 and 6), even though the leaf areas often were less in the Sierra (Figs. 1 and 2). Hence, we asked if environment altered growth in the photoassimilation portion of these potato species. One might speculate that leaves in the cooler Sierra environments (Table I) would be heavier and perhaps less leaf area would be produced. As shown in Figure 7 the generality of more leaf area in the warmer coastal environments was expressed by 7 out of the 10 genotypes. But the leaf area:leaf weight ratio was quite inconsistent with the possibility of the plants producing a heavier leaf in the Sierra than on the Coast (Table III). So we obtained no indication that thicker or heavier leaves, through features such as increased radiation interception, facilitated the increased potato production in the Sierra.

To analyze the effectiveness of leaves in facilitating tuber production, we also compared in Table II Sierra and Coast tuber production on a leaf area and a leaf dry weight basis. On either basis leaves in the Sierra were two- to severalfold more effective in tuber production than leaves on the Coast (Table II). We therefore suspect translocation is facilitated in the Sierra but we do not know the mechanism.

As we considered these results we also realized that we could ask the question: Is there a lower limit of how much leaf area the potato plant requires to grow tubers? In Figure 8 we arrived at this answer by considering that potatoes must be near the upper limit of harvest index at 0.85, e.g. harvest index cannot reach 1.0. Likewise, the leaf area required to produce a tuber cannot be zero. Hence, by graphing plant harvest index versus leaf area (in dm²) per g of tuber produced (dry weight) as in Figure 8, we obtained the minimum leaf area for maximum tuber production. With these *Solanum* genotypes the minimum

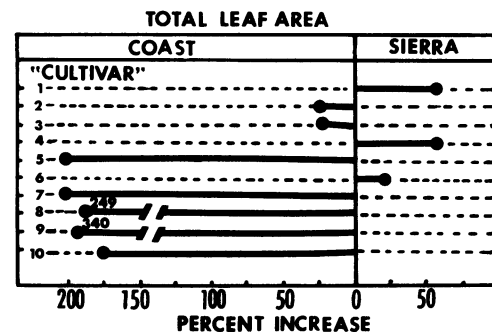


FIG. 7. Percent increase in total leaf area for potatoes comparing Coast with Sierra. No difference is zero.

Table III. Leaf Area:Leaf Weight Ratio or 'Specific Leaf Area' of Potato Genotypes Grown on the Coast and the Sierra at the Final Harvest

'Cultivar' Code No.	Specific Leaf Area	
	Coast	Sierra
	cm ² /g dry wt	
1	104	213
2	93	97
3	100	113
4	83	88
5	138	101
6	44	101
7	86	117
8	147	127
9	103	78
10	79	108

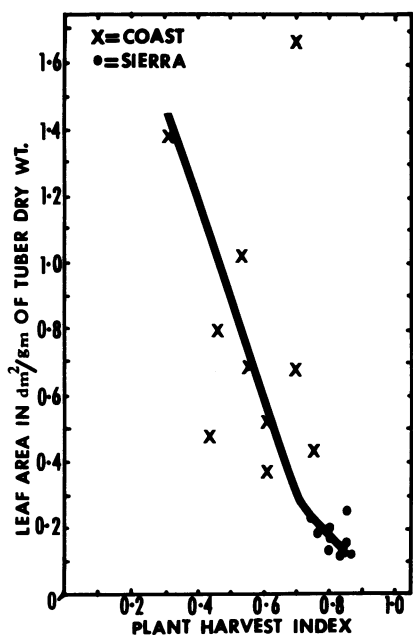


FIG. 8. Determination of the leaf area needed to produce 1 g of tuber dry weight by graphing plant harvest index (see Fig. 5) versus leaf area:tuber dry weight.

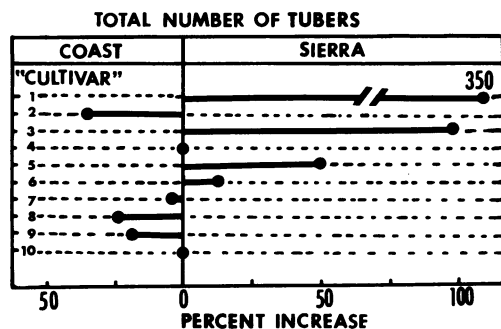


FIG. 9. Percent increase in tuber initiation for potatoes comparing Coast with Sierra. No difference is zero.

leaf area needed to give maximum tuber production lies between 0.12 and 0.16 dm² of leaf surface to produce 1 g of tuber dry weight.

Finally, one might also speculate that tuber initiation differed in the Sierra versus the Coast to support the higher Sierra tuber production. But only 'cultivars' 1, 3, and 5 increased their tuber initiation in the contrasting environments of the Sierra (Fig. 9; also compare Fig. 1 with 2 and 3), while tuber yields increased for all *Solanum* genotypes in the Sierra (Figs. 5 and 6). Hence, increased tuber initiation was not necessary to increase tuber yields in some cultivars.

DISCUSSION

Growth of the potato plant has been analyzed by various groups (1, 2, 5, 7-17), but nearly all of that work was with *Solanum tuberosum* subspecies *tuberosum*. Indeed, predictive agricultural production models for this potato are available because of the widespread interest in potato consumption (1, 5, 12, 13, 17). But understanding partitioning and environmental influence on various potato genotypes still is lacking. It is commonly recognized that root-type crops partition higher amounts of dry matter into the harvested root product than grain crops. Indeed, the grain harvest index seldom rises above 0.5 while root-type

crops often rise to 0.7 or 0.8 (3, 4, 6-8).

As this research indicates, allocation of dry matter into tubers by potato genotypes indeed can be 0.7 to 0.8 (Figs. 5 and 6). But these values are greatly influenced by environment (compare the Coast and Sierra data in Figs. 4-6). The environmental component which is the most determinative is unknown. However, the night temperature was cooler and the day-night temperature differences were greater in the Sierra than on the Coast (see "Materials and Methods"). Hence, thermoperiod is a major environmental component controlling dry matter allocation in potatoes. This conclusion agrees with work with *S. tuberosum* (16) that tuberization and tuber yield increase with lower night temperatures and with large differences between the day versus night temperatures.

Monteith (8) has recognized in analyzing crop growth that there is a linear relationship between intercepted radiation by a crop and its total dry matter yield. Similar data have been presented for *S. tuberosum* varieties in comparing total tuber dry weight and total intercepted radiation (1, 13, 17). We would predict from the data in Figure 4 that a similar relationship is true for the *Solanum* genotypes in this work; unfortunately we did not collect total intercepted radiation either on the Coast or in the Sierra. Certainly, we did not allow water or cultural conditions to limit our studies. It also has been observed (1) that warm weather produces specific leaf area (leaf area:leaf weight ratio) increases in *S. tuberosum*; but there is no consistent indication of heavier leaves being produced in the Sierra in this work even at lower temperatures (compare Table I and III). Hence, the Sierra leaves were not thicker or heavier to potentially intercept more radiation to facilitate increased tuber production.

We do not yet understand how plants react to their environment during development nor in producing a sink such as tubers. But with these *Solanum* genotypes environmental differences between the Coast and the Sierra, such as contrasting temperatures, modulated the partitioning into tuber (Figs. 1-6) without consistently changing leaf area (Fig. 7), tuber initiation (Fig. 9), or specific leaf area (Table III). Plants were consistently shorter in the Sierra (axis 4 of Figs. 1-3) than on the Coast which would reduce translocation distances. This is in agreement with earlier work (9-11, 14) on the environmental responses of potatoes to photoperiod and thermoperiod. In total all of these growth relationships resulted in large differences in yields and harvest index in the integrated plants which we still fail to understand fully in terms of environmental messages and their translation into plant development components.

LITERATURE CITED

1. ALLEN EJ, RK SCOTT 1980 An analysis of growth of the potato crop. *J Agric Sci* 94: 583-606
2. BISCOE PV, JN GALLAGHER 1977 Weather, dry-matter production and yield. In JJ Landsberg and CV Cutting, eds, *Environmental Effects on Crop Physiology*. Academic Press, London
3. BLACK CC 1985 Efficiency of carbon assimilation. In CA Neyra ed. *Biochemical Basis of Plant Breeding*. CRC Press, Boca Raton FL, Vol 1, pp 73-88
4. BOYER JS 1982 Plant productivity and environment. *Science* 218: 443-448
5. BURTON WG 1966 In H Veenman, NW Zonen, eds, *The Potato*. Wageningen, Holland
6. GIFFORD RM, JH THORNE, WD HITZ, RT GIAQUINTA 1984 Crop productivity and photoassimilate partitioning. *Science* 225: 801-808
7. HARRIS PM, ed 1978 *The Potato Crop*, Chapman & Hall, London
8. MONTEITH JL 1977 Climate and the efficiency of crop production in Britain. *Philos Trans R Soc Lond* 281: 277-294
9. MORENO U 1970 Physiological investigations on the potato plant. PhD thesis, Cornell University, Ithaca, NY
10. MORENO U 1974 Respuesta de la planta a los factores edaficos y climaticos de la costa y de los Andes del Peru. *Molina Peru Univ Nac Agraria Anal Cient* 12: 1-11
11. MORENO U 1985 Environmental effects on growth and development of potato plants. In PH Li, ed, *Potato Physiology*. Academic Press, New York, pp 481-501
12. SANDS PJ, C HACKETT, HA NIX 1979 A model of the development and bulking

- of potatoes (*Solanum tuberosum* L I Derivation from well-managed field crops. *Field Crops Res* 2: 309-331
13. SCOTT RK, SJ WILCOCKSON 1978 Application of physiological and agronomic principles to the development of the potato industry. *In* PM Harris, ed, *The Potato Crop*. Chapman & Hall, London, pp 678-704
 14. STEWARD FC, U MORENO, WM ROCA 1981 Growth, form and composition of potato plants as affected by environments. *Ann Bot* 48: S 2. 1-45
 15. VICTORIO, RG 1986 Analisis de crecimiento de diferentes especies e hibridos de papa desarrollados en dos ambientes contrastantes: Costa y Sierra. Thesis, Universidad Nacional San Antonio Abad, Cuzco, Peru
 16. WENT FW 1957 *The Experimental Control of Plant Growth*. Ronald Press Co., New York
 17. ZAAG ED VAN DER 1984 Reliability and significance of a simple method of estimating the potential yield of the potato crop. *Potato Res* 27: 51-73