Improving Adaptation of the Potato (*Solanum* spp.) to Hot Climates - Some Physiological Considerations

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ABSTRACT

A set of characters based on physiological manipulations of the potato crop under field conditions, with potential for improving the adaptation of the potato to hot tropical conditions, is presented. Quick emergence, rapid branching, and large leaf size leading to fast self-shading crop cover of the soil are required if short-season, relatively early tuber initiating and fast bulking clones are desired. Maintenance of canopy effectiveness during tuber bulking by increased leaf longevity, greater leaf reflectivity, and lack of lodging are further requirements that, in addition to less heat stress of photosynthesis and reduced foliage and tuber respiration, could lead to yield improvements. Incorporation of tolerance to aluminum is also desirable.

Introduction

The inability of the potato to tuberize under high temperature has often been cited as the major barrier to its successful production under hot climates (Levy, 1978). Recurrent selection has been largely successful within potato populations at the International Potato Center (Mendoza, 1980) and elsewhere (Levy, 1979) for the ability to tuberize and yield well under hot field conditions; heat-tolerant clones and populations combining both attributes under high temperatures have been developed. Selection frequency was increased from 0.06% to 15% over five cycles of selection, and further work is in progress (Mendoza, 1980). With this level of success, attention can now be turned to the incorporation of certain morpho-physiological characters that, as indicated by agronomic and physiological studies, could better improve adaptation of the potato to hot conditions. A seedling screening technique recently developed (Sattelmacher, 1983) can simplify the efficient screening for tuberization response within large populations while incorporating other important adaptive features.

Tuber yield, particularly under hot conditions, may be limited by a series of morphological, developmental, and physiological functions, independently or in various combinations. Apparent causal relationships between some characters and yield are herein indicated; others, however (e.g., instantaneous photosynthetic rates and yield, Dwelle et al, 1981) although not distinct, merit further attention if yield potential is to be improved.

In this paper, two considerations are presented: First, the benefits of morphological and developmental manipulations, i.e. hastening emergence and early branching, balancing the timing of tuber initiation with the potential for tuber bulking, and maintenance of complete crop cover over the soil. Second, the benefits of physiological criteria related to heat stress on photosynthesis and respiration, and, inasmuch as more than 30% of soils in the tropics present problems with aluminum toxicity, the incorporation of tolerance to aluminum.

Morphological and developmental considerations

Emergence and branching

Quick emergence and rapid crop cover over the soil surface are essential, especially if the crop is to maximize interception of incident radiation, and concommitantly to reduce its soil heating effect. The cooling effect of self-shading on soil temperature can be marked; weighted daytime mean temperatures of 35.5°C for bare soil and 26.0°C under cover of a complete crop have been recorded at 5 cm depth (Midmore, unpublished). Self-shading effects on conservation of soil moisture may also be notable, however, the loss of moisture from an exposed soil surface depends largely on the frequency of rewetting (Milthorpe and Moorby, 1979).

The potato emerges most rapidly when mean soil temperatures at tuber depth are in the range of 22° to 25°C (Sale, 1979; Midmore, 1983); higher temperatures significantly reduce emergence. Genetic differences between north temperate clones and CIP clones, the latter selected for hot climates, have been reported (Midmore, 1983); those with heat-tolerance were the only clones that emerged at the high temperature extreme (30°C), and were quicker to emerge than other clones at soil temperatures closer to the optimum. Hastening emergence from 3 to 5 days as a result of soil cooling during the 35-day period after planting (Midmore, 1983) was accompanied by yield increases of 14% and 28% for two clones. Besides the genetic component, manipulation of age and storage of seed tubers under hot conditions in particular, can be conditioned to hasten emergence and crop cover (Bean and Allen, 1981) with accompanying increase in tuber yield (Table 1). The search for genetic differences between clones for the rate of emergence could be confounded with differences in length of dormancy and physiological age, as is manifested by sprout growth at the time of planting. Proceedures should be sought to reduce this effect.

Table 1. Emergence and tuber yield as influenced by seed tuber storage conditions.

Storage conditions (107 days)	Emergence (days to 50%)		Yield (g/plant)	
	N565.1	DTO-33	N565.1	DTO-33
Diffused light	21	17	314	469
Dark	15	15	458	31

High temperature, apart from its effect on the rate of emergence, has also been noted to reduce the number of emerging main stems (Sattelmacher, 1981), a character that may deserve further attention in a breeding program. Selection for more stems per unit of planting material could be one character favoring a quicker canopy cover of the soil.

Since presprouted tubers may have up to 25 of their total 35 leaves differentiated at the time of planting (Borah and Milthorpe, 1962), the rate of leaf production plays a minor role in achieving a complete canopy cover of the soil in comparison so that of axillary branching.

Improvement in the rate of increase of the canopy cover has been studied by pricking out growing points, releasing apical dominance, and stimulating axillary branching. Self-shading of the soil surface was enhanced; reducing soil temperature and effecting more efficient use of incoming radiation. Mean weighted daytime soil temperatures (5 cm depth) 48 days after planting were 26.9°C for stimulated branching vs 30.7°C for the control, and light interception was 55% and 28%, respectively. Stimulated branching improved yield (Table 2) but not for clones with known rapid branching (e.g. DTO 2). In contrast to previous reports (Hammes and Nel, 1973; Menzel, 1981), our experiments in pricking out of growing points did not promote tuber initiation; therefore, yield improvement was probably due to direct effects upon canopy growth and efficiency of its light interception.

Table 2. Tuber yield on four potato clones as effected by pricking out of growing points 30 days after planting.

1981 Clone	Treatment	Yield (g/plant)	1982 Clone	Treatment	Yield (g/plant)
DTO 2	Control	637	Desiree	Control	708
	Prick	466		Prick	746
LT 4	Control	300	Rosita	Control	515
	Prick	498		Prick	612

The selection for an early canopy-type with large, horizontally displayed leaves, although not corroborated experimentally, should theoretically (Loomis and Rapaport, 1976) assist in achieving a quick crop cover. Circumstancial evidence of the benefit of this character is derived from observations that a Tuberosum-type canopy (fewer and shorter internodes, larger leaves) under high temperature is often associated with heat tolerance. An Andigena-type canopy (long stems, many internodes and small leaves), however, is associated with non-tolerance (Mendoza and Estrada, 1979; Ewing, 1981).

Tuber initiation and bulking period

The dominance of shoot growth early in the crop cycle should later allow a greater allocation of photosynthate to the growing tubers. The photoperiod control of tuber initiation and tuber growth is well documented (Mendoza, 1974; Ewing, 1981) and is strongly stimulated by tropical short days. In the adaptation of potato to hot climates, selection for early tuber initiation and a fast bulking rate has been emphasized, along with selection for high general combining ability (Mendoza, 1980). There is ample opportunity to select for the timing of tuber initiation (Sattelmacher, 1983) as a function of the large amount of genetic variability existing for this trait (Mendoza, 1974). Data exist (Calua and Mendoza, 1982) that indicate that variation in timing of tuber initiation exists within a given maturity class, thus permitting exploitation of a range of initiation and bulking durations to suit local requirements.

Fast emergence and quick crop cover (Figure 1) favored early tuber initiation but at a higher leaf area index (LAI) than that of the slower, later-emerging and initiating treatments. Tuber yields of the former were also greater (Figure 1). Early tuber initiation, but not in combination with a quick foliage growth and crop cover of the soil, can lead to intense competition between developing tubers and foliage (Loomis and Rapaport, 1976). Strong induction to tuberize and a strong sink effect of tubers appear to be related. In some instances, reallocation of assimilates from the haulm to growing tubers compensates for the inability of a small canopy to provide sufficient assimilate (Moorby and Milthorpe, 1975; Midmore and Espinola, 1983). Delay to tuber initiation by planting physiologically younger tubers (Bean and Allen, 1980), by adding extra nitrogen at planting (Simpson, 1962), or by long-day photoperiod treatment (Midmore and Espinola, 1983), enhances canopy size at tuber initiation. The leaf area duration (LAD -- the integral of LAI over time) during the bulking period was markedly increased, as, too, were tuber yields. Excessive delay of tuber initiation, however, may reduce tuber yield since neither extreme self-shading leading to competition for light within the canopy nor the reduced duration available for bulking favor maximum tuber yields.

Maintenance of complete crop canopy

Canopy growth may cease completely after tuber initiation (Moorby and Milthorpe, 1975), although our experience has not indicated such an immediate decline in shoot growth under hot conditions (Figure 1). At least three points appear important when considering canopy characters subsequent to tuber initiation: leaf longevity, leaf reflectivity, and the prevention of lodging.

The potential for new leaf production is reduced as competition for assimilates between growing tubers and leaf surface are effected. The earlier the competitive effect the quicker leaves senesce (Milthorpe, 1963). Extension of leaf longevity is more important for clones with early tuber initiation, especially if LAD during the bulking period and tuber bulking rates are to be optimized. High temperature, in general, hastens leaf senescence (Borah and Milthorpe, 1962), and variation for this character could be sought with selection being made for improved leaf longevity on the basis of leaf-tagging experiments.

Increased leaf (canopy) reflectivity improved economy of water use, an important factor for potato production under both irrigated and rainfed conditions in the hot tropics, even though it did not directly improve canopy persistance or yield (Table 3). Lower leaf temperatures due to greater reflectivity may indirectly extend leaf longevity and delay senescence. Selection for greater leaf pubescence, an important component of increased reflectivity (Ehleringer and Bjorkman, 1978) and important per se in reduction of transpiration (Waggoner, 1966), should be simple since much variation for this character exists within the Solanum genus (Bukasov and Laknovich, 1971).

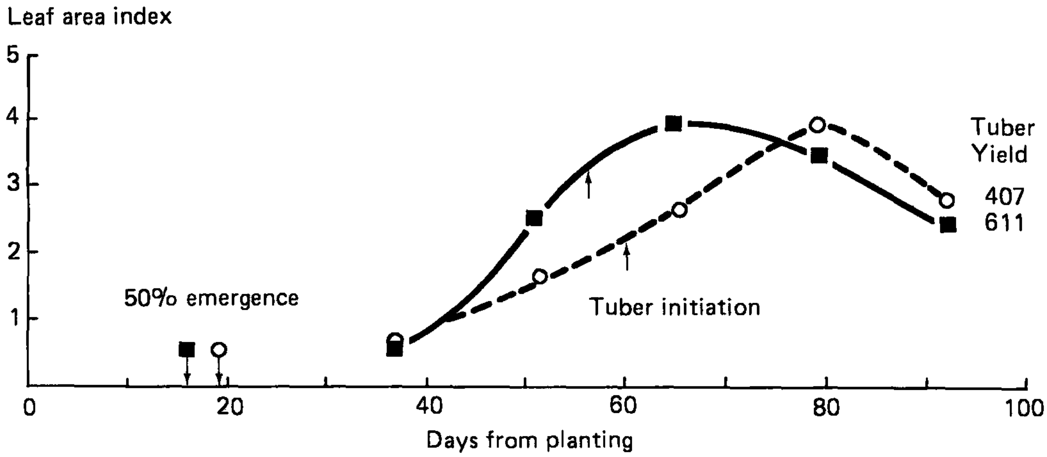

Figure 1. Emergence, tuber initiation, leaf area index and tuber yield (g/plant) as influenced by soil temperature (0 warm, cooler), adapted from Midmore (1983).

Table 3. Effect of leaf reflectant (50 g lime in 1 litre water, plus surfactant) on various physical and biological attributes of potato plants.

Treatment	% Reflected radiation[1]	Leaf temperature[2]	Soil water[3]	LAD[4]	Yield[5]
Control	25.8	28.3	11.8	127	11.74
Leaf reflectant	33.4	28.9	20.7	130	11.95
t[6]	*	*	*	ns	ns

[1] Measured at midday with a Licor pyranometer.
[2] Exposed leaf, daily mean.
[3] Gravimetric, morning of irrigation.
[4] Leaf area duration of crop, mean 2 clones.
[5] t/ha, mean 2 clones.
[6] t values. $*P \leq 0.05$, ns not significant.

Lodging of the canopy should be prevented near the end of the season; this presents dual benefits for the potato crop grown in hot climates. Thus efficient interception of solar radiation is maintained, which in turn favors self-shading and therefore cooling of the soil. Once the canopy has lodged, interception is incomplete and soil heating occurs (Midmore, 1983) leading to loss of yield potential and increased respiratory losses by maturing tubers. Selection for sturdy mainstems and, more particularly, branches, could be effected with consequent yield improvement.

Physiological considerations

Photosynthesis

Variation in, an optimum temperature for, gross photosynthesis has been recognized between potato clones (Dwelle et al., 1981), with the high temperature decline attributed to direct temperature inhibition of photosynthesis rather than to effects on stomatal conductance. Selections for heat tolerance in the field did not have higher photosynthetic rates under heat stressed conditions (Wivutvongvana, 1979). Efforts, however, to identify relative heat tolerance within the potato at the chloroplast thylakoid and cellular membrane levels have been reported using chlorophyll fluorescence (Hetherington et al, 1983) and electrolyte leakage (Palta et al, 1981) techniques. Both methods served to confirm known tolerances of genotypes to heat in the field (i.e. the ability to tuberize and yield under hot conditions). *S. phureja* was identified as the major source of heat tolerance in cultivated species by the chlorophyll flourescence method and *S. chacoense* and *S. acaule* as potential sources of heat tolerance in additional studies (Smillie et al, 1983). The importance of aclimating some genotypes before making comparisons of their heat tolerances has been indicated (Palta et al). Once aclimated, heat tolerance of *S. acaule* was improved, although it was still considered as having a low degree of heat tolerance on the basis of electrolyte leakage. In contrast, *S. comersonii* after aclimation was markedly heat-tolerant as indicated by both the triphenyl tetrazolium chloride reduction and conductivity tests (Palta et al, 1981).

Heat tolerance among potato species in both studies was generally consistent with their ecological distributions. Selection of species for their transfer of that character on the basis of ecological distribution alone would not, however, consistently lead to improvements in heat tolerance. More important, as yet undetermined factors influence the variation in heat tolerance between accessions within species.

Haulm and tuber respiration

Since dark respiration is more heat-resistant than photosynthesis (Berry and Bjorkman, 1980) (i.e. it continues to increase at higher temperatures than does photosynthesis), selection for lower dark respiration rates, as effected by Wilson (1975) in ryegrass, should at increasingly higher temperature lead to proportionally smaller losses in net photosynthesis. Burton (1966) suggested that above 35°C, net photosynthesis in the potato is reduced to zero, and that under normal, hot tropical conditions, 50% of gross production may be lost through respiration (Burton, 1979). Unconscious selection for less foliage respiration at high temperatures has been effected within clones selected for their performance under hot conditions (AVRDS, 1979; Wivuntvongvana, 1979). Selection for reduced dark respiration of potato seedlings (Sattelmacher, unpublished) has been studied and complete evaluation is in progress.

As the growing season progresses, respiratory losses by tubers increase, particularly when soil temperatures rise as a result of lodging and exposure of the soil surface to incident radiation. The extent of the correlation between respiration rates of haulms and tubers is as yet unknown; however, economies of the latter could markedly improve yield under hot conditions. With the onset of tuber enlargement and later maturity, the maintenance component of respiration (the component generally more responsive to selection) (Wilson, 1975) increases in importance. Scope for reduction of the maintenance component of tuber respiration during this important phase is to be studied.

Aluminum tolerance

Haematoxylin staining of young potato seedling roots bathed in nutritive solutions with added Al was linearly related to the susceptibility to acid soils of second generation tubers of the same genotypes. Seedlings may be screened and selected before their transfer to a potting medium and subsequent selection for further characters.

Adaptation of potato to hot climates is a multifaceted task, and herein only the morphophysiological contributions have been discussed. Certain approaches have been suggested that could enhance the adaptation of potato to hot climates and therefore merit further attention. Simultaneous inclusion of all components will not be necessary to achieve yield improvement; step-by-step incorporation and maintenance of the ability to survive, tuberize, and provide acceptable yields under harsh environments should suffice.

Resistance to pests and disease is in process of being incorporated into environmentally adapted genotypes.

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