PHYSIOLOGICAL AND GENETIC STUDIES ON TETRAPLOID AND HAPLOID POTATO (SOLANUM TUBEROSUM L.)

Thesis for the Degree of Ph. D. MICHIGAN STATE UNIVERSITY MARTA T. MORALES 1968



This is to certify that the

thesis entitled PHYSIOLOGICAL AND GENETIC STUDIES ON TETRAPLOID AND HAPLOID POTATO (SOLANUM TUBEROSUM L.)

presented by

Marta T. Morales

has been accepted towards fulfillment of the requirements for

<u>Ph. D.</u> degree in Crop Science

Lowfront Major professor

Date Dec. 27, 196

O-169



ABSTRACT

PHYSIOLOGICAL AND GENETIC STUDIES ON TETRAPLOID AND HAPLOID POTATO (SOLANUM TUBEROSUM L.)

by Marta T. Morales

The physiological relationship between leaf area distribution and dry matter of potato tubers is considered for both tetraploid varieties and haploid derivatives. The genetics of the physiological characters is investigated by diallel cross techniques; this is confined to the haploid plants.

Broadly speaking, there was good agreement between the physiological patterns for haploids and tetraploids. The accumulation of dry matter in the tubers was not only dependent on absolute leaf area, attained by a variety (or group) but was also affected by the pattern of leaf area distribution over the growing season. It was suggested that leaf distribution was primarily influenced by the point where senescence starts and the speed of senescence, coupled with the time at which tuber maturity takes place. The preceding remarks apply to the results from three tetraploid varieties and three groups of haploids. However, more detailed physiological studies on the diallel cross (5 x 5) between haploids confirmed the above statements. Total dry matter of the parents and crosses was linearly related to leaf area. Generally the ratio of tuber dry matter to total dry matter was constant. However, two crosses did not conform to this pattern, one placing more substrate in the tubers, the other in the rest of the plant.

The genetics of the physiological characters indicated that the most important genetic component was specific combining ability. This finding would probably not be an obstacle to breeding, since potato varieties are clonally propagated.

PHYSIOLOGICAL AND GENETIC STUDIES ON TETRAPLOID

AND HAPLOID POTATO (SOLANUM TUBEROSUM L.)

By

.

Marta T. Morales

A THESIS

Submitted to Michigan State University in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

Department of Crop Science

ACKNOWLEDGMENTS

I am indebted to Dr. N. R. Thompsom for his advice and guidance throughout the course of this study.

I would like to thank Drs. R. W. Chase, C. E. Cress, S. T. Dexter and W. T. Magee for their help and critical comments on, the drafts of the thesis.

My gratitude goes to Dr. C. M. Harrison for his encouragement and review of the final draft, to Dr. J. E. Grafius for his concern and to Drs. N. R. Thompson and R. L. Thomas for their help in the revision of the draft.

I wish to acknowledge the Rockefeller Foundation for giving me a travel grant and to NC 84 for financing the project.

Finally, I must mention Mr. R. Kitchen who was of great help with the technical aspects of planting, harvesting, etc.

TABLE OF CONTENTS

	Page
INTRODUCTION	1
REVIEW OF LITERATURE	2
MATERIALS AND METHODS	7
Experiment]	10
a. 1966 Experiment	11
b. 1967 Experiment	11
Experiment 2	12
Experiment 3	13
RESULTS AND DISCUSSION	17
Experiment 1	17
a. 1966 Experiment	17
b. 1967 Experiment	19
Experiment 2	25
Experiment 3	27
a. Physiology	27
b. Genetic studies with haploids	39
SUMMARY AND CONCLUSIONS	47
LIERATURE CITED	49
APPENDIX	52

LIST OF TABLES

Table	Page
 Means and standard deviations of leaf area (LA), yield, tuber dry matter (DMT), starch (S) and economic photosynthetic efficiency (EPE) on a per plant basis of 25 plants for the three varieties. 	· 18
2. Correlation coefficients within varieties for leaf area and each of yield, dry matter of the tubers, and starch (1966 data)	- 19
3. Means of maximum leaf area, day at which maximum leaf area was attained, total photosynthetic leaf area day, maturity, total dry matter, tuber dry matter, net assimilation and economic photosynthe- tic efficiency per plant of Onaway, Katahdin and Russet Burbank (1967 data)	24
 Means and standard deviations for leaf area, yield, tuber dry matter, starch and economic photosyn- thetic efficiency per plant of three groups of haploids (1966 data)	26
5a. Means of cumulative photosynthetic leaf area days at different time intervals and totals for the parental types and the diallel cross F ₁ 's	30
5b. Means of yield, plant dry matter, tuber dry matter, total dry matter, net assimilation and economic photosynthetic efficiency per plant for the pa- rental types and diallel cross F,'s	31
 6. Regression and correlation coefficients of total dry matter, tuber dry matter, plant dry matter, economic photosynthetic efficiency and the percentage of dry matter in the tubers with 2PLAD, 3PLAD, and TPLAD of the parental types and the F₁'s derived from diallel series, with and with-out R₁ and R₂. 	38

Table

7.	Analyses of variance for IPLAD, 2PLAD, 3PLAD, TPLAD, tuber dry matter, yield, starch, net
	assimilation and economic photosynthetic efficiency of parental types and diallel cross F_1 's 42
8.	Estimates of genetic and environmental parameters

Page

of IPLAD, 2PLAD, 3PLAD, TPLAD, tuber dry matter, yield, starch, total dry matter, net assimilation and economic photosynthetic efficiency. - - - - 44

LIST OF FIGURES

Figure		Page
l. Sum of the daul measured at dif Russet Burbank,	y photosynthetic leaf area ferent stages of growth in Katahdin and Onaway	21
2. Typical growth of haploids	patterns of different genotypes	28
3a, b, & c. Total dry haploid types ar against 2PLAD, 3	y matter per plant of parental nd their diallel F,'s plotted 3PLAD and TPLAD, respectively -	32
4a, b, & c. Plant dry and F,'s plotted respectively	w matter per plant of parental types against 2PLAD, 3PLAD and TPLAD,	34
5a,b, & c. Tuber dry types and F _l 's p and TPLAD, respe	matter per plant of parental lotted against 2PLAD, 3PLAD, ctively	35
6. The percentage of tubers of parents against TPLAD	f dry matter accumulated in the al types and F _l 's plotted	37

INTRODUCTION

The advancement in potato processing demands more emphasis on dry matter content rather than fresh weight of tubers. As a consequence, the efficiency of potato leaves becomes of primary impotance in the utilization of solar energy for the production of dry matter through photosynthesis.

There has been only limited study of the genetics of leaf efficiency in the production of dry matter, total leaf area at different stages of growth and their relationship to total dry matter production in the tubers. This research is primarily concerned with the establishment of the relationship of physiological patterns between tetraploid potato varieties (2n = 48) and haploids (2n = 24)and a genetic study of inheritance of these physiological characters in haploids.

LITERATURE REVIEW

Potato (Solanum tuberosum L.) varieties grown under the same environmental conditions differ in yield. To paraphrase Watson (1956), the material a farmer harvests is the end product of the photosynthetic process accumulated throughout the life of the crop in the particular plant organ harvested. Thus, photosynthesis may be regarded, economically as a yield-determining process (Gaastra, 1959).

The obvious and general truism that leaves are the chief organs of photosynthesis has been stated by Watson (1956). The area of the leaf is usually assumed to be the size-attribute that best measures its capacity for photosynthesis. Chapman and Loomis (1953) found that under maximum hydration, rates of carbon dioxide absorption per unit leaf area were nearly equal in all parts of the leaf plane. This was supported by the work of Carraway (1963) using radioactive carbon dioxide ($C_{2}^{14}O_{2}$), who showed that healthy leaves of potatoes fix carbon dioxide from the air uniformly on their entire surface. Goncharik (1963) found that the absorption of growth substances from the stem proceeds at equal rates in the right and left halves of the potato leaf. Watson (1947) showed that in spite of the variation in leaf structure, the net amount of carbon dioxide utilized per unit leaf area is the same in any region of the plane.

The amount of photosynthetic activity on the whole or part of a plant may be measured at basic levels by techniques of gas exchange. According to Pallas, et. al. (1967) the theoretical measure of net photosynthesis is the carbon dioxide difference between incoming and out-going air. Further, Chapman (1951) demonstrated that carbon dioxide absorption by potato leaves is a direct measure of photosynthesis and is free from error due to leaf shrinkage and carbohydrate translocation. Thorne (1959) in his studies on barley leaves, found that the rate of growth of a plant measured by dry weight increase depends on its photosynthetic capacity and total leaf area. He measured photosynthetic activity by the difference of carbon dioxide concentration of air before and after passage over the leaf. However, Chapman and Loomis (1953) and Chapman (1951) did not find any difference in the rate of carbon dioxide absorption per unit leaf area under field conditions, in spite of the fact that potato varieties differ greatly in total yields of dry matter, vine size, date of maturity and leaf type. This method of measuring photosynthetic activity in the field is very difficult and impractical.

A more practical and easily obtained measure of the end products of photosynthetic activity is the increase in dry weight per unit leaf area or net assimilation on a comparative basis between varieties, treatments, etc. This may be regarded as a measure of photosynthetic efficiency (Watson, 1956). This method has been used by several workers in different crops. Williams, <u>et. al</u>. (1965) in their study on corn, used net assimilation rate as an indication

of mean photosynthetic efficiency which is the net gain of dry matter of a community of plants relative to their leaf area. In alfalfa, Thomas and Hill (1937) used this method to measure photosynthetic efficiency.

Leaf area may be regarded as a limiting factor for total dry matter accumulation. This, however, does not mean that greater yield might result from a greater leaf area since the yield of seed, tubers, etc. may not be where the increase is concentrated. Indeed, it has been shown that greater leaf area does not necessarily result in a higher yield of potato tubers. Harper (1963) for instance, found that when there was excess foliage which shaded the lower leaves, the plant could only produce sufficient carbohydrate to meet its own requirements for respiration and did not form any storage organs. There should be an optimum leaf area that produces maximum yield. In kale, Brassica <u>oleracea</u>, Watson and French (1962) actually obtained an optimum leaf area by a thinning procedure. Blackman and Black (1959) found that maximum production of dry matter per unit leaf area under optimal conditions of temperature, nutrient and water supply was limited by the leaf area index and the amount of solar radiation. Optimum leaf area index for dry matter production was dependent on the species under consideration.

Breeding and selection for a greater photosynthetic efficiency could be a feasible means of increasing yield of existing varieties. According to Watson (1956) the total annual photosynthesis by a crop depends not only on the size of the photosynthetic system,

but also on its efficiency and the time during which it is active. Watson (1952) in his studies on leaf growth in relation to yield showed that agricultural yields could be improved by increasing the photosynthetic efficiency of the species presently cultivated. He found significant differences in the net assimilation rate between potatoes and sugar beets and also between varieties of potatoes. He concluded that since the net assimilation rate differs between and within species, new crop types may be found with a higher net assimilation rate than those now grown; or an increase in the net assimilation rate of existing crops by breeding and selection, would increase yields.

Further advances in crop breeding by the manipulation of photosynthetic efficiency is to some degree dependent on the awareness of geneticists to the importance of physiological characters (Loomis, <u>et</u>. <u>al</u>., 1967). At the present time, such measurements are not usually carried out in breeding programs, although, Kumakov (1958) included photosynthetic efficiency as a breeding character in wheat.

In the potato, research on the genetics of photosynthetic efficiency particularly, leaf area at different stages of growth and its effects on total dry matter and dry matter in the tubers, is at best minimal. Swaminathan and Howard (1953) pointed out reasons for lack of information on the genetics of economic and non-economic characters in the potato. Some of the reasons were: (1) tetraploid potato varieties are usually asexually propagated and thus, highly heterozygous (often no attempt is made to obtain

homozygosity); (2) in seedlings derived from selfing a variety, there are usually varying percentages of degenerate individuals which may affect the values of variances and give 'biased' estimates of genetic parameters; (3) there is the difficulty that among offspring, many may not flower, or if they do, may have pollen and/or ovule sterility; and (4) the polyploid constitution of the potato means that segregations are often complex.

Haploids (2n = 24) from autotetraploid potatoes (2n = 48) function as diploids in their inheritance and offer an aid to genetic studies of this crop (Hougas and Peloquin, 1958).

MATERIALS AND METHODS

Economic photosynthetic efficiency and other characters were studied on three tetraploid potato varieties (2n = 48) and groups of haploids (2n = 24). The experiments considered fell into three groups:

 i) Experiment 1 - Physiological observations on three tetraploid varieties grown in two years.

ii) Experiment 2 - Physiological observations on a large group of haploids grown for one year.

iii) Experiment 3 - Physiological and genetic studies on five haploid parents and their F_1 's from a diallel series of crosses.

Measurements taken

Leaf area - The method used in measuring the leaf area
 was that devised by Epstein and Robinson (1965) for potatoes, that
 is, leaf area is based on leaf length alone. The leaf area was
 estimated by the formula:

 $\log \hat{Y} = -0.40 + 1.78 \log X$

where

 $\hat{\mathbf{Y}}$ = estimated leaf area (in square cm.) X = length of compound leaf (in cm.).

The compound leaf is measured from the base of the petiole to

the tip. Epstein and Robinson derived the equation after fitting regression lines of four well known potato varieties, Russet Burbank, Katahdin, Kennebec and Irish Cobbler, in different environmental conditions. The applicability of this equation was found to be general over a wide range of environmental conditions. They found this measure to be a more reliable method of estimating leaf area than that based on length times width and it is less time consuming.

In general, on any one plant in the present work, the lengths of ten (10) compound leaves taken at random from the main stems and five secondary stems were measured. The average of these measurements was the value of X in the formula. The total leaf area per plant was estimated by: \hat{Y} times the average number of leaves per stem times the number of stems per plant.

The arrangement of leaflets in the compound leaves of the haploids was very irregular. Moreover, the leaflets were much smaller and more numerous than those of the tetraploid varieties. Due to these factors, the method used for the varieties could well be a less accurate estimate for leaf area of the haploids. Therefore, the method used by Ludwig, <u>et</u>. <u>al</u>. (1965) in their estimation of leaf area in cotton was employed for the leaflets of the haploids. Samples of leaflets covering the range of shapes and sizes of the experimental plants were collected and the leaf outline traced on graph paper. The area of each leaflet sampled was measured in square centimeters. These different standard sizes and shapes with

corresponding leaf area in sq. cm. were numbered from 1 to 10. Leaf area measurements were made by comparing leaflets of the sampled compound leaves with the standards.

Stratified sampling of the stems and leaves was done. Stems were divided into two groups: main and secondary. Each stem was divided into three parts: base, middle and tip positions. The leaves in each position were counted and leaf was randomly chosen from each position and measured.

The total leaf area of the plant was estimated by:

$$LA = (\Sigma b_i cm_i + \Sigma b_i dm_i + \Sigma b_i em_i + \Sigma b_i ds_i s)$$
 (M)

where

b_i = area in sq. cm. of standard i
cm_i = no. of leaves in position 1 (base) of standard i
dm_i = no. of leaves in position 2 (middle of standard i
em_i = no. of leaves in position 3 (tip) of standard i
ds_i = no. of leaves in secondary stem of standard i
s = ave. no. of secondary stems per main stem
M = no. of main stem per plant
i = 1, 2, ..., 10.

Yield - the fresh weight of the tubers of each plant was recorded.

3. Tuber dry matter (DMT) - was estimated by taking the specific gravity of the tubers and by the use of the table of conversion to percentage of dry matter (Burton, 1948).

4. Plant dry matter (PDM) - all parts of the potato plant other than the tubers were placed in the dryer at 65.5 C for 3-4 days to insure complete dryness.

5. Total dry matter (TDM) - the sum of tuber dry matter (DMT) weight and plant dry matter (PDM) weight.

6. Leaf area index (LAI) - the leaf area per unit area of ground area beneath that plant. Since the plant spacing is constant within the experiment, the pattern of LAI will then follow that of LA. Indeed, the planting distance is more or less constant from experiment to experiment and this enables us to directly compare estimates of LA (or LAI) from experiment to experiment. The results are not included in the discussion but will be presented and discussed in Appendix 1.

<u>Cultural techniques</u>

Fine mist irrigation pipes were set between rows to insure an adequate supply of water and to keep the air and soil temperatures reasonably low. Fertilizer was applied at planting. A regular spray schedule controlled insects and diseases. Weeds were well controlled by a chemical herbicide.

Experiment 1

The plant materials were taken from three well known varieties: Russet Burbank, Katahdin and Onaway. Russet Burbank is a late maturing variety with high specific gravity. Katahdin is medium in maturity and specific gravity. Onaway is early with low specific

gravity.

Twenty five plants were taken at random from a seed-increase plot. All the measurements were taken from these 25 plants for each variety. Data were collected in 1966 and 1967.

a. <u>1966 Experiment</u> - The first-year experiment was conducted at Michigan State University Branch Experiment Station at Lake City in 1966. The plants were spaced 86 x 35 cms. in the field. Leaf area was measured only once - just before the plants reached full maturity. Specific gravity of the tubers was taken. Visual observations on growth habit were made.

b. <u>1967 Experiment</u> - The second-year experiment was conducted at Michigan State University Branch Experiment Station in Montcalm County in 1967. The plants were spaced 91 x 38 cms. in the field. The leaf area was measured 60 days after planting and every twenty days thereafter until the majority of the leaves were yellow or fully matured. The summation of the daily leaf area was estimated by plotting the measurements taken at 60 days, 80 days, 100 days and 120 days against number of days. The points were connected by a smooth curve. Since growth was fairly uniform between points, measuring many points would probably not greatly increase the accuracy of estimating the summation of daily leaf area.

The area under the curve for each particular case is the sum of the daily leaf area for the number of days in each particular time interval. That is, the amount of leaf area for the first 60 days of growth was that estimated from the area covered by the curve

from 0 to 60 days. The leaf area was measured at more than one growth stage: twice in Onaway and three times in Katahdin and Russet Burbank.

As soon as the plants showed full maturity the tops were pulled and dried. However, after 120 days, all were pulled regardless of maturity.

Specific gravity of the tubers and fresh weight were taken for each plant. Tuber dry matter per plant was estimated by the method previously described.

Economic photosynthetic efficiency (EPE) in the first experiment was the tuber dry matter per unit leaf area (g/cm^2) (i.e., the estimated LA for the single measurement). While in the second experiment, EPE was the ratio between the tuber dry matter per plant and the total leaf area days (i.e., the total area of the curve as described above).

All the raw data were punched on IBM cards. Analyses were done by the MSU Computer CDC 3600. Means, standard deviations, correlation coefficients and regression coefficients were evaluated.

Experiment 2

Haploid tubers of <u>Solanum tuberosum</u> were originally obtained from the Wisconsin Experiment Station. In this experiment, the plants were grouped according to their parental source. This experiment was conducted at Lake City in 1966.

Group 1 had 25 individuals, groups 2 and 3 had 4 and 5 individuals, respectively. These individuals cloned into 10 plants.

The 34 clones were planted in randomized-block design with two replications - five plants in each plot.

Leaf area was measured only once - just before full maturity by the same method as that used in the varieties.

Specific gravity and fresh weight of the tubers were determined for each plant and the dry matter in the tubers (DMT) was calculated. Economic photosynthetic efficiency (EPE) was calculated by DMT/LA.

Experiment 3

This experiment was primarily for an estimation of genetic parameters. Haploids of different sources including those tested in the field the previous year were planted in the greenhouse in the winter of 1966 and induced to flower. All possible crosses were made. Because of sterility and incompatibility problems, not all combinations were successful. However, a complete set of a 5 x 5 diallel series without reciprocals was available.

The five parental types of the diallel cross were Parent 1 (5283-4), Parent 2 (5281-6), Parent 3 (5279-23), Parent 4 (5279-21) and Parent 5 (5287-1). The number of F_1 seeds varied from cross to cross.

The seeds were shown in the greenhouse and the plants formed tubers in the summer of 1966. One tuber from each seedling was harvested in the fall of 1966. All the tubers from each cross were bulked and stored in refrigerated conditions (4 C) until the spring of 1967 when they were planted at the Station in Montcalm

County.

Parents and F_1 tubers were planted 45 centimeters between hills and 100 cms. between rows in a randomized block with two replications and four plants in each plot. Two crosses (2 x 4 and 3 x 5) failed due to the fact that they came from very small tubers. Generally, the F_1 's had smaller tubers than the parents.

The leaves were measured 40 days after planting and subsequent measurements were made at intervals of 20 days until the leaves were dead or the majority had turned yellow.

The averages of the estimated leaf areas at each date were plotted on graph paper. The curve was smoothed, cut, and weighed. These values were converted to leaf areas in sq. meter days. The estimated total photosynthetic leaf area days for each particular interval (in this case 40 for the first and 20 days for the rest) is the area under the curve over this particular time interval. That is, the photosynthetic leaf area days from 0 to 40 days after planting was the area under the curve from 0 to the leaf area measured 40 days after planting which was the sum of the daily photosynthetic leaf area for the first 40 days of growth. The estimated photosynthetic leaf area days for 40 to 60 days was the area under the curve from the point at 40 to the leaf area measured 20 days after which was the sum of the photosynthetic leaf area for the next 20 days of growth. The total cumulative photosynthetic leaf area days for the entire growing season was the area under the whole curve.

The plants were pulled the latter part of September, placed

in the dryer at 65.5 C for 3 to 4 days to insure complete dryness and weighed to obtain the dry matter in the portions other than the tubers.

Genetic parameters were estimated by employing Method 4, Model II of Griffing (1956) and Analysis III of Gardner and Eberhart (1966) on the analysis of variance of general and specific combining abilities in a diallel cross. This model assumes that parental genotypes are chosen at random, i.e., genotypic effects were considered random. The gene frequencies of the parental types were arbitrary.

The specific combining ability gives an estimate of the nonadditive genetic variance and the general combining ability an estimate of the additive and non-additive genetic variance. The estimate for environmental variance was the mean square error term in the analysis of variance. Gardner (1966) mentioned that mean square of varieties versus crosses reflects average heterosis and is attributable entirely to non-additive genetic effects.

The analysis of variance for Model II Method 4 of Griffing (1956) and Analysis III of Gardner and Eberhart (1966) giving expected mean square is shown below.

The genetic parameters were estimated as follows:

$\sigma_g^2 = (MSg - MSs)/(n - 2)$	-	variance of general combining ability
$\sigma_s^2 = (MSs - MSe)$	-	variance of specific combining ability
$\sigma_A^2 = 2\sigma_g^2$	=	additive genetic variance



	SOURCE	DF	MEAN SQUARE	EXPECTED MEAN SQUARE
PARENTS		n-1	MSp	
PARENTS	VS. CROSSES	1	МЅрс	
CROSSES	(n ((n-1)/2) -	1 MSc	
GCA		n-1	MSg d	$\sigma_e^2 + \sigma_s^2 + (n-2)\sigma_a^2$
SCA		n (n-3)/2	MSs d	$\sigma_{e}^{2} + \sigma_{s}^{2}$
ERROR			MSe a	2

RESULTS AND DISCUSSION

Experiments 1, 2 and the first part of 3 were conducted to determine the similarity of physiological patterns between the tetraploid potato varieties (2n = 48) and the haploids (2n = 24) derived from tetraploids. The second part of Experiment 3 was a genetic study of inheritance of physiological characters in haploids involving diallel analysis. The tetraploid varieties used were Russet Burbank, Katahdin and Onaway.

Experiment 1:

<u>a. 1966 Experiment</u> - Means and standard deviations of the characters under consideration in Onaway, Katahdin and Russet Burbank are presented in Table 1.

Onaway was the lowest in all the characters studied except yield (962 g. per plant) in which it was the median of the three varieties. Katahdin had the medium leaf area of 5299 sq. cm. but had the highest fresh yield (1019 g. per plant) and dry matter (210 g.). Russet Burbank had the highest leaf area (6790 sq. cm.), but lowest yield. Tuber dry matter of 206 g. in Russet Burbank was about that of Katahdin (210 g.). Starch content follows the pattern for dry matter.

VARIETY		: LA :(sq. cm.)	: YIELD : (g)	: DMT : (g)	: S : (g)	: EPE :(g/sq.cm.)
ONAWAY	x	5050	962	184	129	0.0364
	s _x	2150	356	52	33	
KATAHDIN	x	5299	1019	210	151	0.0396
	s X	2190	317	54	36	
RUSSET BURBANK	x	6790	941	206	15 2	0.0196
	^s īx	3000	210	42	30	

Table 1. Means and standard deviation of leaf area (LA), yield, tuber dry matter (DMT), starch (S) and economic photosynthetic efficiency (EPE) on a per plant basis of 25 plants for the three tetraploid varieties.

If we assume that the difference in mean leaf area measured at one point in time may be regarded as a reliable measure of varietal difference and that this is a valid estimate of active leaf area over the life of the plant, we can proceed to the consideration of the economic photosynthetic efficiency (EPE) Table 1. The results show that Katahdin and Onaway have high EPE, 0.0396 and 0.0364 grams per sq. cm. of leaf area, respectively, and Russet Burbank had the lowest, 0.0196 grams per sq. cm. No standard errors were attached to EPE since this observation was obtained from a calculation based on the mean leaf area and tuber dry matter per plant.

The investigation of the association between leaf area, dry matter of the tubers, starch and EPE was extended to the inter-

relationships of these characters within varieties. In this case, it is possible to examine numerical relationships by means of correlation coefficients (Table 2) rather than verbal associations, since the number of paired comparisons (multiple observations on individual plants) is much larger within than between varieties.

Table 2. Correlation coefficients within varieties for leaf area and each of yield, dry matter of the tubers, and starch (1966 data).

CHARACTERS CORRELATED	CORRELATION COEFFICIENTS						
WITH LEAF AREA	:	ONAWAY	:	KATAHDIN	:	RUSSET BURBANK	
YIELD	0	.77**		0.78**		0.49*	
TUBER DRY MATTER	0	. 76**		0.78**		0.44*	
STARCH	0	.74**		0.77**		0.41*	

*Significant at 5% level

** Significant at 1% level

From Table 2, all characters were positively and significantly correlated with leaf area within these three varieties. Moreover, within any one variety the degree of correlation of yield, DMT, and starch is almost the same. This indicated that these characters could have a high internal relationship between them, i.e., a change in one affects the other two characters.

<u>b. 1967 Experiment</u> - A more comprehensive study of the photosynthetic efficiency of these three varieties was carried out in 1967. Duncan (1967) suggested that in a study of photosynthesis, the time factor should be considered because the product a farmer harvests is not simply a rate per day but an accumulation over a certain time. Also, the 1966 results for these varieties indicate that there was a definite drawback in considering only one measurement of leaf area and in neglecting consideration of maturity times. Accordingly, the leaf area was measured at more than one growth stage: twice in Onaway and three times in Katahdin and Russet Burbank. Onaway had matured before the third measurement. The first measurement was made 60 days after planting and the subsequent measurements were made at 20-day intervals until plants were fully matured.

The average (25 plants) leaf area at these intervals for each of the varieties is indicated by the points on the graphs in Fig. 1.

From Fig. 1, five main characteristics of the curves, which show differences between the varieties, are apparent: - (1) The maximum LA obtained differs; (2) the point (day) at which the maximum was reached is slightly different; (3) the area under the curve differs in bulk, i.e., the integral under the curve, which is termed as photosynthetic leaf area day (PLAD) (the term is derived from the naming of the x and y axes and was calculated by weighing out the total graphed area and converting it to sq. m. days); (4) the shapes are different; (5) the end point, i.e., the time of maturity varies. However, the harvested yield and tuber dry matter changed only slightly from variety to variety (Table 3). This table includes measures of points 1, 2, 3, and 5,



<u>Figure 1</u>. Sum of the daily photosynthetic leaf area measured at different stages of growth in Russet Burbank, Katahdin and Onaway

mentioned above, and also estimates of total dry matter (TDM), tuber dry matter (DMT), net assimilation (NA), and economic photosynthetic efficiency (EPE). Figure 1 and Table 3 should be examined to account for the lack of differences in tuber dry matter: - (1) The maximum LA was highest in Onaway, median in Russet Burbank and lowest (about 1/2 of Russest Burbank) in Katahdin. These large differences in maximum levels obviously did not result in differences in yield dry matter. (2) There was a difference in the time when maximum LA was attained. (3) The area under the curve (TPLAD) did not follow the level of maximum LA in the two varieties Onaway and Russet Burbank. They were, in fact, reversed. However, it was again lowest in Katahdin. Since there was no substantial difference in the tuber dry matter content it must be concluded that TPLAD by itself cannot account for dry matter accumulation in the tubers.

It is necessary to emphasize that although TPLAD (and/or maximum LA) are the most likely factors which might affect dry matter accumulation - neither did so. The explanation is thought to lie in the next two considerations: (4) Shape of the curve and (5) end point or maturity.

The pattern of leaf area development is quite different from variety to variety (Fig. 1). The most striking difference is between Russet Burbank and Katahdin and Onaway. All three varieties accumulated leaf area at a rapid rate during the early growth stages. Onaway and Katahdin attained maximum LA at approximately

the 60-day point. While Russet Burbank attained its maximum LA at the 100-day point the increase after the 60-day point was very small. After this point the first two varieties (Russet Burbank and Katahdin) more or less leveled off. The third variety (Onaway) decreased in LA until all the leaves senesced at the 100-day point, at which time 'maturity', if defined as the complete laying down of substrate in the tubers, has been reached. Nevertheless, there were less striking differences in pattern between Russet Burbank and Katahdin. After th 60-day point, LA of Russet Burbank increased slightly, then leveled off and decreased very little by the time the experiment was terminated. On the other hand, Katahdin started a slow almost imperceptible decrease in LA and all the leaves had senesced completely by the end of the experiment.

Leaf area alone whether measured as TLA or TPLAD does not seem to account for DMT. It would seem logical to suppose that the distribution of leaf area over the growing season, the onset of senescence, and the time of maturity are modifying forces. Further, the critical time for the accumulation of dry matter in the tubers is the period after maximum leaf area has been attained. This could be a function of senescence/maturity and could be due to variation in efficiency of leaf areas at any given time. For example, too much leaf area could decrease photosynthesis and increase respiration.

The results of the estimated LA of the three varieties in relation to each other did not entirely agree in both years. In

the 1966 results Katahdin had the medium LA among the three varieties studied and Russet Burbank had the highest, while the 1967 results showed that Katahdin had the smallest LA both in the total and at any time interval of measurement. Russet Burbank had the highest TPLAD because of the longer growing period. Onaway had the median TPLAD with a very short growing period.

Table 3. Means of maximum leaf area, day at which maximum leaf area was attained, total photosynthetic leaf area day, maturity, total dry matter, tuber dry matter, net assimilation and economic photosynthetic efficiency per plant of Onaway, Katahdin and Russet Burbank (1967 data).

CUADACTEDS	·VARIETY						
	: ONAWAY :	KATAHDIN :	RUSSET BURBANK				
(1) MAXIMUM LA (sq. cm.)	15,454	5,840	10,141				
(2) MAX. LA ATTAINED (DAY)	60	60	100				
(3) TPLAD (sq. m. days)	51.43	32.19	60.15				
(5) MATURITY (DAYS)	100	120	120				
TDM (grams)	318	342	325				
DMT (grams)	209	223	227				
NA (gr am s /s q. m. d	lay) 6.17	10.63	5.40				
EPE (g/sq. m. day)	4.06	6.92	3.77				

The discrepancy in the LA measurements could be that Katahdin had its maximum LA between the second and third measuring time and/ or the measurement in Onaway in the 1966 experiment had been made

so late in the season that the leaf area had already decreased due to the onset of leaf senescence or tuber maturity. Another reason could be that the 1967 LA was presented as the cumulative photosynthetic leaf area days while in the 1966 results, LA was the actual estimation at one particular time of measurement.

The other characters followed the same pattern for the two years' experiments. That is, Katahdin had the highest TDM, NA and EPE, although, NA and EPE for the 1967 experiment are not comparable with those of 1966 because the latter was based on LA while the former was based on PLAD. However, the trend was the same. Dry matter of the tubers was almost the same as that of Russet Burbank. Net assimilation (NA) was the ratio of TDM and EPLAD and economic photosynthetic efficiency (EPE) was DMT/TPLAD in the 1967 experiment.

Of the three varieties studied, Katahdin had the highest NA and EPE. The data suggested that plants which had moderate LA during the early stage of growth and remained that way for a period of time before maturity, stored most of the photosynthate in the tubers. When leaf area continued to increase, much of the photosynthate was used in the production of more leaves. If there are too many leaves, there is a possibility of shading, thus, these plants will not be as efficient as those with fewer leaves. This suggestion would be compatible with the results of Watson (1958).

Experiment 2:

The main object of this experiment was to determine whether

similar physiological patterns exist between the tetraploids and the haploids. Means and standard deviations were calculated between individual clones within the three groups (progenies), Table 4. The standard deviations for LA for each of the three groups were very large, but were not significant between groups. It seems pointless, therefore, to discuss the influence of LA on tuber dry matter, yield, etc. for this experiment particularly since it is felt that the large errors were due to errors in measurements arising from the inability of the method of Epstein and Robinson (1965) to deal with the different morphological type of the haploids. This situation was corrected in the main experiment with haploids, Experiment 3. The results, however, showed a pattern of the relationships between LA and yield, DMT, starch and EPE similar to that obtained in the varieties (Expt. 1).

Table 4. Means and standard deviations for leaf area, yield, tuber dry matter, starch and economic photosynthetic efficiency per plant of three groups of haploids (1966 data).

(GRO	DUPS			: LA :(sq. cm.:	: Y ; (g)	: DMT : (g)	: S : (g)	: EPE : (g/sg. cm.)
Group	1	(25	plots) ^{a/}	x	4211	493	90	65	0.0214
				s _v	4 79 7	401	72	47	
Group	2	(4	plots)	x	6427	729	125	84	0.0195
				s _ī	4191	325	45	29	
Group	3	(5	plots)	x	4506	756	129	86	0.0286
				s _x	3281	769	120	76	

<u>a</u>/number of progenies in each group.

Experiment 3:

More intensive observations were made on the haploids. The parental haploids, 5283-4, 5279-23, 5279-21, 5287-1 and 5281-6 and the F_1 's of the diallel cross were evaluated. The experiment was broken down into two parts: (a) Physiological and (b) Genetic investigations.

<u>a. Physiology</u> - It was apparent in the results of Expt. 2 that there was a very high variation in leaf area measurement. One of the causes might be that the method used in measuring LA was the same as that used in the varieties.

All the parental types matured in 100 days. Parent 1 (5283-4) consistently had the greatest PLAD followed by Parents 3 and 4 (5279-23 and 5279-21, respectively) with the smallest PLAD found in Parents 2 and 5 (5281-6 and 5287-1). Maximum LA was attained by all the parental types at the 60-day measurement. This agreed with Onaway and Katahdin varieties and the results of Carolus (1937).

The F_1 's of the diallel cross had variable maturity. Crosses (1×4) , (1×5) , (2×3) and (1×3) were not fully matured after 120 days when they were all harvested. Maximum LA or PLAD of the F_1 's was obtained at different stages of growth. For instance, cross (1×4) had its maximum PLAD during the 80-100 day interval, (2×5) on the 40-60 day interval and (2×3) on the 100-120 day interval. The last measurement on the (2×3) F_1 might not have been the maximum LA because all were harvested after 120 days regardless of maturity. All the other crosses reached maximum.





mum PLAD during the 60-80 day interval. Typical growth patterns are shown in Fig. 2.

The results are summarized in Tables 5a and 5b. It was shown by the parental types and the F_1 's that there was a direct relationship between 1PLAD and 2PLAD with the TPLAD. However, if the plant matured early even if it had higher 1PLAD and 2PLAD it did not have as high TPLAD as the one with a longer growing period of moderate 1PLAD and 2PLAD. The parental types were generally more vigorous than the F_1 's.

In the potato, the interest is in the proportion of the photosynthate that is translocated to the tubers from the leaves. The values of 2PLAD, 3PLAD and TPLAD for both parents and F_1 's are plotted against total dry matter (TDM) in Figs. 3a, b, and c, respectively. In general, there is a linear increase in TDM with increase in leaf area (PLAD) for all three measurements of PLAD. In the earlier stages the increase is steeper, i.e., a given increase in PLAD at stage 2 (2PLAD) gave a greater increase in dry matter than a similar increase at the later stages. It may be seen from the fitted values that there is a decrease in regression slopes, i.e., b (2PLAD) = 0.216 b (3PLAD) = 0.146. Photosynthetic efficiency (as defined by the TDM/TPLAD) tended to decrease with plant age.

To obtain a clearer idea of the relationship of PLAD and dry matter distribution in the plant, 2PLAD, 3PLAD, and TPLAD were graphed against both tuber dry matter (DMT) and dry matter of the

	:	CUMULA	TIVE PHO	TOSYNTHETIC	LEAF ARE	A DAYS
	: 0-40 : days	:40-60 ; days	: 60-80 : days	:80-100 : : days :	100-120; days :	TOTAL
PARENT 1	4.34	16.74	24.32	14.54	0	58.50
PARENT 2	1.30	4.40	6.82	3.59	0	15.59
PARENT 3	1.98	11.55	15 .98	8.04	0	36.16
PARENT 4	3.96	12.03	16.85	11.30	0	42.51
PARENT 5	1.35	4.09	5.88	2.97	0	13.66
1 x 2	2.13	3.48	3.89	1.35	0	8.88
1 x 3	2.55	5.62	6.84	5.35	3.77	21.92
1 x 4	3.15	8.15	12.18	13.52	12.63	48.09
1 x 5	3.25	10.37	13.19	6.03	1.19	33.14
2 × 3	2.06	4.37	5.65	5.76	5.90	22.31
2 x 5	2.72	3.13	2.29	0.45	0	6.83
3 x 4	1.59	2.73	3.45	1.68	0	7.60
4 x 5	2.70	5.62	9.61	6.63	0	22.95

Table 5a. Means of cumulative photosynthetic leaf area days at different time intervals and totals for the parental types and the diallel cross F_{l} 's.

6**1**1

٨.

TYPES		: YIELD :(g/plt.)	: PDM):(g/plt.	: DMT):(g/plt.)	: TDM :(g/plt	: NA : :.): :	EPE:(D	MT/TDM)100 er cent
PARENT	1	1354	140	282	422	7.33	4.92	66.82
PARENT	2	554	58	106	164	11.05	7.47	64.63
PARENT	3	1106	132	207	339	9.35	5.68	61.06
PARENT	4	9 42	116	179	295	7.99	5.04	60.68
PARENT	5	410	32	92	124	9.55	6.93	74.19
1 x 2		244	60	63	123	13.87	7.08	51.22
1 x 3		422	95	96	191	8.63	4.51	50.26
1 x 4		360	226	76	303	6.73	1.63	25.08
1 x 5		644	104	133	236	7.81	4.44	56.36
2 × 3		364	108	84	192	8.37	3.63	43.75
2 x 5		248	41	59	100	14.40	8.40	59.00
3 x 4		162	63	45	108	14.33	5.93	41.67
4 x 5		474	49	106	155	7.67	5.33	68.39

Table 5b. Means of yield, plant dry matter, tuber dry matter, total dry matter, net assimilation and economic photosynthetic efficiency per plant for the parental types and diallel cross F_l 's.



plant (leaves, stems, etc.) (PDM) in Figs. 5a, b, and c and 4a, b, and c, respectively. It can be seen from all 6 figures that generally, there was a linear increase both in DMT and PDM with an increase in PLAD. It may be seen that the pattern for the 3 measurements of PLAD was similar for both DMT and PDM within the qualification stated in the preceding paragraph, i.e., there were decreasing regression slopes as the plant ages. In this case, it is better to concentrate on the differences in the patterns between DMT and PDM from Figs. 4c and 5c.

The components of total dry matter (TDM), DMT and PDM are not as clear as the TDM. Consider first Fig. 4c. Generally, there seems to be a linar response to increase in PLAD. However, there are two points designated as R_1 and R_2 (encircled on the graphs) which are off the trend (Fig. 4c). At this point, consider also Fig. 5c. There is also a general linear response, i.e., DMT increases as PLAD increases, but one of the two points (R_2) which was off the trend in Fig. 4c also disturbed the trend in Fig. 5c (encircled as R_2 which corresponds to the R_2 in Fig. 4c). By considering the two points in Fig. 4c, the plants belonging to R_1 were least efficient in the production of tops while those in R_2 were most efficient. In Fig. 5c, R₁ plants were more efficient in accumulating photosynthate in the tubers and R plants were less efficient. It would appear, therefore, (Figs. 4c and 5c) that R_1 plants are more economically efficient, i.e., a greater proportion of the photosynthate was accumulated in the tubers and R plants $\frac{2}{2}$





<u>Lignits 5s é.b.</u> Tuber dry matter per plant of perents and P₁' haploids plotted against 2 and 3 photosynthetic lasf area days respectively.

were not economically efficient.

This is amplified in Fig. 6 where the ratio (DMT/TDM) times 100 is plotted against TPLAD. The ratio seems to be constant for both parents and F_1 's (the line through the points appears to be horizontal) except again for the two points, R_1 and R_2 (encircled). If these points R_1 and R_2 be examined closely considering the maturity of these plants, the differences may be explained.

Plants in R_1 (cross 4 x 5) matured in 100 days and plants in R_2 (cross 1 x 4) matured in 120 days. Plants in R_1 were more economically efficient because they matured earlier than those in R_2 . In fact, R_2 plants were not fully matured when harvested. Had these plants been allowed to reach full maturity, they might have had greater DMT and therefore might have had higher efficiency. However, in field plots the growing season is limited by frost. Therefore, R_1 plants may be considered the ideal with an optimum TPLAD of approximately 23 sq. m. days at 100-day maturity. The PLAD during the attainment of the maximum LA and before full maturity, however, must be considered.

The amount of photosynthetic leaf area at the 60-day and 80-day period have a greater influence on the total leaf area and DMT, i.e., 2PLAD and 3PLAD, respectively.

To return to a more statistical treatment of Figs. 4c and 5c, regression and correlation coefficients were calculated with and without the points R_1 and R_2 . These are shown in Table 6.





Table 6. Regression and correlation coefficients of total dry matter, tuber dry matter, tops dry matter, economic photosynthetic efficiency and the percentage of dry matter in the tubers with 2PLAD, 3PLAD and TPLAD of the parental types and the F_1 's derived from diallel series, with and without R_1 and R_2 .

	HAPAC	TE	ÞC		:_		2PL/	AD	:		3	PLA	D	_	: TPLAD				
					:	r	:	b		:	r	:	Ь		:	r	:	Ł	>
TDM	(w/o	R	£	R ₂)*	0.	97	0.	.216		0.9)7	0.	. 146		0.9	98	6	.17	14
	(w/	R	8	R ₂). **	* 0.	95	0.	.220		0.9	5	0	. 148		0.9	6	5	.86	2
DMT	*				0.	97	0.	.149		0.9	8	0.	. 102		0.9	6	4	. 19	9
	**				0.	94	0.	146		0.9	3	0.	.098		0.7	9	3	. 22	1
PDM	*				0.	85	0.	070		0.8	4	0.	046		0.9	0	2	. 08	8
	**				0.	62	0.	078	I	0.6	2	0.	052		0.8	3	2	.73	8
EPE	*				-0.	47	-0.	001	-	0.4	6	-0.	001	-	0.5	9	-0	. 05	3
	**				-0.	39	-0.	002	-	0.4	2	-0.	001	-	0.6	6	-0	. 07	2
(DMT	/TDM)	100)	*	0.	39	0.	800	(0.4	2	0.	006		0.3	4	0.	. 20	0
				**	0.	19	0.	006	(0.2	1	0.	004	-	0.0	7	-0.	.06	0

A much better relationship is obtained between both DMT and PDM with TPLAD when these two points were omitted. It seems logical, on the basis of biological considerations, to accept the better fit as describing the general relationship and to consider, R_1 and R_2 as special cases. Plant breeders would, however, be interested in the special cases.

The physiological patterns for both tetraploids and haploids were discussed in detail under their separate headings, however, general similarities are summarized here. (1) The distribution of LA over the growing season, the onset of senescence and the time of maturity are modifying forces in the accumulation of DMT. (2) The critical time for the laying down of dry matter in the tubers is the period after maximum LA is attained. Leaf area at the 60- and 80-day periods has the greatest influence on the accumulation of dry matter in the tubers. (3) Plants with moderate maximum LA which senece slowly and mature in reasonable time are more economically efficient than those with more LA, long maturity and rapid senescence. On this basis the genetic action of the physiological characters under consideration in the genetic experiment with haploids would apply to the tetraploid potato.

b. Genetic studies with haploids:

To attain the objective of maximum production it is necessary to have strains or varieties that have highly efficient leaves. Blackman and Black (1959) concluded that optimum LAI for dry matter production is dependent on the species. According to Watson and French (1962) a better way to remedy the inefficiency of the kale crop in dry matter production when LAI was high would be to decrease the leaf-density dependence of net assimilation rate by breeding and selection.

Breeding and selection can be utilized effectively by knowwing the genetics of the characters under consideration. In this experiment the diallel set was utilized to study the genetic behaviour of the different characters. To test the null hypotheses

that there are no genotypic differences among the parents and F₁ progenies, a randomized-block analysis of variance for each character was performed.

The analyses showed that all the characters under study had highly significant values of F. This means that the null hypotheses were rejected and it can be assumed that genotypic differences exist.

The potato is an autotetraploid plant. It is asexually propagated and thus highly heterozygous. In this study, haploids derived from autotetraploids were used. Haploidy provides a means of obtaining a high degree of homozygosity. Hougas and Peloquin (1958) stated 'The haploids in themselves as initially derived from an autotetraploid closely approximate, assuming random chromosome segregation and not more than two alleles for any one locus, the degree of homozygosity obtained following three generations of selfing the autotetraploid. If one assumes random chromatid segregation the degree of homozygosity would be slightly less.'

The analyses of general and specific combining abilities for the different characters under consideration are given in Table 7.

The methods of analyses of Griffing (1956) were performed by least squares as described by Gardner and Eberhart (1966).

The analyses of the parental types were separated from the progenies due to the differences in their physiological behavior. The parental types were more vigorous than the crosses. This could be due to the fact that parental types were grown from larger

seed pieces while the F_1 's were from small, some very small, tubers. The parental types had higher PLAD at any time than their F_1 's. Most of the F_1 's had lower PLAD than their mid-parents. However, some of the F_1 's had yield and DMT lower than their mid-parents. Most approached their mid-parents in NA and EPE.

The parental types showed significant differences for 1PLAD, 2PLAD, 3PLAD, and TPLAD. There were also significant differences between parents and crosses in all the traits mentioned above except for 1PLAD. The non-significance between parents and crosses for 1PLAD could be that the plants were starting to develop.

The photosynthetic leaf area at early development, IPLAD, 2PLAD and 3PLAD among the crosses (Table 7) did not show any significant differences at the 5 percent level in general and specific combining abilities.

The non-significance of the general and specific combining abilities for IPLAD, 2PLAD, and 3PLAD indicates that the ability of the parents to transmit these characters was very low or nonexistent.

Specific combining ability for TPLAD was significant at the one percent level. This character then, can be improved through breeding and selection by using parental lines that combined or nick well. However, it did not show any significant additive genetic variance (σ_{A}^{2}) but very high non-additive genetic variance (σ_{NA}^{2}) . It may be possible that the genes for 1PLAD were different from those for 2PLAD or for 3PLAD and that there might have been

starch,	he	
TPLAD, tuber dry matter, yield, s	efficiency of parental types and t	
, 2PLAD, 3PLAD,	photosynthetic	
ance for IPLAD	and economic	's.
Analyses of vari	net assimilation	diallel cross F _l
Table 7.		

CONTRACT OF VABLANCE	10				MEAN SQ	UARE				
SOURCE OF VARIANCE	5	: I PLAD	2PLAD	3PLAD	TPLAD	DMT	TDM	۲	NA	EPE
PARENT S	4	2.12 ^{##}	29.51 ^{**}	59.04 **	356.90 ^{**}	6031 ^{***}	15259 ^{***}	151,635 ^{#1}	2.11	1.30
PARENTS VS. CROSSES	-	0.01	57.74 ^{**}	43.63**	429.74 **	5173	26498**	795,450**	4.23	2.43
CROSSES	7	1.45	29.96	65.16	356.57	7567	14633	215,714	5.03	2.98
GENERAL COMBINING ABILITY	4	0.40	6.71	15.61	136.57	757	2736	21,803	5.29	3.49 *
SPECIFIC COMBINING ABILITY	ŝ	0.20	5.12	13.94	258.00*	* 665	6320 ^{***}	18,176	18.52 [*]	*5.77
ERROR	24	0.15	4.70	9.29	71.10	614	1439	10,333	3.27	1.07

gene interaction within a locus and between loci, giving the total effect of very high σ_{NA}^2 , thus lowering the estimate of heritability in the narrow sense. It is also possible that this leaf area days (IPLAD, etc.) is not the best physiological measure of genetic difference.

The analysis showed that there was a highly significant difference in the tuber yield between the parental types. The difference between parents and crosses was significant at the one percent level. However, this character did not show significance in general and specific combining abilities of the parents. The σ_{NA}^2 was about three times that of the σ_A^2 , thus giving a heritability percentage of 11.7 per cent, Table 8.

The differences in tuber dry matter in the parental types was significant at the one percent level. There was also high significant at the one percent level. There was also high significance between parental types and crosses. The parents did not show any significant difference in general and specific combining abilities for this trait. The σ_{NA}^2 was about 4 times as much as the σ_A^2 . Heritability percentage was 8.4 percent which is very low. This might be due to the high σ_{NA}^2 and σ_e^2 . It could mean that this trait had an overdominance effect.

Total dry matter included all the dry matter produced by the plant throughout its life, i.e., DMT and PDM. The analysis showed that there were significant differences of TDM among parents and between parents and crosses. There was a significant difference among parents in specific combining ability for TDM. Total dry

2PLAD, 3PLAD, TPLAD,	vilation and economic	
of IPLAD,	net assim	
parameters	dry matter,	
mates of genetic and environmental	ir dry matter, yield, starch, total	osynthetic efficiency.
Esti	tube	phot
Table 8		

TRAIT	ENVIRONMENTAL : VARIANCE	:ADDITIVE :GENETIC VAR	:MON-ADDITIVE: .:GENETIC VAR.:	TOTAL GENET VARIANCE	IC: PHENOTYPIC : VARIANCE	:HERITABILITY BROAD SENSE:N	PERCENTAGE IARROW SENSE
1 PLAD	0.15	0.14	0.05	0.19	0.33	55.91	40.87
2PLAD	4.70	1.06	0.43	1.48	6.18	24.00	17.08
3PLAD	9.29	11.1	4.65	5.76	15.05	38.25	7.38
TPLAD	71.10	0	186.90	186.90	258.00	72.44	0
DMT	419.07	61.05	246.38	307.43	726.49	42.32	8.40
۲	10,333	2418	7843	10261	40594	49.83	11.74
TOM	1,439	0	1881	1881	6320	77.23	0
S	226	31	66	130	356	36.54	8.60
NA	3.27	0	15.25	15.25	18.52	82.35	0
EPE	1.07	0	4.70	4.70	5.77	81.46	0

44

A

matter appeared to be a complex character as exhibited by its lack of σ_A^2 and very high σ_{NA}^2 , i.e., zero σ_A^2 and 4,881 σ_{NA}^2 . The heritability in the broad sense was 77.23 percent compared with zero percent heritability in the narrow sense. The non-additivity could be accounted for by gene interaction within a locus or between loci. Like TPLAD, this trait may be improved through breeding and selection by using parental lines that combined well and taking advantage of the non-additive effects.

The efficiency of the plant to utilize the radiation energy for the production of usable energy is the ultimate factor to consider. It was divided into two categories, viz.: (1) the production of dry matter of the whole plant per unit leaf area (NA) and (2) the dry matter stored in the tubers per unit leaf area (EPE). These two were considered but the latter was the more important.

The analyses showed that in these two characters, there were no significant differences among the parental types or between parents and crosses. However, the parents showed highly significant specific combining abilities for both NA and EPE. The σ_{NA}^2 for each trait was high but zero σ_{A}^2 . The heritability percentages in the broad sense were 82 and 81 for NA and EPE, respectively. Both had zero heritability in the narrow sense because of the lack of additivity, i.e., zero σ_{A}^2 .

One of the possible explanations for the non-additivity in these traits is that there must have been a very high frequency of dominant genes. It could also be that the distribution of genes

for the transport of photosynthate to the tubers, and of the genes for the process of photosynthesis was probably unequal between the parents, since the parents were not homozygous at all loci. It was assumed that a majority of the loci are homozygous.

Overdominant or epistatic effects may be responsible for the large non-additive variances. In either case the best genetic combination must be specifically evaluated. For the traits measured in this study, it would appear that mass selection, or other selection methods which depend on additive genetic variance, would be ineffective with this gene base. However, in the potato, overdominant or epistatic effects can be an aid to improvement, since the potato is an asexually propagated crop. Superior characteristics can be propagated and maintained without the problem of loss through sexual generations.

SUMMARY AND CONCLUSIONS

Service of the servic

A comparison of physiological patterns of growth within and between tetraploid potato (2n = 48) varieties and haploids (2n = 24)were studied in three experiments. The first experiment was a physiological study of tetraploids using three well known varieties, Russet Burbank, Katahdin and Onaway. The second experiment was a physiological study of haploid groups, grouped according to parental source. The third experiment was the physiological and genetical study of the haploids. Five parental types and their F_1 's derived from diallel series were used.

The following conclusions may be stated: (1) The varieties and haploids examined showed similar physiological patterns (i.e., DMT, TDM, etc., increased as LA increased with only two exceptions which were considered as special cases). (2) The amount of DMT produced depended upon the total leaf area distribution throughout the life of the plant and is discussed in terms of the size, shape, and end point of the growth curve. (3) There are some plants that are very efficient in producing and accumulating photosynthates in the tubers, while others used a greater proportion of the photosynthate in the production of more tops and maintenance of the normal metabolic processes. (4) Accumulation of photosynthate in

47.

the tubers occurred after the maximum LA was attained. Maximum LA occurred in most plants at the 60- and 80-day measurements. Moderate LA and slow senescence produced more DMT than large LA and rapid senescence or too much LA and too long a maturity. The cause of less accumulation of DMT was due to a limited growing season, the problem of shading or a very short period of accumulation, thus resulting in less efficiency. Plant Breeders will be interested in plants which have (a) moderate maximum LA attained around 60 or 80 days after planting, (b) that senesce slowly to take full advantage of the accumulation of dry matter in the tubers and that mature within the normal growing season. (5) All the traits studied appeared to be complex with low heritability. Thus, the breeder must plan selection systems to take advantage of the non-additive variance, if this population is representative, or devise a better evaluation of the genetic differences. (6) Most of the traits studied showed overdominance or epistatic effects. Non-additive effects can be an aid rather than a hindrance to breeding and selection for the improvement of the potato, since this crop is asexually propagated.

LITERATURE CITED

- Anderson, A. K. 1960. Essentials of physiological chemistry. Fourth Ed. John Willey and Sons. Inc. N. Y, Lond.
- Blackman, G. E. and J. N. Black. 1959. Physiological and ecological studies in the analysis of plant environment. XII. The role of the light factor in limiting growth. Ann. Bot. N. S. 23: 131.
- Burton, W. G. 1948. The Potato. Chapman & Hall Ltd. 37 Esses Street W.C.2. 319 pp.
- Carolus, R. L. 1937. Chemical estimations of the weekly nutrient level of a potato crop. Amer. Potato J. 14: 141-153.
- Carraway, Michael 0. 1963. Movement of the products of photosynthesis in potato plants infected with leaf blight. Phytoprotection 44 (1): 60 Abst.
- Chapman, H. W. 1951. Absorption of carbon dioxide by leaves of potato. Amer. Potato J. 28: 602-615.

and W. E. Loomis. 1953. Photosynthesis in the potato under field conditions. Plant Physiol. 28: 702-716.

- Duncan, William G. 1967. Model building in photosynthesis. Harvesting the Sun. Symp. Photosynthesis in Plant Life. Ed. A. San Pietro, F. A. Greer and T. J. Armey. Acad. Press, N.Y., London. 309-314.
- Epstein, E. and R. R. Robinson. 1965. A rapid method for determining leaf area of potato plants. Agron. J. 57: 515-516.
- Gaastra, P. 1959. Photosynthesis of crop plants as influenced by light, carbon dioxide, tempeature and stomatal diffusion resistance. Mededelingen van de Landbouwhogeschool te Wageningen, Nederland. 59 (13): 1-68.

1962. Photosynthesis of leaves and field crops. Repr. Neth. J. Agric. Sci. 10 (5): 311-324.

- Gardner, C. O. and S. A. Eberhart. 1966. Analysis and interpretation of the variety cross diallel and related populations. Biometrics 22(3): 439-451.
- Goncharik, M. N. 1963. The method of halves in photosynthesis measurement. Biological Abst. 24896 (44).
- Griffing, B. 1956. Concept of general and specific combining ability in relation to diallel crossing systems. Australian J. Biol. Sci. 9: 463-493.
- Harper, Peter. 1963. Optimum leaf area index in the potato crop. Nature (London) 197: 917-918.
- Hougas, R. W. and S. J. Peloquin. 1958. The potential of potato haploids in breeding and genetic research. Amer. Potato J. 35: 701-707.
- lvins, J. D. and P. M. Bremner. 1965. Growth, development and yield in the potato. Outlook in Agric. 4: 211-217.
- Kumakov, V. A. 1958. Photosynthesis indices as a breeding character in wheat (Sel'skohoz. Biol. 1967. 2: 551-558 (Russian)). Plant Breeding Abst. 415. 38(1): 53.
- Loomis, R. S., W. A. Williams and W. G. Duncan. 1967. Community architecture and the productivity of terrestial plant community. Harvesting the Sun. Symp. Photosynthesis in plant life. Ed. A. San Pietro, F. A. Greer and T. J. Army. Academic Press. N.Y., London. 291-308.
- Ludwig, L. J., T. Saeiki, and L. T. Evan. 1965. Photosynthesis in artificial communities of cotton plants in relation to leaf area. Australian J. Biol. Sci. 18: 1103-1118.
- Pallas, J. E. Jr., B. E. Mikel and D. G. Harris. 1967. Photosynthesis, transpiration, leaf temperature and stomatal activity of cotton plants under varying water potentials. Plant Physiol. 42: 76-88.
- Swaminathan, M. S. and H. W. Howard. 1953. The cytology and genetics of the potato (<u>Solanum tuberosum</u> L.) and related species. Repr. Bibliographia Genetica XVI: 1-192.
- Thomas, M. D. and G. R. Hill. 1937. The continuous measurement of photosynthesis, respiration and transpiration of alfalfa and wheat growing under field conditions. Plant Physiol. 12: 285-307.

- Thorne, Gillian N. 1959. Photosynthesis of lamina and sheath of barley leaves. Ann. Bot. N. S. 23: 365-370.
- Watson, D. J. 1947). Comparative physiological studies in the growth of field crops. Ann. Bot. N. S. 11(41): 41-76.

______ 1952. The physiological basis of variation in yield. Advan. Agron. 4: 101-145.

1956. Leaf growth in relation to crop yield. Proc. Third Easter School Agric. Sci. Univ. Nottingham, Lon. Butterworths Scientific Publ.

1958. The dependence of net assimilation rate on leaf area index. Ann. Bot. Lond. N. S. 22: 37-54.

and G. A. W. French. 1962. An attempt to increase yield by controlling leaf area index. Ann. Appl. Biol. 50: 1-10.

Williams, W. A., R. S. Loomis, and C. R. Lepley. 1965. Vegetative growth of corn as affected by population density. II. Components of growth, net assimilation rate and leaf area index. Crop Sci. 5: 215-219.

APPENDIX I

Some leaf area estimates (only one was used, maximum LA) from Experiments 1 and 3 are presented in the table below along with the corresponding leaf area index (LAI) calculated as described in the Materials and Methods Section.

VARIETIES	: EXPERIMENT	la (1966)	: EXPERIMENT 15 (1967)
	<u>: LA</u>	<u>: LAI</u>	:MAX. LA : MAX. LAI
ONAWAY	5050	1.64	15,454 4.44
KATAHDIN	5299	1.72	5,840 1.68
RUSSET BURBANK	6790	2.21	10,141 2.91
HAPLOIDS	:	EXPERIMENT	3 (HAPLOIDS, 1967)
	.	MAXIMUM LA	: MAXIMUM LAI
P ₁ (5283-4)		₩6,246	3.61
P, (5281-6)		4,349	0.97
P, (5279-23)		1 0, 994	2.44
P ₁ (5279-21)		10,808	2.40
P ₅ (5287-1)		3,840	0.85
1 x 2		2,570	0.57
1 x 3		4,657	1.03
1 x 4		9 , 394	2.09
l x 5		9,604	2.13
2 × 3		4,155	0.92
2 × 5		1,567	0.35
3 × 4		2,178	0.48
4 × 5		6,293	1.40

Since the experiments have virtually the same spacing, any LAI may be computed by multiplying LA by the constant (.0003). The trend of LA is thus, exactly followed by LAI. The term LAI could have been substituted for LA in the discussion of results, thus needs little further consideration here. It is included in the above table mainly, so that other authors may compare these results with those obtained in other crops. Nevertheless, it may be briefly noted that the LAI results are not in agreement with Watson (1958) with kale and Harper (1963) on potato who stated that the optimum LAI should be about 3.5, whereas, the most efficient variety here (Katahdin) and haploid cross (4 x 5) had much lower LAI's. It was suggested that the reasons for the efficiency of these two low LAI types lie in their pattern of growth, which was fully discussed in the results and discussion section.

