INHERITANCE OF MATURITY IN BASIC GRAINS AND

OTHER TROPICAL CROPS.   A REVIEW

Gustavo A. Enríquez

ENRIQUEZ, GUSTAVO A.   Inheritance of maturity in basic grains and other tropical crops.   A review.   Turrialba, Costa Rica, CATIE 1977.   30 p.*

SUMMARY

The review summarizes the genetic relationships controlling the expression of earliness or lateness in 16 crop plants.   It discussed the different interpretations of the results found in the literature.

Several categories of genetic postulates have been found which explain the results obtained for maturity of these crops.

RESUMEN

La presente revisión hace un resumen de las relaciones genéticas que controlan la expresión genética de tempranos o tardíos en 16 cultivos comunes. Se discuten las discrepancias entre algunos autores y se plantean algunas explicaciones.

Varias categorías de postulados genéticos fueron encontrados y discutidos para la explicación de la herencia de esta característica de los cultivos en estudio.

CONTENT

INHERITANCE OF MATURITY IN BASIC GRAINS AND

OTHER TROPICAL CROPS. A REVIEW*

Gustavo A. Enriquez**

INTRODUCTION

The genetic relationships controlling the expression of earliness or lateness in plants are complex and their expression is often altered by the environment. This trait has been observed in several crops for several years and a great disagreement is found in the literature in some crops.

The flowering process does not occur in one stage, but rather in a series of physiological and morphological stages which eventually lead to anthesis.

In some plants earliness or lateness can be observed most accurately by keeping daily records of the date of first heading of each plant; in other crops the number of days from planting or emergence to the opening of the first flower can be recorded. The data can be expressed as the mean of all the individuals records of the population under observation.

The objective of the present paper is to give a general idea of some of the mechanisms found to control this trait in several crops by reviewing part of the available literature, which is very extensive, in the most

---

important crops.

Several catagories of genetic postulates have been offered in order to explain the control of maturity in plants: monogenic, digenic or polygenic control of the trait, being dominant, recessive, partial dominant, or overdominant; epistatic, complementary or idependent action has been reported.

BARLEY (Hordeum vulgare L.)

In a short review Smith (69) concluded that expression of earliness in barley has been reported to be dependent on one to many genes, and cited Wilson (1907) who reported that lateness was dominant to earliness. While Griffee (29) reported that earliness is dominant over lateness and that it is controlled by a single gene pair.

Frey (26) found that the variety 'Ogalitsu' differes from 'Harlam' by one factor pair for date of heading, while 'Jet' and 'Anoidium' differ from 'Harlam' by two. Both 'Jet' and 'Anoidium' contain the same gene pairs for determining heading date. He reported that date of heading has been shown to be determined by two or three genes by Neatby (1929) and Wexelsen (1933).

Johnson and Paul (33) working with the F_1, F_2 and F_3 of 7 crosses between spring barley varieties of differential maturity periods that were grown in the same year, found that parents in each late x early cross differed by additive increaser alleles at two loci giving a_i a_i b_i b_i x aabb. Theorically such a cross produces 6 F_2 breeding types: late, intermediate, and early homozygotes; and late, intermediate and early heterozygotes; the ration geing: 1:2:1:4:4:4. Observed frequencies being in good agreement with these expectactions, they concluded that

the hypothesis accounted satisfactorily for the main features of in-
heritance. Minor discrepancies were attributed to modifying genes, the
nature of which could not be determined.

Based on the same data, Eunus (21) re-analyzed five of these cros-
ses by following biometrical techniques developed by Mather in 1949. He
found that the number of effective factors controlling earliness in the
varieties studied varies from two to five. The low estimation may be due
to non-isodirectional accumulation of polygenes of unequal effects.

On the other hand the study showed that there was over-dominance
in three of the five crosses and no dominance in the remaining two
crosses. Overdominance was also evident in the F_2 days-to-heading data
of one cross. Comparing the F_1 and F_2 data he found that earliness is
dominant over lateness in two crosses, while lateness is dominant over
earliness in one cross (Atrel x Tulare). This must be the same case as
that of Wilson cited by Smith (69). The other case must be the same as
reported by Griffee (29) (see above). Transgressive segregation was ob-
served in two crosses.

BEANS (Phaseolus vulgaris L.)

Coyne (13, 14) and Yarnell (78) found that the time of flowering in
bean is dependent upon a major dominant gene with modifying factors in
crosses like While Seeded Tendergreen x Blue Lake OSC 949-1864.

When Coyne (15) crossed G.N. 1140 x G.N. Nebraska #1 Sel. 27 he
found two major genes governing the inheritance, earliness being dominant.
When he crossed White Seeded Tendergreen x G. N. Nebraska #1 Sel. 27
(12, 13, 15) he found 3 genes involved in the inheritance of time of
flowering and late flowering was dominant in the F_1. In crosses of

Harvester x OSC 949-1864 he found (12, 13) that additive effects were more important for late flowering. For cross G.N. Nebraska #1 Sel. 27 x G.V.-50, he found (13) that the trait was quantitatively inherited.

Studying a diallel cross with snap beans, Dickson (19) found an additive inheritance pattern. Overdominance apparently influenced earliness. 'Harvest King' was the earliest variety and contain the most dominant genes for earliness. 'Wade' and 'Earliwax' contain recessive genes for earliness and show transgressive segregation when crossed with 'Harvest King'.

Coyne (14) studied the lines 'Great Northern-1140' and Introduction PI-165078 found that when these two varieties were grown in growth chambers with 14-hour daylenth and 30° and 27°C (day and night) temperatures, where like in the field. There was no significant difference in data of flowering of the varieties under the 14 hours photoperiod and 27° and 21°C. A temperature of 30° and 27°C under 14 hours day produced a differential respond in time of flowering of these varieties.

Padda (50) and Padda and Munger (51) found an interaction between 3 temperatures and photoperiod affecting the flowering response of varieties 'Red Kidney' and 'Great Northern UI 1'. Under an 18-hour photoperiod the response of these two varieties can be classified into 3 categories depending upon the temperature prevailing during the test. Under high temperature conditions 'Red Kidney' was delayed; under low temperature 'Great Northern' was delayed; but under medium temperature neither of these varieties was delayed. A hypothetical model was presented in these papers. Under this hypothesis, 'Red Kidney' carried a gene designate Ht which caused delay in flowering under 18 hours photoperiod and high temperature. 'Great Northern' on the other hand has a second gene, Lt which causes

delay in flowering under 18 hour photoperiod and low temperature condition. The double recessive plants should flower normally under all combinations of 18 hours photoperiod and temperature regimes.

They found that although floral initiation had occurred at both long and short photoperiods, the further development of flower primordia into flowers was delayed or completely inhibited by long photoperiods. When the plants with inhibited floral buds were transferred from long photoperiods to short photoperiods, they developed normal flowers.

Rudorf (65) and Yarnell (78) said that the gene for indeterminate growth of beans, fin^+, retards flowering as compared with fin. The F_2 of crosses between the indeterminate (fin^+) short-day (neu^+) Phaseolus aborigeneus and the determinate (fin day-neutral (neu) P. vulgaris gives a 3:1 ration when grown with a short-period, but with long days segregates 9 indeterminate short-day (fin^+ neu^+): 3 indeterminate day neutral (fin^+ neu): 4 determinate day-neutral (fin neu^+ and neu). A third generation established that fin is epistatic to neu^+. This accounts for the lack of shortday varieties of bush beans.

Bliss (7) found that in common beans the segregated ratios observed in the F_2 and F_3 of crosses of true bush cultivars and OSC410 and both backcross populations show that sprawling growth habit is completely dominant to true bush type and controlled by a single gene. The mean flowering time of OSC410 was nearly 2 weeks later than that of true bush cultivars. In general true bush plants flowered early and sprawling plants were late flowering in the segregating population.

The ratios observed in populations resulting from the cross 'Polaris' x OSC410 support the hypothesis that indeterminate is dominant to deter-

minate habit. 'Polaris' and OSC410 differed greatly in plant height and growth habit, but there was little difference in flowering time.

When he crossed 'Mexico 80R' (normal) x OSC410 he found that in this population height and plant type were controlled by 2 epistatic genes, with indeterminance being dominant. Segregation data from 5 F_2 progenies were pooled and the observed ratios did not differ significantly when tested against a 9:3:3:1 ration which would be expected if expression resulted from epistatic gene action as it was suggested when he studied the F_1 phenotypes. There was little variability with respect to flowering time; however, the indeterminate phenotypes appeared to be slightly later.

Studies at Cornell show that some photoperiod insensitive lines are temperature sensitive and that this sensitivity is regulated by the daylength. Under low temperatures and long days the plants flowering earlier than at low temperatures and short days, but at high temperature the difference is almost nil. In the photoperiod sensitive group, lines grown under short days, higher temperatures reduce the number of days to flowering. When the same lines are grown under long days (14 hours or more), higher temperatures delay flowering.

BIRDSFOOT TREFOIL (Lotus corniculatus L.)

Buzzell and Wilsie (9) working with birdsfoot trefoil crosses believe that a dependency of flowering time on the rate and amount of vegetative growth may be an explanation for a different segregation of the clone 578, an early flowering, short stemmed clone, when crossed with late flowering, short-stemmed clones 540 or 567 and when crossed

with the late flowering, long stemmed clones E-7 or 533. Earliness or lateness of flowering in trefoil may be regulated by a number of genes, some of which may have opposing effects. The F_2 data did not show a consistente relationship between late flowering and long stems.

Transgressive segregation for earliness in the F_2 progenies ranged from 4 to 8 days, while for lateness it ranged from 13 to 21 days. In the F_2 families, phenotypic dominance for early flowering was indicated when a cross involved early by late flowering and short by short stem length. Little or no dominance was observed in crosses involving early by late flowering and short by long stem length.

The earliness of the F_1 may be due to dominance, a heterotic effect or non-allelic interaction. The heritability estimates for flowering time among F_2 progenies was 40%. For the purpose of selection for time of flowering, the total backcross population might be more useful than an F_2 population obtained from chain or diallel crossing.

CASTOR BEAN (Ricinus comunis L.)

In a diallel cross study of Castor beans, Hook, Williams and Gardner (31) found significant heterosis for earliness. Eleven hybrids flowered earlier than the earliest parent. Reciprocal effects were significant for time of flowering. Sixteen F_1's flowered earlier than the reciprocal cross when the female was earlier than the male parent. Three of five crosses not showing a maternal effect had a common variety ('Baker 296') as pollen parent. This may indicate that this line has more potential to bring the flowering of its hybrids nearer to its own level when used as male or female parent. Both additive and non-additive effects were involved in the expression of this trait. The mean square

for line effect was larger than that for heterosis. Earliness of flowering was a partially dominant trait in most of the F_1's progenies.

CORN (Zea mays L.)

Jones (35) reported from a study in corn that in the inheritance of maturity in six crosses of "early x late" varieties, earliness appeared to be due mainly to dominant genes. He found some degree of heterosis that was expressed in each cross. Early silking showed complete genetic dominance, but classification of inbredes entirely on the basis of silking date may not furnish the desired information on maturation. The dominant genes for earliness in two inbreds were epistatic (R-53 and A-158). It was calculated that minimum gene numbers ranged from 5 to 19 for silking date.

Dessureaux et al. (18) found that in general, strains that flowered early in corn tend to mature more rapidly than those that flowered late. However, the rate of kernel maturation may be relatively slow in some early strains and relatively rapid in some late ones.

Mohamed (41) found that "fewer" days from seeding to silking and to pollen shedding showed complete phenotypic dominance over "more" days. The genetic variance indicated also complete genic dominance. Silking date was determined by at least 3 major gene pairs by which the two inbred lines studied were differentiated. The number of days from seeding to pollen shedding was found to be governed by at least 2 major gene pairs. The difference in days between pollen shedding and silking indicated complete phenotypic and genic dominance for longer duration with at least one major gene pair controlling the difference.

Giesbrecht (28), studying the inheritance fo maturity, found that the trait as measured by days to silking and days to pollen shedding gave evidence of partial phenotypic dominance for earliness: Some interallelic interaction was found. The results from the two characters, days to silking and pollen shedding, both support the hypothesis of a 4 effective factor pair difference; it therefore appears that they are controlled by the same factors.

Francis et al. (25) found extremes from photoperiod insensitive to sensitive corn varieties when they studied tropical maize varieties and corn belt hybrids growing in both areas, but the tropical varieties seldom made anthesis early enough to set seed in a corn belt field.

COTTON (Gossypium hirsutum L.)

White (76) from crosses of a diallel found that epistasis (interaction) was all but ruled out in the chi-square test, so he concluded that the significance of the interaction multiple allelism component in earliness was due to multiple allelism. Estimates of dominance were reasonably repeatable over 2 experiments using the same parents.

Al-Rawi and Kohel (1) found that 5.3% of heterosis was caused by epistatic genes only, since epistasis chi-square values were significant and the dominance component H_1* was not significant in their diallel analysis.

Murray and Verhalen (44) found from their studies in cotton that the results suggest that the genetic system for earliness was primarily

---

* According to the notation of K. Mather, 1949 Biometrical Genetics. Methuen & Co. Ltd. London. pp. 56.

additive. Based upon the fact that actual and predicted genetic advances

are different (4.8% and 9.1%) and that broad-sense rather than narrow-

sense heritabilities were used to make the prediction, one can assume that

earliness has relatively more dominance or epistatic varieance. The con-

sistently heritability obtained suggests that little progress for this

character could be made in this population by selecting among single F_2

plants for the performance of their F_3 progeny rows.

Verhalen et al. (73) found that the additive genetic variance (D)*

was significant over two years, for earliness. The relative frequency

of dominant versus recessive alleles of the parents (F)* was positive and

significant in the F_2 for earliness suggesting a predominance of dominant

alleles in the parents for this trait in this generation. Earliness

has the highest narrow-sense heritability compared with the other traits

studied.

COWPEA (Vigna sp.)

Roy and Richharia (64) working in V. sinensis found in the F_2 that

maturity was controlled by two complementary factor segregating 9:7. Some

transgressive segregation found at both sides, early and late, were at-

tributed to environmental factors.

The analysis of the F_1, of the F_2 segregation and of the F_3 families

of V. unguiculata L. Walp, made by Sene (67) show that the characters of

"no susceptibility to photoperiod" and of "short-day flowering" are con-

trolled by a pair of major genes with the allele of "short-day flowering"

---

* According to the notation of K. Mather, 1949 Biometrical Genetics.
  Methuen & Co. Ltd. London. pp. 56.

** Vigna sinensis is synonymous of V. unguiculata.

prevailing. Days shorther than 12 hours were considered short days.

Ojomo (49) working with <u>V. unguiculata</u> L. Walp. found that the F_1 showed little or no segregation and that the high proportion in the early class indicated that early flowering was dominant to late flowering. In the F_2 and F_3 a 1:15 segregation ration of late and early flowering plants were observed, suggesting that the date of flowering might be controlled principally by two major gene pairs. He found that most of the exotic varieties used in breeding at Moor Plantation are high yielding, early flowering, and possess a short flowering interval, and consequently are early maturing. The local varieties, on the other hand, are relatively lower yielding and late flowering, and their long flowering period extends the harvest over a long period, during which time insect damage to the crop reduces the yield. He found that 'Mala' and 'Local Brown' were late and must be recessive at both loci $ef_1 ef_1$, $ef_2 ef_2$, and that 'Westbred' and 'Dixielle', early and intermediate varieties, must be $Ef_1 Ef_1 Ef_2 Ef_2$ or $Ef_1 ef_1 Ef_2 ef_2$. In the F_2 and F_3 in some crosses he found transgressive segregation for late and early flowering, suggesting the presence of minor modifiers in addition to the major genes.

FLAX (Linum usitatissimum L.)

Baker <u>et al</u>. (3) studying the flowering time in flax concluded that at least two genes are concerned in this trait in each of the crosses they studied. Early flowering time appears to be dominant over late flowering time. Additive, dominant and epistatic gene actions are important. It was evident that the study involved at least five and probably six different genotypes insofar as flowering time is concerned. In

either case at least three genes would be required to explain the differences among the parents. It is possible that only one gene was involved in one or several of the crosses. Early and late flowering genotypes are more subject to environmental variation than intermediate-flowering genotypes.

JUTE (Corchorus capsularis)

Eunus and Salam (22) working with different crosses of jute, found that the number of effective factors conditioning earliness was one; the estimation is low considering that for some crosses transgressive segregation was found. The low estimation may be due to non-isoderectional distribution of polygenes. One of the crosses showed partial dominance, but the F_1 and F_2 means of the cross exhibited overdominance. They found complementary epitasis for all crosses except one. Another cross showed epistasis for earliness; this may be due to the presence of the interaction of three or more genes.

OATS (Avena sativa L.)

Muehlbauer et al. (42) found that the variance caused by reciprocal effects was significant for days to first head in the group of crosses between spring and hardy winter parents. This may have resulted from an interaction between the cytoplasm and nuclear genes. The same was observed for maturity in some crosses in some locations. General combining ability was the major component of variation for maturity. Heritability (h^2%) estimate for maturity in one location was 60.7 and for the other location 24.2%.

PEANUTS (Arachis hypogea L.)

In Virginia type peanuts, Gupton and Emery (30) found very little difference between corresponding mean square values for the F_4 and F_5 generations. Genetic variance of the F_5 generation equals the sum of the additive variance and 1/64 of the dominance variance. Since dominance variance is negligible at the F_4 and F_5 generation levels and only a fraction of it is used, dominance effect can be practically ignored, so the genetic effects are essentially additive and heritable. The progressive increase in mean square from the early to the late pegging group found in both generations signified a greater difference among genotypes in the ability to mature late-appearing fruit than the first fruit on the plant. The first fruit are apparently set early enough to approach maturity in the normal growing season regardless of genotype. The later appearing fruit are more dependent upon the rate of maturation conditioned by the genotypes. This suggests that the greatest gain in the maturity level of a crop could be made by selecting lines in which fruit maturation is rapid at the later-appearing fruit positions.

PEA (Pisum sativum L.)

Keeble and Pellew (39) studying the varieties 'Autocrat' and 'Bountiful' found 30 days of difference in the flowering time. They concluded that there is an incomplete dominance of lateness over earliness and that there are two or more factors connected with time of flowering. The combination of both, dominant and antagonic factors, from either parent in the F_1 plants, result in an intermediate time of flowering.

Working with six pea cultivars in crosses in diallel fashion, Watts,

Stevenson and Crompton (74) found that the genetic system controlling

time of flowering was mainly additive in effect. Gene action in specific

combination appear to be present in this experiment. There were indi-

cations that lateness was largely dominant, although not controlled by

major genes. There was no sign of transgressive segregation, apart from

one day's earliness in one plant out of 25 in 5 of the crosses.

Murfet (43) in the same crop, crossing a late variety (L) with

an early developing variety (ED) obtained an early initiating progeny

(EI) and in the F_2 a ratio of 4ED: 9EI: 3L, all crosses being fully

discrete. With these results he assumed two dominant genes S_2 and E which

interact as follows: genotype es_2 is ED; S_2 by itself gives an L type;

E is epistatic to S_2 in terms of flowering mode, but by itself has no

effect so that Es_2 is EI and Es_{x_2} is ED. This theory was confirmed by

growing F_3 and F_4. The E/e pair segregate normally but the S_2/s_2 pair

have a disturbed segregation with a slight deficiency of recessives. S_2

is sometimes impenetrant in terms of flowering node, and has pleiotropic

effects on flower initiation, floral development, ability to respond to

photoperiod, senescence, height and yield. Mayor genes E and S_2, by dosage

and combination effects, also contribute substantially to within -class

variation.

Dolan (20) found that optimal conditions for growth of peas would

combine medium temperature, long photoperiod, and high light intensity.

Genetic studies cannot be evaluated without considering the interaction

with temperature and light intensity.

RICE (Oriza sativa L.)

Several categories of interpretation were generally offered in the literature of rice: Monogenic or digenic control of heading date (25, 36, 37, 46). Three genes interacting with different levels of dominance and additivity (10, 45, 47, 60, 61, 62, 63, 70, 71). Several alleles which conditioned heading time (27). Multiple factors (6, 43, 64, 68). Photoperiod sensitivity (10, 11, 66, 72). Temperature sensitivity (27). All of them give different levels of dominance and additivity or interaction between genes and alleles.

Inheritance of the duration from seeding to heading in rice was analyzed by dividing the vegetative growth period into the basic vegetative phase and the photoperiod-sensitive phase, by Chang, Li and Vergara (11). Concurrent determination of the two physiological phases on pure lines and hybrids was facilitated by testing vegetative tillers of the same plant under two photoperiods.

With this information it is feasible to reconcile some of the apparently divergent findings in previous genetic studies by considering both the genetic constitution of the parents and the prevailing environment. A short optimum photoperiod appears to be dominant to a long one.

Nagai (45) cited an interesting linkage trait that was observed by Ramiah and Ramuswami. They reported that the floating habit behaved as a double recessive to the normal habit. A linkage was found between the floating habit and lateness with a crossing over value of 30%. In the F_2 the time from seeding to flowering varied from 70 to 114 days. By classifying the segregates into two groups, early and late, at 90 days

from seeding, the numbers agreed with the expectation on the basis of a monohybrid segregation, lateness being dominant over earliness.

Kawai and Soto (38) studying an early heading mutation in rice found that some mutant strains show grain yields of 80% or more of the original variety. Early heading mutations, even if their yielding capacity was reduced, would be of direct use under some cultivation systems or climatic conditions. Six mutants were obtained from 1.322 R_2 strains; these could have direct practical use.

In 1926 Nagai, cited by Nagai (45) discovered an extremely late mutant in a pedigree line of the variety 'Togo'. The mean date of heading of the mutant was 29 days after the mean of the variety. The mutant plant was a heterozygote and in the next generation segregated to give 3 early: 1 late. Apparently AA had mutated to Aa in the preceding year. Dominance was complete so that Aa and AA were phenotypically alike. When they were grown in a warm climate (Kyushu) the mode of segregation was not so conspicuous as shown elsewhere and the range between the mean of the early and late groups became closer.

The components into which heading behavior in rice has been partitioned by Chandraratna (10) include: a) photoperiod sensitivity, b) minimum flowering duration, and c) optimum photoperiod. He argued that each of these components should be treated as a character and should form the subject of separate study.

Fuke (27) stated that six alleles which he designated Z, M, K, G. O and F, conditioned heading time in rice. He claimed that K was the most effective of the sensitivity alleles. Z and M were inferior in potency only to K. The sensitivity created by G, O, and F was conspicuously less than that derived from the other three alleles. The former

three alleles appeared to produce pleiotropically marked sensitivity to temperature. Interaction of K and F resulted in extreme sensitivity.

SORGHUM (Sorghum sp.)

Quinby and Kaper (58) reported three maturity genes in milo (Sorghum subglabrencens) var lotum Snowden). Lateness is dominant over earliness. The second and third genes, Ma_2 and Ma_3, do not express themselves except in the presence of dominant Ma_1. Also, the third gene, Ma_3, does not express itself in the presence of dominant Ma_2.

A fourth maturity locus was found when 'Hegari' (S. caffrorum var. albofuscum Snowden) was studied by Quinby (54) who showed that 'Hegari' is recessive at a fourth locus at which the 'Milos' are dominant.

Dominant Ma_1 interacting with dominant at other loci cause the formation of many leaves, late floral initiation, long duration of growth, and flowering as late as 100 days after planting.

Recessive ma_1, regardless of dominant or recessive alleles at other loci, produces early floral initiation and flowering as early as 50 days after planting. Combinations of dominant and recessive at the three loci produce a number of intermediate maturities.

In sorghum, (55) leaves continue to be laid down in the meristem until a floral bud is initiated. If floral initiation is delayed, more leaves are formed. Sieglinger (1936) was the first to pointed out the relationship between leaf number and maturity and observed that each additional leaf delayed heading by about 3 days. Sieglinger's data also showed that varieties of about the same maturity have different numbers of leaves, indicating a difference in the rate at which varieties initiate leaves.

Another linked trait in sorghum has been presented by Quinby and Karper (57). They found that gene Ma_1 was linked with Dw_2, a gene that influences length of internode. The gene Ma_3 was found to be linked with R, a gene that controls presence or absence of a plant pigment, and showed (59) the relations between the three Ma genes and the mutation ma^R3, that comes from the ma_3 gene.

Quinby (56) found that the earliest genotypes initiated floral buds at the same time, but flowered at slightly different times, indicating periods of panicle development of different lengths.

Sorghum was recognized as a short-day specie by Garner and Allard in 1923. The characteristic of being sensitive to short photoperiod, acts as dominant. A variety is considered to be sensitive if, under a 10-hour photoperiod, it differentiates its head, or is florally induced in about 21 to 23 days. It is also possible to find different critical photoperiod, so critical photoperiod and sensitivity to photoperiod are distinct manifestations (58).

Quinby and Karper (57) found that the action of the gene Ma is influenced by photoperiod. When grown under a 10-hour photoperiod, the early, intermediate, late, and ultralate genotypes of the 14-hour photoperiod were identical in appearance. The genes Ma_2 and Ma_3 were not able to express themselves if the plants were grown under the 10-hours photoperiod, and under the 14-hour photoperiod only when the gene Ma was present in the dominant condition.

They found (58) that the three Ma genes all influence the critical photoperiod and that the inheritance of sensitivity to photoperiod is not simple as that of critical photoperiod.

Lame cited by Quinby (55) determined the length of the light period or critical photoperiod needed to delay the floral initiation of 4 Milo genotypes. The data show that different critical photoperiods account for different time of flowering in sorghum.

SOYBEAN (Glycine max L. (Merr.)

Woodworth (77) reported that the large luxuriant, late maturing type is a simple Mendelian dominant to the small, low compact, early maturity type of soybean plant. Dominance appers to be complete. The symbols S and s were suggested. Owen cited by Norman (48) found that maturity tends to be linked with pubescens color and assigned the symbols E and e to this maturity factor. There is the possibility that this is the same as Woodworth's S and s factor pair.

Singh and Anderson cited by Norman (48) studied the maturity of segregating progenies from several crosses of soybean and found evidence for a few major genes and a number of minor ones. They reported evidence for the dominance of earliness in some crosses and for the dominance of lateness or the absence of dominance in others.

Two independent gene pairs affecting time of flowering and maturity in soybean were identified by Bernard (4) and studied in a common genetic background developed by backcrossing to the commercial variety 'Clark'.

Some soybean research workers (48) in the U.S.A. and Canada have divided soybean varieties and selections into 10 maturity classes, from 00 to VIII. Group 0 and 00 were added to the original numbering scheme with the northward expansion of soybean production. Group VIII is

adapted to the Gulf Coast area.

Bernard (5) said that Ting 1946 and Nagota 1960, pointed out a basic difference between the two types, namely that indeterminate plants continue growth in stem length and leaf production for a long while after flowering, but determinate plants terminate stem growth when flowering begins or soon afterward. The term 'determinate' is preferable to 'dwarf'.

From the data Bernard (5) obtained he found that determinate (dt$_1$) has an effect on plant growth when heterozygous and is therefore not completely recessive. Semi-determinate Dt$_2$ dt$_2$ and Dt$_2$ Dt$_2$ plants appeared similar in the field, but more study may prove that dt$_2$ is not completely recessive.

In other genetic backgrounds, modifiers can cause Dt$_2$ plants to be as short and determinate as dt$_1$ dt$_1$ plants; and dt$_1$ dt$_1$ varieties can be as tall or taller than the semi-determinate plants oberserved in the 'Harosoy' or 'Clark' backcross.

Crosses between the indeterminate types Dt$_1$-dt$_1$ x Dt$_2$-dt$_2$ show the expected ratio of 1 indeterminate; 11 semi-determinate: 4 determinate, for two independent loci with dt$_1$ epistatic to Dt$_2$-dt$_2$, confirmed by the F$_3$. In tests at Urbana of dt$_1$ and Dt$_2$ in BC$_5$ isolines of the indeterminate (Dt$_1$-dt$_2$) commercial varieties 'Harosoy' and 'Clark', plant height was reduced by 45 - 61% by dt$_1$ and 12-15% by Dt$_2$. Seed yield was only slightly reduced by dt$_1$ and was unaffected by Dt$_2$. Time of maturity and seed size and composition were slightly affected in some cases. The gene dt$_1$ produced a dwarfing effect when introduced into Northern U.S. soybean varieties.

Studies of the effect of photoperiod, time of planting, and rate of development, examined independently or in combination, lead to the general conclusion that genetic studies of the time of flowering and maturity cannot be evaluated without considering the interaction of environmental factors (8, 16, 32).

WHEAT (Triticum aestivum)

Pinthus (52) and Johnson et al. (34) working with spring and winter wheat respectively, found that time of maturity was controlled by one pair factor, earliness being dominant over lateness.

Florell (23, 24), in a series of studies found that earliness depends on more than one factor. Three or more factors probably are responsible for the differences in earliness observed in these studies, earliness being dominant.

Crumpacker and Allard (17) found three levels of dominance: 1) high dominant, 2) moderately recessive, and 3) highly recessive. A few genes with major effects appear to be responsible for most of the differences among the parents. The gene B, b has somewhat less effect on heading date than A, a. Another gene C, c which is partially dominant for lateness may differentiate a variety from the other members of the moderately recessive group. They obtained evidence that the remaining genetic variability in the diallel cross is governed by a system of minor genes displaying little or no dominance. Some of these minor genes appear to interact with one another and/or with the major genes to produce minor epistatic effects in certain crosses.

Anwar and Chowdhry (2) studied earliness of heading in four crosses of spring wheat. In three crosses earliness appeared to be partially

dominant, with each F_1 heading earlier than the midparent values and the F_2s' heading even earlier. Dominance was more pronounced in the fourth cross, with the F_1's heading in 58 days as compared to 59 days for the early parent. The broad-sense heritabilities for the character in all the crosses were considerably larger than the corresponding narrow-sense estimate. The broad-sense heritability ranged from 57 - 64% and the narrow sense (h^2) from 23 - 37%. Transgressive segregation also occurred, which suggests that desirable gene combinations occurred in these populations and that selection may be advantageous.

Pugsley (53), using the backcrossing procedure for developing a pair of near isogenic lines which differed in their response to vernalization, found a single-gene difference governing the vernalization.

Klaimi and Qualset (40) found a continuous series of intergrades between the extremes in time of maturity that appeared to exist in the species as a whole. There may be no clear distinction among early, intermediate, and late cultivars. They emphasize that the segregation ratios obtained depend on the environmental conditions under which the plants are grown and on the method of classification into spring and winter characters.

The association of the absence of response to a cold treatment with a single gene, with several genes, or several dosages of a gene, need not be mutually exclusive events on the assumption that a threshold level of some product is indeed a prerequisite for this type of response.

From the evolutionary point of view, time of flowering (heading time) is a character directly related to fitness. Thus natural selection must have operated on the widely available genetic variability to sort out genotypes closely adapted to their environments.

REFERENCES

1. AL-RAWI, K.M. and KOHEL, R.J. Diallel analysis of yield and other agronomic characters in *Gossypium hirsutum* L. Crop Science. 9:779-783. 1969.

2. ANWAR, A.R. and CHOWDHRY, A.R. Heritability and inheritance of plant height, heading date and grain yield in four spring wheat crosses. Crop Science 9:760-761. 1969.

3. BAKER, R.J., PESEK, J. and McKENZIE, R.I.H. A genetic study of flowering time in flax. Crop Science 12:84-86. 1972.

4. BERNARD, R.L. Two major genes for time of flowering and maturity in soybeans. Crop Science 11:242-244. 1971.

5. _____. Two genes affecting stem termination in Soybeans. Crop Science 12:235-239. 1972.

6. BHIDE, R.K. Inheritance and correlation of certain characters in rice crosses. Poona Agricultural College Magazine 18:76-85. 1926.

7. BLISS, F.A. Inheritance of growth habit and time of flowering in beans. *Phaseolus vulgaris* L. J. Amer. Soc. Hort. Sci. 96-715-717. 1971.

8. BORTHWICK, H.A. and PARKER, M.W. Photoperiodic responses of several varieties of soybeans. Botanical Gazette 101:341-365. 1939.

9. BUZZELL, R.I. and WILSIE, C.P. Inheritance of flowering time and lenght of flowering stem in 'Empire' by 'Viking' Birdsfoot Trefoil Crosses. Crop Science 5:526-529. 1965.

10. CHANDRARATNA, M.F. Genetics and Breeding of Rice. Longmans. London. 1964. 389 p.

11. CHANG, T.T., LI, C.C. and VERGARA, B.S. Component analysis of duration from seeding to heading in rice by the basic vegetative phase and the photoperiod-sensitive phase. Euphytica 18:79-91.

12. COYNE, D.P. The genetics of photoperiodism and the effect of temperature on the photoperiodic response for time of flowering in *Phaseolus vulgaris* L. Proc. Amer. Soc. Hort. Sci. 89:350-360. 1966.

13. COYNE, D.P. The inheritance of a temperature and a photoperiodic response on time of flowering in *Phaseoulus vulgaris* L. . Intern. Hort. Congress. Vol. 1 Work 65. n.p. 1966.

14. _____. Genetic control of a photoperiod-temperature response for time of flowering in beans (*Phaseolus vulgaris* L.) Crop Science 10:246-248. 1970.

15. _____, and MATTSON R.H. Inheritance of time of flowering and lenght of blooming period in *Phaseolus vulgaris* L. Proc. Amer. Soc. Hort. Sci. 85:366-373. 1964.

16. CRISWELL, J.G. and HUME, D.J. Variation in sensitivity to photoperiod among early maturing soybean strains. Crop Science 12:657-660. 1972.

17. CRUMPACKER, D.W. and ALLARD, R.W. A diallel cross analysis of heading date in wheat. Hilgardia 32:275-318. 1962.

18. DESSUREAUX, L., NEAL N.P. and BRINK R.A. Maturation in Corn. J. of Amer. Soc. of Agronomy 40:733-745. 1948.

19. DICKSON, M.H. Diallel analysis of seven economic characters in snap beans. Crop Science 7:121-124. 1967.

20. DOLAN, D.D. Temperature, photoperiod, and light intensity effects on gorwth of *Pisum sativum* L. Crop Science 12:60-62. 1972.

21. EUNUS, A.M. Inheritance of earliness in barley. Euphytica 13: 49-56. 1964.

22. _____ and SALAM, M.A. Epistasis in the inheritance of quantitative characters in Jute. Crop Science 9:167-169. 1969.

23. FLORELL, V.H. Studies on the inheritance of earliness in wheat. Jour. of Agr. Research 29:333-347. 1924.

24. _____. A study of certain characters in wheat back-crosses. Jour. of Agr. Research 43:475-498. 1931.

25. FRANCIS, C.A., GROGAN C.O. and SPERLING D.W. Identification of photoperiod insensitive strains of maize. Crop Science 9:675-677. 1969.

26. FREY, K.J. Inheritance and heritability of heading date in barley. Agronomy Journal. 46:226-228. 1954.

27. FUKA, Y. Genetical study of the photoperiodic reaction in the rice plant. Tokyo National Institute of Agricultural Sciences. Serie D. Bull 5:72-91. 1955.

28. GIESBRECHT, J. The inheritance of maturity in maize. Canadian Jour. of Plant Sci. 40:490-499. 1960.

29. GRIFFEE, F. Correlated inheritance of Botanical characters in barley, and manner of reaction to *Helminthosporium sativum*. Journal of Agricultural Research. 30:915-936.

30. GUPTON, C.L and EMERY, D.A. Heritability estimates of the maturity of fruit from specific growth periods in Virginia type peanuts (*Arachis hypogea* L.) Crop Science 10:127-129. 1970.

31. HOOKS, J.A., WILLIAMS, J.H. and GARDNER, C.O. Estimates of heterosis from a diallel cross of inbred lines of Castors. *Ricinus communis* L. Crop Science 11:651-655. 1971.

32. JOHNSON, H.W., BORTHWICK, H.A. and LEFFEL, R.C. Effects of photoperiod and time of planting on rate of development of the soybean in various stages of the life cycle. Botanical Gazette 122:77-95. 1960.

33. JOHNSON, L.P.V., and PAUL, G.I. Inheritance of maturity period in barley (Abs.) Genet. Soc. Canada Proc. 3:50. 1958.

34. JOHNSON, V.A., BIEVER, K.J., HAUNOLD A. and SCHMIDT, J.W. Inheritance of plant height, yield of grain, and other plant and seed characteristics in a cross of hard red and winter wheat. *Triticum aestivum* L. Crop Science 6:336-338. 1966.

35. JONES, C.M. An inheritance study of corn maturity Diss. Abstracts. 1954: Publ. N°. 7469:445-446. (Abst.). Plant Breeding Abstracts. 25:176. 1955.

36. JONES, J.W. Inheritance of earliness and other agronomic characters in rice. Journ. of Agri. Research 36:581-601. 1928.

37. JONES, J.W. Inheritance of characters in rice. Journal of Agri. Research 47:771-782. 1933.

38. KAWAI, T. and ' , H. Studies on early heading mutation in rice. Bot. Nat. Inst. of Agr. Science D 20:1-34. 1969.

39. KEEBLE, F. and PELLEW, C. The mode of inheritance of stature and time of flowering in peas (*Pisum sativum*) J. Genet. 1:47-56. 1910.

40. KLAIMI, Y.Y. and QUALSET, C.O. Genetics of heading time in wheat (*Triticum aestivum* L.). II The inheritance of vernalization response. Genetics 76:119-133. 1974.

41. MOHAMAD, ALY H. Inheritance of quantitative characters in *Zea mays*. I Estimation of the number of genes controlling the time of maturity. Genetics 44:713-724. 1959.

42. MUEHLBAUER, F.J., MARSHALL, H.G. and HILL, Jr. R.R. Combining ability, heritability and cytoplasmic effects in oats. Crop Science 11:375-378. 1971.

43. MURFET. I.C. Flowering in *Pisum*. Three distinct phenotypic classes determined by the interaction of a dominant early and a dominant late gene. Heredity 26:243-257. 1971.

44. MURRAY, J.C. and VERHALEN, L.M. Genetic studies of earliness, yield, and fiber properties in cotton (*Gossypium hirsutum* L.) Crop Science 9:752-755. 1969.

45. NAGAI, I. Japonica rice. Its breeding and culture. Tokyo Yokendo Ltd. 842 p. 1959.

46. NANDI, H.K. and GANGULI, P.M. Inheritance of earliness in Surma Valley rices. Indian Jour. of Agric. Science 11:9-17. 1941.

47. NOMURA, M and YAMAZAKI, R. A study on the inheritance of the shooting time on the Rice-plant. Japanese Journal of Genetics 3:129-130. 1925.

48. NORMAN, A.G. The Soybean. Ed. Academic Press N.Y. 2nd. Printing. 1967. 239 p.

49. OJOMO, O.A. Inheritance of flowering date in cowpeas (*Vigna unguiculata* L. Walp.) Trop. Agr. 48:279-282. 1972.

50. PADDA, D.S. Physiological genetics studies of photoperiodic responses in beans (*Phaseolus vulgaris* L.). Ph.D. Thesis. 1968 Cornell University. Ithaca, New York. 97 p.

51. PADDA, D.S. and MUNGER, H.M. Photoperiod, temperature and genotype interaction affecting time of flowering in bean *Phaseolus vulgaris* L. J. Amer. Soc. Hort. Sci. 94:157-160. 1969.

52. PINTHUS, M.J. Inheritance of heading date in some spring wheat varieties. Crop Science 3:301-304. 1963.

53. PUGSLEY, A.T. The inheritance of a vernalization response in Australian spring wheats. Australian J. of Agri. Research 14: 622-627. 1963.

54. QUINBY, J.R. Fourth maturity gene locus in sorghum. Crop Science 6:516-518. 1966.

55. _____. The maturity genes of sorghum. Advances in Agronomy 19:267-305. 1967.

56. _____. Influence of maturity genes on Plant Growth in sorghum. Crop Science 12:490-492. 1972.

57. _____, and Kerper, R.E. The inheritance of three genes that influence time of floral initiation and maturity date in Milo. J. Am. Soc. Agron. 37:916-936. 1945.

58. _____ and _____. The effect of short photoperiod on Sorghum varieties and first generation hybrids. Jour. Agr. Res. 75: 295-300. 1947.

59. _____ and _____. Inheritance of duration of growth in the milo group of Sorghum. Crop Science 1:8-10. 1961.

60. RAMIAH, K. Inheritance of flowering duration in rice (*Oryza sativa* L.) Indian Journal of Agricultural Science 3:377-410. 1933.

61. _____. Inheritance of height of plants in rice (*Oryza sativa* L.). Indian Journal of Agricultural Science 3:411-432. 1933.

62. _____. Genetic association between flowering duration and plant height and their relationship to other characters in rice (*Oryza sativa* L.) Indian Journal of Agricultural Science 3:433-445. 1933.

63. _____. Inhibitory factor hypothesis and the inheritance of flowering duration and plant height in rice (*Oryza sativa* L.) Indian Journal of Agricultural Science 3:446-459. 1933.

64. ROY, R.S. and RICHHARIA, R.H. Breeding and inheritance studies on cowpea, *Vigna sinensis*. Jour. Am. Soc. Agr. 40:479-489. 1948.

65. RUDORF, W. Genetics of *Phaseolus aborigineus* Burkart. Proc. X International Congress of Genetics 11:243. 1958.

66. SAMPATH, S. and SESHU. Genetics of photoperiod response in rice. Indian Journal of Genetics and Plant Breeding. 21:38-42. 1961.

67. SENE, D. Determinisme genetique del a Precocite chez *V. unguiculata* (L.) Walp. L'Agronomic Tropicale 3:309-318. 1967.

68. SETHI, R.L., SETHI, B.L. and MEHTA, R.R. Inheritance of earliness in united provinces rice, II. Indian J. Agr. Sci. 8:1-20. 1938.

69. SMITH, L. Genetics and Cytology of Barley. Botanical Review 17: 133-202. 1951.

70. SYACUDO, K. and KAWASE, T. Studies on the quantitative function of the causal genes in its determination. (1) On the quantitative function of the genes E_1, E_2 and D_1. Japanese Journal of Breeding 3:6-12. 1954. (Summary in English).

71. SYACUDO, K., KAWASE, T. and YOSHIBO, K. Studies on the quantitative inheritance (13). A. Rice (*Oryza sativa* L.) (a) Inheritance of the heading period and the quantitative function of the causal genes in its determination (2) on the quantitative function of the genes E_3, E_4 and E_5, Japanese Jour. of Breeding 4:83-91. 1954.

72. VERGARA, B.S., CHANG, T.T. and LILIS, R. The flowering response of the rice plant to photoperiod Int. Rice Res. Inst. Tech. Bull. 8.

73. VERHALEN, L.M., et al. A diallel analysis of several agronomic traits in Upland Cotton (*Gossypium hirsutum* L.) Crop. Sci. 11:92-96. 1971.

74. WATTS, L.E., STEVENSON, E. and CROMPTON, M.J. Inheritance of flowering time in six pea cultivars (*Pisum sativum* L.) Euphytica 19:405-410. 1970.

75. WELSH, J. R., et al. Genetic control of photoperiod response in wheat. Proc. Inter. Wheat Genetic Symposium. 4:879-884. 1973.

76. WHITE, T.G. Diallel analysis of qunatitatively inherited characters in *Gossypium hirsutum* L. Crop Science 6:253-255. 1966.

77. WOODWORTH, C.M. Inheritance of growth habit, pod color, and flower color in soybeans. J. Amer. Soc. Agron. 15:481-495. 1923.

78. YARNELL, S.H. Cytogenetics in vegetables crops IV Legumes. Bot. Rev. 31:247-330. 1965.