CROP GENETICS AND PHYSIOLOGY

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Summary

Plants evolve primarily for their own survival and not to feed the now burgeoning population of the world. Thus, crop physiologists should elucidate existing physiological systems and determine how genetic manipulation can be used to optimize achieving human objectives. Through these efforts, physiologists and geneticists have

been able to develop elaborate models and predict crop performance in given environments. An understanding of underlying genes is being incorporated to design new crops using plant breeding techniques. The greatest challenge to these efforts is the realization that complex physiological processes are controlled by multiple genes, not simple by Mendelian inheritance. Hence, efforts are made to utilize knowledge of quantitative trait loci in physiological studies and crop improvement. This integrated information is useful in developing a close relationship between the genotype and the phenotype, which is essential to genetic modeling and manipulation of crop plants.

Crop physiology research is predicated on three efforts: (i) understanding existing physiological systems, (ii) determining the genetic and environmental factors that affect these systems and (iii) manipulating these two variables to optimize crop performance. Pure research into photosynthetic and hormonal systems that control plant metabolism have illuminated understanding of these biochemical processes. Manipulation of the genes involved in these pathways has demonstrated the roles of many molecular signals in plant structure and function. Studies of quantitative traits under varying environmental regimens have allowed crop breeders to determine the role of each in crop phenotypes. Genetic manipulation, using physical and chemical mutagenesis, has permitted crop scientists to both study gene function and to generate additional genetic diversity for use in crop breeding efforts.

The findings of modern crop research demonstrate the efficacy in uniting plant physiology efforts with the tools of molecular biology for the improvement of the crop plants upon which the world's growing population depends.

1. Introduction

How do plants work? What is it that makes the physiology of plants unique and different compared to other organisms? These questions have driven plant biologists to seek a deep understanding of the impact of genetic and environmental factors on the evolution of plant physiology. Crop physiologists have specifically pursued the genetic mechanisms by which angiosperms, the group to which most crop species belong, manage nutrient mobilization.

Over millions of years of evolution, the basal angiosperm evolved in complexity, often by duplicating genes and sometimes entire sets of chromosomes. During this process there were changes in how and at what rate certain physiological processes take place. For instance cereals store starch in their grain but most fruits in the rose family store sorbitol. The driving force in these processes is the interplay of genes and their interaction with the environment that ultimately determine the physiological quality of any given plant. Modern research methodology has uncovered many of the mechanisms by which plants control their metabolism and development, and studies of physiological traits have allowed crop scientists to track and manipulate genetic changes.

2. Mendelian Principles of Plant Inheritance

In 1865, Gregor Mendel, in his publication "*Experiments in Plant Hybridization*", established basic principles of inheritance based on empirical data from his experiments

with hybrid pea plants. Mendel's conclusions, in modern terminology, can be summarized in three basic statements:

- A given trait or gene is determined by a pair of factors, which come in various forms called *alleles*;
- When an organism reproduces, the two alleles of a pair separate into different gametes and only one is passed on to a given offspring;
- Unless two genes are linked on the same chromosome, alleles of different genes segregate in a random pattern with respect to each other.

This third principle is of particular importance to crop scientists, whose goal is often the synthesis of many unique combinations of alleles that will alter or enhance the physiology of the plant for new applications. Furthermore, Mendel introduced the idea of allelic dominance when he demonstrated that some alleles are capable of completely masking the expression of their partners. This discovery was essential in establishing the critical recognition that an organism's genotype, the combination of alleles it possesses, is distinct from its phenotype, the physical trait it exhibits (*see also: Plant Genomics*). The cytological basis for Mendel's principles is the behavior of chromosomes during meiosis, as outlined in Figures 1, 2 and 3.
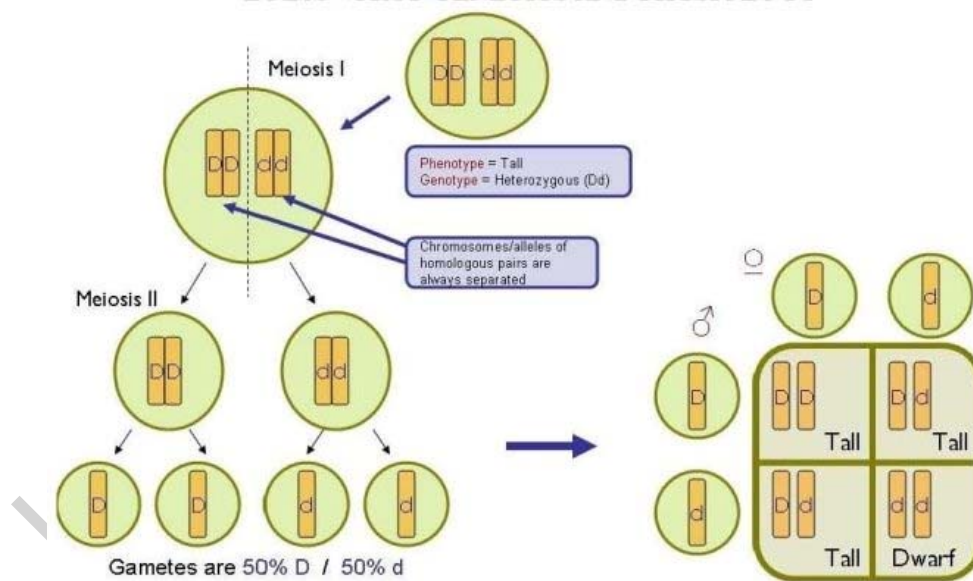

Figure 1. Meiosis I ensures segregation of alleles on homologous chromosomes into separate cells. The second division merely distributes one copy of the allele into each gamete. In this example, a carrier of a recessive dwarf gene will produce offspring with a phenotypic ratio of 3 tall : 1 dwarf.
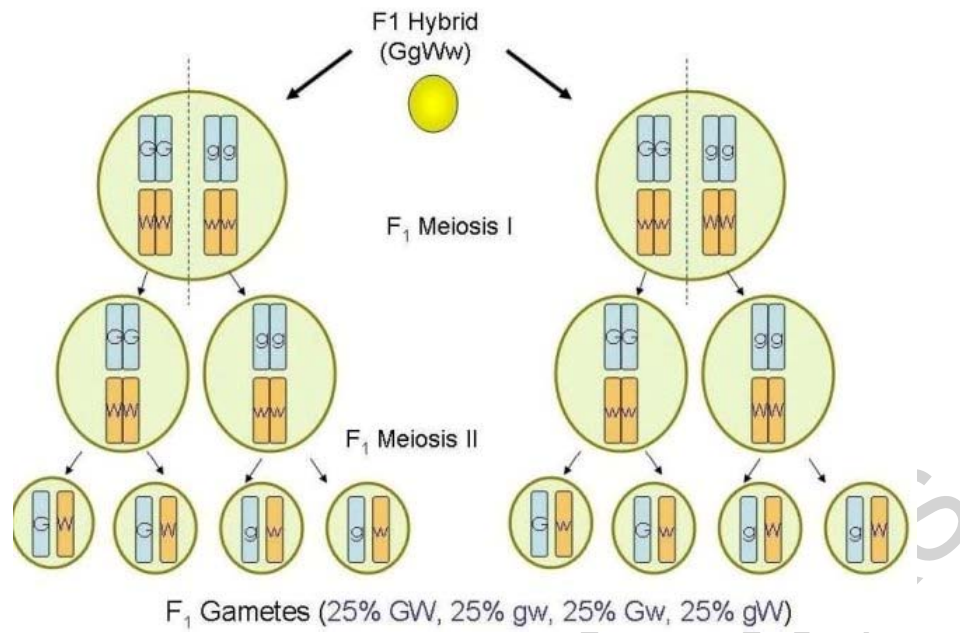
Figure 2. In an experiment crossing yellow and round peas with green and wrinkled peas, Mendel demonstrated independent assortment of alleles at different loci. Because of the random possible arrangements of chromosomes during meiosis, there is an equal chance of forming gametes with the four possible allelic combinations.
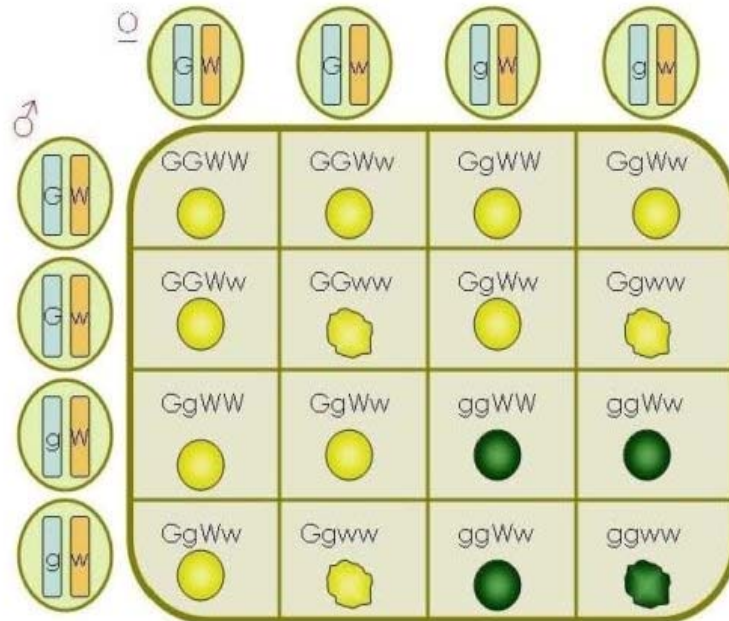
Genotypic Ratio → 1/16GGWW : 1/8GGWw : 1/8GgWw: 1/8Ggww : 1/8ggWw: 1/4 GgWw : 1/16 ggWW : 1/16ggww

Phenotypic Ratio → 9 : 3 : 3 : 1

Figure 3. Upon self-pollination, random fertilization will result in equal proportions of all 16 possible allelic combinations. The phenotypic ratio will be 9:3:3:1.

2.1. Quantitative Traits in Plants

Mendelian analysis is only effective on a relatively small number of traits that are caused by single genes. If the major agronomic traits for various crop species were qualitative traits caused by one or two genes, crop research would be a relatively simple affair. However, many of the traits that are of greatest interest to plant researchers are far more complex than single-gene qualitative traits that have an either/or classification (ex: yellow or green seeds). Most agronomic traits are determined by a large number of genes, working concertedly and often in very complex patterns. The final plant phenotype is the result of the many interactions of these genes, each of which has a small effect, and of the environmental influences of the plants. Such traits are called quantitative traits, and the phenotype is expressed as a quantity, such as a yield of 40 metric tons/km^2, rather than an either/or value.

As an example, consider plant height. Genetically, this trait is affected by rapidity of cell division, hormonal responses, mineral utilization efficiencies, rooting depth, and hundreds of other factors, each directed by a set of genes. Environmentally the trait is affected by hydration, sunlight, soil composition, biotic stresses such as pests or disease and other factors. The sum total of the hundreds (or thousands) of genes in a specific plant variety, coupled with the organism's environment, determines the height of the plant. To reflect and analyze these complex interactions, we assign numerical values, such as 48.6 cm, to describe quantitative traits, rather than simple designators such as "short" and "tall."

The principles of segregation are not different for quantitative traits, but the numbers of genes involved are so high that the ratios generated are incalculably complicated. In 1909, Herman Nilsson-Ehle demonstrated that kernel color in wheat was determined by two genes in which the two allelic variants (ex: A or a) either contribute to overall pigment production or do not, as outlined in Figure 4. When heterozygous populations segregate for quantitative traits, the majority exhibit phenotypes close to the average value, because there are more possible gene combinations for these phenotypes.
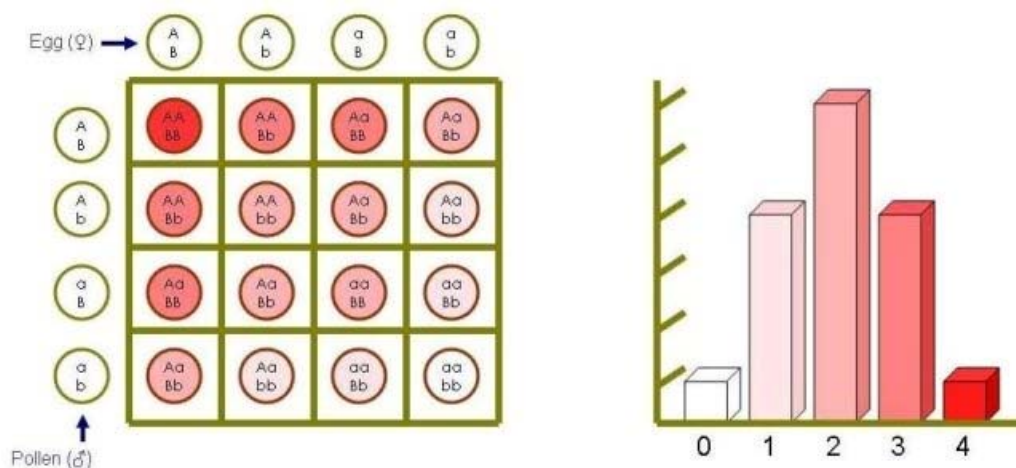

Figure 4. Some quantitative traits are additive. In this example, red kernel color trait is caused by genes A and B. Alleles denoted a or b provide no pigment while alleles A or B do.
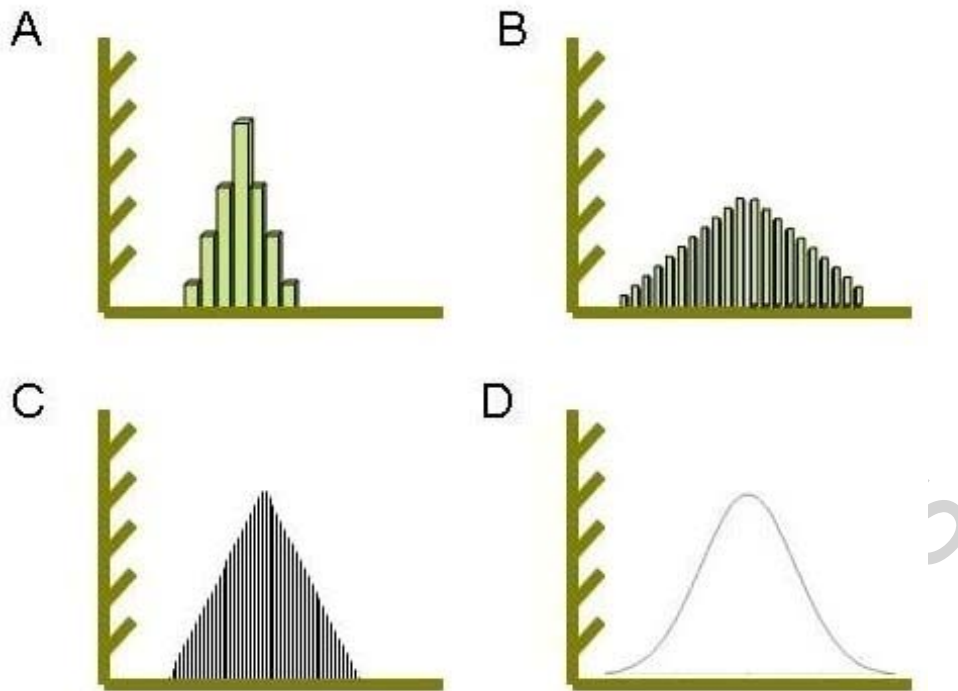
Figure 5. Examples of simple additive traits controlled by (A) three genes, (B) ten genes and (C) 50 genes, assuming equal contribution of alleles at each locus. With many genes, histograms become insufficient to depict the range of phenotypes (Panel D).

Even when multiple genes are involved, inheritance of simple qualitative and additive traits is still conceptually straightforward, particularly if only two alleles are present in the population. However, the complex nature of cellular physiology and the intricacies of the chemical interactions between gene products require that more complicated gene interaction patterns occur for many traits.
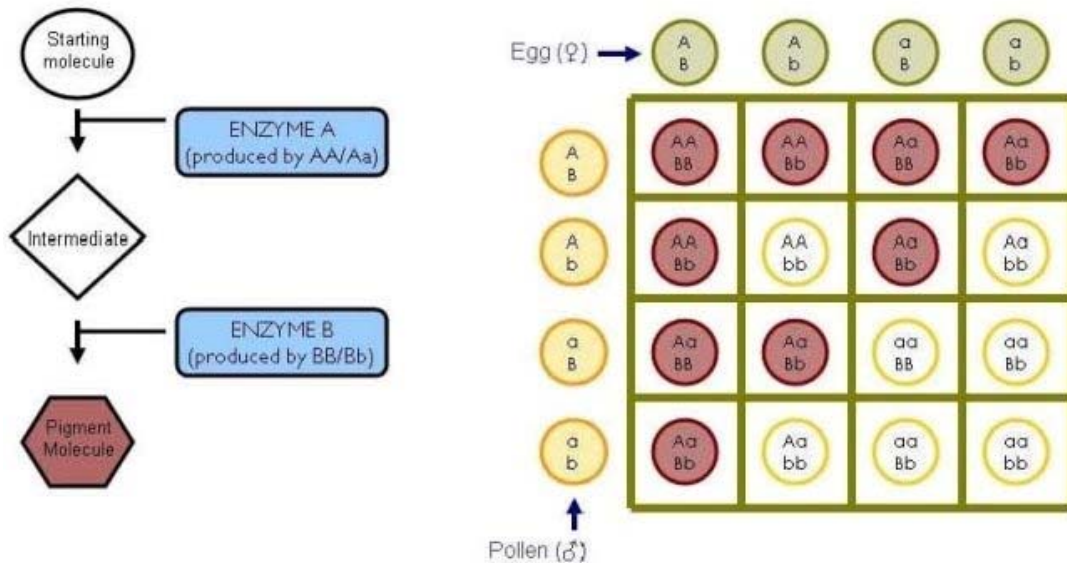

Figure 6. A hypothetical example where red seed color is determined by two gene epistasis. Mutations in the genes for either result in white seed. A heterozygous self-pollinating plant will thus produce offspring in the ratio 9 red : 7 white.

Additivity, co-dominance, incomplete dominance and multiple alleles for the same trait greatly complicate the concept of allelic interaction. Many alleles are also "leaky" and are not always apparent due to aberrant expression or untraceable physiological or environmental occurrences. Epistasis, the interaction of genes such that the genotype of one locus affects the function of another, has a significant effect on inheritance patterns. The simplest form of epistasis, outlined in Figure 6, occurs when two loci are reliant upon each other for expression of a trait.

In this situation, both loci must have functional (usually dominant) alleles present in order for expression to occur. However, many epistatic relationships are possible, including gene action at one locus having an inhibitory effect on another, genes which have the same function, or gene products that compete for a particular substrate.

The converse of epistasis, in which the action of multiple genes affects a single phenotype, is pleiotropy, in which a single gene affects many phenotypes. Any novel allele that affects physiology is likely to have an impact on multiple traits. In plants, genes involved in photosynthesis, resource allocation or nutrient mobilization will have effects on yield, height, biomass, rooting depth, stress tolerance and many other traits. This is very common, and difficult to quantify, in classical crop breeding, because of the level of genetic diversity in the populations being assessed. The diversity in a segregating breeding population often makes it difficult to distinguish between the actions of several genes and a single pleiotropic gene. The statistical association of molecular markers with quantitative traits makes this theoretically possible, although still challenging.

Loci that demonstrate over-dominance are worth special mention. Over-dominance describes a novel phenotype, resulting from heterozygosity at a given locus that provides greater fitness than in either homozygote. This is often related to the concept of heterozygote advantage, hybrid vigor or heterosis and might be a key promoter of out-breeding among populations undergoing natural selection. This is one basis for hybrid cultivar breeding as practiced on cross-pollinating crops. However, it is difficult to quantify whether enhanced characteristics in hybrid progeny are due to over-dominance at individual loci rather than inter-locus interactions in hybrids that are unaffected, at least in expression level, by homozygosity or heterozygosity. Furthermore, crop scientists are most interested in characteristics that are of use under cultivation, which are often in conflict with what natural selection would produce. The role of hybrid vigor is obviously critical in allogamous crops which suffer from inbreeding depression.

2.2. Environmental Effects on Crop Populations

In 1903, shortly after the rediscovery of Mendel's work, Wilhelm Johanssen conducted the first comprehensive study of the effect of environment on phenotype. Working with self-pollinating dry beans, he selected the largest and smallest beans and established pure-breeding subpopulations based on seed size. However, when he selected true-breeding lines from the small and large phenotypic groups, he still observed levels of variation in their offspring. Because these lines were purportedly isogenic, Johanssen concluded that both heritable and environmental effects were impacting the phenotype.

Even in cases of very complex gene interactions between many genes, inheritance ratios could still theoretically be predicted and phenotypes described with discrete values. It is largely the environmental effects on phenotype that cause trait values to become indiscrete. While it is obvious that plants grown in two distinct environments can result in different phenotypes, it is important to emphasize that variation in a quantitative trait, such as plant height, will occur even in plants grown in the same field or greenhouse. Small, often undetectably subtle, differences in the local environment of the plant translate to phenotypic variation.

Consider two plants grown only a meter apart in the same field, and what factors might be different between these two. Perhaps the local topography causes the field to slope slightly, causing water to trickle down toward one plant? Perhaps one plant is on the edge of a plot, and has higher exposure to wind or sun? Perhaps there is a slightly larger concentration of soil-borne minerals near one plant, or a higher concentration of symbiotic microbes? Soil-borne aggregates of nutrients, such as nitrogen hotspots, are not uncommon. Even with the very careful experimental designs employed in crop studies, it is impossible to eliminate all the subtle environmental variations between individual plants. Such differences translate to changes in the plant's physiological regulation, as they alter cellular events to cope with changing conditions.

Crop scientists thus refer to each plant existing in a microenvironment, a term which encompasses the immediate surroundings of the plant, with which it exchanges resources, as well as the plant's internal physiology. For crops, soil is a critical component of microenvironment and one that is difficult to assay without physically disrupting a field experiment.

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Biographical Sketches

Matthew Arterburn is Assistant Professor of Biology at Washburn University, in Topeka, Kansas. He has a B.S. in Biology from George Mason University and a Ph.D. degree in Genetics and Cell Biology from Washington State University. His research focus is on the genetic mechanisms that cause the switch between annual and perennial life cycles in wheat and its relatives. The primary goal of his research is to contribute to the production of perennial wheat for use in sustainable agriculture systems. He teaches courses in Genetics, Cell Biology and Immunology, and contributes to interdisciplinary courses in bioethics and the socially responsible use of genetic research.

Amit Dhingra is Assistant Professor of Horticultural Genomics and Biotechnology at Washington State University, in Pullman. He earned his Ph.D. through the University of Delhi, India, and Rutgers, The State University of New Jersey, supported by a Rockefeller Foundation pre-doctoral fellowship. His post-doctoral training, initiated at Rutgers and completed at the University of Florida, represents a confluence of disciplines within plant biology.

Dr. Dhingra has widely published in top plant science journals in the areas of genomics, plastid transformation, photobiology, and photosynthesis engineering. Some of his work on green-light responses in plants is redefining the established paradigms in photobiology. He has also developed a novel biological and computational method in collaboration with a WSU colleague for targeted re-sequencing that is enabling biologists to conduct genomics research faster at lower cost. Some of his previous work on engineering photosynthesis holds great potential for increasing energy production in plants.