Biochemical Basis of Plant Breeding

Volume I
Carbon Metabolism

Editor

Carlos A. Neyra, Ph.D.

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Carlos A. Neyra, Ph.D.
Associate Professor of Plant Physiology
Biochemistry and Microbiology Department
Rutgers University
New Brunswick, New Jersey

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THE EDITOR

Carlos A. Neyra, Ph.D., is an Associate Professor of Plant Physiology in the George H. Cook College of Agriculture and Environmental Sciences at Rutgers University, New Brunswick, New Jersey. Dr. Neyra received his B.S. degree in Agronomy in 1965 from the Universidad Nacional de Tucuman in Argentina and his Ph.D. degree in Plant Physiology in 1974 at the University of Illinois at Urbana-Champaign.

In addition to being a prolific writer in the fields of Agronomy, Agricultural Biochemistry, and Plant Physiology, Dr. Neyra is widely known internationally for his activities as a Teacher, Researcher, and Scientific Advisor in several countries including Argentina, Brasil, Dominican Republic, Panama, Peru, and the United States.

Dr. Neyra is a tenured member of the Rutgers faculty with full-member status in the following graduate programs: Botany and Plant Physiology; Horticulture; Microbiology; and Soils and Crops. He teaches formally both undergraduate and graduate courses of Plant Physiology and has served in numerous University Committees. He is a reviewer for a number of referred journals including *Plant Physiology, Canadian Journal of Botany, Canadian Journal of Microbiology, Soil Sciences,* and others. He has also collaborated as a peer reviewer for various granting agencies (USDA, NAS, NSF, AID, BARC, BOSTID, etc.). Dr. Neyra was elected full-member of the honorary societies of Sigma Xi and Gamma Sigma Delta in 1974.

CONTRIBUTORS

James T. Bahr, Ph.D.
Research Manager
Rhone-Poulenc, Inc.
Agrochemical Division
Monmouth Junction, New Jersey

Clanton C. Black, Jr., Ph.D.
Research Professor of Biochemistry
Biochemistry Department
Boyd Graduate Studies Research Center
University of Georgia
Athens, Georgia

Charles D. Boyer, Ph.D.
Associate Professor of Plant Breeding and Genetics
Department of Horticulture
Pennsylvania State University
University Park, Pennsylvania

Chee-Kok Chin, Ph.D.
Associate Professor
Department of Horticulture and Forestry
Cook College
Rutgers University
New Brunswick, New Jersey

John J. Gaynor, Ph.D.
Assistant Professor of Plant Molecular Biology
Department of Botany
Rutgers University
Newark, New Jersey

Ravinder Kaur-Sawhney, Ph.D.
Research Associate
Department of Biology
Yale University
New Haven, Connecticut

C. R. Somerville, Ph.D.
Associate Professor
Department of Botany and Plant Pathology
MSU-DOE Plant Research Laboratory
Michigan State University
East Lansing, Michigan

S. C. Somerville, Ph.D.
Assistant Professor
MSU-DOE Plant Research Laboratory
Michigan Plant University
East Lansing, Michigan

Barbara A. Zilinskas, Ph.D.
Associate Professor of Plant Physiology
Department of Biochemistry and Microbiology
New Jersey Agricultural Experiment Station
Cook College
Rutgers University
New Brunswick, New Jersey

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Part I
Introductory Chapters

Chapter 1

PLANT BREEDING: BIOCHEMISTRY AND CROP PRODUCTIVITY

Carlos A. Neyra

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I. INTRODUCTION

One of the major challenges for scientists, at present, is to help increase effectively world food production to meet the ever increasing demands of a rapidly expanding population. A projection of current statistical figures indicates that world population will reach 8 billion by the first decade of the 21st century.[1] By that time, food supply will still be dependent, for the most part, on agricultural farming, but the efficiency of utilization of cultivated land will have to be greatly improved by the adoption of better farming practices and the development of new genotypes capable of achieving higher yields than those currently under cultivation.

The significant growth of agricultural productivity over the past few decades can be attributed in large part to the application of modern concepts of genetics to the breeding of superior crops. Most of the gains have come from the exploitation of the genetic diversity present in species that have long been domesticated but so far, all genotypes available for farming have been developed by conventional methods based on phenotypic characters associated with crop yields. To some extent, the goal of increasing crop productivity and the rate of achievements depends on our ability to understand and manipulate the biochemical and genetic mechanisms controlling plant productivity. Several biochemical criteria have been proposed for the selection of superior cultivars and have been under evaluation for almost 25 years. Yet, they are still to be implemented into a successful plant breeding program of economic importance.

This book presents a comprehensive survey of progress and current knowledge of those biochemical processes with greater potential for the development of superior cultivars: photosynthesis, photorespiration, nitrate assimilation, biological nitrogen fixation, and starch and protein synthesis. Each chapter addresses the major features of the physiological processes involved: the indentification of rate-limiting steps; regulatory properties of key enzymes; and a discussion of alternatives to overcome the limitations for enhanced crop productivity.

The contents of this book are presented in two volumes: Carbon Nutrition (Volume I) and Nitrogen Nutrition (Volume II). Throughout the contents, we have attempted to provide sufficient background information and discussion of biochemical tools to strengthen the approach and goals of plant breeding programs. Special attention was given to analyze the possibility of using genetic engineering methods for raising the genetic yield potential of crops. Modern plant breeding, in the context of this book, is seen as a combination of both the conventional or traditional plant breeding approach with the more novel molecular and cellularly based genetic engineering methodologies.

Because of the vast knowledge needed to make an in-depth presentation of the subjects under consideration, I chose to invite some of the best regarded scientists to contribute with their expertise to this book. As the editor, I was also responsible for the selection of the topics to be included. Within broad editorial guidelines, the contributors have been responsible for the precise content and approach of their chapters. A list of contributors and their institutional affiliations has been included for anyone willing to make further contacts and expand on the topics covered under this book.

II. PLANT BREEDING AND CROP PRODUCTIVITY

A. Food Crops and Partitioning of Assimilates

The welfare of mankind largely depends upon plants as a source of food and fiber. Of all plants known to have economical value (about 1500 species), only a few (around 30 species) have been developed as food crops.[1-3] One half of those species (eight cereals and seven legumes) is known as grain crops (pulses in the case of legumes), and these provide most of the calories and protein for human nutrition. In fact, 50% of those requirements is met by only three cereal crops: wheat, rice, and corn. Among the pulses, soybeans (*Glycine max*) and drybeans (*Phaseolus vulgaris*) are the most important food crops. Potatoes (*Solanum tuberosum*) and cassava (*Manihot esculenta*) are the most important among the crops harvested for their underground parts.[4] All of the crops cited above have been developed because of their capability to mobilize and accumulate in defined structures of the plant a large proportion of their biosynthetic production. Thus, the increase of the genetic yield potential, within a given crop species, has usually been accompanied by an increase in harvest index (dry matter accumulated in storage organs/total dry matter produced by the plant).[1,5-9]

The partitioning of assimilates among various plant parts is of major importance for agricultural productivity. We also know that an important variation exists in the relative allocation of dry matter to different organs. Crops grown for their vegetative aerial portion tend to reinvest more into the development of new leaves. Grain crops, on the other hand, tend to allocate more assimilates into the production of reproductive structures, and other crops (potato, cassava, etc.) invest relatively more into the underground plant parts. However, we know relatively very little about the physiological and biochemical mechanisms controlling a defined pattern of assimilate partitioning. Research in these areas should help provide the knowledge needed to devise modern plant breeding strategies. Further understanding of the specific nature of assimilate partitioning may lead to further manipulation of harvest indexes and maximization of reproductive yields in grain crops and vegetative yields in forage and root crops.

In principle, assimilate partitioning is based upon the relative strength of source and sink structures. Source tissues are those capable of exporting assimilates. Sinks, on the other hand, are represented by structures that exhibit a net import of assimilates, and their activity will be dependent upon size, position in relation to the source, geometry, physiological stage, and competition among different sinks.[5,9] All actively growing, storing, or metabolizing tissues may be considered as strong sinks. Mobilization of assimilates from source to sink occurs primarily via phloem.[9,10] Sucrose (and, to a lesser extent, amino acids) is universally recognized as the main form of carbon transported. Organic nitrogen, on the other hand, is primarily transported in the form of amino acids.[9,10] The interrelationships between primary carbon assimilation, and sucrose and starch metabolism are schematically presented in Figure 1 and will be discussed in more detail in Chapters 6 and 8 (Volume I). The interrelationships between the primary assimilation of inorganic nitrogen, temporary storage of organic nitrogen in vegetative structures, and the remobilization and transport of organic nitrogen to the seeds are also shown in Figure 1. For further details, see Chapters 4 and 5 (Volume II) and also Pate,[10] Below et al.,[11] Miflin and Lea,[12] and Reed et al.[13]

B. Wheat, Rice, and Corn Breeding

Plant breeders have been successful in developing cultivars that allocate a larger proportion of their assimilates to the harvestable organ without increasing the total biomass production (dry matter/ha), and this suggested that a genetic basis for partitioning exists.[1,5,9] In wheat and rice, the release of semi-dwarf varieties with an improved plant architecture led to higher harvest indexes with a larger fraction of the assimilates being partitioned into the grains.[1] The development of semi-dwarf varieties of wheat and rice, by incorporation of dwarfing genes through conventional breeding practices, marked the beginning of a new era in agriculture: the green revolution of the 1960s and 1970s, but required, in addition to the new varieties, the development of "technological packages" that included an increased use of fertilizers, irrigation, and chemical pesticides to allow maximum yield potentials to be expressed.

Another significant contribution made to agriculture by conventional breeding was the commercial introduction of the first corn hybrids in the U.S. about 40 years ago.[1]

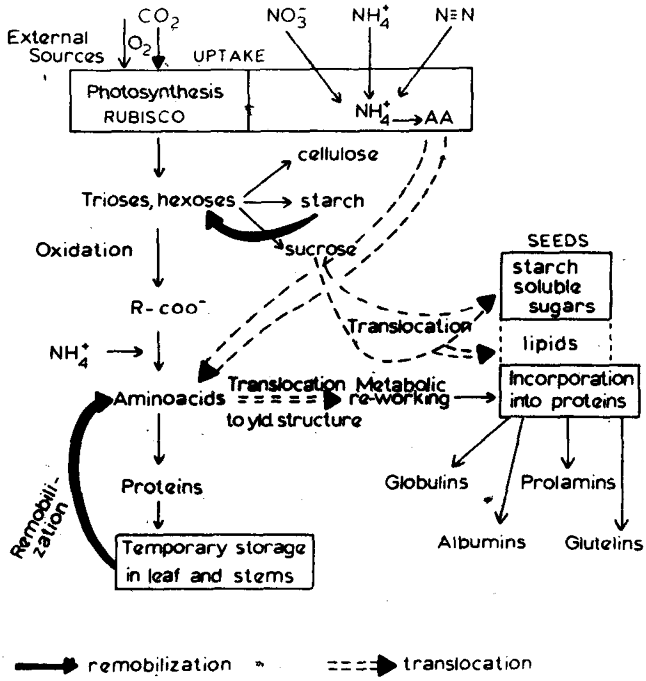

FIGURE 1. Schematic illustration of the conversion of inorganic carbon and nitrogen into plant organic constituents. This scheme also illustrates the remobilization of carbon and nitrogen from vegetative to reproductive structures. Box on the top left represents a chloroplast where CO_2 fixation takes place with the participation of ribulose bisphosphate carboxylase. Box on the top right represents a chloroplast or a nodule for the assimilation of nitrate (NO_3^-), or atmospheric nitrogen (N_2) into amino acids, respectively.

Since then, many improved elite hybrids with continuously higher yields, disease and insect resistance, and shorter and stronger stalks suitable for mechanical harvesting have been developed. In spite of the fact that hybrid corn has been predominantly cropped in the last 25 to 30 years in the U.S., a marked increase in yields was further associated with the use of progressively (year after year) larger quantities of fertilizer N.[6,14]

The development of semi-dwarf wheat and rice genotypes together with the advent of corn hybrids is a clear example of successful plant breeding aimed at increasing crop productivity. Nonetheless, it should be pointed out that yield increases in all of those three cases were highly dependent on the availability and responsiveness to fertilizer nitrogen.[14] It is not surprising then that 50% of the total fertilizer nitrogen used in agriculture goes to cereal production.[15] However, economic considerations and protection of environmental quality would eventually limit the amounts of fertilizer nitrogen to be used in farming. The ever increasing prices of fertilizer nitrogen and the need of fossil fuels for its manufacture make it desirable to find alternative ways to lessen the dependence on high nitrogen inputs for obtaining maximal yields.[15] Genotypic differences in nitrogen utilization have been demonstrated, indicating that there is potential for developing superior, nitrogen-efficient genotypes.[16-20] Later, in Volume II (Chapter 4), a method will be discussed that uses dry matter and total N measurements to describe some of the traits which may indicate the effectiveness with which nitrogen assimilation processes contribute to dry matter or grain production and how these methods could help facilitate genetic selection of specific genotypes with improved efficiency for the utilization of available nitrogen.

C. Grain Legumes

Grain legumes represent some of the earliest agricultural crops cultivated for direct consumption of their seeds but currently they amount to only 10% of the total world production of cereal grains.[15] Even though legumes and cereals complement each other nutritionally and agriculturally in terms of cropping patterns, their progress has not run in parallel in recent years with cereal production increasing at a much faster rate than that of legumes.[14,15] The increased use of fertilizer N, together with the development of genotypes highly responsive to added N, is given as the main reason for the steady increase in cereal grain yields over the last 25 to 30 years.[14,15] Obviously, grain legumes have not been selected for their responsiveness to fertilizer N and many attempts to supplement nitrogen fixation with fertilizer N have not succeeded in increasing yields.[14,15,21,22,23] Nevertheless, there are reports indicating that grain legumes may still benefit from adequate timing and quantity of fertilizer N applied[24,25] and that the lack of appropriate agronomical practices to use fertilizer N in legumes may have prevented its use on a larger scale.

Geneticists and plant breeders have been effective in the use of existing genetic variability for the improvement of crop yields, but symbiosis and N_2-fixation characteristics have rarely been considered in plant breeding programs. The potential capability of legumes for nitrogen self-sufficiency should be pursued to its maximum, but yields have to be enhanced or at least maintained. Increasing N input for increasing grain legume yields will place a larger demand on photosynthate to satisfy the energy required for the reduction of nitrate (NO_3^- assimilation) or atmospheric nitrogen (N_2-fixation). Thus, legume breeding programs should consider the increase of photosynthetic productivity simultaneously with the enhancement of N incorporation by these crops. For more detailed discussions on these topics, please refer to Chapters 2 and 6 (Volume II).

D. Root and Tuber Crops

On a world-wide basis, roots and tubers represent nearly half the volume of all horticultural crops and over 30% of the staple grains.[26] Potatoes are grown mainly in cool climates (highland tropics or northern and southern latitude temperate climates) and are considered the world's fourth most important food crop after rice, wheat, and corn.[27] Cassava, on the other hand, is a basic staple in the tropics and the leading horticultural crop in the developing world.[26,28] Cassava is regarded as one of the most efficient crops under water and nutrient stress conditions. Under optimum conditions, yields of over 80 tons of fresh roots per hectare per year (equivalent to $\sim$30 tons of dry matter) have been reported.[28] Under nutrient or water stress conditions, yields could be significantly reduced to 9 or 10 tons of fresh roots per hectare per year but still outyields most crops under such limiting conditions. The yield potential of cassava under stress conditions is a consequence of several physiological adaptive features of the plant. Cassava has a remarkably high harvest index of about 0.6 to 0.8 (ratio of root weight to total biomass production) even under the influence of stress factors. In fact, under nutrient or water stress conditions, cassava increases the relative allocation of dry matter to the roots.[28] Furthermore, during drought stress, cassava follows a conservative pattern of water use by reducing stomatal aperture and decreasing the formation of new leaves. Stomatal closure is quite sensitive to vapor pressure differences and they may respond even before bulk leaf water potential is affected.[29,30] Photosynthetic activity can be recovered immediately after rehydration. All of those adaptive characteristics, and their tolerance to acid-infertile soils with relatively high aluminum allow the use of cassava on the marginal lands of the tropics and subtropics to help increase total agricultural production.[28]

Currently cultivated cassava and potato cultivars have been developed from a rather narrow genetic base. Both of these crops originated in America but were broadly dispersed throughout the world. Large, untapped genetic resources still exist in the centers of origin but their potential value is, for the most part, unknown; however, they could serve as the basic genetic resources for wider climatic flexibility with higher yields and better resistance to pests and disease.[27] With the organization of the International Research Centers having specific mandates, it has been possible to broaden the genetic base of both potatoes and cassava. A world potato collection is being organized and maintained by the International Potato Center (CIP), headquartered at LaMolina, Lima, Peru. The size of the collection now stands at 5000 accessions of primitive cultivars and 1291 accessions of wild tuber-bearing species. On the other hand, the International Center of Tropical Agriculture (CIAT) has developed a germplasm bank for cassava containing about 2600 accessions obtained from 13 Latin American and 2 Asian countries.

Innovative in vitro methods have been integrated to breeding programs for the conservation and exchange of potato and cassava germplasm.[31,32] Because of their high genetic stability and disease-free conditions, meristem and shoot tip cultures have become increasingly important as a means of propagation, conservation, and germplasm exchange. The in vitro system has been well accepted by several countries as a means to improve the phytosanitary aspects of germplasm exchange.[31,32] Meristems, isolated cells, and protoplast cultures have all been shown to regenerate normal plantlets and may add a new dimension to the breeding efforts in root and tuber crops. For further information on these topics, please refer to Chapters 2 and 3 of this book (Volume I).

III. PLANT BIOCHEMISTRY AND BREEDING RESEARCH

A. An Overview

Man has come a long way since we learned, about 10,000 years ago, how to cultivate plants. Until late in the 19th century, however, crop improvement was in the hands of farmers who selected the seed from preferred plant types or populations for subsequent sowing.[1,2,33] Genetics, on the other hand, was only known as a science at the start of the 20th century, after the laws of heredity proposed by Gregor Mendel were finally accepted.[1,34] Since genetics is basic to rational plant breeding, we should consider the practice of controlled breeding a rather new happening. Even though plant breeding is considered both an art and a science,[2,7] it should be remembered that breeding is central to the problem of enhancing crop productivity and must be scientifically based.[7] At least two scientific disciplines, genetics and biochemistry, are expected to provide the supporting basis to plant breeding research for the development of improved cultivars.

In the process of cultivar selection, traditional breeders have generally made use of phenotypic characters in their search for higher yielding varieties.[2,7] However, one would expect that in this process of selection, biochemical and physiological modifications have taken place. With the advent of new biochemical methods, plant physiologists and biochemists have been able to elucidate and interpret a large number of biochemical reactions associated with plant function, rate-limiting steps in pathways, and regulatory properties of the enzymes involved.

The detailed description of biochemical pathways and regulatory mechanisms of key enzymes in microorganisms have greatly contributed to the development of highly efficient and profitable industrial processes.[35-37] Advanced research into the biochemistry and genetics of the microorganisms involved has been the key to the success of industrial microbiology. On the other hand, the use of biochemical criteria for the development of superior plant genotypes is not a new idea,[38,39] but these genotypes have not been used directly, in any successful plant breeding program of economical importance, including the genotypes developed during the "green revolution" years of the 1960s and 1970s. Nonetheless, substantial progress has been made in the last two decades towards our understanding of plant biochemical reactions, most noticeably in the fields of carbon and nitrogen metabolism. The current knowledge on these two fields and its applicability to future plant breeding programs will be dealt with in more detail throughout this book.

Plants are largely dependent on solar energy, carbon, and nitrogen for maximal productivity. The production of dry matter on earth is estimated to be around 200 billion metric tons per year. This would require the reduction, using part of the solar energy fixed, of 70 billion and 0.2 billion tons of carbon and nitrogen, respectively. Since carbon is obtained from a highly oxidized atmosphere (20% O_2) and the concentration of CO_2 is relatively low (0.03%), the interactions between photosynthesis and photorespiration are of major concern for the purpose of maximizing yields (see Chapter 7, Volume I) in addition to the relationships between rates, duration of photosynthesis, and yield output.[40] Solar radiation, on the other hand, is the primary source of energy for the assimilation of both carbon and nitrogen,[41] but the efficiency of conversion of light energy into plant products is still very low. Since energy is lost in diverse ways between the arrival of sunlight at canopy level and the reduction of CO_2 to carbohydrate in the leaf,[40] more must be learned about the efficiency of light energy capture and conversion to make a fuller use of the energy available for crops. The potential for improvement of crop yields through changes in the efficiency and/or capacity of the light-dependent photosynthetic reactions is discussed in Chapter 4 (Volume I).

On a global scale, it has been estimated that biological nitrogen fixation contributes about 100×10^6 tons of nitrogen fixed per annum in agricultural soils.[15,27,30] Chemically produced fertilizer N contributes an additional 50×10^6 tons of nitrogen to agriculture.[15] These figures speak for themselves about the importance of both nitrogen sources (biologically and chemically fixed) for plant growth and agricultural productivity. Nonetheless, the efficiency of utilization of those N sources will depend upon the rate and duration of N uptake (either from soil or atmospheric sources), translocation, transient accumulation in vegetative organs, redistribution and accumulation of N in harvestable organs, sink size for N, etc. A broader discussion on all of these parameters will be found in Volume II of this book which is devoted entirely to nitrogen nutrition.

B. Gene Mutations and Cellular Approaches to Breeding

The primary goal of selection in plant breeding is the identification of desirable genotypes and effective selection is dependent upon the existence of genetic variability.[42] The extent of genetic variability in a specific breeding population depends on the germplasm included in it and its selection history. When genetic variability in a breeding program is insufficient to permit attainment of a specific goal, it will be necessary to increase the variability by using either mutagenic treatments or introduction of new germplasm.[42]

Gene mutation provides the basic material for natural selection.[2,34,43] The use of strains carrying a mutant gene can be useful probes in physiological investigations (see Chapters 4, 7, and 8, Volume I), or the mutation may carry a desirable characteristic that may be important to perpetuate.[39,44] The identification of specific mutants of agronomically important genes and regulation of their expression is also important to expand our understanding of plant molecular biology as the basis for future applications to the development of new genotypes by genetic engineering.[39,44,45] Gene mutation may be assumed to have proceeded at a more or less steady rate, age after age, throughout evolution.[2] The frequency of occurrence of spontaneous mutants is, however, very low, and special screening procedures should be adopted for their identification.[46] Alternatively, specific mutations may be induced by a number of chemical and physical treatments.[47] The latter have been very useful and extensively applied to microbial biochemistry research, but induction of stable mutations in higher plants presents a number of practical and methodological problems. However, the recent advances in plant cell and tissue culture techniques have set the stage for genetic manipulations of higher plant cells in much the same manner as microbial populations.[39,47] As plant cells are totipotent, for some species one could obtain adult plants from callus tissue; from this emerges the outline of new systems for investigating plant genetics and breeding for the development of superior plant genotypes. First, individual cells can be isolated from plant tissues and grown in a defined culture media. A large population of cells may then be available in a matter of days or weeks, depending on the type of tissue used as a source material and the plant of origin. Second, in such cell cultures, the rate of mutation may be increased, making possible the needed genetic variability and diversity of phenotypes from which to select. Third, foreign genetic material may be introduced directly into plant cells by following DNA-manipulation procedures.

A major limitation of phenotypic selection in vitro is that it may identify modifications of traits that are expressed at the cellular level only. The developmental complexity of higher plants imposes a severe limitation on the number of possible applications of the new methodologies based on cell or tissue culture techniques. Many traits of agronomic importance are the products of the organization of highly differentiated cells and, therefore, they may not appear in culture.[37,45,48] All of these limitations, however, may be resolved with the progress of research, and we have a better understanding and ability to manipulate the molecular and biochemical principles controlling correlative functions in differentiated organisms. The techniques available for the culture of cells and plantlets in vitro will certainly improve rapidly in the next few years and the use of in vitro selections applicable to the improvement of crop plants may be a reality sooner than expected (see Chapters 2 and 3, Volume I). Modern plant breeding may then be seen as a combination of both the conventional or traditional plant breeding approach with the more novel, molecular and cellularly based genetic engineering methodologies. Integration of these two approaches will certainly benefit science and agricultural productivity. This new era of research must rely strongly on the progress made in plant biochemistry research and its extension to modern plant breeding and the goal of improving the genetic potential of crops.

C. Protein Quantity and Quality

The explosive yield increases of cereal grains in recent decades are the best indicator of how successfully genetic resources can be exploited.[49] Because the percent protein content of grains has remained virtually unchanged over the last 30 years,[14] we could deduce that the total quantity of crude protein per unit of land has increased in proportion to the increase in grain yields. Quantitatively, it is estimated that cereal grains provide about 50% of the world protein needs; grain legumes and animal products, 20 and 30%, respectively.[50]

Grain protein concentration can be influenced by heredity as well as cultural conditions.[14,49,51] Genetic constitution is, however, the most important single factor affecting protein levels in grains.[51] There is ample evidence showing that substantial genetic variation exists for grain protein concentration.[49,51] Even though it would be highly desirable to increase the protein concentration in cereal grains, yields and desirable commercial characteristics should be maintained. Frey[52] reported that in various cereal species the protein concentration and grain yields are negatively correlated, with some exceptions.[53] Also, Lambert et al.[54] found that opaque-2 corn hybrids had higher pro-