专业外语第二部分

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Chapter 11 Cellular Organization

According to the Cell Theory, all living things are composed of one or more cells. Cells fall into prokaryotic and eukaryotic types. Prokaryotic cells are smaller (as a general rule) and lack much of the internal compartmentalization and complexity of eukaryotic cells. No matter which type of cell we are considering, all cells have certain features in common: cell membrane, DNA, cytoplasm, and ribosomes.

11.1 Cell Size and Shape

The shapes of cells are quite varied with some, such as neurons, being longer than they are wide and others, such as parenchyma (a common type of plant cell) and erythrocytes (red blood cells) being equidimensional. Some cells are encased in a rigid wall, which constrains their shape, while others have a flexible cell membrane (and no rigid cell wall).

The size of cells is also related to their functions. Eggs (or to use the latin word, *ova*) are very large, often being the largest cells an organism produces. The large size of many eggs is related to the process of development that occurs after the egg is fertilized, when the contents of the egg (now termed a zygote) are used in a rapid series of cellular divisions, each requiring tremendous amounts of energy that is available in the zygote cells. Later in life the energy must be acquired, but at first a sort of inheritance/trust fund of energy is used.

11.2 The Cell Membrane

The cell membrane functions as a semi-permeable barrier, allowing a very few molecules across it while fencing the majority of organically produced chemicals inside the cell. Electron microscopic examinations of cell membranes have led to the development of the lipid bilayer model (also referred to as the fluid-mosaic model). The most common molecule in the model is the phospholipid, which has a polar (hydrophilic) head and two nonpolar (hydrophobic) tails. These phospholipids are aligned tail to tail so the nonpolar areas form a hydrophobic region between the hydrophilic heads on the inner and outer surfaces of the membrane. This layering is termed a bilayer since an electron microscopic technique known as freeze-fracturing is able to split the bilayer.

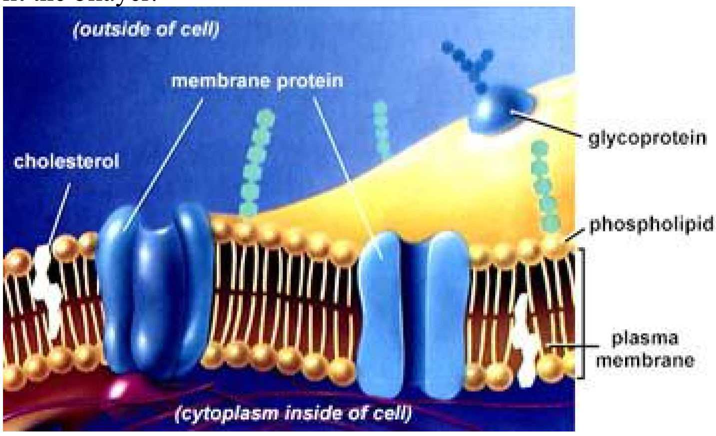


Diagram representing the cell membrane. The above image is from http://www.biosci.uga.edu/almanac/bio_103/notes/may_15.html.

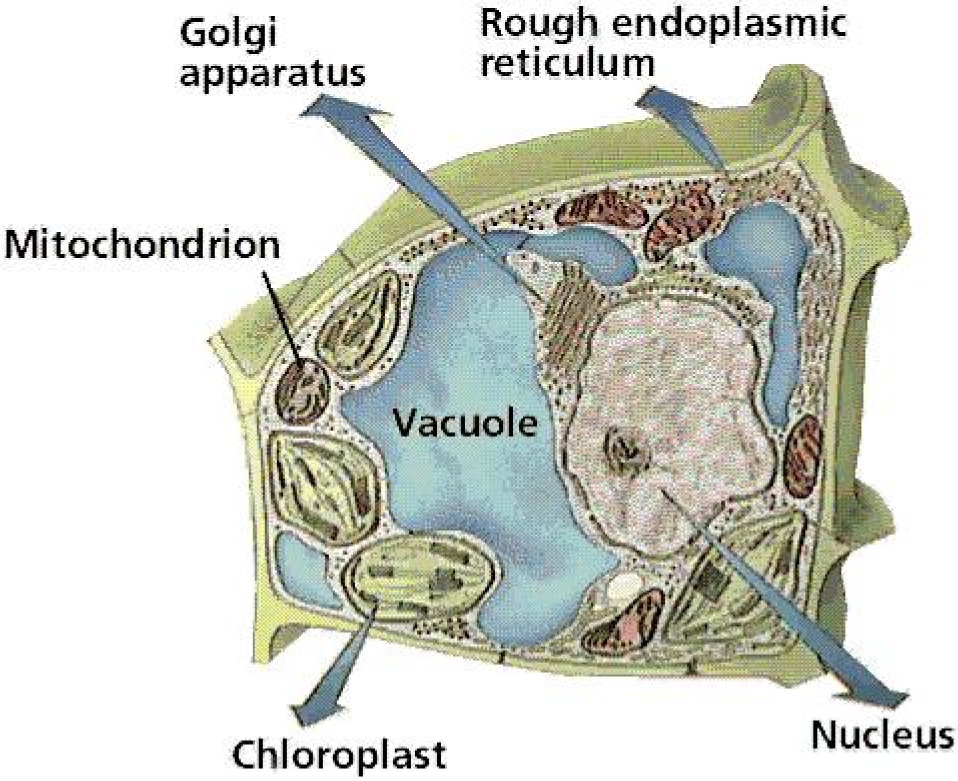
Cholesterol is another important component of cell membranes embedded in the hydrophobic areas of the inner (tail-tail) region. Most bacterial cell membranes do not contain cholesterol.

Proteins are suspended in the inner layer, although the more hydrophilic areas of these proteins "stick out" into the cells interior and outside of the cell. These proteins function as gateways that will, in exchange for a price, allow certain molecules to cross into and out of the cell. These integral proteins are sometimes known as gateway proteins. The outer surface of the membrane will tend to be rich in glycolipids, which have their hydrophobic tails embedded in the hydrophobic region of the membrane and their heads exposed outside the cell. These, along with carbohydrates attached to the integral proteins, are thought to function in the recognition of self.

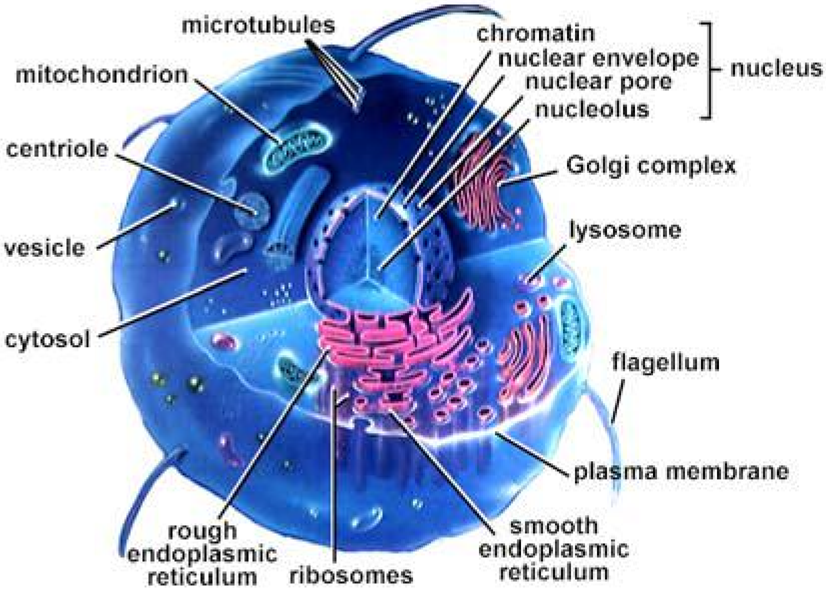
The contents (both chemical and organelles)of the cell are termed protoplasm, and are further subdivided into cytoplasm (all of the protoplasm except the contents of the nucleus) and nucleoplasm (all of the material, plasma and DNA etc. within the nucleus).

11.3 The Cell Wall

Not all living things have cell walls, most notably animals and many of the more animal-like Protistans. Bacteria have cell walls containing peptidoglycan. Plant cells have a variety of chemicals incorporated in their cell walls. Cellulose is the most common chemical in the plant primary cell wall. Some plant cells also have lignin and other chemicals embedded in their secondary walls. The cell wall is located outside the plasma membrane. Plasmodesmata are connections through which cells communicate chemically with each other through their thick walls. Fungi and many protists have cell walls although they do not contain cellulose, rather a variety of chemicals (chitin for fungi).



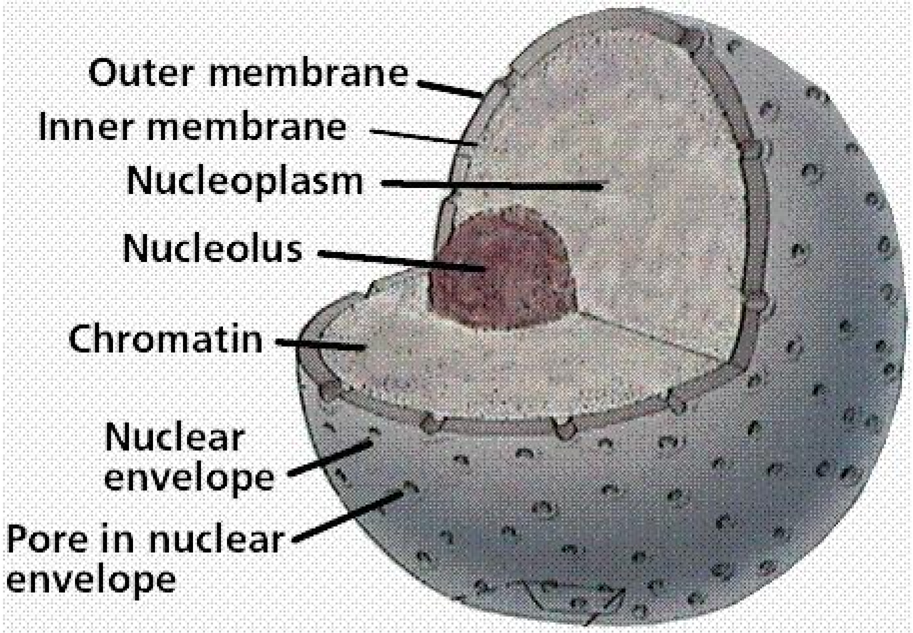
Structure of a typical plant cell. Image from Purves et al., Life: The Science of Biology, 4th Edition, by Sinauer Associates (www.sinauer.com) and WH Freeman (www.whfreeman.com), used with permission.



Structure of an animal cell. The above image is from http://www.biosci.uga.edu/almanac/bio_103/notes/may_15.html.

11.4 The nucleus

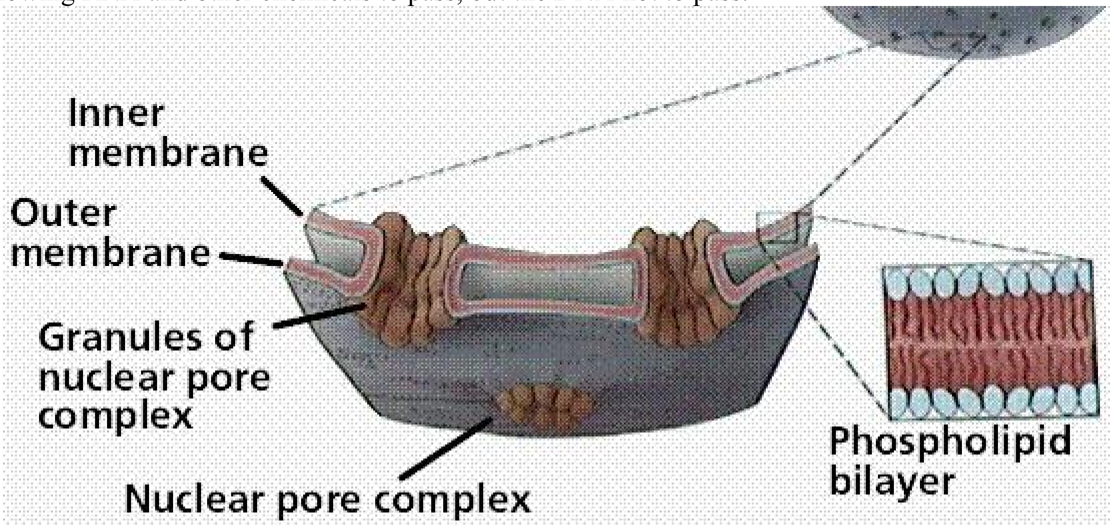
The nucleus occurs only in eukaryotic cells, and is the location of the majority of different types of nucleic acids. Van Hammerling's experiment (click here for a diagram) showed the role of the nucleus in controlling the shape and features of the cell. Deoxyribonucleic acid, DNA, is the physical carrier of inheritance and with the exception of plastid DNA (cpDNA and mDNA, see below) all DNA is restricted to the nucleus. Ribonucleic acid, RNA, is formed in the nucleus by coding off of the DNA bases. RNA moves out into the cytoplasm. The nucleolus is an area of the nucleus (usually 2 nucleoli per nucleus) where ribosomes are constructed.



Structure of the nucleus. Note the chromatin, uncoiled DNA that occupies the space within the nuclear envelope. Image from Purves et al., Life: The Science of Biology, 4th Edition, by

Sinauer Associates (www.sinauer.com) and WH Freeman (www.whfreeman.com), used with permission.

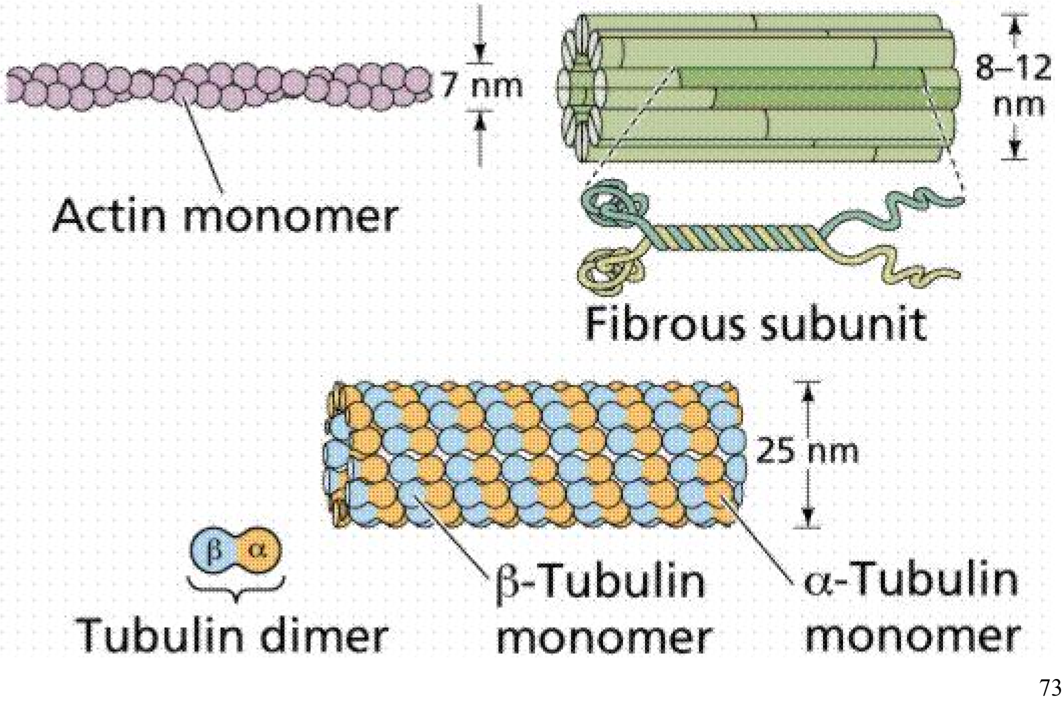
The nuclear envelope is a double-membrane structure. Numerous pores occur in the envelope, allowing RNA and other chemicals to pass, but the DNA not to pass.



Structure of the nuclear envelope and nuclear pores. Image from Purves et al., Life: The Science of Biology, 4th Edition, by Sinauer Associates (www.sinauer.com) and WH Freeman (www.whfreeman.com), used with permission.

11.5 Cytoplasm

The cytoplasm was defined earlier as the material between the plasma membrane (cell membrane) and the nuclear envelope. Fibrous proteins that occur in the cytoplasm, referred to as the cytoskeleton maintain the shape of the cell as well as anchoring organelles, moving the cell and controlling internal movement of structures. Microtubules function in cell division and serve as a "temporary scaffolding" for other organelles. Actin filaments are thin threads that function in cell division and cell motility. Intermediate filaments are between the size of the microtubules and the actin filaments.



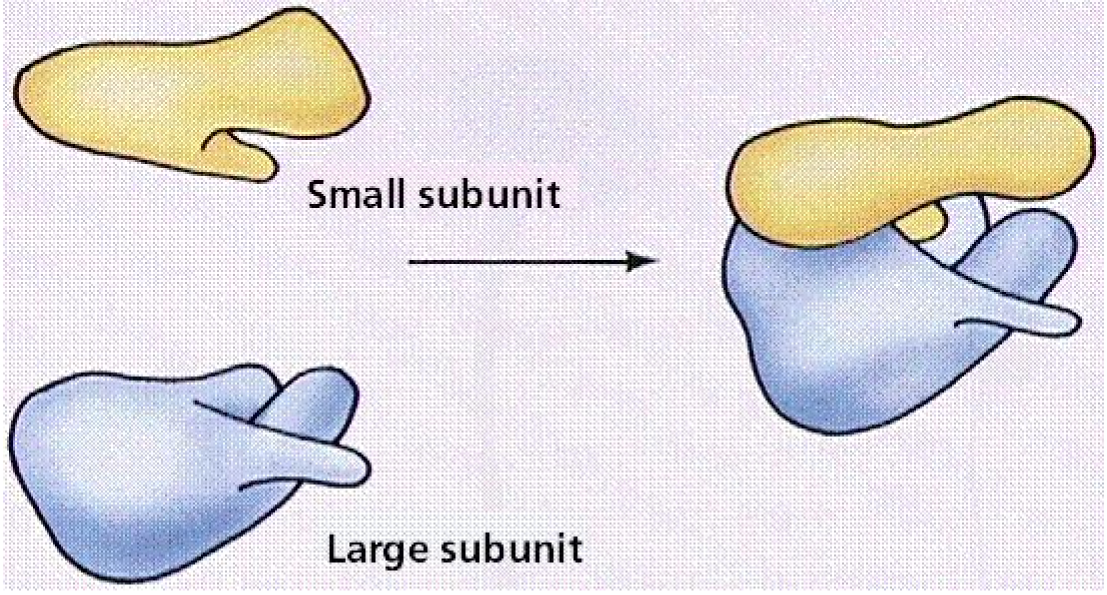
Actin and tubulin components of the cytoskeleton. Image from Purves et al., Life: The Science of Biology, 4th Edition, by Sinauer Associates (www.sinauer.com) and WH Freeman (www.whfreeman.com), used with permission.

11.6 Vacuoles and vesicles

Vacuoles are single-membrane organelles that are essentially part of the outside that is located within the cell. The single membrane is known in plant cells as a tonoplast. Many organisms will use vacuoles as storage areas. Vesicles; are much smaller than vacuoles and function in transport within and to the outside of the cell.

11.7 Ribosomes

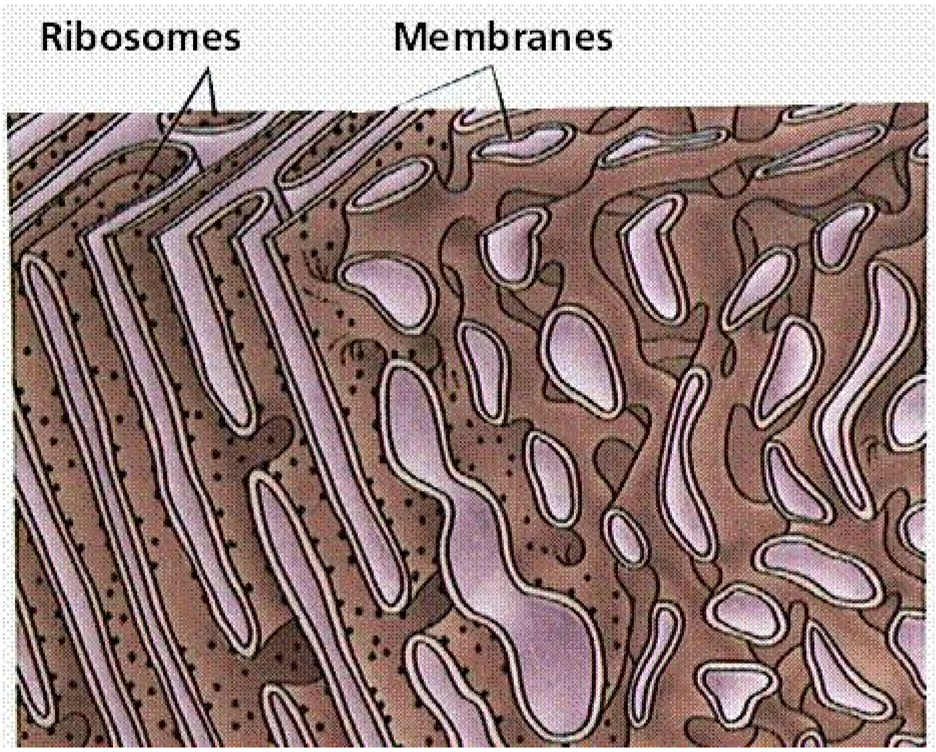
Ribosomes are the sites of protein synthesis. They are not membrane-bound and thus occur in both prokaryotes and eukaryotes. Eukaryotic ribosomes are slightly larger than prokaryotic ones. Structurally the ribosome consists of a small and larger subunit. Biochemically the ribosome consists of ribosomal RNA (rRNA) and some 50 structural proteins. Often ribosomes cluster on the endoplasmic reticulum, in which case they resemble a series of factories adjoining a railroad line. Click here for Ribosomes (More than you ever wanted to know about ribosomes!)



Structure of the ribosome. Image from Purves et al., Life: The Science of Biology, 4th Edition, by Sinauer Associates (www.sinauer.com) and WH Freeman (www.whfreeman.com), used with permission.

11.8 Endoplasmic reticulum

Endoplasmic reticulum is a mesh of interconnected membranes that serve a function involving protein synthesis and transport. Rough endoplasmic reticulum (Rough ER) is so-named because of its rough appearance due to the numerous ribosomes that occur along the ER. Rough ER connects to the nuclear envelope through which the messenger RNA (mRNA) that is the blueprint for proteins travels to the ribosomes. Smooth ER; lacks the ribosomes characteristic of Rough ER and is thought to be involved in transport and a variety of other functions.



The endoplasmic reticulum. Rough endoplasmic reticulum is on the left, smooth endoplasmic reticulum is on the right. Image from Purves et al., Life: The Science of Biology, 4th Edition, by Sinauer Associates (www.sinauer.com) and WH Freeman (www.whfreeman.com), used with permission.

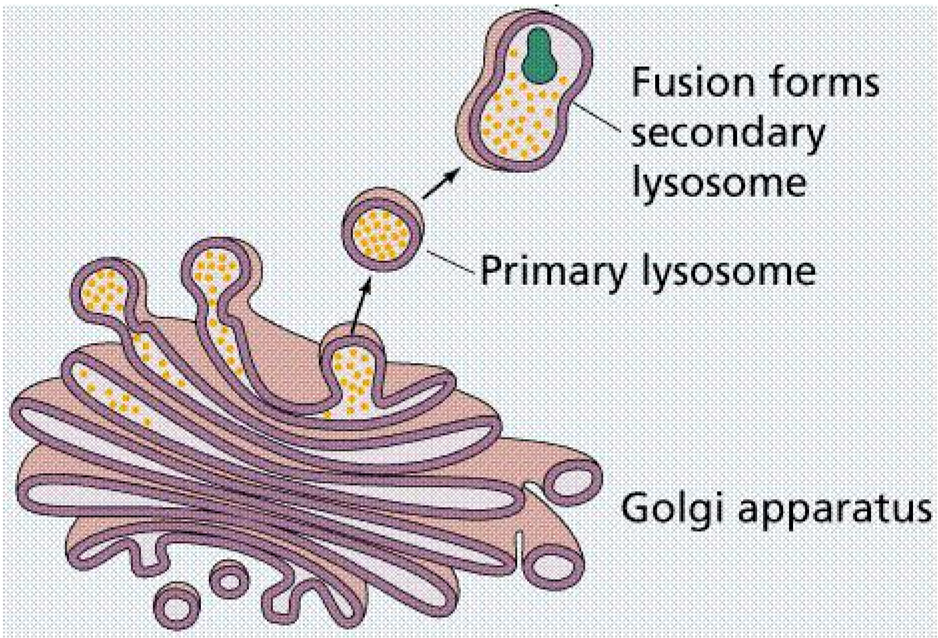
Rough Endoplasmic Reticulum with Ribosomes (TEM x61,560). This image is copyright Dennis Kunkel at www.DennisKunkel.com, used with permission.

11.9 Golgi Apparatus and Dictyosomes

Golgi Complexes are flattened stacks of membrane-bound sacs. They function as a packaging plant, modifying vesicles from the Rough ER. New membrane material is assembled in various cisternae of the golgi.

11.10 Lysosomes

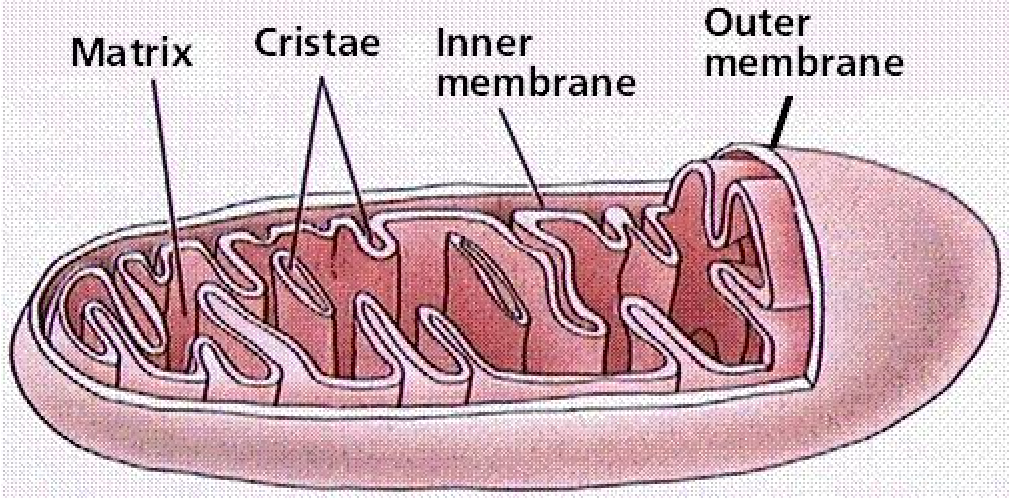
Lysosomes are relatively large vesicles formed by the Golgi. They contain hydrolytic enzymes that could destroy the cell. Lysosome contents function in the extracellular breakdown of materials.



Role of the Golgi in forming lysosomes. Image from Purves et al., Life: The Science of Biology, 4th Edition, by Sinauer Associates (www.sinauer.com) and WH Freeman (www.whfreeman.com), used with permission.

11.11 Mitochondria

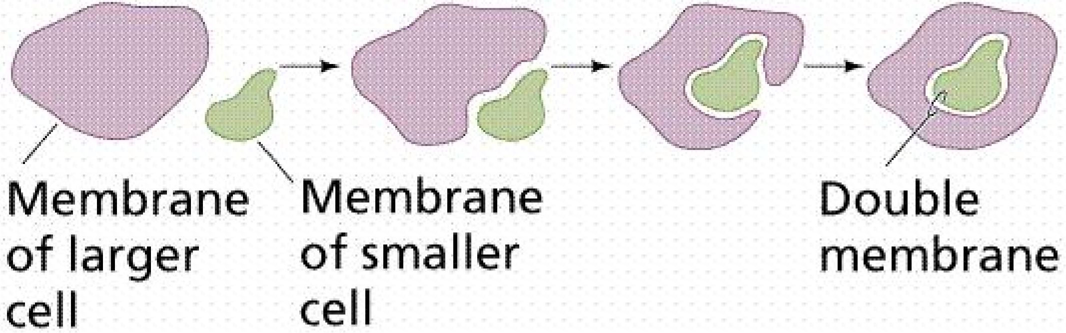
Mitochondria contain their own DNA (termed mDNA) and are thought to represent bacteria-like organisms incorporated into eukaryotic cells over 700 million years ago (perhaps even as far back as 1.5 billion years ago). They function as the sites of energy release (following glycolysis in the cytoplasm) and ATP formation (by chemiosmosis). The mitochondrion has been termed the powerhouse of the cell. Mitochondria are bounded by two membranes. The inner membrane folds into a series of cristae, which are the surfaces on which ATP is generated.



Structure of a mitochondrion. Image from Purves et al., Life: The Science of Biology, 4th Edition, by Sinauer Associates (www.sinauer.com) and WH Freeman (www.whfreeman.com), used with permission.

11.12 Mitochondria and endosymbiosis

During the 1980s, Lynn Margulis proposed the theory of endosymbiosis to explain the origin of mitochondria and chloroplasts from permanent resident prokaryotes. According to this idea, a larger prokaryote (or perhaps early eukaryote) engulfed or surrounded a smaller prokaryote some 1.5 billion to 700 million years ago.



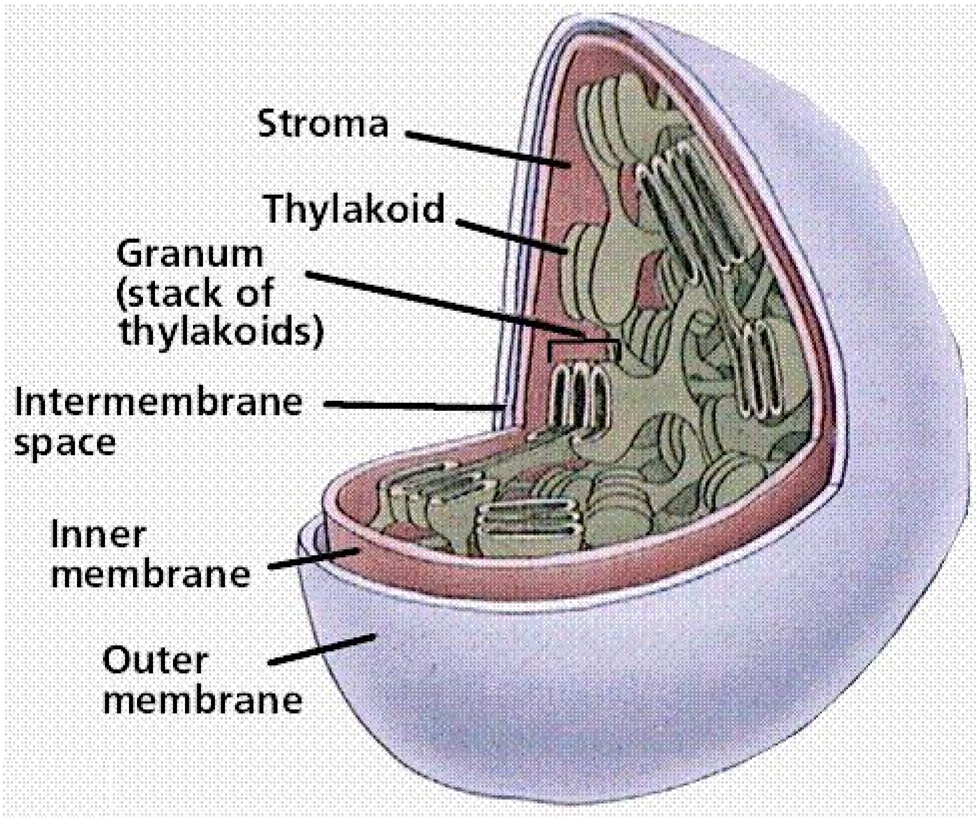
The basic events in endosymbiosis. Image from Purves et al., Life: The Science of Biology, 4th Edition, by Sinauer Associates (www.sinauer.com) and WH Freeman (www.whfreeman.com), used with permission.

Instead of digesting the smaller organisms the large one and the smaller one entered into a type of symbiosis known as mutualism, wherein both organisms benefit and neither is harmed. The larger organism gained excess ATP provided by the "protomitochondrion" and excess sugar provided by the "protochloroplast", while providing a stable environment and the raw materials the endosymbionts required. This is so strong that now eukaryotic cells cannot survive without mitochondria (likewise photosynthetic eukaryotes cannot survive without chloroplasts), and the endosymbionts can not survive outside their hosts. Nearly all eukaryotes have mitochondria. Mitochondrial division is remarkably similar to the prokaryotic methods that will be studied later in this course. A summary of the theory is available by clicking here.

11.13 Plastids

Plastids are also membrane-bound organelles that only occur in plants and photosynthetic eukaryotes.

Chloroplasts are the sites of photosynthesis in eukaryotes. They contain chlorophyll, the green pigment necessary for photosynthesis to occur, and associated accessory pigments (carotenes and xanthophylls) in photosystems embedded in membranous sacs, thylakoids (collectively a stack of thylakoids are a granum [plural = grana]) floating in a fluid termed the stroma. Chloroplasts contain many different types of accessory pigments, depending on the taxonomic group of the organism being observed.



Structure of the chloroplast. Image from Purves et al., Life: The Science of Biology, 4th Edition, by Sinauer Associates (www.sinauer.com) and WH Freeman (www.whfreeman.com), used with permission.

11.14 Chloroplasts and endosymbiosis

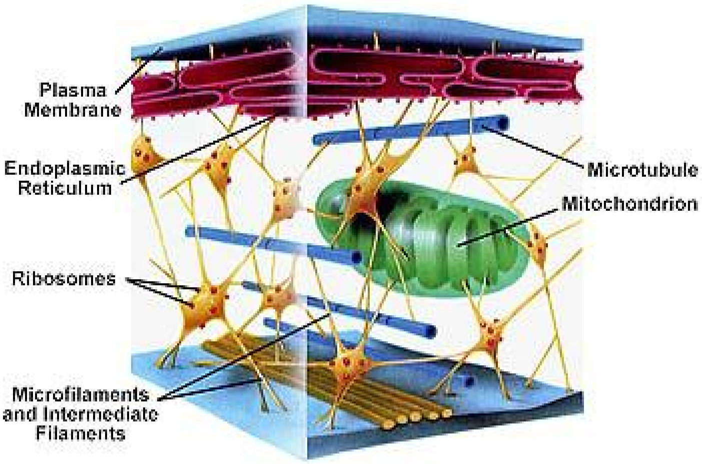
Like mitochondria, chloroplasts have their own DNA, termed cpDNA. Chloroplasts of Green Algae (Protista) and Plants (descendants of some Green Algae) are thought to have originated by endosymbiosis of a prokaryotic alga similar to living *Prochloron* (Prochlorobacteria). Chloroplasts of Red Algae (Protista) are very similar biochemically to cyanobacteria (also known as blue-green bacteria [algae to chronologically enhanced folks like myself :)]). Endosymbiosis is also invoked for this similarity, perhaps indicating more than one endosymbiotic event occurred.

Leukoplasts store starch, sometimes protein or oils.

Chromoplasts store pigments associated with the bright colors of flowers and/or fruits.

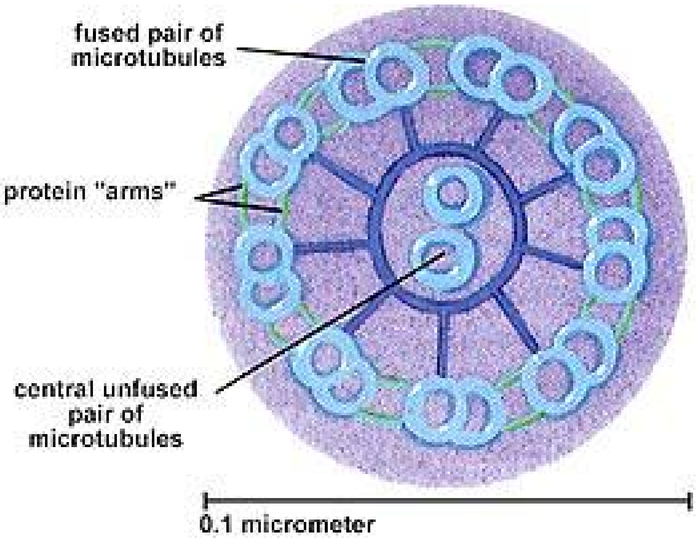
11.15 Cell Movement

Cell movement; is both internal, referred to as cytoplasmic streaming and external, referred to as motility. Internal movements of organelles are governed by actin filaments. These filaments make an area in which organelles such as chloroplasts can move. Internal movement is known as cytoplasmic streaming. External movement of cells is determined by special organelles for locomotion.



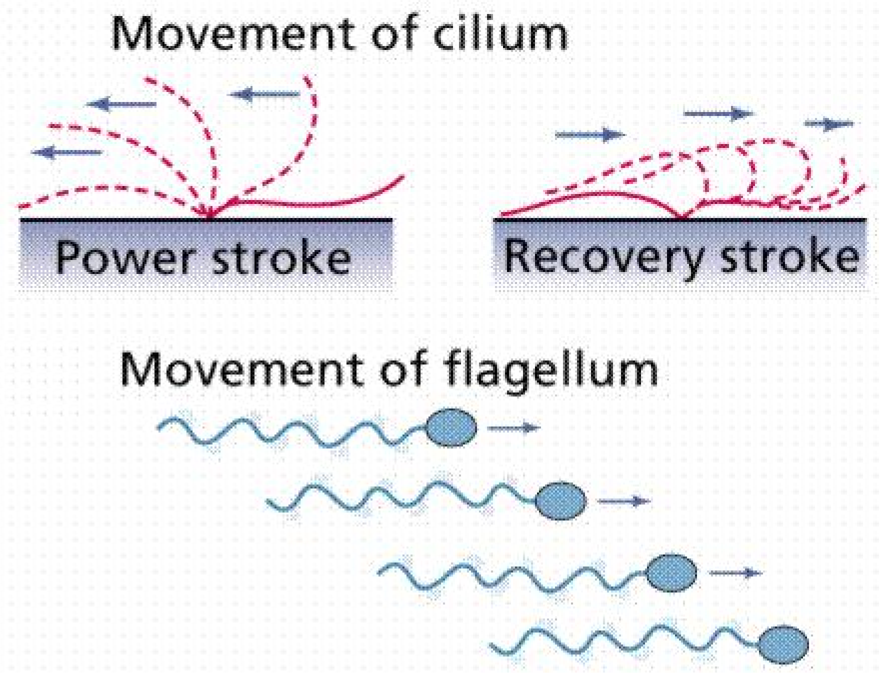
The cytoskeleton. Image from Prentice Hall.

Cilia and flagella are similar except for length, cilia being much shorter. They both have the characteristic 9 + 2 arrangement of microtubules.



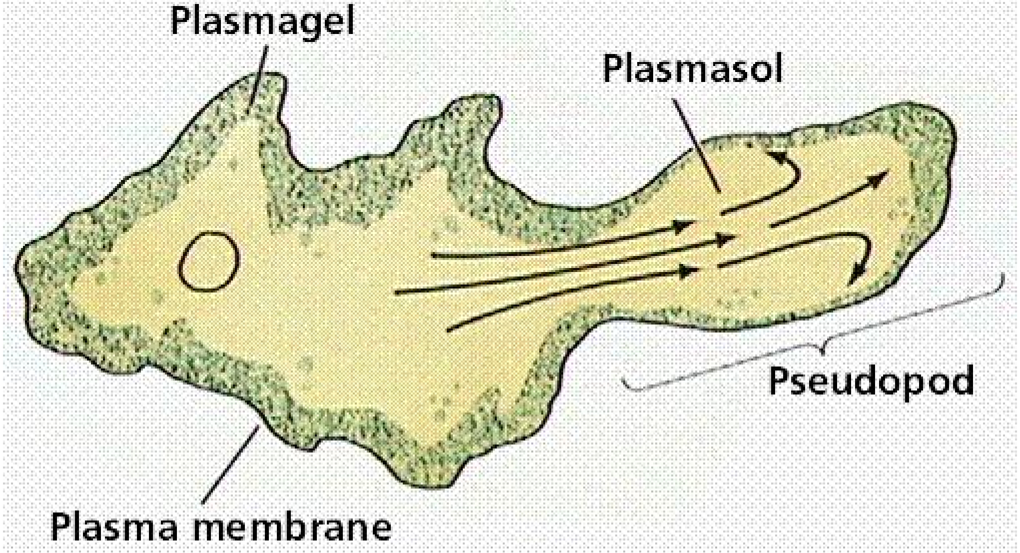
The 9+2 arrangement of microtubules in a flagellum or cilium. Image from Prentice Hall.

Flagella work as whips pulling (as in *Chlamydomonas* or *Halosphaera*) or pushing (dinoflagellates, a group of single-celled Protista) the organism through the water. Cilia work like oars on a viking longship (*Paramecium* has 17,000 such oars covering its outer surface).



Movement of cilia and flagella. Image from Purves et al., Life: The Science of Biology, 4th Edition, by Sinauer Associates (www.sinauer.com) and WH Freeman (www.whfreeman.com), used with permission.

Pseudopodia are used by many cells, such as *Amoeba*, *Chaos (Pelomyxa)* and human leukocytes (white blood cells). These are not structures as such but rather are associated with actin near the moving edge.



Formation and functioning of a pseudopod by an amoeboid cell. Image from Purves et al., Life: The Science of Biology, 4th Edition, by Sinauer Associates (www.sinauer.com) and WH Freeman (www.whfreeman.com), used with permission.

Learning Objectives

- Give the function and cellular location of the following basic eukaryotic organelles and structures: cell membrane, nucleus, endoplasmic reticulum, Golgi bodies, lysosomes, mitochondria, ribosomes, chloroplasts, vacuoles, and cell walls.

- A micrometer is one-millionth of a meter long. A nanometer is one-billionth of a meter long. How many micrometers tall are you?
- Describe the function of the nuclear envelope and nucleolus.
- Describe the details of the structure of the chloroplast, the site of photosynthesis.
- Mature, living plant cells often have a large, fluid-filled central vacuole that can store amino acids, sugars, ions, and toxic wastes. Animal cells generally lack large vacuoles. How do animal cells perform these functions?
- Microtubules, microfilaments, and intermediate filaments are all main components of the cytoskeleton.
- Flagella and cilia propel eukaryotic cells through their environment; the microtubule organization in these organelles is a 9+2 array.

Terms

actin, carotenes, cellulose, cell walls, chemiosmosis, chitin
chlorophyll, cristae, cyanobacteria, cytoplasm, cytoskeleton, dinoflagellates
endoplasmic reticulum, erythrocytes, eukaryotic, fluid-mosaic, Golgi complexes, grana
Green Algae, hydrophilic, hydrophobic, leukocytes, lysosomes, microtubules
mitochondria, mutualism, neurons, nucleus, nucleolus, *ova*
parenchyma, phospholipid, photosystems, plasmodesmata, plastid, pseudopodia
Red Algae, ribosomal RNA, ribosomes, stroma, symbiosis, thylakoids
vacuoles, zygote

Topic 5.1

Chapter 12 Mineral Nutrition of Plants

12.1 Visual Symptoms of Nutrient Deficiency In Plants

Visual nutrient deficiency symptoms can be a very powerful diagnostic tool for evaluating the nutrient status of plants. One should keep in mind, however, that a given individual visual symptom is seldom sufficient to make a definitive diagnosis of a plant's nutrient status. Many of the classic deficiency symptoms such as tip burn, chlorosis and necrosis \nə-ˈkrō-səs, ne-\ are characteristically associated with more than one mineral deficiency and also with other stresses that by themselves are not diagnostic for any specific nutrient stress. However, their detection is extremely useful in making an evaluation of nutrient status. In addition to the actual observations of morphological and spectral symptoms, knowing the location and timing of these symptoms is a critical aspect of any nutrient status evaluation. Plants do not grow in isolation, they are part of the overall environment and as such they respond to environmental changes as that affect nutrient availability. Also, plants do influence their environment and can contribute to environmental changes, which in turn can affect the nutrient status of the plant.

necrosis *usu. localized death of living tissue(局部坏死)*

12.1.1 Sources of Visual Symptoms

Stresses such as salinity, pathogens \ˈpa-thə-jən\, and air pollution induce their own characteristic set of visual symptoms. Often, these symptoms closely resemble those of nutrient deficiency. Pathogens often produce an interveinal chlorosis *（脉间失绿）*, and air pollution and salinity stress can cause tip burn. Although at first these symptoms might seem similar in their general appearance to nutrient deficiency symptoms, they do differ in detail and/or in their overall developmental pattern. Pathological \ˌpa-thə-ˈlä-ji-kəl\ symptoms can often be separated from nutritional symptoms by their distribution in a population of affected plants. If the plants are under a nutrient stress, all plants of a given type and age in the same environment tend to develop similar symptoms at the same time. However if the stress is the result of pathology, the development of symptoms will have a tendency to vary between plants until a relatively advanced stage of the pathology is reached.

Pathological：

1: of or relating to pathology

2: altered or caused by disease; also : indicative of disease

3: being such to a degree that is extreme, excessive, or markedly abnormal <a pathological liar ，pathological fear

Pathogen：*a specific causative agent (as a bacterium or virus) of disease*

12.1.2 Environmental Associations

Plants remove substantial amounts of nutrients from the soil during their normal growth cycle and many long-term environmental changes occur as a result of this process. Effects on the soil go considerably beyond the straight removal or depletion of nutrients. Charge balance must be maintained in the plant-soil system during nutrient uptake. Charge balance is usually achieved by the excretion of proton and/or hydroxyl ions by the plant to replace the absorbed nutrient cations or anions. For example when plants are fertilized with ammonia, they acquire most of their nitrogen in the form of the ammonium cation, rather than from the usual nitrate anion. Because nitrate is the only anion used by the plant in large amounts, the net result of this change is that during normal nutrient uptake the proton excretion will far exceed that of hydroxyl ions. In the case of vigorously growing plants, the amount of excreted \ik-ˈskrēt\ protons can be sufficiently large as to decrease the pH of the soil by several pH units. Changes in soil pH of such magnitude *can have large implications for* a number of soil processes such as soil structure, nutrient availability and leaching of nutrients. The immediate effect on the soil may be favorable for some plants, especially acid-loving plants, in that it tends to make iron more available. However, in the long run, lowering the soil pH can be deleterious \ˌde-lə-ˈtir-ē-əs\ to plants in that the availability of nutrients will change. A lower soil pH will allow micronutrients to be more readily leached from the soil profile, eventually resulting in deficiencies of nutrients such as Cu and Zn. Additionally, when the pH of the soil drops much below pH 5, the solubility of Al and Mn can increase to such an extent as to become toxic to most plant growth (see textbook Figure 5.4).

: harmful often in a subtle or unexpected way deleterious effects <deleterious to health>

Plants are often thought of as passive in relation to the environment. However this is not always a valid assumption; for there are many plants that clearly manipulate their environment in a fashion that tends to makes certain nutrients more readily available. For example, iron is a limiting nutrient in many agricultural areas, but it comprises about 3% of the average soil which, if available, would be far in excess of the needs of the average plant. Some plants actively excrete protons, and the resulting decrease in pH increases the solubility of iron in their environment. In addition, other plants excrete phytosiderophores/铁载体/ that chelate the soil iron rendering it a more available form for the plants (see p. 277 of the textbook).

12.1.3 Pathways of Symptom Development

At first glance, it would appear that the distinction of deficiency symptoms for the 13 known essential mineral nutrients should be relatively simple. But such an assumption is incorrect. In fact, the deficiency symptoms are quite complex because each nutrient has a number of different biological functions and each function may have an independent set of interactions with a wide range of environmental parameters. In addition, the expression of these symptoms varies for acute or chronic deficiency conditions. **Acute deficiency** occurs when a nutrient is suddenly no longer available to a rapidly growing plant. **Chronic deficiency** occurs when there is a limited but continuous supply of a nutrient, at a rate that is insufficient to meet the growth demands of the plant.

Most of the classic deficiency symptoms described in textbooks are characteristic of acute deficiencies. The most common symptoms of low-grade, chronic deficiencies are a tendency towards darker green leaves and stunted or slow growth. Typically most published descriptions of deficiency symptoms arise from experiments conducted in greenhouses or growth chambers where the plants are grown in hydroponics or in media where the nutrients are fully available. In these conditions, nutrients are readily available while present, but when a nutrient is depleted, the plant suddenly faces an acute deficiency. Thus, hydroponic studies favor the development of acute deficiencies.

In experiments designed to study **micronutrient** deficiency symptoms, micronutrients are usually omitted from the nutrient solution. Micronutrients are often present in the seed or as contaminants in the environment, so a plant of adequate size will exhaust these trace amounts of micronutrient and develop characteristic acute deficiency systems. When deficiency symptoms of **macronutrients** are sought, the macronutrient is removed suddenly from a suitable sized rapidly growing plant. Alternatively the plant can initially be given a one-time supply of the nutrient that is sufficient for a limited amount of growth. Because macronutrients are continuously required in relatively large amounts by rapidly growing plants, the available nutrients will be rapidly depleted, resulting in an acute deficiency.

In natural systems, the plant encounters many degrees and types of stresses that result in different types of symptoms occurring over time. Perhaps the most common nutrient deficiency in natural environments is the case of a limited nutrient supply that is continuously renewed at a low rate from soil weathering processes. In such cases, the limited nutrient availability results in chronic nutrient deficiency symptoms.

12.1.4 Effect of Nutrient Mobility on Symptom Development

The interaction between nutrient mobility in the plant, and plant growth rate can be a major factor influencing the type and location of deficiency symptoms that develop. For very mobile nutrients such as nitrogen and potassium, deficiency symptoms develop predominantly in the older and mature leaves. This is a result of these nutrients being preferentially mobilized during times of nutrient stress from the older leaves to the newer leaves near the growing regions of the plant. Additionally, mobile nutrients newly acquired by the roots are also preferentially translocated to new leaves and the growing regions. Thus old and mature leaves are depleted of mobile nutrients during times of stress while the new leaves are maintained at a more favorable nutrient status.

The typical localization of deficiency symptoms of very weakly mobile nutrients such as calcium, boron, and iron is the opposite to that of the mobile nutrients; these deficiency symptoms are first displayed in the growing regions and new leaves while the old leaves remain in a favorable nutrient status. (This assumes that these plants started with sufficient nutrient, but ran out of nutrient as they developed). In plants growing very slowly for reasons other than nutrition (such as low light) a normally limiting supply of a nutrient could, under these conditions, be sufficient for the plant to slowly develop, maybe even without symptoms. This type of development is likely to occur in the case of weakly mobile nutrients because excess nutrients in the older leaves will eventually be mobilized to supply newly developing tissues. In contrast, a plant with a similar supply that is growing rapidly will develop severe deficiencies in the actively growing tissue such as leaf edges and the growing region of the plant. A classic example of this is calcium deficiency in vegetables such as lettuce where symptoms develop on the leaf margins (tip burn) and the growing region near the meristems \ˈmer-ə-ˌstem\. The maximal growth rate of lettuce is often limited by the internal translocation rate of calcium to the growing tissue rather than from a limited nutrient supply in the soil.

When moderately mobile nutrients such as sulfur and magnesium are the limiting nutrients of the system, deficiency symptoms are normally seen over the entire plant. However the growth rate and rate of nutrient availability can make a considerable difference on the locations at which the symptoms develop. If the nutrient supply is marginal compared to the growth rate, symptoms will appear on the older tissue, but if the nutrient supply is very low compared to the growth rate, or the nutrient is totally depleted, the younger tissue will become deficient first.

12.1.5 Plant Competition and Induced Deficiencies

When the observed symptoms are the direct result of a nutrient deficiency, the actions needed for correction are relatively straight-forward. However symptoms are often the result of interactions with other environmental factors limiting the availability of the nutrient whose symptoms are expressed. The classic instance is that of iron deficiency induced by an excess of heavy metals in the environment. Transition metals such as Cu, Zn Cr and Ni compete with Fe and each other for plant uptake. Competition for uptake is not specific to Fe and heavy metals but is true for all mineral nutrients that are chemically similar and have similar uptake mechanisms \ˈme-kə-ˌni-zəm\. For example if the availability of Cu or Zn is relatively less than that of Fe, then excessive concentrations of some other metal such as Ni or Cr will induce a deficiency of one of these nutrients rather than Fe. In the case of the macronutrients, excessive amounts of Mg will compete with K for uptake and can possibly induce a K deficiency. The barrenness of serpentine soils is the result of such competition, *with the high Mg of these soils inducing a Ca deficiency.* The toxicity of a low pH soil is another example of a basic nutrient deficiency. Low pH has a two-fold effect on soil nutrients: It enhances the leaching of cations, reducing their availability *in the soil, and the relatively abundant protons in the soil compete with Ca and other cations for uptake.* Thus, nutrient deficiencies can be induced by a number of different mechanisms often working in concert to limit the availability of a nutrient.

12.1.6 Nutrient Demand and Use Efficiency

Although all plants of the same species respond similarly to nutrient stress, plants of similar species will often show significant differences in their nutrient use efficiency. This results from differences in growth rate, root distribution, phase of development, and efficiency of nutrient uptake and utilization. This implies that in any given location, plants from one species may become nutrient-deficient, while those from another species growing in the same environment right next to them, may not show any deficiency symptoms.

Growth rate also affects nutrient status. When the nutrient supply is barely inadequate for growth under existing environmental conditions, many plants adjust their growth rate to match that supported by the available nutrient supply without displaying typical visual deficiency symptoms.

Agricultural systems differ from natural systems in that crop plants have been selected primarily for rapid growth under low stress conditions. This rapid growth rate results in a high nutrient demand by these plants and a higher incidence of nutrient deficiency unless supplemental fertilizers are supplied. It is not uncommon to find agricultural crops showing severe signs of nutrient stress, with native plants growing in the same area showing little or no indication of nutrient stress. In agriculture systems chronic deficiency symptoms develop mostly in crops with little or limited fertilization. Acute nutrient deficiency symptoms most often occur when new crops with a higher nutrient demand are introduced, or less productive lands are brought under cultivation for the production of rapidly growing crop plants.

12.1.7 Uniformity of Nutrient Status

Not all tissues of a plant are at the same nutrient status during times of stress. Leaves on the same plant that are exposed to different environmental conditions, (such as light), or those of different ages may have considerable differences in nutrient status. Mineral nutrients are for the most part acquired by the roots and translocated throughout the plant. The distance of any part of the plant to the roots will influence nutrient availability, particularly in the case of the less mobile nutrients. In plants recovering from nutrient deficiency, the root and conductive tissues recover first. For example, in the case of recovery from Fe deficiency, it is common to see the veins re-green while the interveinal tissue remains chlorotic and Fe-deficient.

In order to maintain rapid, optimal growth, all plant tissues must have a favorable nutrient status. Although a plant may be marginally low in a number of nutrients, only one nutrient at a time will limit overall growth. However, if the supply of that limiting nutrient is increased even slightly, the resulting increase in growth will increase the demand for all other nutrients and another nutrient, the next lowest in availability, will become limiting.

12.1.8 Other Diagnostic Tools

Although visual diagnostic symptoms are an extremely valuable tool for the rapid evaluation of the nutrient status of a plant, they are only some of the tools available. Other major tools include microscopic studies, spectral analysis, and tissue and soil analysis. These methods all vary in their precision, rapidity and their ability to predict future nutrient status. Because of the close interaction between plant growth and the environment, all predictions of future nutrient status must make assumptions about how the environment will change in that time frame.

The principle advantage of visual diagnostic symptoms is that they are readily obtained and provide an immediate evaluation of nutrient status. Their main drawback \ˈdrȯ-ˌbak\（缺点） is that the visual symptoms do not develop until after there has been a major effect on yield, growth and development.

Tissue analysis is nutrient-specific but relatively slow; tissues must be sampled, processed and analyzed before the nutrient status can be determined. An analysis of the mineral nutrient content of selected plants tissues, when compared against Critical Level values (which are available for most crop plants, see textbook Figure 12.3), can be used to evaluate the plant nutrient status at the time of sampling with a relatively high degree of confidence and can be extrapolated to project nutrient status at harvest. Soil analysis is similar to tissue analysis but evaluates the potential supplying power of the soil instead of plant nutrient status. Plant analysis provides information as to what the plant needs, while soil analysis provides information about the status of the nutrient supply.

Spectral analysis of nutrient status is still in its infancy and is presently used primarily in the inventory of global resources and in specialized studies. Microscopic studies are most valuable in looking at the physiological aspects of nutrient stress rather than the evaluation of plant nutrient status on a whole plant or crop basis.

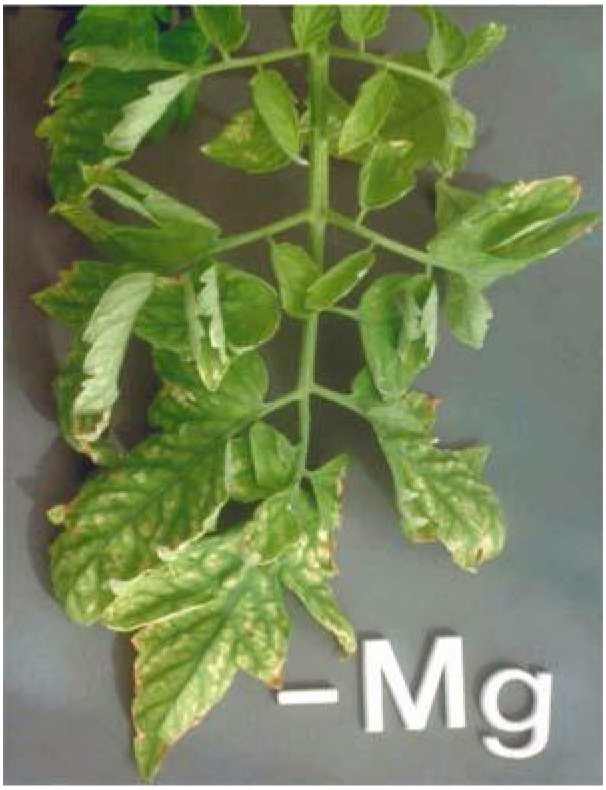
12.1.9 Symptom Descriptions

It is unusual to find any one leaf or even one plant that displays the full array\ə-ˈrā\ of symptoms (一系列的) that are characteristic of a given deficiency. It is thus highly desirable to know how individual symptoms look, for it is possible for them to occur in many possible combinations on a single plant. Most of the terms used below in the description of deficiency symptoms are reasonably self evident; a few however have a distinct meaning in the nutrient deficiency field. For example, the term *chlorotic,* which is a general term for yellowing of leaves through the loss of chlorophyll \ˈklȯr-ə-ˌfil, -fəl\, cannot be used without further qualification because there may be an overall chlorosis as in nitrogen deficiency, interveinal, as in iron deficiency, or marginal, as in calcium deficiency. Another term used frequently in the description of deficiency symptoms is *necrotic,* a general term for brown, dead tissue. This symptom can also appear in many varied forms, as is the case with chlorotic symptoms.

Nutrient deficiency symptoms for many plants are similar, but because of the large diversity found in plants and their environments there is a range of expression of symptoms. Because of their parallel veins, grasses and other monocots generally display the affects of chlorosis as a series of stripes rather than the netted interveinal chlorosis commonly found in dicots. The other major difference is that the marginal necrosis or chlorosis found in dicots is often expressed as tip burn in monocots.

Web Figures 12.1.A–M show deficiency symptoms for macronutrients and micronutrients in tomato.

Magnesium. The Mg-deficient leaves (see Web Figure 12.1.A) show advanced interveinal chlorosis, with necrosis developing in the highly chlorotic tissue. In its advanced form, magnesium deficiency may superficially resemble potassium deficiency. In the case of magnesium deficiency the symptoms generally start with mottled chlorotic areas developing in the interveinal tissue. The interveinal laminae tissue tends to expand proportionately more than the other leaf tissues, producing a raised puckered surface, with the top of the puckers progressively going from chlorotic to necrotic tissue. In some plants such as the Brassica (The mustard family, which includes vegetables such as broccoli \ˈbrä-kə-lē, ˈbrä-klē\, brussel sprouts, cabbage, cauliflower \ˈkȯ-li-ˌflau̇(-ə)r, ˈkä-, -lē-\（菜花）, collards \ˈkä-lərd\, kale/keil/ 羽衣甘蓝, kohlrabi \kōl-ˈrä-bē also -ˈra-\球茎甘蓝, mustard \ˈməs-tərd\芥末, rape, rutabaga \ˌrü-tə-ˈbā-gə, ˌru̇-, -ˈbe-; ˈrü-tə-ˌ, ˈru̇-\芜菁甘蓝 and turnip.), tints of orange, yellow, and purple may also develop.

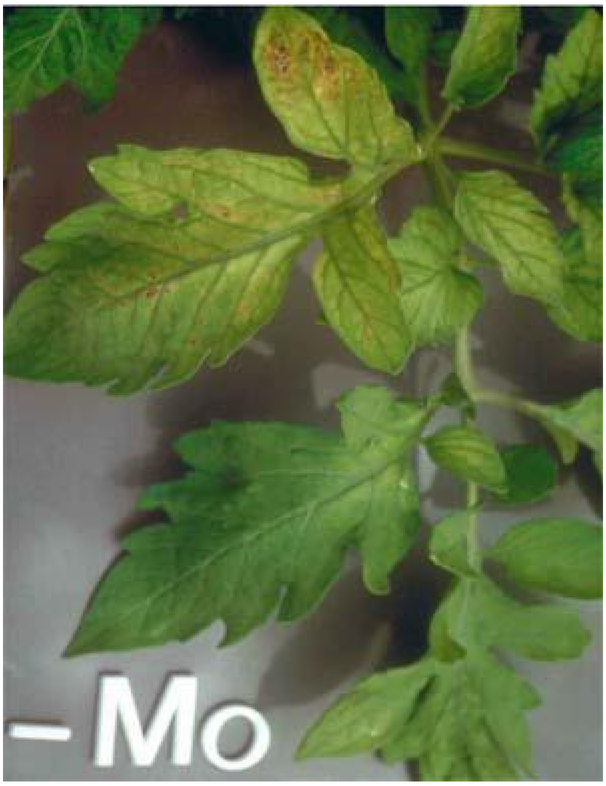


Web Figure 12.1.A Magnesium deficiency symptoms in tomato. (Epstein and Bloom 2004) **(Click image to enlarge.)**

Manganese. These leaves (see Web Figure 12.1.B) show a light interveinal chlorosis developed under a limited supply of Mn. The early stages of the chlorosis induced by manganese deficiency are somewhat similar to iron deficiency. They begin with a light chlorosis of the young leaves and netted veins of the mature leaves especially when they are viewed through transmitted light. As the stress increases, the leaves take on a gray metallic sheen and develop dark freckled and necrotic areas along the veins. A purplish luster may also develop on the upper surface of the leaves. Grains such as oats, wheat, and barley are extremely susceptible to manganese deficiency. They develop a light chlorosis along with gray specks which elongate and coalesce, and eventually the entire leaf withers and dies.

Web Figure 12.1.B Manganese deficiency symptoms in tomato. (Epstein and Bloom 2004) **(Click image to enlarge.)**

Molybdenum. These leaves (See Web Figure 12.1.C) show some mottled spotting along with some interveinal chlorosis. An early symptom for molybdenum deficiency is a general overall chlorosis, similar to the symptom for nitrogen deficiency but generally without the reddish coloration on the undersides of the leaves. This results from the requirement for molybdenum in the reduction of nitrate, which needs to be reduced prior to its assimilation by the plant (see Textbook chapter 12). Thus, the initial symptoms of molybdenum deficiency are in fact those of nitrogen deficiency. However, molybdenum has other metabolic functions within the plant, and hence there are deficiency symptoms even when reduced nitrogen is available. In the case of cauliflower, the lamina of the new leaves fail to develop, resulting in a characteristic whiptail appearance. In many plants there is an upward cupping of the leaves and mottled spots developing into large interveinal chlorotic areas under severe deficiency. At high concentrations, molybdenum has a very distinctive toxicity symptom in that the leaves turn a very brilliant orange.



Web Figure 12.1.C Molybdenum deficiency symptoms in tomato. (Epstein and Bloom 2004) **(Click image to enlarge.)**

Nitrogen. The chlorotic symptoms (see Figure 4) shown by this leaf resulted from nitrogen deficiency. A light red cast can also be seen on the veins and petioles. Under nitrogen deficiency, the older mature leaves gradually change from their normal characteristic green appearance to a much paler green. As the deficiency progresses these older leaves become uniformly yellow (chlorotic). Leaves approach a yellowish white color under extreme deficiency. The young leaves at the top of the plant maintain a green but paler color and tend to become smaller in size. Branching is reduced in nitrogen deficient plants resulting in short, spindly plants. The yellowing in nitrogen deficiency is uniform over the entire leaf including the veins. However in some instances, an interveinal necrosis replaces the chlorosis commonly found in many plants. In some plants the underside of the leaves and/or the petioles and midribs develop traces of a reddish or purple color. In some plants this coloration can be quite bright. As the deficiency progresses, the older leaves also show more of a tendency to wilt under mild water stress and become senescent much earlier than usual. Recovery of deficient plants to applied nitrogen is immediate (days) and spectacular.

Web Figure 12.1.D Nitrogen deficiency symptoms in tomato. (Epstein and Bloom 2004)

Phosphorus. These phosphorus-deficient leaves (see Figure 12) show some necrotic spots. As a rule, phosphorus deficiency symptoms are not very distinct and thus difficult to identify. A major visual symptom is that the plants are dwarfed or stunted. Phosphorus deficient plants develop very slowly in relation to other plants growing under similar environmental conditions but without phosphorus deficiency. Phosphorus deficient plants are often mistaken for unstressed but much younger plants. Some species such as tomato, lettuce, corn and the brassicas develop a distinct purpling of the stem, petiole and the under sides of the leaves. Under severe deficiency conditions there is also a tendency for leaves to develop a blue-gray luster. In older leaves under very severe deficiency conditions a brown netted veining of the leaves may develop.

Web Figure 12.1.E Phosphorus deficiency symptoms in tomato. (Epstein and Bloom 2004)

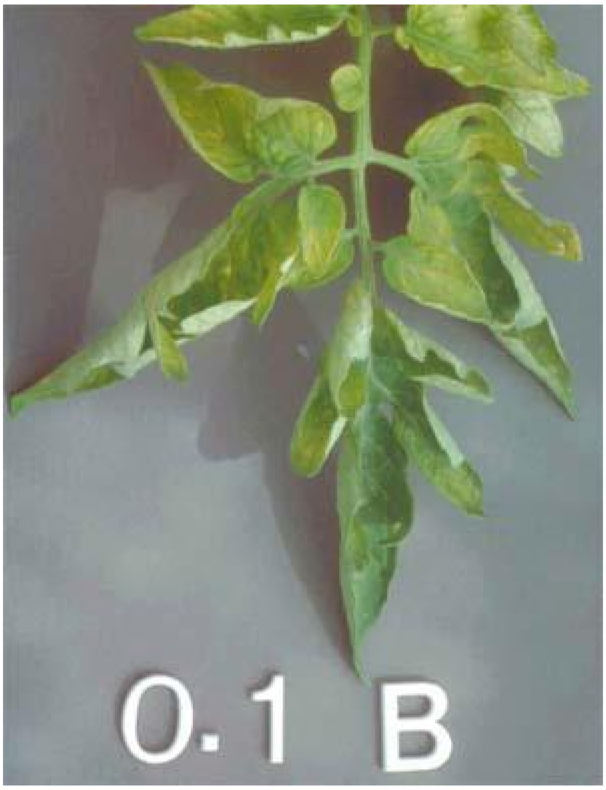
Sulfur. This leaf (see Figure 6) shows a general overall chlorosis while still retaining some green color. The veins and petioles show a very distinct reddish color. The visual symptoms of sulfur deficiency are very similar to the chlorosis found in nitrogen deficiency. However, in sulfur deficiency the yellowing is much more uniform over the entire plant including young leaves. The reddish color often found on the underside of the leaves and the petioles has a more pinkish tone and is much less vivid than that found in nitrogen deficiency. With advanced sulfur deficiency brown lesions and/or necrotic spots often develop along the petiole, and the leaves tend to become more erect and often twisted and brittle.

Web Figure 12.1.F Sulfur deficiency symptoms in tomato. (Epstein and Bloom 2004)

Zinc. This leaf (see Figure 7) shows an advanced case of interveinal necrosis. In the early stages of zinc deficiency the younger leaves become yellow and pitting develops in the interveinal upper surfaces of the mature leaves. Guttation (see textbook Figure 4.5) is also prevalent. As the deficiency progress these symptoms develop into an intense interveinal necrosis but the main veins remain green, as in the symptoms of recovering iron deficiency. In many plants, especially trees, the leaves become very small and the internodes shorten, producing a rosette like appearance.

Web Figure 12.1.G Zinc deficiency symptoms in tomato. (Epstein and Bloom 2004)

Boron. These boron-deficient leaves (see Figure 8)show a light general chlorosis. The tolerance of plants to boron varies greatly, to the extent that the boron concentrations necessary for the growth of plants having a high boron requirement may be toxic to plants sensitive to boron. Boron is poorly transported in the phloem of most plants, with the exception of those plants that utilize complex sugars, such as sorbitol, as transport metabolites. In a recent study, (see Brown et al., 1999) tobacco plants engineered to synthesize sorbitol were shown to have increased boron mobility, and to better tolerate boron deficiency in the soil.



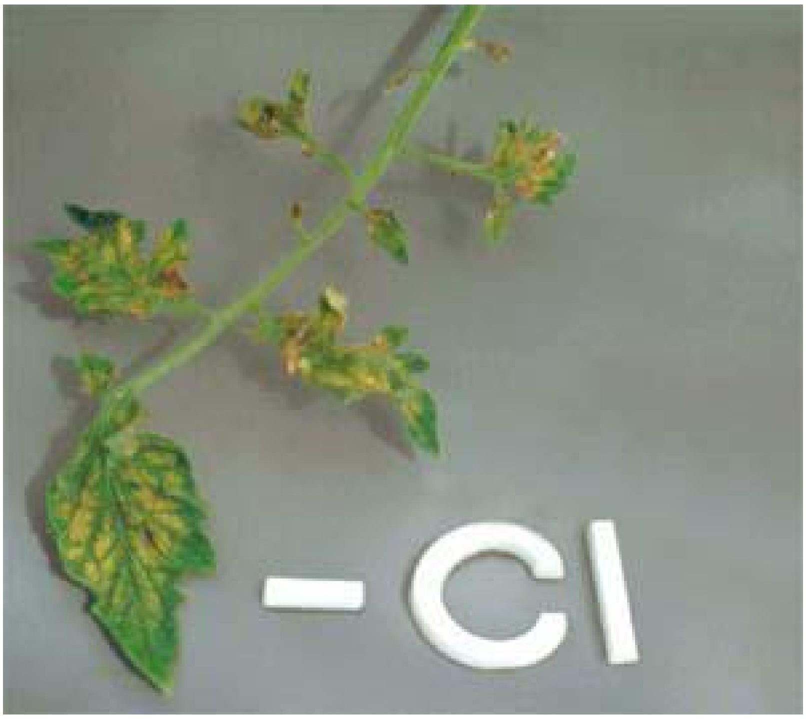
Web Figure 12.1.H Boron deficiency symptoms in tomato. (Epstein and Bloom 2004)

In plants with poor boron mobility, boron deficiency results in necrosis of meristematic tissues in the growing region, leading to loss of apical dominance and the development of a rosette condition. These deficiency symptoms are similar to those caused by calcium deficiency. In plants in which boron is readily transported in the phloem, the deficiency symptoms localize in the mature tissues, similar to those of nitrogen and potassium. Both the pith and the epidermis of stems may be affected, often resulting in hollow or roughened stems along with necrotic spots on the fruit. The leaf blades develop a pronounced crinkling and there is a darkening and crackling of the petioles often with exudation of syrupy material from the leaf blade. The leaves are unusually brittle and tend to break easily. Also, there is often a wilting of the younger leaves even under an adequate water supply, pointing to a disruption of water transport caused by boron deficiency.

Calcium. These calcium-deficient leaves (see Figure 9) show necrosis around the base of the leaves. The very low mobility of calcium is a major factor determining the expression of calcium deficiency symptoms in plants. Classic symptoms of calcium deficiency include blossom-end rot of tomato (burning of the end part of tomato fruits), tip burn of lettuce, blackheart of celery and death of the growing regions in many plants. All these symptoms show soft dead necrotic tissue at rapidly growing areas, which is generally related to poor translocation of calcium to the tissue rather than a low external supply of calcium. Very slow growing plants with a deficient supply of calcium may re-translocate sufficient calcium from older leaves to maintain growth with only a marginal chlorosis of the leaves. This ultimately results in the margins of the leaves growing more slowly than the rest of the leaf, causing the leaf to cup downward. This symptom often progresses to the point where the petioles develop but the leaves do not, leaving only a dark bit of necrotic tissue at the top of each petiole. Plants under chronic calcium deficiency have a much greater tendency to wilt than non-stressed plants.

Web Figure 12.2.I Calcium deficiency symptoms in tomato. (Epstein and Bloom 2004)

Chloride. These leaves (see Figure 10) have abnormal shapes, with distinct interveinal chlorosis. Plants require relatively high chlorine concentration in their tissues. Chlorine is very abundant in soils, and reaches high concentrations in saline areas, but it can be deficient in highly leached inland areas. The most common symptoms of chlorine deficiency are chlorosis and wilting of the young leaves. The chlorosis occurs on smooth flat depressions in the interveinal area of the leaf blade. In more advanced cases there often appears a characteristic bronzing on the upper side of the mature leaves. Plants are generally tolerant of chloride, but some species such as avocados, stone fruits, and grapevines are sensitive to chlorine and can show toxicity even at low chloride concentrations in the soil.



Web Figure 12.1.J Chloride deficiency symptoms in tomato. (Epstein and Bloom 2004)

Copper. These copper-deficient leaves (see Figure 11) are curled, and their petioles bend downward. Copper deficiency may be expressed as a light overall chlorosis along with the permanent loss of turgor in the young leaves. Recently matured leaves show netted, green veining with areas bleaching to a whitish gray. Some leaves develop sunken necrotic spots and have a tendency to bend downward. Trees under chronic copper deficiency develop a rosette form of growth. Leaves are small and chlorotic with spotty necrosis.

Web Figure 12.1.K Copper deficiency symptoms in tomato. (Epstein and Bloom 2004) **(Click image to enlarge.)**

Iron. These iron-deficient leaves (see Figure 12) show strong chlorosis at the base of the leaves with some green netting. The most common symptom for iron deficiency starts out as an interveinal chlorosis of the youngest leaves, evolves into an overall chlorosis, and ends as a totally bleached leaf. The bleached areas often develop necrotic spots. Up until the time the leaves become almost completely white they will recover upon application of iron. In the recovery phase the veins are the first to recover as indicated by their bright green color. This distinct venial re-greening observed during iron recovery is probably the most recognizable symptom in all of classical plant nutrition. Because iron has a low mobility, iron deficiency symptoms appear first on the youngest leaves. Iron deficiency is strongly associated with calcareous soils and anaerobic conditions, and it is often induced by an excess of heavy metals.

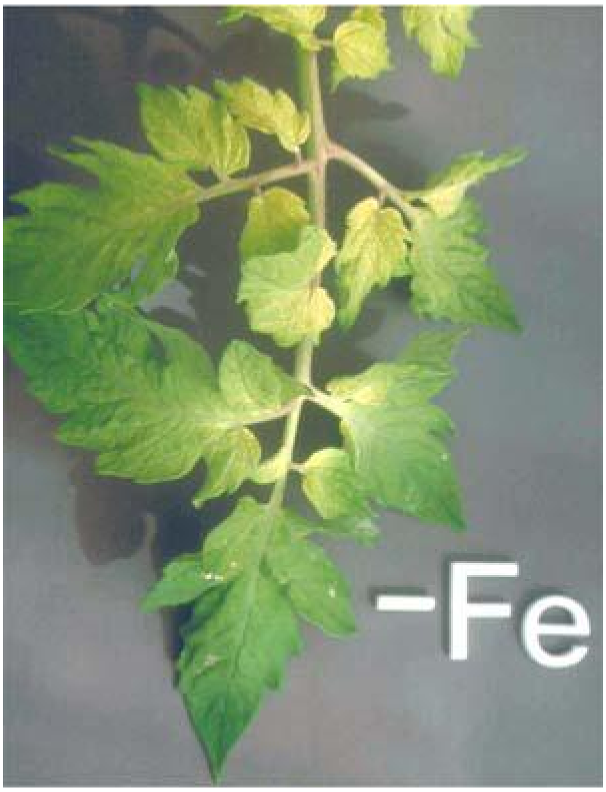
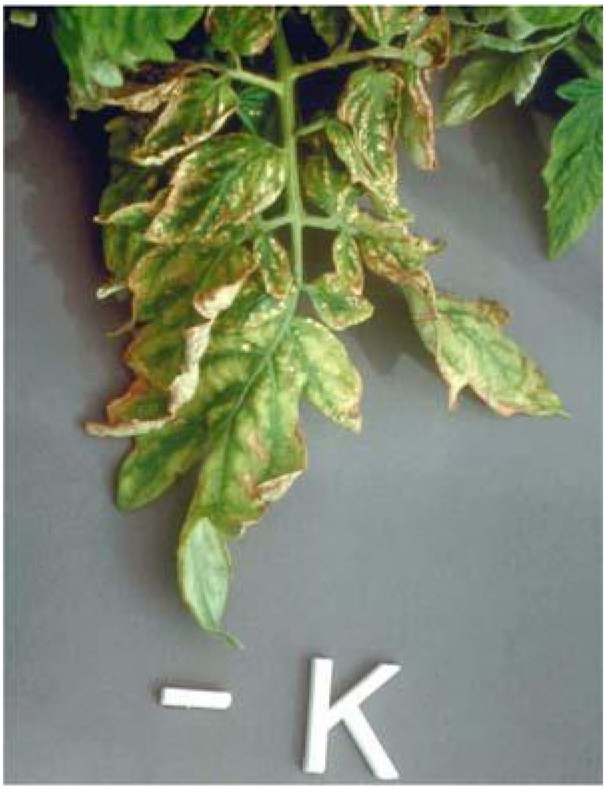


Figure 12.1.L Iron deficiency symptoms in tomato. (Epstein and Bloom 2004)

Potassium. Some of these leaves (see Figure 13) show marginal necrosis (tip burn), others at a more advanced deficiency status show necrosis in the interveinal spaces between the main veins along with interveinal chlorosis. This group of symptoms is very characteristic of K deficiency symptoms.



Web Figure 12.1.M Potassium deficiency symptoms in tomato. (Epstein and Bloom 2004)

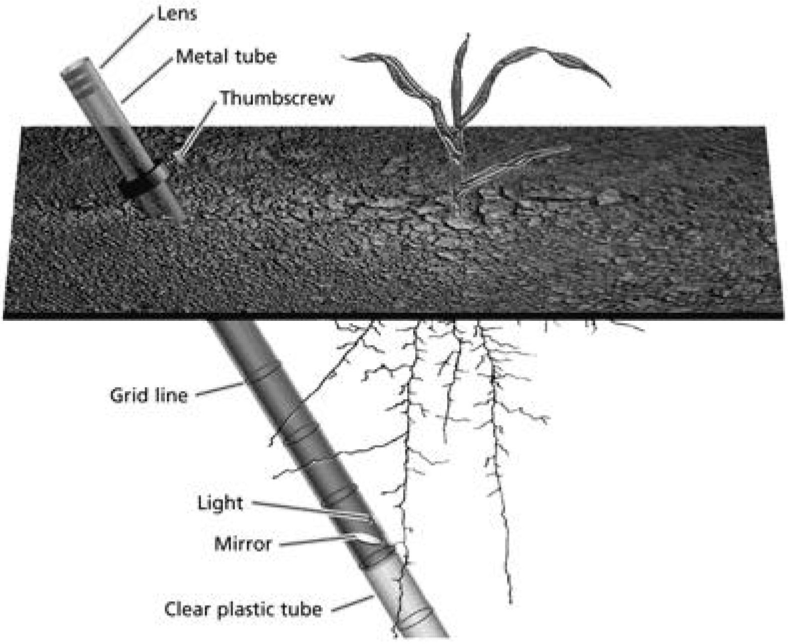
The onset of potassium deficiency is generally characterized by a marginal chlorosis progressing into a dry leathery tan scorch on recently matured leaves. This is followed by increasing interveinal scorching and/or necrosis progressing from the leaf edge to the midrib as the stress increases. As the deficiency progresses, most of the interveinal area becomes necrotic, the veins remain green and the leaves tend to curl and crinkle. In some plant such as legumes and potato, the initial symptom of deficiency is white speckling or freckling of the leaf blades. In contrast to nitrogen deficiency, chlorosis is irreversible in potassium deficiency, even if potassium is given to the plants. Because potassium is very mobile within the plant, symptoms only develop on young leaves in the case of extreme deficiency. Potassium deficiency can be greatly alleviated in the presence of sodium but the resulting sodium-rich plants are much more succulent than a high potassium plant. In some plants over 90% of the required potassium can be replaced with sodium without any reduction in growth.

12.2 Observing Roots below Ground

Studying root growth below the soil surface requires a means of observing the root system directly. As early as 1873, the German botanist Julius von Sachs studied root systems by using simple soil-filled boxes with one glass wall. Since that time, facilities for studying root growth in the soil have become much more complex. Large laboratories with subterranean chambers for the observation of root growth have been constructed and allow the analysis of root growth while the aerial parts of the plant are exposed to natural field conditions (Klepper and Kaspar 1994). These laboratories are called **rhizotrons** (from the Greek *rhizos*, meaning "root," and *tron*, meaning "a device for studying").

In a rhizotron, roots grow in glass-walled chambers that line underground passageways. Grid lines on the glass walls indicate soil depth. Details of root morphology (root size and distribution) under natural growing conditions can be observed with specially designed microscopes, mounted adjacent to the glass walls of the root chambers. In addition, the growth of the roots over a period of time can be measured with time-lapse photography.

Because rhizotrons are expensive to construct and maintain, they have been largely supplanted by minirhizotrons or root periscopes. Minirhizotrons are transparent plastic tubes previously buried at an angle in the soil near the plants to be observed. An optical device such as a tilted mirror with a magnifying lens or a miniature videocamera is inserted into a tube to monitor roots growing along its surface (Web Figure 12.2.A). This device provides information on rooting density in the bulk soil, as well as on root growth and phenology. Plant physiologists use such information in conjunction with changes in nutrient and water levels in the soil to assess root activity through the soil profile.



Web Figure 12.2.A Drawing of a minirhizotron installed near an oat seedling. A metal tube that slides within a clear plastic tube is held in place by a thumbscrew. The metal tube contains the optics for viewing roots growing along the surface of the plastic tube. A dark grid scribed onto the surface of the plastic tube assists in positioning the metal tube. The optics include lenses, mirror, and lights. Many modern configurations use a miniature television camera instead of lenses to obtain the image.

Chapter 13 Growth Stages of Wheat

13.1 INTRODUCTION

fficient, economic wheat management systems A sound understanding of plant growth and development is an essential element of efficient, economic wheat management systems. The impact of frost, heat, drought, diseases, insects, and weeds can be more accurately predicted with a clear picture of the relationships between growth stage and plant response to stress. The optimum timing of fertilizer, irrigation, herbicide, insecticide, and fungicide applications are also best determined by crop growth stage rather than calendar date.

The ten major growth stages that the wheat plant progresses through during its life cycle are all familiar to farmers:

1. Germination
2. Seedling
3. Tillering
4. Stem elongation or Jointing
5. Booting
6. Heading
7. Flowering or Anthesis
8. Milk
9. Dough
10. Ripening

13.2 MEASURES OF GROWTH AND DEVELOPMENT

Several systems have been developed to provide numerical designations for growth and developmental stages. Among these, the **Feekes**, **Zadoks**, and **Haun** scales are used the most frequently (Table 1).

The **Haun** scale growth stages key on rate of development of the main shoot (Table 1). In the early stages, the description of each new leaf is related to the previous leaf that was produced. For example, a seedling with one fully extended leaf and a second leaf that is half as long as the fully extended leaf is at Haun stage 1.5. Similarly, a plant with five fully extended leaves on the main shoot and an emerging sixth main shoot leaf that is 30% as long as the fifth leaf is at Haun stage 5.3. The booting stage numerical designation starts at one more than the number of leaves produced by the main shoot, i.e., the flag leaf number plus one. This can cause confusion because the flag number is not a constant for all cultivars. For this reason, the Haun scale has been used mainly to describe the growth stages before the booting stage.

Table 1. A comparison of wheat growth stages for Haun, Feekes, and Zadoks scales.

Haun scale	Feekes scale	Zadoks scale	General Description
			Germination
		00	Dry seed
		01	Water uptake (imbibition) started
		03	Imbibition complete
		05	Radicle emerged from seed
		07	Coleoptile emerged from seed
0.0		09	Leaf just at coleoptile tip
			Seedling developmet
	1	10	First leaf emerged
1.+		11	First leaf unfolded
1.+		12	2 leaves unfolded
2.+		13	3 leaves unfolded
3.+		14	4 leaves unfolded
4.+		15	5 leaves unfolded
5.+		16	6 leaves unfolded
6.+		17	7 leaves unfolded
7.+		18	8 leaves unfolded
8.+		19	9 or more leaves unfolded
			Tillering
		20	Main shoot only
	2	21	Main shoot and 1 tiller
		22	Main shoot and 2 tillers
		23	Main shoot and 3 tillers
		24	Main shoot and 4 tillers
		25	Main shoot and 5 tillers
	3	26	Main shoot and 6 tillers
		27	Main shoot and 7 tillers
		28	Main shoot and 8 tillers
		29	Main shoot and 9 or more tillers
			Stem elongation or jointing
	4-5	30	Pseudo stem erection
	6	31	1st node detectable
	7	32	2nd node detectable
		33	3rd node detectable
		34	4th node detectable
		35	5th node detectable
		36	6th node detectable
	8	37	Flag leaf just visible
	9	39	Flag leaf ligule/collar just visible

			Booting
		40	----
8-9 note		41	Flag leaf sheath extending
9.2	10	45	Boot just swollen
		47	Flag leaf sheath opening
10.1		49	First awns visible
			Heading
10.2	10.1	50	First spikelet of head visible
	10.2	53	1/4 of head emerged
10.5	10.3	55	1/2 of head emerged
10.7	10.4	57	3/4 of head emerged
11.0	10.5	59	Emergence of head complete
			Flowering of Anthesis
11.4	10.51	60	Beginning of flowering
11.5		65	Flowering half complete
11.6		69	Flowering complete
			Milk
		70	----
12.1	10.54	71	Kernel watery
13.0		73	Early milk
	11.1	75	Medium milk
		77	Late milk
			Dough
		80	----
14.0		83	Early dough
	11.2	85	Soft dough
15.0		87	Hard dough
			Ripening
		90	----
	11.3	91	Kernel hard (difficult to separate by fingernail)
16.0	11.4	92	Kernel hard
		93	Kernel loosening in daytime
		94	Overripe, straw dead and collapsing
		95	Seed dormant
		96	50% of viable seed germinates
		97	Seed not dormant
		98	Secondary dormancy
		99	Secondary dormancy lost

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* **Note:** Remember, Haun scale values from the booting to ripening stages are dependent on the number of leaves produced on the main stem. The example given here is for a plant with eight leaves on the main stem.

The **Feekes** scale recognizes eleven major growth stages starting with seedling emergence and ending with grain ripening (Table 1). The Feekes scale is frequently used to identify optimum stages for chemical treatments, such as fungicide applications, that focus on the plant development period from the start of stem elongation (Feekes stage 6) to the completion of flowering (Feekes stage 10.53).

The **Zadoks** scale provides the most complete description of wheat plant growth stages (Table 1, Figure 1). It uses code based on ten major stages that can be subdivided, making it particularly suited for computerization. When using the Zadoks scale, the main growth stages, e.g., seedling versus tillering, should be identified before proceeding to a description of the secondary stages, e.g., seedling leaf number or tiller number.

13.3 THERMAL TIME

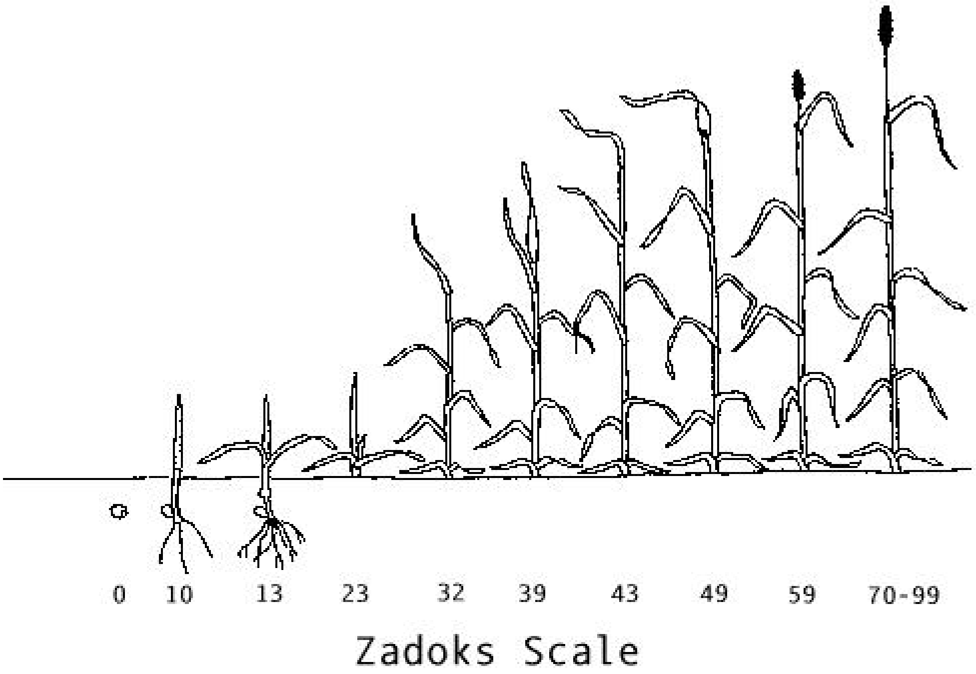
Crop growth and development is often described in terms of time, e.g., 60-day barley, frost-free days, heading date, etc. However, a consideration of temperature is also important in these discussions because temperature determines the rate of growth and development. The time/temperature relationship that governs plant growth and development is known as **thermal time** and it is measured in heat units or growing-degree days. Heat units have been chosen as the measure of thermal time in this discussion to avoid confusion between growing-degree days and calendar days.

13.3.1 Heat Units

The thermal time required for crop production is determined by adding the daily heat units together for the period between planting and harvest. When the centigrade temperature scale is used, the heat units generated each day is determined by adding the minimum and maximum daily temperatures together and dividing by two. For example, a day with minimum and maximum temperatures of 10 and 20°C respectively, would generate 15 heat units [(20 + 10) / 2 = 15]. Days with average daily temperatures below 0°C do not contribute to the heat unit total.

13.3.2 Thermal Time Requirements For Wheat Production

The heat unit requirements to produce a mature crop are approximately 1550 for spring and 2200 for winter wheat. Translated into calendar days, this means that it would take 103 (103 ×15 = 1545) days to produce a spring and 147 (147 ×15 = 2205) days to produce a winter wheat crop if the average daily temperature was a constant 15°C. As we all know, there are large variations in temperature from day to day and growing season to growing season. The use of thermal time rather than calendar time takes this variability into consideration and provides an explanation for differences in crop maturity when observations from different years are compared. For example, we harvested Norstar winter wheat on July 20 in 1988 and August 24 in 1993 at Saskatoon. The 1988 growing season was much warmer with the result that the thermal time requirements to produce a mature Norstar crop were met five weeks earlier in 1988 than in 1993.



ZADOKS SCALE

Figure 1. Wheat growth and developmental stages according to the Zadoks scale. See Table 1 for comparisons with Feekes and Haun scales.

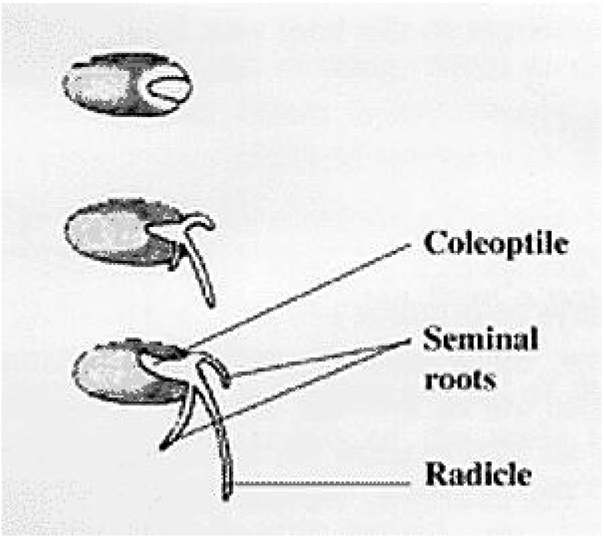


Figure 2. Wheat germination.

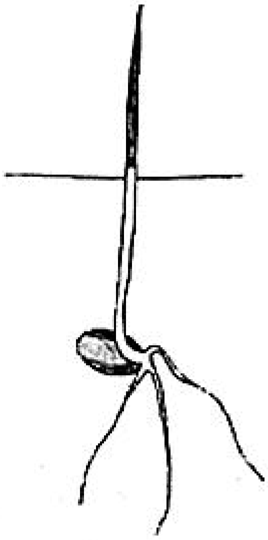


Figure 3. Wheat emergence. Zadoks stage 10.

Development of the roots, leaves, tillers, and spikelets on the head of the wheat plant takes place in an orderly, predictable pattern that is dependent upon thermal time. It takes approximately 105 heat units for a wheat plant to germinate and emerge from a seeding depth of less than one inch (2.54 cm). The appearance of each successive leaf on the main shoot and tillers then proceeds at a constant rate that is determined by cultivar, sowing date, and latitude. Most wheat cultivars require between 80 to 100 heat units to produce each leaf on the main shoot. After the requirements for leaf development have been met, another 650 heat units are normally required to complete the heading and maturation stages.

13.4 WHEAT GROWTH AND DEVELOPMENT

See Table 1 for Haun, Feekes, and Zadoks scale numerical designation for the following growth and developmental stages.

13.4.1 The Wheat Kernel

The mature wheat kernel (caryopsis) is composed of approximately 83 percent endosperm, 14.5 per cent bran, and 2.5 percent embryo. Once germination starts, the endosperm provides the developing plant with an energy source until its roots are established and newly expanded leaves allow it to harvest energy from the sun. The embryo of the mature wheat kernel has already undergone the first stages of plant development before the kernel is separated from the parent plant. In a mature kernel the embryo includes the **coleoptile**, which protects the first leaf as it pushes its way through the soil to the surface during germination, the **radicle**, which becomes the first root, and **primodia**, which develop into the first three leaves and seminal roots.

13.4.2 Germination

Germination starts with the uptake of water (imbibition) by a wheat kernel that has lost its post-harvest dormancy. Plant development is resumed once the embryo is fully imbibed. With the resumption of growth, the radicle and coleoptile emerge from the seed (Figure 2). The first three seminal roots are produced and then the coleoptile elongates pushing the growing point toward the soil surface.

13.4.3 Seedling Stage

The seedling stage begins with the appearance of the first leaf (Figure 3) and ends with the emergence of the first tiller. Up to six seminal roots and three leaves support the plant at this stage. The crown of the plant usually becomes noticeably distinct after the third leaf has emerged (Figure 4).

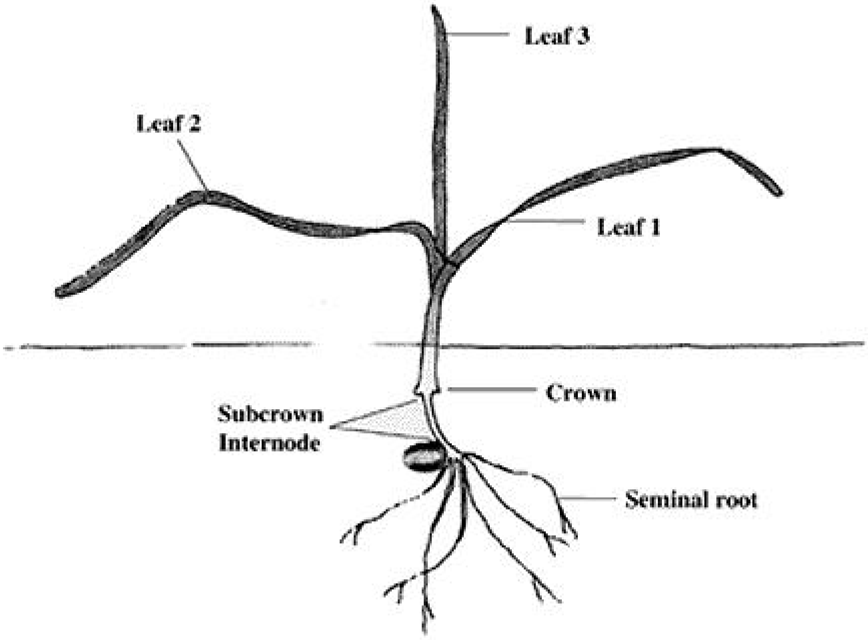


Figure 4. Wheat seedling with three leaves and a developing crown. Zadoks stage 13. Haun stage 2.6.

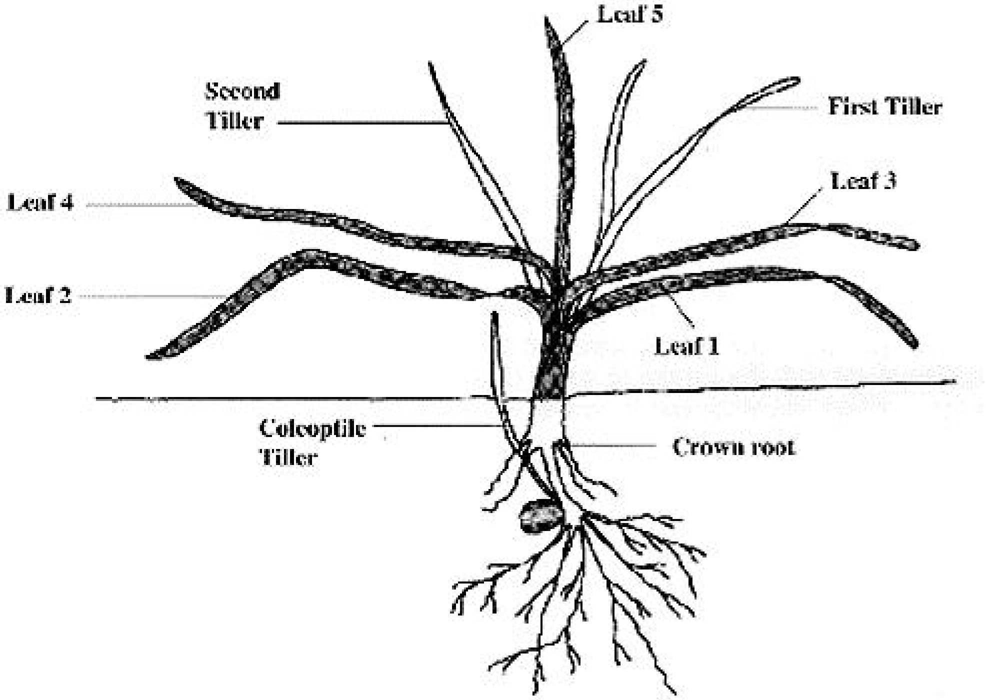


Figure 5. A wheat plant with five leaves, two tillers, and a well developed crown. Zadoks stage 22. Haun stage 4.7.

13.4.4 Tillering Stage

Crown formation is soon followed by the appearance of tillers and development of a secondary or crown root system (Figure 5). The crown root system provides the plant with most of its nutrients and water during the growing season.

The distance between the wheat kernel and the crown is determined by the length of the subcrown internode (Figure 4). The subcrown internode can elongate several inches and, depending on soil temperature, usually positions the crown within 1.2 inches (3.0 cm) of the soil surface. At Saskatoon, crown depths of 0.7 inches (1.8 cm) and 1.2 inches (3.0 cm) have been recorded when soil temperatures were 18 and 11°C, respectively, at the time of seeding. The recommended planting depth for winter wheat is less than one inch (2.54 cm). Consequently, a clearly defined subcrown internode is **not** usually found on seedlings of properly managed winter wheat.

The roots, leaves, tillers, and spikelets on the head of the wheat plant develop from primodia at nodes. While the first tiller is not produced until the third leaf has fully emerged, the appearance of later tillers is usually synchronized with the emergence of each subsequent new leaf that develops on the main shoot. For example, emergence of the fifth leaf is normally accompanied by the appearance of the second crown tiller (Figure 5) which originates from an auxiliary bud (primodium) located in the node at the base of the second leaf (leaf axil). Similarly, a tiller can start producing its own subtillers once it has three fully developed leaves.

Each tiller that is produced represents the potential for a wheat plant to develop an additional stem complete with its own leaves, roots, and head. Root and shoot development of the plant is synchronized so that the number of crown roots is related to the number of leaves produced. However, root production by a tiller is usually delayed until its third leaf has emerged. Consequently, tillers that do not produce at least three leaves are not competitive and usually die off once the stem elongation stage starts.

Coleoptile tillers can develop when environmental conditions are favorable (Figure 5). The development of coleoptile tillers is not closely synchronized with the development of the rest of the plant, but their appearance often coincides with the emergence of the third leaf on the main shoot. They develop from a node at the base of the coleoptile and are separated from the main shoot by the subcrown internode. However, when wheat is seeded shallow the subcrown internode does not elongate and the coleoptile tiller will originate from a position adjacent to the crown of the main shoot.

A major change in the development of the wheat plant occurs at the end of the tillering stage. At this time, the growing points of the main shoot and tillers stop initiating new leaves and start producing reproductive structures. Conversion of the growing point signals the end of the vegetative and the start of the reproductive period.

Early maturing spring wheat cultivars change from the vegetative to the reproductive phase after seven to eight leaves have been initiated on the main shoot. However, many commercial wheat cultivars have a vernalization (growth at low temperature - see Chapter 7) or photoperiod (growth under long day length) requirement that extends the vegetative period allowing for the production of more main shoot leaves and a larger number of tillers. An extended vegetative period due to a vernalization requirement is the main reason why more heat units are needed to produce a winter than a spring wheat crop.

13.4.5 Stem Elongation or Stem Jointing Stage

The nodes from which leaves develop are telescoped at the crown during the tillering stage. Once jointing starts, the internode region elongates, moving the nodes and the growing point upward from the crown to produce a long stiff stem that will carry the head. Appearance of the first node (Zadoks stage 31) can usually be detected without dissecting the plant by pressing the base of the main (largest) stem between your fingers.

Each successive tiller on a wheat plant normally has one less leaf than its predecessor. This synchronizes the start of the stem elongation stages of the main stem and tillers.

Synchronization of growth and development at this stage ensures there will be no more than a few days difference in the maturity of all heads on the plant.

Spikelet development on the microscopic head is usually completed by the time the first node is 0.4 inches (1 cm) above the soil surface. The terminal spikelet is produced at about Zadoks stage 31. A rapid loss of younger, poorly developed tillers also normally starts at this stage.

The stem elongation or jointing stage comes to an end with the appearance of the last (flag) leaf.

13.4.6 Booting Stage

The developing head within the sheath of the flag leaf becomes visibly enlarged during the booting stage. The booting stage ends when the first awns emerge from the flag leaf sheath and the head starts to force the sheath open.

13.4.7 Heading Stage

The heading stage extends from the time of emergence of the tip of the head from the flag leaf sheath to when the head has completely emerged but has not yet started to flower.

13.4.8 Flowering or Anthesis Stage

The flowering or anthesis stage lasts from the beginning to the end of the flowering period. Pollination and fertilization occur during this period. All heads of a properly synchronized wheat plant flower within a few days and the embryo and endosperm begin to form immediately after fertilization.

13.4.9 Milk Stage

Early kernel formation occurs during the milk stage. The developing endosperm starts as a milky fluid that increases in solids as the milk stage progresses. Kernel size increases rapidly during this stage.

13.4.10 Dough Development Stage

Kernel formation is completed during the dough development stage. The kernel accumulates most of its dry weight during dough development. The transport of nutrients from the leaves, stems, and spike to the developing seed is completed by the end of the hard dough stage. The developing kernel is physiologically mature at the hard dough stage even though it still contains approximately 30 percent water.

13.4.11 Ripening Stage

The seed loses moisture, and any dormancy it may have had, during the ripening stage.

13.5 CRITICAL GROWTH STAGES

Successful adaptation of a crop species is dependent upon the programming of critical growth stages so that the plant can capitalize on favorable weather periods during the growing season. Plants have evolved a variety of adaptive mechanisms that allow them to optimize growth and development while coping with environmental stresses. Plant breeders have selected and recombined the variability that exists in natural populations to produce cultivars with increased production potential and adaptation to a wide range of environments. An understanding of how plants respond to environmental stresses at different growth stages can assist in the assessment of crop condition and production potential throughout the growing season.

Winter wheat plants must survive the many stresses of winter (see Chapter 12). Roots and leaves that develop in the fall are often killed off during the overwintering period. However, as long as the crown remains alive, new roots and leaves can be regenerated. Therefore, plants that enter the winter with well developed crowns have the best chance of winter survival.

Grain yield can be expressed as the product of three variables (yield components):

Grain yield = (number of heads) × (kernels per head) x (kernel weight).

The impact of each yield component on final grain yield is determined at different stages during the growing season.

The number of viable seeds planted and the number of tillers produced per plant sets the upper limit on the number of heads that can be produced by a wheat crop. Tiller production is favored by moist, warm weather and good soil fertility, especially nitrogen fertility, prior to the stem elongation stage.

Tillers produced during the tillering stage must survive to maturity to contribute to grain yield. The developing head and elongating stem start making large demands on the plants' resources once stem elongation starts and younger, poorly developed tillers that are unable to compete are quickly lost. Tiller mortality level is especially dependent on environmental conditions immediately after terminal spikelet formation (Zadoks stage 31).

Drought and heat stress during the stem elongation and booting stages increase the rate of tiller mortality by placing added restrictions on resource availability. For example, nearly 250,000 tillers per acre per day were lost from winter wheat stands subjected to extreme drought and heat stress in the late spring of 1988 at Saskatoon. Only the main stem of each plant was left to set seed after this period of extreme environmental stress. If a drought is broken or a late application of nitrogen fertilizer suddenly becomes available during this period, the developmental synchrony of the plant may be disrupted producing a flush of later maturing heads. A dry spring followed by cool damp weather during the last half of June in Saskatchewan in 1993 produced many examples of this type of maturity problem (Figure 6).

Environmental stress prior to flag leaf appearance can result in a loss of spikelets on the developing head (Figure 7). As many as twelve florets per spikelet can be initiated under favorable conditions for development. However, later forming florets abort and normally only two to four florets actually set seed in each spikelet (Figure 8). Floret initiation starts in the lower central region and progresses toward the base and tip of the head. Under extreme environmental stress, all of the florets in the spikelets at the top and bottom of the head may abort prior to flowering.

The number of tillers and florets initiated by the wheat plant is usually far in excess of the number of heads and kernels that can be supported through to maturity. As we have seen, a downward adjustment in yield potential normally starts with tiller loss at the beginning of stem elongation and continues with floret abortion prior to flowering. Environmental conditions experienced during these developmental stages determine the magnitude of the loss in yield potential. The final adjustments in yield potential are made during the grain filling period when kernel size is determined.

figure 6. **Asynchronous tiller development caused by a dry spring followed by cool, damp weather during the booting stage. Note the large differences in stage of tiller maturity.**

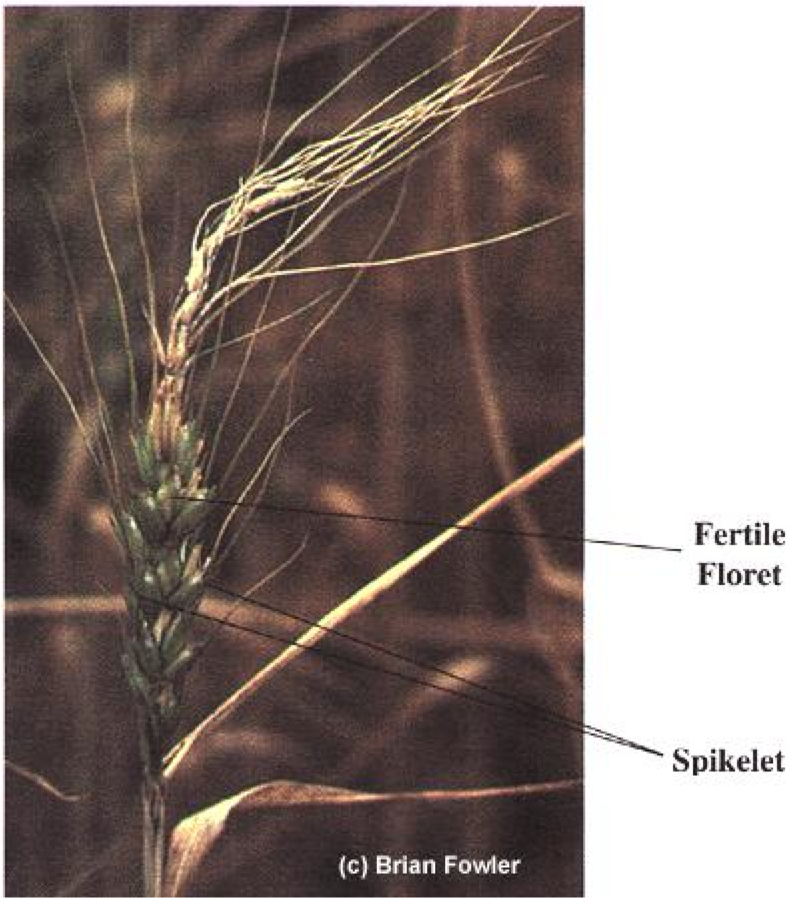
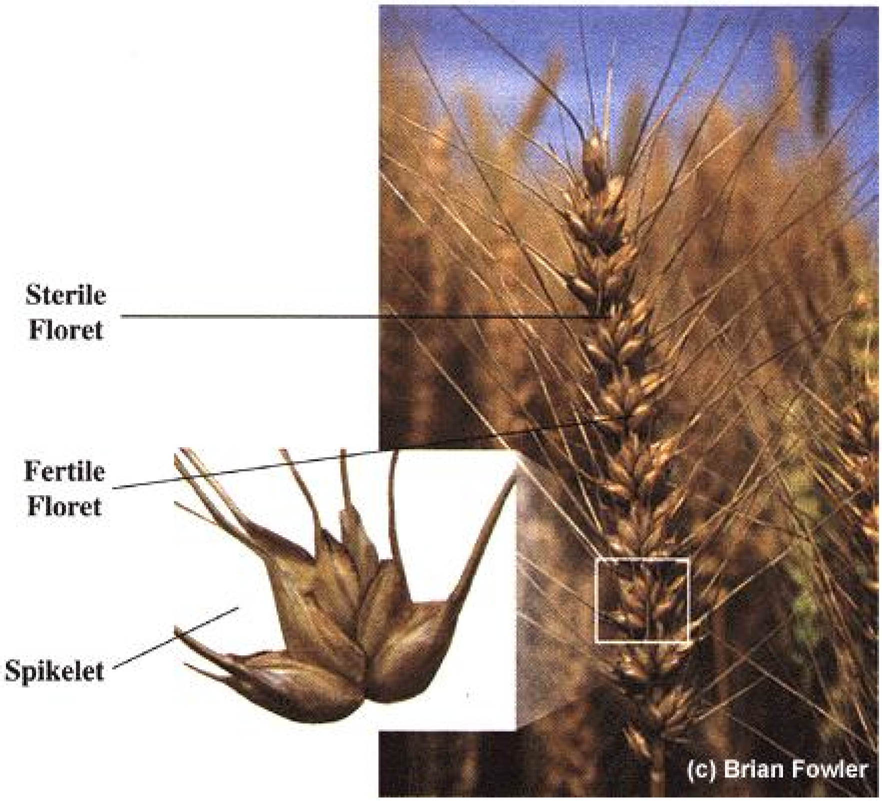


Figure 7. Drought stress immediately before flowering can cause floret abortion (blasting).



Five 8. Under favorable conditions of moisture and temperature, winter wheat can produce as many as five kernels per spikelet.

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Chapter 14 Nitrogen Fertilization of Wheat

14.1 INTRODUCTION

Maintenance of a snow cover during the winter is necessary for successful winter wheat production in most areas of the Canadian prairies outside of southern Alberta. Direct seeding into standing stubble (no-till or stubbling-in) has proven to be the most reliable method of ensuring a uniform snow cover on winter wheat fields.

Most stubble fields are deficient in available soil nitrogen (N) and residual soil N levels are often less than 30 lb/acre in the surface two feet of soil. Low residual soil N levels usually result in crop responses to added N that are very dramatic making N fertilizer a highly profitable input. The large N requirements of stubbled-in winter wheat also makes N fertilizer a major cost factor, often exceeding 50 percent of the variable input costs. Consequently, N fertilization has an important influence on both the income and expense columns of the winter wheat balance sheet. For this reason, N fertilization of stubbled-in winter wheat has been the focus of numerous research studies in the past several years. These studies have identified a number of important factors that should be considered by producers when formulizing their fertilizer management strategies to produce Maximum Economic Yield of stubbled-in winter wheat.

14.2 A COMPREHENSIVE MANAGEMENT PACKAGE IS NECESSARY TO OBTAIN MAXIMUM ECONOMIC N FERTILIZER RESPONSE

Winter survival and a healthy, vigorous spring stand are required for economic fertilizer response with winter wheat. The winter survival potential of the hardiest winter wheat cultivars is not sufficient to ensure overwintering without snow cover protection on most of the Canadian prairies. Consequently, **strict** attention must be paid to management factors that maximize the winter hardiness potential of the crop and maintain a uniform snow cover during the coldest part of the winter.

No amount of N fertilizer will salvage a crop that has been winterkilled or severely winter damaged. In addition, any management factor that limits the yield potential of a crop that survives the winter will also result in reduced N fertilizer response and lower Maximum Economic Yields. In the stubbling-in production system, the most important management decisions are made before winter wheat seeding moves into high gear. For example, effective trash management, seeding at the optimum date and depth, and correcting phosphate deficiencies have a major influence on the degree of success that can be achieved in the production of stubbled-in winter wheat.

14.3 EARLY SPRING BROADCAST AMMONIUM NITRATE (34-0-0) GIVES THE HIGHEST, MOST CONSISTENT N RESPONSE

Significant N losses have been reported for surface applied urea (46-0-0), especially when broadcast on snow. These losses arise primarily through ammonia volatization (loss as a gas) that occurs before urea moves into the soil.

Nitrogen losses of more than 50 percent have been reported for fall and spring broadcast applications of urea in the absence of snow. When both fertilizer price and potential yield are considered, the nitrogen loss from broadcast urea can often be very costly. However, significant yield reductions with broadcast urea are only observed about 1/3 of the time indicating that specific weather conditions are required for volatization losses to occur. This means that potential losses with urea are as unpredictable as the weather. Consequently, losses with broadcast urea often cannot effectively be corrected for by simply increasing application rates to compensate for average losses.

Application of nitrogen fertilizer immediately after the soil has thawed in the spring has provided the most consistent, predictable grain yield response. When applied in the early spring, average grain yield responses have been 100 percent for broadcast ammonium nitrate (34-0-0), 90 percent for broadcast urea (46-0-0), 89 percent for urea banded on the soil surface, 88 percent for surface dribble banded urea-ammonium nitrate solution (28-0-0), and 81 percent for urea-ammonium nitrate solution applied as a spray.

Banding beneath the soil surface has been the main method of minimizing losses for N forms that are vulnerable to volatization. These N forms include anhydrous ammonia, aqua ammonia and urea.

Attempts to band fertilizer in the stubbled-in production system have exposed several problems and variables such as:

- precision of seed placement,
- horsepower requirements,
- seedbed disturbance,
- labour availability during seeding,
- time priorities,
- method of N application for other crops produced,
- type of drill required to seed other crops produced,
- ammonium nitrate availability,
- climatic factors, and
- relative cost of different N forms.

These and other factors must all be assessed before the best fertilizer management system can be identified for an individual producer.

14.4. **POST-HARVEST OPERATIONS THAT REDUCE THE SNOWTRAPPING POTENTIAL OF A STUBBLE FIELD, DRY OUT THE SEEDBED, OR DAMAGE THE WINTER WHEAT STAND MUST BE AVOIDED**

Height and density of stubble determine the snowtrapping potential of a stubble field and any post harvest operation, including fertilizer banding below the soil surface, that breaks down the stubble will increase the risk of winter damage. Soil moisture in stubble fields is also often limiting for germination and establishment of winter wheat. When soil moisture is poor, a fall banding operation prior to seeding may result in further moisture loss and poor seed germination. Excessive tillage associated with fertilizer banding during the seeding operation can also create similar problems.

If banding below the soil surface is done after emergence of the winter wheat there will be damage to the stand. This will result in greater susceptibility to winterkill, delayed maturity and increased weed competition.

Spring banding below the soil surface into established winter wheat stands will result in delayed maturity and increased weed competition.

14.5. SEED PLACEMENT MUST RECEIVE PRIORITY OVER FERTILIZER PLACEMENT

Shallow seeding (approximately one inch) into a firm, moist seedbed provides optimum seed placement for stubbled-in winter wheat. Improper seed placement can result in increased winterkill, later maturity and lower yields. For example, in the severe winterkill winter of 1984-85, a difference in seeding depth of one inch (2.5 cm) compared to two inches (5 cm) often meant the difference between a crop and no crop the following spring.

Accurate seed placement is often difficult to accomplish, especially when drill openers create considerable soil disturbance and seeding is followed by a rain or other factor resulting in furrow cave-in. Straw and chaff can present obstacles to proper seed placement with the stubbling-in production system. Consequently, most successful winter wheat producers invest in the equipment necessary to provide for chopping of straw and uniform spreading of straw and chaff to facilitate their seeding operations, thereby maximizing the opportunity for uniform stand establishment and winter survival. In addition, when selecting seeding equipment, they will remember that trash clearance and seed placement should not be sacrificed for fertilizer placement.

14.6. **KEEP THE WINTER WHEAT PRODUCTION SYSTEM AS SIMPLE AND STRAIGHTFORWARD AS POSSIBLE**

Stubbled-in winter wheat involves seeding directly into standing stubble with a no-till drill. Phosphate fertilizer, if required, should be applied with the seed. Winter annual weeds are sprayed for in the late fall or early spring. Nitrogen fertilizer should be applied by early spring at the latest. The crop is then harvested. While only minor changes appear to be required to accommodate winter wheat on a farm geared for spring crops, many producers have run into problems inserting winter wheat into their rotations. Most western Canadian farmers are not experienced in either the production of a crop with a winter growth habit or the no-till production system. Consequently, the production scheme for stubbled-in winter wheat presents a major change in management philosophy for most farmers. Unfortunately, this production system is often too simple for modern hi-tech agriculture and many of the production problems with winter wheat can be directly attributed to a tendency to make some of these operations overly complicated.

Most of the problems that producers have with the stubbling-in production system are associated with the seeding operation. Winter wheat is seeded in late August or early September. This often results in a conflict with harvesting of late-season, spring sown crops. Time means money during harvest and winter wheat seeding. Too much experimentation or excessive labor demands at this busy period are a sure formula for disaster. Forward planning and the postponement of operations that could be completed at a later date help to reduce these conflicts ensuring priority can be given to essential production steps, such as getting the seed into the ground properly at the optimum date.

Interest in fertilizer banding drills has accompanied the growth of winter wheat. While the concept of banding urea and urea based fertilizers during the seeding operation has merit because N losses with urea are reduced, most producers have had little or no experience with banding drills. Also, compared to conventional no-till drill openers, some types of banding drill openers increase the horsepower requirement per unit width of drill by 2 to 3 times, depending upon soil characteristics. This means that drill size has to be reduced by 1/2 to 2/3's, or tractor horsepower has to be increased by 2 to 3 times when the seeding of winter wheat is accompanied by N fertilizer banding with these openers. Therefore, the advantages gained from eliminating the need for a broadcast fertilizer application and reductions in urea N losses with banding during the seeding operation must be weighed against reduced horsepower requirements and quicker seeding when ammonium nitrate is broadcast later as a separate operation.

14.7 **RISK OF WINTER DAMAGE IS INCREASED WHEN N IS SEED PLACED**

The response of winter wheat to seed-placed N is dependent upon the N source, row spacing and opener type. Drill row spacing and opener type determine the concentration of fertilizer in the row and immediately adjacent to the seed. For instance, moving from a 6 to 12 inch row spacing has the effect of doubling the fertilizer concentration in each row while a disc opener places the fertilizer in a narrower band than a broad hoe opener.

Urea (46-0-0) and ammonium nitrate (34-0-0) are the two most common N forms that are seed placed. Urea has become the main form of granular N and many fertilizer distributors have little interest in stocking ammonium nitrate.

Field trials have indicated that, when placed in the seed row, both urea and ammonium nitrate can reduce seedling number and size, especially when the soil is dry at seeding. In the absence of winter damage, seed placement of 34-0-0 at 30,60 and 90 lbs N/acre in 3/4 inch wide seed rows spaced 8 inches apart has produced grain yields that are 100, 86 and 70% of comparable early spring broadcast N rates, respectively. The effect of seed-placed urea is more insidious and yield performance is often significantly lower than with ammonium nitrate. Placement of urea a minimum of one inch from the seed row will minimize seedling damage.

Table 1.The effect of seed-placed ammoniun nitrate (34-0-0)fertilizer on winter survival. The seed and fertilizer were placed in 3/4 inch wide rows spaced 8 inches apart in this study.

Seed placed N (lb/acre)	Subtract (FSI)
0	0
30	17
60	34
90	51

FSI = Field Survival Index.

Similar grain yield responses for 30 lb N/acre seed-placed and spring broadcast ammonium nitrate indicates that ammonium nitrate can be safely seed placed at low rates (see Chapter 12). However, even at low rates, increased damage to winter wheat stands has been observed following high stress winters (Table 1). The importance of this seed-placed N induced reduction in winter hardiness is emphasized by the following example. The reduction in winter survival potential with 30 lb/acre seed-placed N is equivalent to the difference in winter hardiness potential between Norstar (FSI=514) and Sundance (FSI=496) winter wheat cultivars (514-496=18). In other words, the winter survival advantage of Norstar over Sundance is eliminated if 30 lb/acre N is seed placed with Norstar. The use of high rates of phosphate fertilizer will not counteract the effect that seed row banded N has in reducing winter hardiness.

14.8 NITROGEN FERTILIZER MUST BE APPLIED BY EARLY SPRING TO ACHIEVE MAXIMUM N RESPONSE WITH WINTER WHEAT

Under average conditions, 90 percent of the total N accumulated by the winter wheat plant will have been taken up by the start of heading, which normally occurs near the 3rd week in June. Therefore, N fertilizer must be applied early in the season if Maximum Economic Yields are to be achieved. For maximum yield response and minimum N loss, broadcast N fertilizer should be applied as early as possible after the soil thaws in the spring. This increases the probability of subsequent rainfall moving the fertilizer N into the rooting zone before the soil N reserves become insufficient to meet the plants' N demands for healthy growth.

Yield responses to N will be small if the plants' early season demands are not met because of delays in N fertilization. A three week delay in spring N application has produced average grain yield responses that are only 69 percent of those observed when fertilizer is applied as soon as the soil thaws in the spring. Delaying N fertilizer application until early June often results in no grain yield response at all.

Poor yield responses from late May or early June N fertilization are often associated with increased grain protein percentages. However, percent protein is simply the ratio of grain protein yield to total grain yield and the higher percent protein is normally a result of the reduced grain yield response with late compared to early N application dates. Consequently, if protein premiums are available, rather than attempting to improve percent protein with late N fertilization, it is much more profitable to obtain both higher percent protein and grain yield by increasing early season N fertilizer rates.

Stranding of fertilizer N at the soil surface, due to dry weather following early spring broadcast applications, has the same effect as delaying N fertilizer application date. Late fall N fertilization avoids this problem. However, reduced grain yield and percent protein, attributed primarily to denitrification losses and immobilization, have been observed for fall applied broadcast N in regions with cool, damp weather conditions in early spring. Therefore, late fall broadcast N fertilization of dryland stubbled-in winter wheat should be restricted to the brown and dark brown soil zones where the risk of spring surface stranding are greatest and losses from denitrification are lowest.

14.9. **GROWING SEASON WEATHER CONDITIONS HAVE A LARGE INFLUENCE ON WINTER WHEAT N RESPONSE**

Winter wheat grain yield response to N is highest for the first pound of N added (Figure 1). After the initial increment of N, the grain yield N response gradually decreases reaching zero when maximum yield is achieved. The response becomes negative at excessively high N rates and there is a loss in grain yield for N added beyond that required for maximum yield.

The grain yield N response for each pound of added N is larger and the N requirement for maximum yield is higher when weather conditions create a high yield potential (Figure 1). This strong interdependence of N fertilizer grain yield response and weather demonstrates the difficulty there is in predicting the N fertilizer requirements for winter wheat. Because N responses are so dependent upon growing season weather, N requirement predictions are only going to be as good as our ability to predict the weather.

The influence of weather on stubbled-in winter wheat grain yield has been studied in detail in Saskatchewan. Evaporation during the two week period immediately prior to heading, root zone extractable soil water at heading and evaporation during the last two weeks in July were found to be the primary weather factors determining grain yield in these studies.

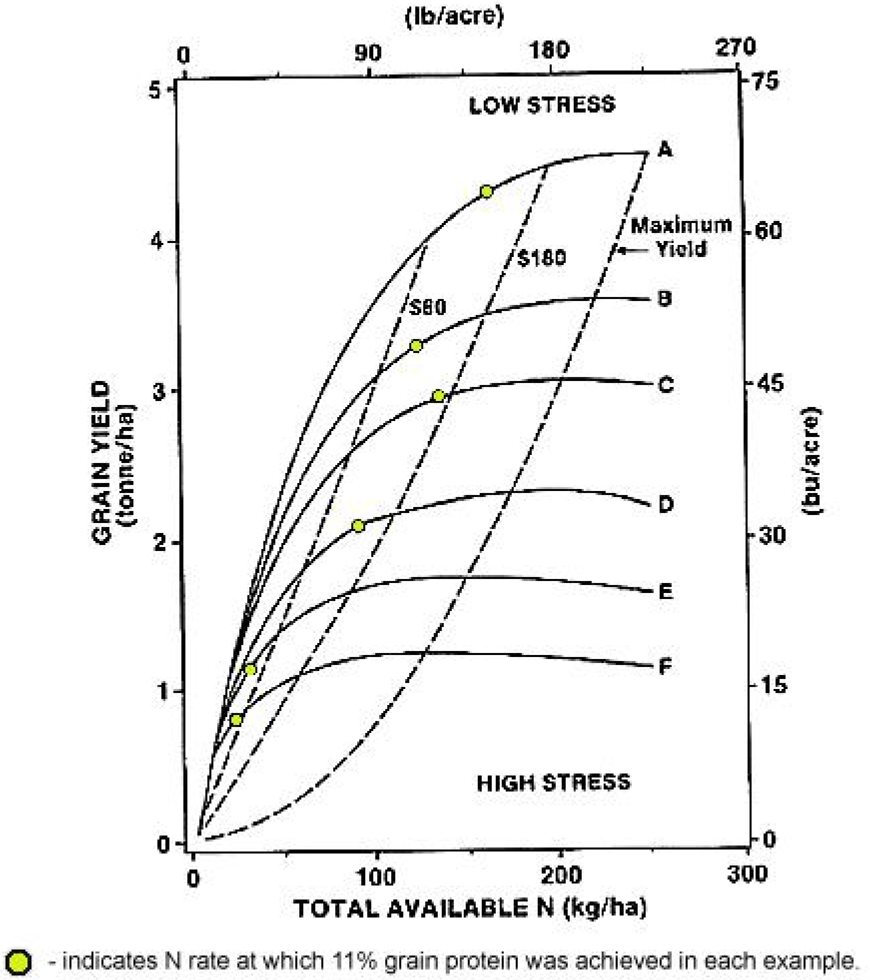


Figure 1. Norstar winter wheat grain yield response to total available N for six levels of drought stress. Intersect lines identify the N rates that give 1) maximum grain yield, 2) Maximum Economic Yield when wheat prices are $180 and 3) $60/tonne and N fertilizer price is $0.66/kg ($0.30/lb). Total available N = Soil test N for the surface two feet + fertilizer N.

Evaporation rates during the growing season generally increase gradually from May to July and then drop off quickly in August. On average, evaporation rates are highest in the southwest and lowest in the north and east of the agricultural region of western Canada. Consequently, maximum potential grain yield and N fertilizer requirements should increase as we move from the brown soil zone to black and grey soil zones.

The growth and development of winter wheat is normally 10 days to two weeks ahead of spring wheat and therefore coincides more favorably with the mean temperature and precipitation patterns experienced in western Canada. However, stubbled-in winter wheat is by definition a stubble crop. This makes it highly dependent upon precipitation that occurs between the harvest of the previous crop and pre-heading, the critical period for moisture availability.

Snow trapped in the standing stubble provides additional spring moisture that can be especially valuable to crop production following dry years. Consequently, moisture availability from fall rains and the snow trap can provide useful guides to decisions on N fertilizer rates. However, field studies have demonstrated that soil water reserves only contribute approximately

20 percent to the total annual water use indicating that, unless irrigation water is available, the yield potential of stubbled-in winter wheat is very dependent upon growing season rainfall. These studies also demonstrated that stubbled-in winter wheat often exhausts most of its available soil water reserves by heading. This makes later season growth even more dependent upon growing season rainfall. Because N has to be applied by early spring at the latest, this strong influence of growing season rainfall makes it extremely difficult to accurately determine N requirements for Maximum Economic Yield of stubbled-in winter wheat.

14.10 **GRAIN AND FERTILIZER PRICES INFLUENCE THE N RATES AT WHICH MAXIMUM ECONOMIC YIELDS OF STUBBLED-IN WINTER WHEAT ARE ACHIEVED**

The last few years have seen dramatic reductions in grain prices, especially for winter wheat where the price of #1 Canada Western Red Winter Wheat (CWRW) fell from $194/tonne in 1981/82 to $109/tonne in 1986-87 (basis Thunder Bay). Because grain yield N responses gradually decrease with increases in total available N, the largest returns are realized on the first increments of fertilizer N (Figure 2). For this reason price changes do not have a straight line influence on the "break-even" (marginal cost = marginal return) N fertilizer rates and as price per tonne of wheat increases the amount of N fertilizer required to achieve Maximum Economic Yield increases (Figure 1).

With most farm chemicals, such as herbicides, rates cannot be modified without compromising the performance of the chemical. Consequently, rate cutting is usually not an economic option for farmers faced with increases in the price of farm chemicals. However, not only is N fertilizer rate cutting an option, it is a requirement if Maximum Economic Yield is to be achieved following an N fertilizer price increase (Figure 3).

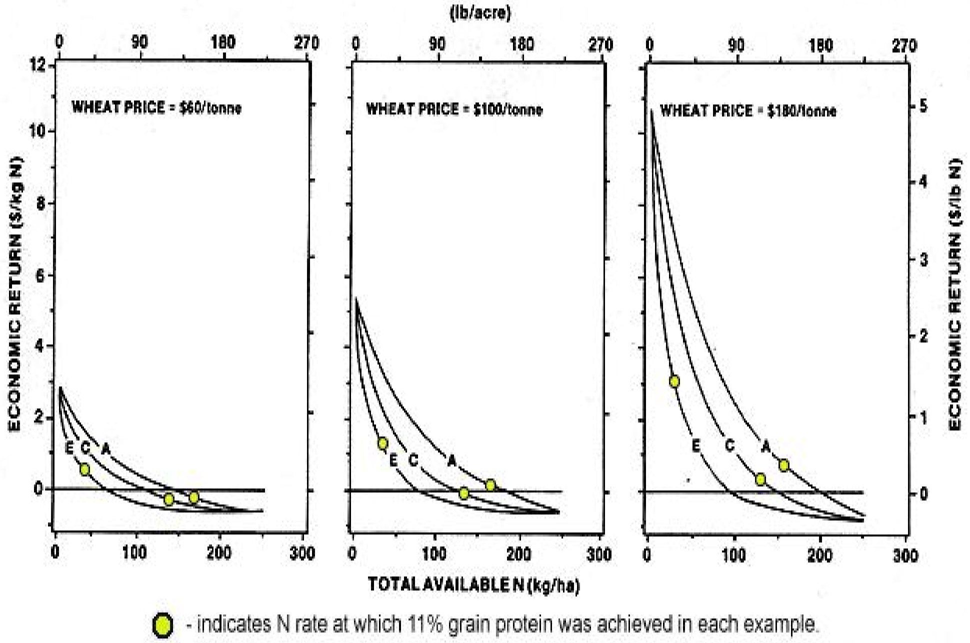


Figure 2. Economic return on N fertilizer ($/kg N) for three levels of drought stress (see Figure 1) when wheat prices are $60, 100 and 180/tonne and N fertilizer price is $0.50/kg ($0.23/lb).

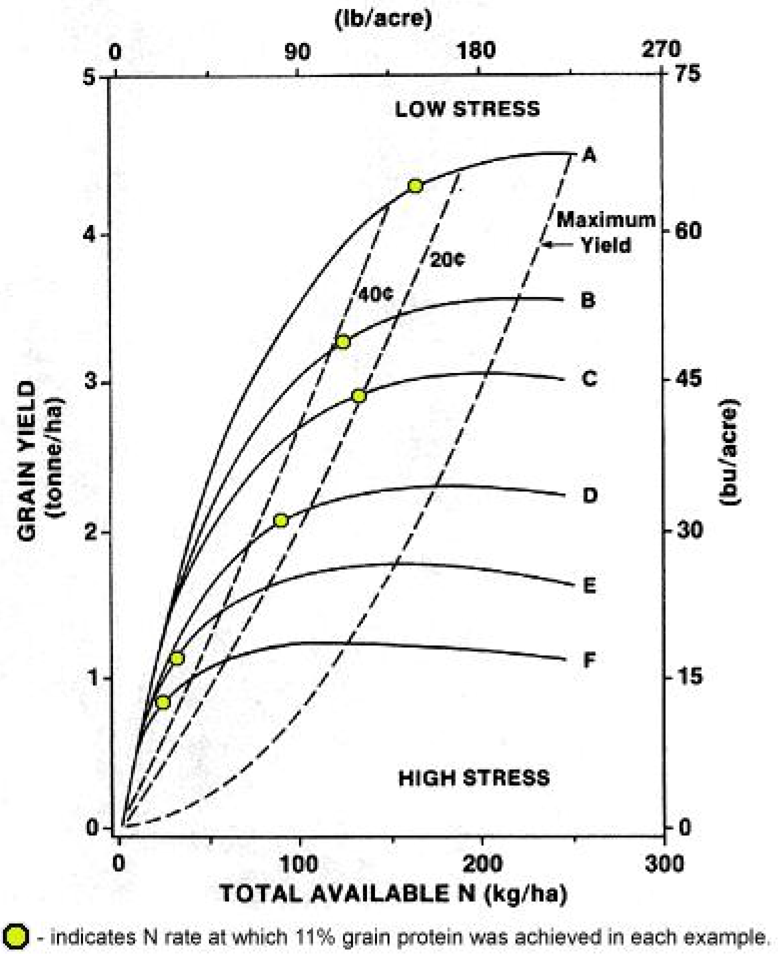


Figure 3. **Grain yield response to total available N for six levels of drought stress. Intersect lines identify the N rates that give 1) maximum grain yield, 2) maximum economic yield when N fertilizer prices are $0.44/kg ($0.20/lb) and 3) $0.88/kg ($0.40/lb) and wheat price is $100/tonne.**

HIGH N RATES ARE NECESSARY TO MAINTAIN QUALITY

Cereal protein contains approximately 17.5 percent protein. Because N is obtained from the soil, plant-available soil N also has a direct influence on grain protein yield. The ratio of grain protein yield to total grain yield determines grain protein concentration (percent protein). Consequently, the influence that N fertilizer has on this ratio determines its influence on percent grain protein.

The following general grain yield, grain protein and grain protein concentration N response patterns have been observed for winter wheat grown in Saskatchewan. There is a minimum N level for plant growth that results in a constant ratio of total grain yield to grain protein yield and a minimum grain protein concentration of approximately 8.0 percent protein. Consequently, when conditions are favorable for growth, the correction of severe N stress by the addition of fertilizer N produces a lag phase in the protein concentration N response curves (Figure 4).

Once cultivar yield potential or weather factors become limiting to growth and subsequent yield increases, excess N is utilized mainly for grain protein production and the protein concentration N response curve enters an increase phase. Maximum grain yield is achieved at N rates that coincide with the end of the increase phase of the protein concentration - N response curve (

Figure 4).

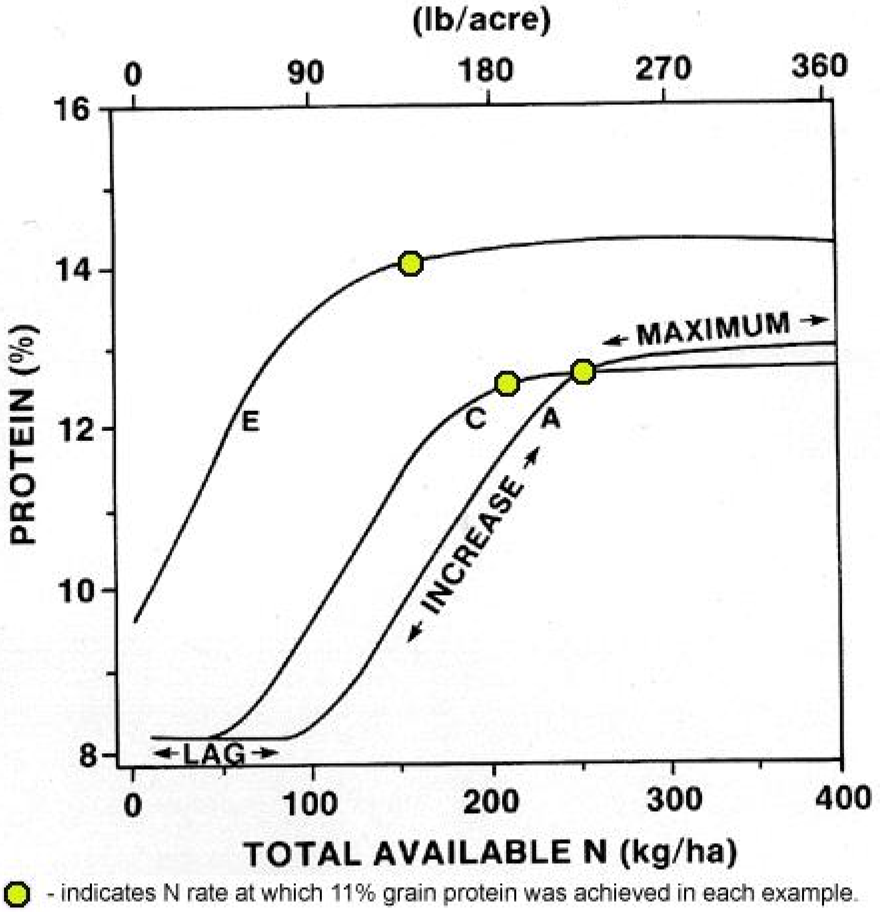


Figure 4. Percent grain protein response to total available N for three levels of drought stress (see Figure 1).

These observations indicate that high percent grain protein can only be achieved at N fertilizer rates that are in excess of those required for Maximum Economic Yield (Figures 1, 3, and 4). Under average to good weather conditions, the maximum N requirements of the winter wheat plant can be expected to have been met when the grain protein concentration N response curve reaches approximately 12.5 percent. The protein concentration N response curve will reach a maximum near this level unless spring environmental conditions favorable for plant growth and N uptake are followed by extreme drought that severely limits grain yield. Maximum protein concentrations ranging from 14.5 percent to 20 percent have been observed for Norstar winter wheat produced under these conditions.

It is clear from the above observations that, because most stubble fields are deficient in plant-available soil N, N fertilization is also required to maintain grain protein concentration at an acceptable level. Low percent protein (less than 11 percent) is reflected in a high frequency of "piebald", "yellow berry" or "starchy kernels" in a sample. If the frequency of piebald kernels is high, a sample will be degraded to No. 3 CWRW, which usually sells for the same price as feed wheat. Therefore, grain quality can become an important consideration in determining N fertilization rates required for Maximum Economic Yield (Figures 1, 2 and 3).

Identification of the N levels required for 11 percent protein in our examples has demonstrated that both reductions in grain price and increases in fertilizer price can shift the economic N rate curves below the N levels required for 11 percent grain protein concentration (Figures 1 and 3). Consequently, market opportunities and penalties for low protein concentration, such as degrading to feed wheat prices, or premiums for high protein concentration should receive attention when determining N fertilizer requirements for Maximum Economic Yield of winter wheat.

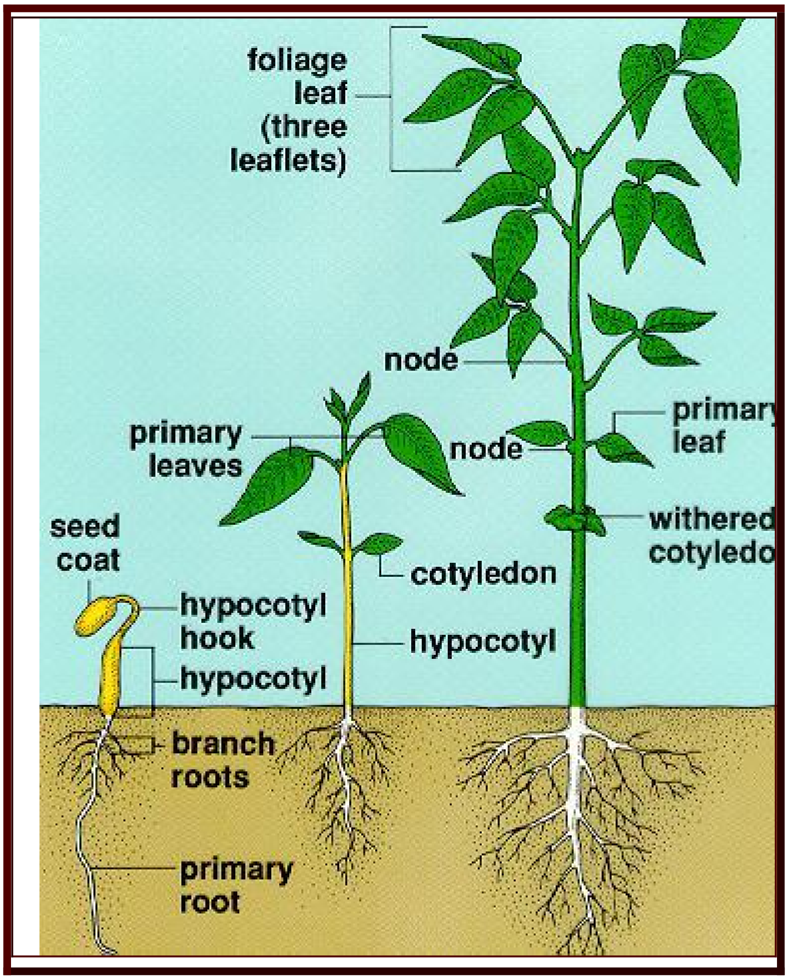
Chapter 15 Growth Stages of Soybean Plant

Growth, development and yield of soybeans are a result of a variety's genetic potential interacting with environment and farming practices. Correct production decisions using plant growth staging and timing are important for successful soybean production. Minimizing environmental stress will optimize seed yield. Farmers who understand how a soybean plant grows and develops can establish their field practices to maximize the genetic potential of the varieties grown. Management practices that may influence crop growth include seedbed preparation, variety selection, planting rate, planting depth, row width, pest management (diseases, insects and weeds), fertilization and harvesting.

As soybean seed takes on the water and swells, the radical is the first part of embryo to penetrate the seed coat . it develops rapidly into a root which must become firmly anchored for seedling to develop enough leverage to force its way to the soil surface. Lateral roots are formed soon after the radical or primary root begins to elongate. Root Hair appear on the primary root with in 4 or 5 days after germination and on the lateral roots soon after they are formed . These hair are the main absorbing surface of the root system. They are very small nearly invisible without a lens and might be extensions of single epidermal cells. They are actively growing part of the root just behind the growing point.

Short day length and warm temperatures control soybean flowering. Soybeans must reach at least the first trifoliolate in growth before they can be induced to flower.

A fully developed leaf node for the vegetative stages has a leaf above it with unrolled or unfolded leaflets. These unfolded leaflets have their edges no longer touching. Stages are counted from the unifoliolate leaf node and upward. All other stages have true leaves that are trifoliolate and produced singularly on different nodes with these leaves alternating on the stem. The reproductive stages are divided into 4 parts: R1 and R2 describe flowering; R3 and R4 describe pod development; R5 and R6 describe seed development; and R7 and R8 describe plant maturation.



Identifying Stages of Development

The staging system employed here divides plant development into vegetative (V) and reproductive (R) stages (table 1). The eight subdivisions of the R stages are designated numerically with their common names in below.

Vegitative Stages	Reproductive Stages
	R1(beginning bloom)
VE (emergence)	R2 (full bloom)
VC (cotyledon stage)	R3 (beginning pod)
V1 (first trifoliolate)	R4(full pod)
V2(Second trifoliolate)	R5 (beginning seed)
V3(Third trifoliolate)	R6(full size seed)
V(n)(nth trifoliolate)	R7 (beginning maturity)
V6(flowering will start)	
	R8 (full maturity)

This system accurately identifies the stages of a soybean plant. However, all plants in a given field will not be in the same stage at the same time. When staging a field of soybeans, each specific V or R stage is defined only when 50 percent or more of the plants in the field are in or beyond that stage.

15.1 VEGETATIVE STAGES AND DEVELOPMENT

15.1.1. Germination and Emergence

The planted soybean seed begins germination by absorbing water in amounts equal to about 50 percent of its weight. The radical or primary root is first to grow from the swollen seed (see fig. 3) where it elongates downward and anchors itself in the soil. Shortly after initial primary root growth, the hypocotyl (small section of the stem between the cotyledonary node and the primary root; see fig. 1), begins elongation toward the soil surface pulling the cotyledons (seed leaves) with it. The anchored primary root and elongating hypocotyl provide leverage for pulling the cotyledons to the soil surface for VE or emergence, fig. 3. VE typically occurs 1 to 2 weeks after planting, depending on soil moisture, soil temperature, and planting depth. Lateral roots begin to grow from the primary root just prior to emergence.

Shortly after VE, the hook-shaped hypocotyl straightens out and discontinues growth as the cotyledons fold down. The unfolding of the cotyledons exposes the growing epicotyl (young leaves, stem, and growing point located just above the cotyledonary node). The subsequent expansion and unfolding of the unifoliolate leaves marks initiation of the VC stage, which is followed by the numbered (nodal) V stages.

Nutrients and food reserves in the cotyledons supply the needs of the young plant during emergence and for about 7 to 10 days after VE, or until about the V1 stage. During this time, the cotyledons lose 70 percent of their dry weight. Loss of one cotyledon has little effect on the young plant's growth rate, but loss of both cotyledons at or soon after VE will reduce yields 8 to 9 percent.

After V1, photosynthesis by the developing leaves is adequate for the plant to sustain itself.

New V stages will appear about every 5 days from VC through V5, and every 3 days from V5 to shortly after R5 when the maximum number of nodes is developed.

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In most cases, soybeans should be planted at a depth of 2.5 to 3.8 cm (1 to 11/2 inches) and never deeper than 5.1 cm (2 inches). The ability of the germinating soybean seedling to push through a crusted soil decreases with deeper planting. Some varieties are especially sensitive to deep planting. In addition, the cooler soil temperatures at greater depths cause slower growth and decreased nutrient availability.

Small amounts of fertilizer placed in a band 2.5-5.1 cm (1 to 2 inches) to the side and slightly below the seed may stimulate early plant growth if soil temperatures are still cool. Roots are not attracted to this fertilizer band, so the fertilizer must be placed where the roots will be. Fertilizer placement too near or with the seed can injure the young plant.

Weeds compete with soybeans for moisture, nutrients, and sunlight. Tillage operations, herbicides, uniform stands, and crop rotations are useful methods for controlling weeds. The rotary hoe is an excellent tool for early weed control before and shortly after the soybeans have emerged .

Seed inoculation with Rhizobium japonicum bacteria is generally not recommended unless the field has never grown soybeans, or has not grown soybeans for the past 5 or more years.

15.1.2. Cotyledon Stage (VC)

The VC stage is begun when these unifoliolate leaves are fully expanded. During the VC stage, the cotyledons supply the nutrient needs of the young plant (for about seven to 10 days). The cotyledons will lose about 70% of their dry weight to this nutrient reallocation. If one cotyledon is lost during this time, there is little affect on the plant's growth rate. However, loss of both cotyledons at or soon after VE will reduce yields 8-9%. Later, after V1, photosynthesis in the developing leaves allows the plant to sustain itself. New V stages will now begin appearing around every three to five days through V5 and then every two to three days from V5 to shortly after R5 when node number usually reaches a maximum.

15.1.3. First trifoliolate (V1)

This stage is achieved when the first trifoliolate is fully emerged and opened. The V stages after VC are defined and numbered by the upper, fully-developed leaf node on the main stem (the stage is numbered by fully-developed trifoliolates). Trifoliolate leaves on branches are not counted when determining V stages, only the trifoliolates off the main stem are used in the count.

fig. 3, fig. 1

15.1.4 V2 Stage (second node)

At the V2 stage, the plants are 15.2 to 20.3 cm (6 to 8 inches) tall and three nodes have leaves with unfolded leaflets (the unifoliolate node and the first two trifoliolate leaf nodes), fig. 4.

Soybean roots normally become infected with Rhizobium japonicum bacteria, which cause formation of round or oval shaped root growths termed nodules, fig. 1 and 5. Millions of these bacteria are located within each nodule and provide much of the soybean plant's nitrogen supply through a process called nitrogen fixation. Through nitrogen-fixation, the bacteria change nonavailable N_2 gas from the air into nitrogen products that the soybean plant can use. The plant in turn provides the bacteria's carbohydrate supply. A relationship such as this, where both the bacteria and plant profit from the other, is called a symbiotic relationship. Nodules actively fixing nitrogen for the plant appear pink or red on the inside (fig. 6) , but are white, brown, or green if N-fixation is not occurring.

Under field conditions, nodule formation can be seen shortly after VE, but active nitrogen-fixation does not begin until about the V2 to V3 stages. After this, the number of nodules formed and the amount of nitrogen fixed increases with time until about R5.5 (midway between R5 and R6) when it decreases sharply.

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Nitrogen fertilization of soybeans is not recommended because it generally does not increase grain yields. The total number of root nodules that form decreases proportionately with increasing amounts of applied N. In addition, N fertilizer applied to a soybean plant with active nodules will render the nodules inactive or inefficient proportionately to the amount of N applied. Thus, the soybean plant can utilize both fixed N from bacteria and soil N (both mineralized and fertilizer N), but soil N is utilized over fixed N if available in large amounts.

At V2, the lateral roots are proliferating rapidly into the top 15 cm (6 inches) of soil between the rows, and by V5 will completely reach across a 76 cm (30-inch) row. Because these roots are growing close to the soil surface, cultivation to control weeds should be shallow.

fig. 1, fig. 4, fig. 5, fig. 6

15.1.5. V3 and V5 Stages (third and fifth nodes)

Plants at V3 are 18-23 cm (7-9 inches) tall and four nodes have leaves with unfolded leaflets, fig. 7.

Plants at V5 are about 25.4-30.5 cm (10-12 inches) tall and six nodes have leaves with unfolded leaflets, fig. 8.

The upper angle junction between the main stem and a leaf petiole is called an axil. In each axil is an axillary bud (fig. 1), which is similar in nature to the main stem growing point. This bud, however, may develop into a branch, develop into a flower cluster and finally pods, or it may remain dormant (inactive).

The number of branches that develop increases with wider row spacings and lower plant densities, depending on the variety grown. From zero to six branches typically develop under field conditions. Generally the largest branch is the lowest on the main stem and progressively smaller branches develop farther up. Each branch develops trifoliolate leaves, nodes, axils, axillary buds, flowers, and pods similar in nature to the main stem. The first branch beginning to develop can be seen in the axil of the first trifoliolate leaf node in fig. 7.

At about two node stages (one week) from R1, or at V5 in this publication, the axillary buds in the top stem axils appear bushy and are beginning to develop into flower clusters called racemes. A raceme is a short, stem-like structure that produces flowers and finally pods along its length, see fig. 21.

The total number of nodes that the plant may potentially produce is set at V5. The potential total number of nodes that an indeterminate type soybean plant may produce is always higher than the actual number of nodes that fully develop (have a leaf on the node above with unfolded leaflets).

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The axillary buds of the unifoliolate and trifoliolate leaves and of the cotyledons, allow a tremendous capacity for the soybean plant to recuperate from damage such as hail. The stem apex, or tip growing point, normally exhibits dominance over the axillary buds (axillary growing points) during vegetative growth of the plant. If the stem apex is severed or broken off along with part of the stem, however, the remaining axillary buds are released from this dominance and branches grow profusely. The plant, therefore, has the ability to produce new branches and leaves after hail destroys almost all of the above ground foliage. Severing the plant below the cotyledonary node kills it because there are no axillary buds below this node.

fig. 1, fig. 7, fig. 8, fig. 21

15.1.6. V6 Stage (sixth node)

Plants at V6 are 30.5 to 35.6 cm (12 to 14 inches) tall, fig. 9. Seven nodes have leaves with unfolded leaflets and both of the unifoliolate leaves and cotyledons may have senesced and fallen from the plant at this time. New V stages are now appearing every 3 days.

Lateral roots are present completely across row spacings of 76 cm (30 inches) or less by this stage.

Fifty percent leaf loss at V6 reduces yield approximately 3 percent.

15.2.1. R1 Stage (beginning bloom)

Plants at R1 are 38 to 46 cm (15 to 18 inches) tall and are vegetatively in the V7 to V10 stage (7 to 10 nodes fully developed). Flowering begins on the third to sixth node of the main stem, depending on the V stage at the time of flowering, and progresses upward and downward from there. The branches begin flowering a few days later than the main stem. Flowering on a raceme occurs from the base to the tip, see fig. 12. Basal raceme pods are thus always more mature than pods from the raceme tip, see fig. 21. Flowering and pod set mostly occur on primary racemes, but secondary racemes may develop to the side of the primary raceme in the same axil. The appearance of new flowers peaks between R2.5 and R3, and is, almost complete by the R5 stage.

At R1, vertical root growth rates sharply increase and stay relatively high to the R4 to R5 stage. Proliferation of secondary roots and root hairs within the top 0 to 23 cm (0 to 9 inches) of soil is extensive during this period also but roots in this zone generally begin to degenerate thereafter.

fig. 12, fig. 21

15.2.2. R2 Stage (full bloom)

Plants at R2 are 43 to 56 cm (17 to 22 inches) tall and are in the V8 to V12 stage. At this stage, the plant has only accumulated about 25 percent of its total mature dry weight and nutrients, attained about 50 percent of its mature height, and has produced about 50 percent of its total mature node number. This stage marks the beginning of a period of rapid and constant daily dry matter and nutrient accumulation rates (see figures 38, 39, 40 and 41) by the plant that will continue until shortly after the R6 stage. This rapid accumulation of dry weight and nutrients by the whole plant initially occurs in the vegetative plant parts (leaves, stems, petioles, and roots), but accumulation gradually shifts into the pods and seeds as they begin to develop, and as vegetative parts finalize their development. In addition, the rate of nitrogen-fixation by the root nodules is also increasing rapidly by the R2 stage. Figure 14 shows that a large number of root nodules may develop on a single plant.

Roots are present completely across the inter-row space of 102 cm (40 inch) rows by R2 and growth of several major lateral roots has turned downward by this time. These major lateral roots along with the tap root continue to elongate deeply into the soil profile until shortly after the R6.5 stage.

Fifty percent defoliation at this stage reduces yield about 6 percent.

fig. 38, fig. 39, fig. 40, fig. 41

15.2.3. R3 Stage (beginning pod)

Plants at R3 are 58 to 81 cm (23 to 32 inches) tall and are in the V11 to V17 stage. It is not uncommon to find developing pods, withering flowers, open flowers, and flower buds on the same plant at this time. Developing pods are located on the lower nodes where flowering first began.

If plant densities are adequate, yield (total seed weight) can be divided into three components: the total number of pods produced per plant, the number of beans produced per pod, and the weight per bean (seed size). Yield increases or decreases may be described as increasing or decreasing one or more of these three components.

Yield increases most generally result from increases in total number of pods per plant, especially large yield increases. The upper limits on number of beans per pod and seed size are genetically confined; however, these two components can still fluctuate enough to produce sizable yield increases.

Stressful conditions such as high temperature or moisture deficiency reduce yield due to reduction in one or more of the components. Reductions in one component, however, may be compensated by another component so yields are not significantly changed. Which yield component is reduced or increased depends on the R stage of the plant when the stress occurs. As the soybean plant ages from R1 through R5.5, its ability to compensate after a stressful condition decreases, and the potential degree of yield reduction from stress increases.

Management Guides R1 - R3

Under Corn Belt conditions, about 60 to 75 percent of all soybean flowers produced typically abort and never contribute to yield. About half of this abortion occurs before the flowers develop into young pods, and the other half is due to pod abortion. The over production of flowers and pods and the extended period of flowering (from R1 to R5) seems desirable because it offers a degree of escape from short periods of stress. Stressful conditions (which cause even higher abortion rates) from R1 through R3 generally do not reduce yields greatly because some flowers (and finally pods) can still be produced until R5 to compensate. In addition, stress at these stages may result in an increase in the number of beans per pod and weight per bean, which also help compensate for the aborted flowers and young pods.

Scientists and producers haven't learned to take full advantage of the soybean plant's potential. Practices such as fertilization, narrow rows, proper planting rates, irrigation, and weed control are all attempts to reduce the amount of floral and pod abortion and thus increase yields.

15.2.4. R4 Stage (full pod)

At stage R4 a pod is 2 cm (3/4 inch) long at one of the four uppermost nodes on the main stem with a fully developed leaf, fig. 17 and fig. 18.

Plants at R4 are 71 to 99 cm (28 to 39 inches) tall and are in the V13 to V20 stage. This period is characterized by rapid pod growth and by beginning seed development.

The period from R4 to shortly after R5.5 is a period of rapid steady dry weight accumulation by the pods. Some individual pods on the lower nodes of the main stem are full size or close to full size now (fig. 18), but many pods will be full size by the R5 stage, see fig. 25. Pods normally attain most of their length and width before the beans begin to develop rapidly, see fig. 27. Thus, toward the end of this period, some beans within the lower node pods have begun rapid growth.

Some of the last flowering to occur on the plant is at the main stem tip where a floral cluster appears, fig. 20. This cluster consists of axillary flowers bunched together from the tip nodes that haven't separated. Flowering at the upper nodes of the branches is also the last to occur on the plant.

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The R4 stage marks the beginning of the most crucial period of plant development in terms of seed yield determination. Stress (moisture, light, nutrient deficiencies, frost, lodging, or defoliation), occurring anytime from R4 to shortly after R6, will reduce yields more than the same stress at any other period of development. The period from R4.5 (late pod formation) to about R5.5 is especially critical because flowering becomes complete and can not compensate, and because young pods and seeds are more prone to abort under stress than older pods and seeds. Yield reductions at this time result mainly from reductions in total pod numbers per plant, with lesser reductions occurring in beans per pod and possibly seed size. Seed size may actually compensate somewhat if growing conditions are favorable after R5.5. However, compensation by seed size is genetically limited. Thus, the plant essentially has limited ability to compensate for abortion-causing stresses that occur during R4.5 to R5.5.

Where possible, irrigate to ensure adequate moisture during these crucial periods.

fig. 17, fig. 20, fig. 25, fig. 27

15.2.5. R5 Stage (beginning seed)

Plants at R5 are 76 to 109 cm (30 to 43 inches) tall and are in the V15 to V23 stage. This period is characterized by rapid seed growth or seed filling, fig. 27 and 28, and redistribution of dry weight and nutrients within the plant to the growing seeds, see fig. 38, 39, and 40.

At initial R5, reproductive development ranges from flowers just open to pods containing seeds 8 mm long, fig. 27. Midway between the R5 and R6 stages, several events occur close to the same time. At about R5.5: (1) the plant attains its maximum height, node number, and leaf area; (2) the high nitrogen fixation rates peak and begin to drop rapidly; and (3) the seeds begin a period of rapid, steady, dry weight, and nutrient accumulation. Shortly after R5.5 dry weight and nutrient accumulation in the leaves, petioles, and stems maximizes and then be gins to redistribute (relocate) from these plant parts to the rapidly developing seeds. The period of rapid, steady seed dry weight accumulation continues until shortly after R6.5, during which time about 80 percent of the total seed dry weight is acquired.

Seed yields depend upon the rate of dry weight accumulation in the seeds and the length of time that dry weight accumulates in the seeds. There is often relatively little difference between adapted varieties in the rate of dry weight accumulation, but they do vary in the length of time that dry weight accumulates in the seeds. Stress may influence both the rate and length of time that dry weight accumulates in seeds.

Management Guides

Demand for water and nutrients is large throughout the rapid seed filling period. During this entire period, the beans acquire about half of their N, P, and K by redistribution from vegetative plant parts, and about half by soil uptake and nodule activity. This redistribution of nutrients from plant parts occurs regardless of the soil nutrient avail ability. Water deficiencies may reduce nutrient availability because roots cannot take up nutrients or grow in upper soil areas where the soil dries. Thus, at least part of the P and K must be located where the soil will likely be moist and the nutrients will be available to the plant.

One hundred percent leaf loss (such as by hail) anytime between R5.0 to R5.5 can reduce soybean yields by about 75 percent. Stress conditions occurring from the R5.5 to R6 period also may cause large yield reductions. Yield reductions during R5.5 to R6 occur mainly as fewer pods per plant and fewer beans per pod; and to a lesser degree, as less weight per bean.

fig. 27 , fig. 28, fig. 38, fig. 39, fig. 40

15.2.6. R6 Stage (full seed)

Plants at R6 are 79 to 119 cm (31 to 47 inches) tall and are in the V16 to V25 stage. Because plant height and node number maximized at about R5.5, little increase in these factors is evident between R5 and R6.

The R6 bean or "green bean" (fig. 31) is characterized by width equal to its pod cavity; however, beans of all sizes, as in fig. 27 and 28, may be found on the plant at this time. Total plant pod weight maximizes at about R6.

Growth rate of the beans and whole plant at R6 is still very rapid. This rapid rate of dry weight and nutrient accumulation begins to slow in the whole plant shortly after R6, and at shortly after R6.5 in the seeds. Dry weight and nutrient accumulation maximizes in the whole plant shortly after R6.5 and in the seeds at about R7, fig. 38, 39, and 40.

Rapid leaf yellowing (visual senescence) over the plant begins shortly after R6 and continues rapidly to about R8, or until all leaves have fallen. Leaf senescence and falling begins on the older lowest node leaves, and subsequently spreads upward to the younger leaves. Three to six trifoliolate leaves may have already fallen from the lowest nodes before rapid leaf yellowing begins.

Root growth is essentially complete shortly after R6.5.

fig. 27, fig. 28, fig. 31, fig. 38, fig. 39

15.2.7. R7 Stage (beginning maturity)

Physiological maturity of an individual soybean seed occurs when the accumulation of dry weight ceases. This first occurs when the seed (and generally the pod) turns or has completely lost all green color Although not all pods on the R7 plant (fig. 32 and 33) have lost their green color the plant is essentially at physiological maturity because very little additional dry weight will be accumulated. The soybean seed at physiological maturity is about 60 percent moisture and contains all necessary plant parts to begin the next generation soybean plant.

Figure 34 displays a green R6 pod and beans, a completely yellow pod and beans at physiological maturity and a pod and beans at mature color ready for harvest.

Management Guides R6-R7

As pods and seeds mature, they become less prone to abort. As a result, the total number of pods per plant and number of beans per pod gradually become set with plant maturity. Although an older seed may not abort (fall from the plant) under stressful conditions, the length of the period of rapid seed dry weight accumulation may be shortened, which in turn causes smaller seed size and reduced yields.

As the soybean plant matures past R6, the potential degree of yield reduction by stress gradually declines. From R6 to R6.5 stress may cause large yield reductions mostly by reducing seed size, but also by reducing pods per plant and beans per pod. Yield reductions from stress occurring from R6.5 to R7 are much smaller because the seeds have already accumulated a sizable portion of their mature dry weight. Stress occurring at R7 or thereafter essentially has no effect on yield.

Fig.35 shows the redirection of leaf growth toward the sun after a soybean plant partially lodges. The tendency for lodging increases as plants grow taller. High plant populations, irrigation, and high seasonal rainfall increase plant height and lodging. Lodging reduces yields by causing increased harvest losses and inefficient use of sunlight by the plan.

fig. 32, fig. 33, fig. 34, fig. 35

15.2.8. R8 Stage (full maturity)

Ninety-five percent of the pods have reached their mature pod color, fig. 36. Five to 10 days of drying weather are required after R8 before the soybeans have less than 15 percent moisture.

Figure 37 displays the sequence of color and size changes the soybean pod and beans undergo from the green R6 beans (left) to the mature beans ready for harvest (right). The second from right pod and beans in fig. 37 are at their mature color, but have not attained their harvest shape and moisture content. Thus, mature pod color does not always indicate harvestable readiness of the beans within. With favorable drying weather, soybeans will lose moisture quickly.

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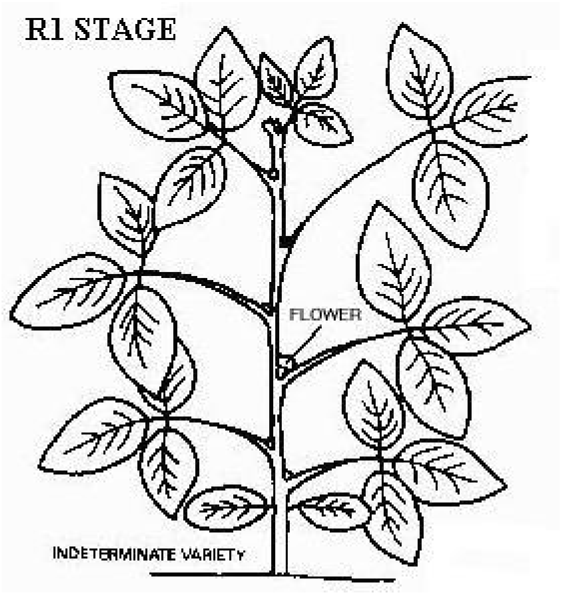
Sub-optimum plant densities become readily apparent at harvest time. Above-optimum plant densities cause lodged plants that are difficult to harvest, thus leaving potential yield in the field. Below-optimum plant densities cause branching and low pod set. Heavily podded branches may break off easily and fall to the ground. Also, pods produced very close to the ground are difficult or sometimes impossible to harvest mechanically.

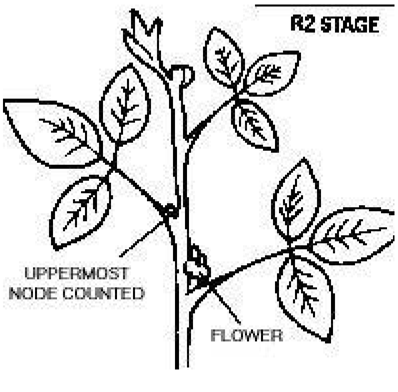
Timeliness of harvest is very crucial for soybeans. Ideal bean moisture content at harvest and for storage 13 percent. Although harvest may begin at higher moisture percentages, some drying costs will be encountered for safe storage. In contrast, harvest delayed to less than 13 percent moisture causes increased pre-harvest shatter loss, sickle-bar shatter loss during harvest, increased number of split beans, and loss of weight to sell.

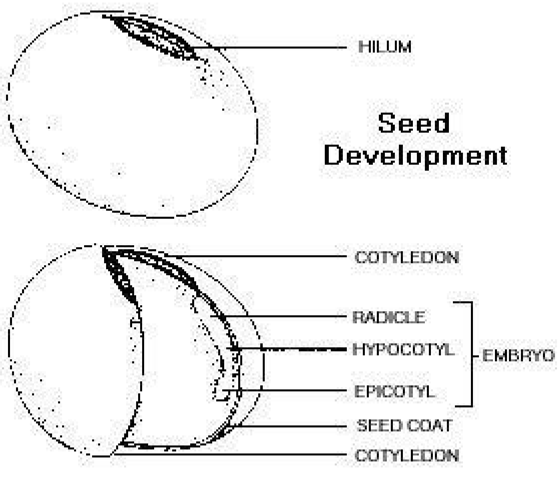
To reduce harvest losses: drive at proper speed, and check concave clearance, cylinder speed, sieves, and air velocity. Be sure reel speed and ground travel are synchronized to minimize sickle-bar shatter loss. Leave a short stubble. A 9 cm (3.5 inch) stubble contains 5 percent of the crop; a 16.5 cm (6.5 inch) stubble, 12 percent.

fig. 36

fig. 37







Chapter 16 Growth Stages of Rice

16.1. **Overview and Objectives**

This reference guide discusses the growth stages of the rice plant. The information presented is based on the data and characteristics of IR64, a modern, high-yielding, semidwarf variety, but applies generally to other rice varieties.

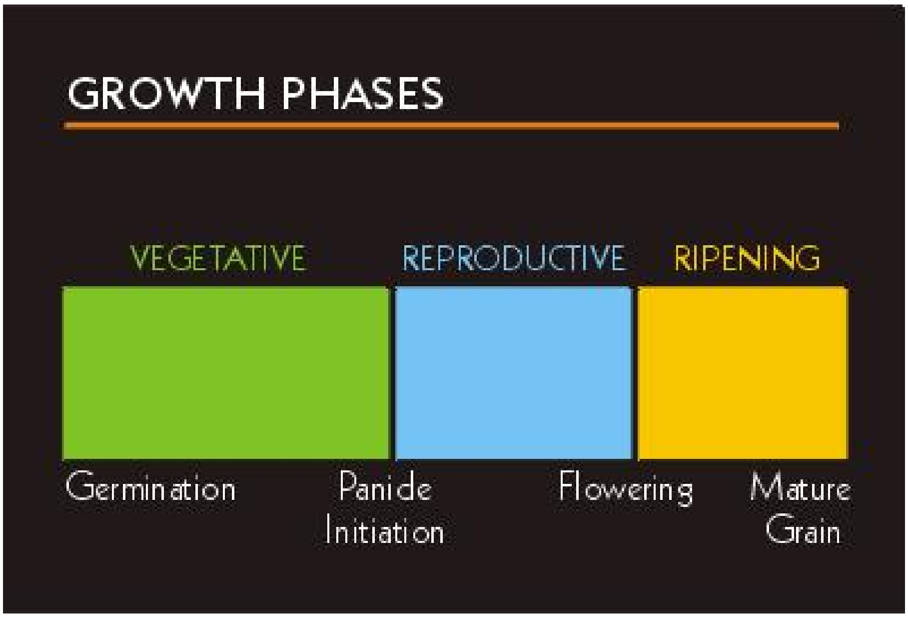
This reference guide will enable you to:

- recognize the 3 basic growth phases of the rice plant and the stages of development in each phase.
- identify the growth stages of a rice plant according to a 0-9 numerical scale. Each number in the scale corresponds to a specific growth stage.
- explain the specific physical changes in a growing rice plant.

Three growth phases

The growth of the rice plant is divided into three phases:

1. **vegetative** (germination to panicle initiation);
2. **reproductive** (panicle initiation to flowering); and
3. **ripening** (flowering to mature grain)



- In the tropics, the reproductive phase is about 35 days and the ripening phase is about 30 days.
- The differences in growth duration are determined by changes in the length of the vegetative phase.
- For example, IR64 which matures in 110 days has a 45-day vegetative phase, whereas IR8 which matures in 130 days has a 65-day vegetative phase.

Growth stages 0-9

These 3 growth phases consist of a series of 10 distinct stages. These stages are numbered and described as follows:

Stage 0 is from germination to emergence:

Stage 1 is called seedling:

Stage 2, tillering:

and Stage 3 is stem elongation:

These first 4 stages make up the **vegetative phase**, the first phase of rice plant growth.

Stage 4 is panicle initiation to booting:

Stage 5 is heading or panicle exsertion:

and Stage 6 is flowering:

Stages 4, 5, and 6 constitute the **reproductive phase**, the second phase of rice growth.

Stage 7 is the milk grain stage:

Stage 8, the dough grain stage:

and Stage 9, the mature grain stage:

Stages 7 through 9 correspond to the **ripening phase**, the last phase in the development of the rice plant.

16.2. Vegetative Phase

Stage 0 - Germination to emergence

Seeds are usually pregerminated by soaking for 24 hours and incubating for another 24 hours. After pregermination the radicle and plumule protrude through the hull.

By the second or third day after seeding in the seedbed, the first leaf breaks through the coleoptile.

The end of stage 0 shows the emerged primary leaf still curled and an elongated radicle.

16.2.1. Stage 1 - Seedling

The seedling stage starts right after emergence and lasts until just before the first tiller appears. During this stage, seminal roots and up to five leaves develop.

As the seedling continues to grow, two more leaves develop. Leaves continue to develop at the rate of 1 every 3-4 days during the early stage.

Secondary adventitious roots that form the permanent fibrous root system rapidly replace the temporary radicle and seminal roots.

This is an 18-day-old seedling ready for transplanting. The seedling has 5 leaves and a rapidly developing root system.

16.2.2. Stage 2 - Tillering

This stage extends from the appearance of the first tiller until the maximum tiller number is reached.

Tillers emerge from the axiliary buds of the nodes and displace the leaf as they grow and develop.

This seedling shows the position of the two primary tillers with respect to the main culm and its leaves.

After emerging, the primary tillers give rise to secondary tillers. This occurs about 30 days after transplanting.

The plant is now increasing in length and tillering very actively. Here is a field with plants at the early tillering stage. Note the tiller size and canopy development due to increased leafing and tiller development.

Besides numerous primary and secondary tillers, new tertiary tillers arise from the secondary tillers as the plant grows longer and larger.

By this stage, the tillers have multiplied to the point that it is difficult to pick out the main stem. Tillers continuously develop as the plant enters the next stage which is stem elongation.

16.2.3. Stage 3 - Stem elongation

This stage may begin before panicle initiation or it may occur during the latter part of the tillering stage. Thus, there may be an overlap of stages 2 and 3.

The tillers continue to increase in number and height, with no appreciable senescence of leaves noticeable. Ground cover and canopy formation by the growing plants have advanced.

Growth duration is significantly related to stem elongation. Stem elongation is more in varieties with longer growth duration. In this respect, rice varieties can be categorized into two groups: the short-duration varieties which mature in 105-120 days and the long-duration varieties which mature in 150 days.

In early-maturing semidwarfs like IR64, the fourth internode of the stem, below the point where the panicle emerges, elongates only from 2 to 4 cm before panicle initiation becomes visible. This slide shows stems which have been dissected to show the length of the fourth internode at the panicle initiation stage.

Maximum tillering, stem elongation, and panicle initiation occur almost simultaneously in short-duration varieties (105-120 days).

In long-duration varieties (150 days), there is a so-called lag vegetative period during which maximum tillering occurs. This is followed by stem or internode elongation, and finally by panicle initiation.

16.3. Reproductive Phase

16.3.1. Stage 4 - Panicle initiation to booting

The initiation of the panicle primordium at the tip of the growing shoot marks the start of the reproductive phase. The panicle primordium becomes visible to the naked eye about 10 days after initiation. At this stage, 3 leaves will still emerge before the panicle finally emerges.

In short-duration varieties, the panicle becomes visible as a white feathery cone 1.0-1.5 mm long. It occurs first in the main culm and then in tillers where it emerges in uneven pattern. It can be seen by dissecting the stem.

As the panicle continues to develop, the spikelets become distinguishable.

The young panicle increases in size and its upward extension inside the flag leaf sheath causes the leaf sheath t bulge. This bulging of the flag leaf sheath is called booting.

Booting is most likely to occur first in the main culm.

At booting, senescence (aging and dying) of leaves and nonbearing tillers are noticeable at the base of the plant.

16.3.2. Stage 5 - Heading

Also known as the panicle exsertion stage. Heading is marked by the emergence of the panicle tip from the flag leaf sheath. The panicle continues to emerge until it partially or completely protrudes from the sheath.

16.3.3. Flowering

Stage 6 is called flowering. It begins when anthers protrude from the spikelet and then fertilization takes place.

At flowering, the florets open, the anthers protrude from the flower glumes because of stamen elongation, and the pollen is shed. The florets then close.

The pollen falls on the pistil, thereby fertilizing the egg. The pistil is the feathery structure through which the pollen tube of the germinating pollen (round, dark structures in this illustration) will extend into the ovary.

The flowering process continues until most of the spikelets in the panicle are in bloom. From left to right, this frame shows anthesis or flowering at the top of the panicle, 1st day after heading; anthesis at the middle of the panicle, 2nd day after heading; anthesis at the lower third of the panicle, 3rd day after heading.

Flowering occurs a day after heading. Generally, the florets open in the morning. It takes about 7 days for all spikelets in a panicle to open. At flowering, 3-5 leaves are still active.

The tillers of this rice plant have been separated at the start of flowering and grouped into bearing and nonbearing tillers.

16.4. Ripening Phase

16.4.1. Stage 7 - Milk grain stage

The last 3 stages of growth, stages 7, 8, and 9 comprise the ripening phase.

Stage 7. Milk grain stage

In this stage, the grain has begun to fill with a milky material.

The grain starts to fill with a white, milky liquid, which can be squeezed out by pressing the grain between the fingers.

The panicle looks green and starts to bend. Senescence at the base of the tillers is progressing. The flag leaves and the two lower leaves are green.

16.4.2. Stage 8 - Dough grain stage

During this stage, the milky portion of the grain first turns into a soft dough and later into a hard dough.

The grains in the panicle begin to change from green to yellow. Senescence of tillers and leaves is noticeable.

The field starts to look yellowish. As the panicle turns yellow, the last two remaining leaves of each tiller begin to dry at the tips.

16.4.3. Stage 9 - Mature grain stage

The individual grain is mature, fully developed, hard, and has turned yellow.

This slide shows rice plants at the mature grain stage. Ninety to one hundred percent of the filled grains have turned yellow and hard.

The upper leaves are now drying rapidly although the leaves of some varieties remain green. A considerable amount of dead leaves accumulate at the base of the plant.

Chapter 17 Growth Stages of Maize

17.1. Principal growth stage 0: Germination

00 Dry seed (caryopsis)
01 Beginning of seed imbibition
03 Seed imbibition complete
05 Radicle emerged from caryopsis
06 Radicle elongated, root hairs and/or side roots visible
07 Coleptile emerged from caryopsis
09 Emergence: coleoptile penetrates soil surface (cracking stage)

17.2. Principal growth stage 1: Leaf development

10 First leaf through coleoptile
11 First leaf unfolded
12 2 leaves unfolded
13 3 leaves unfolded Stages continuous till
. .
1 Stages continuous till…
.
19 9 or more leaves unfolded

17.3. Principal growth stage 3: Stem elongation

30 Beginning of stem elongation
31 First node detectable
32 2 nodes detectable
33 3 nodes detectable
Stages continuous till . . .
39 9 or more nodes detectable3

17.4. Principal growth stage 5: Inflorescence emergence, heading

51 Beginning of tassel emergence: tassel detectable at top of stem
53 Tip of tassel visible
55 Middle of tassel emergence: middle of tassel begins to separate
59 End of tassel emergence: tassel fully emerged and separated

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[1] A leaf may be described as unfolded when its ligule is visible or the tip of next leaf is visible

[2] Tillering or stem elongation may occur earlier than stage 19; in this case continue with principal growth stage 3

[3] In maize, tassel emergence may occur earlier, in this case continue with principal growth stage 5

17.5. Principal growth stage 6: Flowering, anthesis

61 Male: stamens in middle of tassel visible. Female: tip of ear emerging from leaf sheath
63 Male: beginning of pollen shedding. Female: tips of stigmata visible
Male: upper and lower parts of tassel in flower. Female: stigmata fully emerged
67 Male: flowering completed. Female: stigmata drying
69 End of flowering: stigmata completely dry

17.6. Principal growth stage 7: Development of fruit

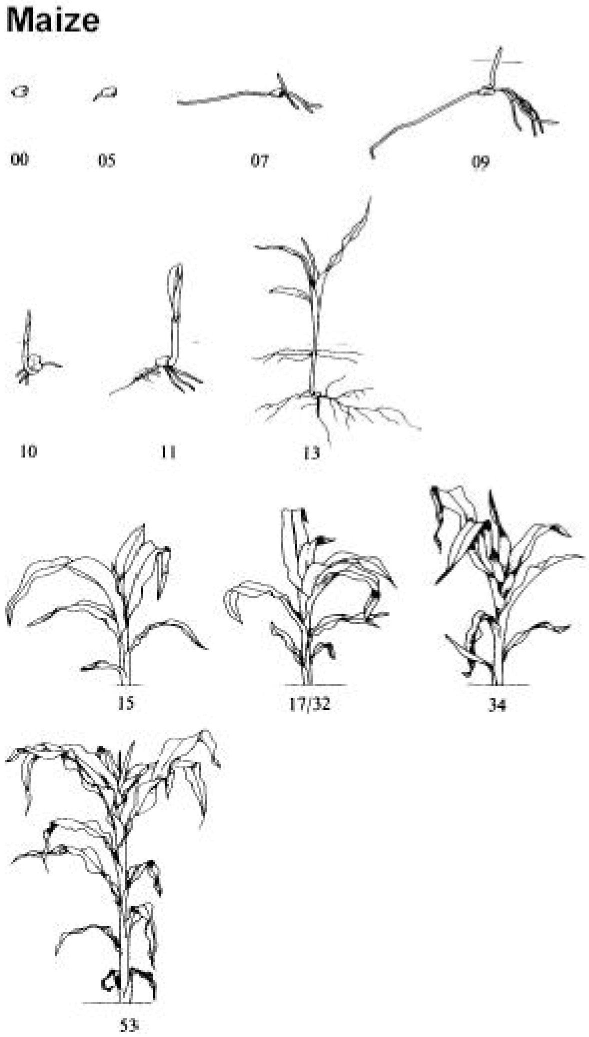
71 Beginning of grain development: kernels at blister stage, about 16% dry matter
73 Early milk
75 Kernels in middle of cob yellowish-white (variety-dependent) content milky about 40% dry matter
79 Nearly all kernels have reached final size

17.7. Principal growth stage 8: Ripening

83 Early dough: kernel content soft about 45% dry matter
85 Dough stage: kernels yellowish to yellow (variety dependent) about 55% dry matter
87 Physiological maturity: black dot/layer visible at base of kernels about 60% dry matter
89 Fully ripe: kernels hard and shiny about 65% dry matter

17.8. Principal growth stage 9: Senescence

97 Plant dead and collapsing
99 Harvested product



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Growth Stages

Corn growth stages are divided into vegetative (V) and reproductive (R) growth stages. The vegetative growth stages start with the corn emergence and reproductive growth stages start with silking.

Vegetative (V) growth stages

The vegetative growth stages start with corn emergence (VE) and finish with tasseling (VT) (Table 1). During the VE stage, the mesocotyl elongation pushes the growing coleoptile to the soil surface and the radicle root and some lateral roots develop from the seed. This seminal root system absorbs water and nutrients until the V3 growth stage (3 leaves with collars).

Following emergence, the coleoptile and mesocotyl elongation stops, and the growth continues from the growing point (stem apex), which is located just above the mesocotyl and below the soil surface until the V5 - V6 growth stage (5 - 6 corn leaves with collars). The rapidly developing embryonic leaves grow through the coleoptilar tip.

Stages between VE and VT are designated numerically as V1, V2, …through V(n). The (n) represents stage with top leaf fully expanded before the VT stage. A leaf is considered fully expanded if the leaf collar (discolored line between the leaf blade and leaf sheath) is visible. The eventual number of leaves to be produced by a plant is determined by V6 - V7 growth stage.

Table 1. Vegetative growth stages of corn.

Vegetative stage	Description
VE	Emergence (Fig. 2)
V1	First fully expanded leaf with the leaf collar (Fig. 3)
V2	Second fully expanded leaf with the leaf collar (Fig. 4)
V3	Third fully expanded leaf with the leaf collar
V(n)	nth fully expanded leaf with the leaf collar
VT	Tassel fully emerged (Fig. 5)

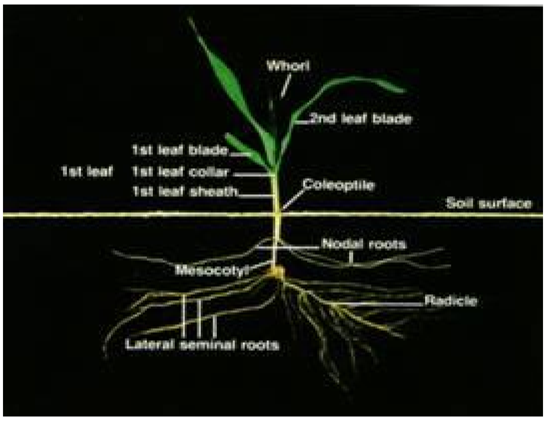

Fig. 1. Description of corn plant during early development.

Fig. 2. VE - Corn emergence.

http://www.agronext.iastate.edu/corn/

Fig. 3. V1 - First fully expanded leaf with the leaf collar.

Fig. 4. V2 - Second fully expanded leaf with the leaf collar.

Fig. 5. VT - Tassels fully emerged.

Reproductive (R) growth stages

The reproductive (R) stages are designated with R1 through R6 (Table 2). These stages start with silking (R1) and finish with physiological maturity (R6). Following R1, stage R2 refers to blister, R3 - milk, R4 - dough, R5 - dent, and R6 - physiological maturity (grain black layer).

At R1 , silks are first visible outside the husks. Pollination occurs when the falling pollen grains are caught by these silks. All silks emerge from the base to the tip in 2 to 5 days and remain receptive for up to two weeks. The silks will continue to elongate until fertilized. The ears pollinate from the base to the tip. Silks are pollinated within 2 - 3 days. For successful pollination it is important that silks emerge and pollinate at the same time. Moisture stress at this time causes poor pollination and reduced seed set, and therefore reduced yield. More information on conditions affecting corn can be found in chapter on "Environmental conditions affecting corn growth".

At R2 stage, the kernels are white on the outside and have a blistered appearance. At R3, kernel is yellow outside and filled with a milk-colored fluid which is mainly starch. Kernels at this stage have 80% moisture. During the R4 stage, starch continues to accumulate and thickens to a pasty consistency. At R5 stage, most kernels are dented. The kernels at the R5 stage are drying down, beginning at the top, where a small hard white layer of starch is forming. The line indicating the hard starch layer will advance toward the base of the kernel.

The kernels reach their maximum dry matter weight at R6 stage when the hard starch layer has advanced completely to the cob and formed a brown or black abscission layer ('black layer') right above the kernel tip. The 'black layer' is an indication of physiological maturity. Kernels at the R6 stage have about 30 - 35% moisture content.

Table 2. Reproductive stages of corn.

Reproductive stage	Description
R1	Silking (Fig. 6)
R2	Blister
R3	Milk
R4	Dough
R5	Dent
R6	Physiological maturity (grain black layer) (Fig. 7)

Fig. 6. R1 - Silking stage.

Fig. 7. R6 - Physiological maturity (grain black layer).