Chapter 3

Crop Physiology

I. IMPORTANCE

Crop physiology is the study of plant functions and responses of crops grown in various environments. It is the underlying science that helps us to understand questions such as:

- What causes a plant to grow?
- Do the largest plants produce the largest yield?
- How is yield related to the environment?
- Why do overcrowded plants grow tall and spindly?
- How is sunlight converted into food?

Knowing why and how crop plants react to their field environment is essential for crop improvement, solving crop management problems, and making good management decisions.

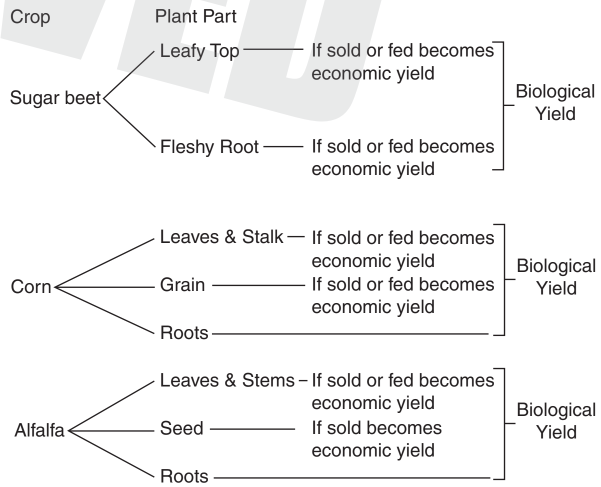
II. YIELD

A. Definition

Yield is the amount of product produced per unit of land area. The amount of product in many agronomic crops is usually expressed as the weight of dry matter (weight of dried product). Water content in plants can commonly vary from 55 to 90%, depending on plant age, environment, and other factors. Thus, wet weight yields (weight of non-dried product) is a poorer indicator of actual organic matter production by the plant than dry matter yields. The unit of land area frequently used in yield measurements is the hectare (metric) or acre (English). Examples of yield measurements are:

Grain yield (maize) = 150 bu/A or 8400 lbs/A (English)
= 94 q/ha or 9400 kg/ha (metric)

Forage yield (hay) = 6 tons/A or 12,000 lbs/A (English)
= 13 mt/A or 13,450 kg/ha (Metric)



B. Types of Yield

There are two general types of yield:

1. **Biological Yield** — The total dry matter produced per plant or per unit area. It includes all of the leaf, stem, grain, and root dry matter produced by the plant.

2. **Economic or Agricultural Yield** — The volume or weight per unit area of only those plant parts that have marketable value. It may refer to seed or grain yield for species like wheat or maize, leaf and stem yield for forage species and root and tuber yield for beets and potatoes. Each species usually has a standardized market moisture content.

Harvest index (the ratio of economic yield to biological yield) is frequently used by scientists to determine the efficiency of crop species and varieties in converting biological yield into an economically desirable product under different management practices or environments. Conditions or practices that promote very high biological yield and low economic yield result in a low harvest index.

C. Components of Yield

1. The economic yield of grain crops is usually determined by the following equation (all other factors being present in optimum amounts):

$$\text{YIELD} = \text{Plants/area} \times \text{Heads/plant} \times \text{Seeds/head} \times \text{Weight/seed}$$

For a given species, each yield component has an optimum level for each level of the other components. Some yield components may affect all of the other components and some may be affected more than another. For example, increasing plants per acre may greatly reduce the heads per plant, which causes a moderate increase in seeds per head, which may cause a slight reduction in the weight per seed.

Breaking yield into individual components is also a way to model yield development over time. For example, plants/area is established first, then tillers/plant, then heads/tiller, etc. . . . This way of modeling yield development over time helps one to identify reasons for yield reductions occurring at different times in different environments.

III. RATE OF GROWTH

A. Plant Growth Curve

The rate of plant growth follows a general pattern altered by environmental factors. This pattern is called the growth curve (see Figure 1). The curve typifies the growth of all organisms or parts of organisms, such as a maize plant, a bacterium, or an ear or leaf on a maize plant. The growth curve is divided into three parts:

1. Logarithmic growth phase — The period of ever increasing rate of growth — includes the germination and vegetative stages.
2. Linear growth phase — The period of constant growth rate — includes the flowering and seed filling stages.
3. Maturation phase — Growth slows and declines with age. Growth eventually ceases.

NOTE: Departure from the optimum curve indicates that dry matter is not being accumulated very efficiently and usually indicates the species is not well adapted to the environment or to a particular geographic location.

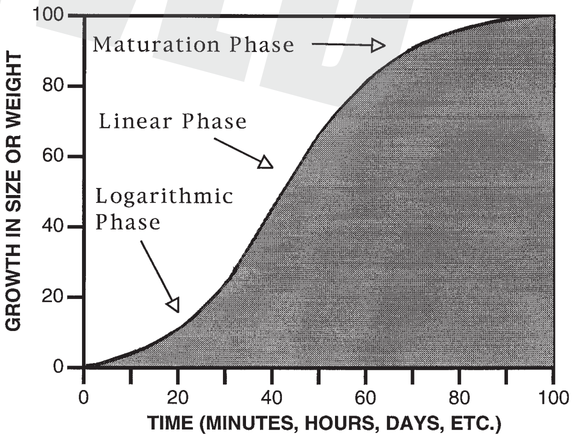


FIGURE 1. Plant Growth Curve

B. Plant Growth Regulators

A wide range of plant responses to environment are mediated through plant growth regulators, which are minute amounts of organic substances that influence and regulate plant growth and development. These substances are active within the plant at very low concentrations and may be produced in one plant organ which stimulates or inhibits a response in another location. Plant growth regulators may be naturally produced within the plant ("plant hormones" or "phytohormones") or synthetically produced ("synthetic hormones"). There are five major groups of plant growth regulators:

1. **Auxins** — stimulate cell and stem elongation, control apical dominance, and many other growth responses. *Example:* indoleacetic acid (IAA). Used commercially to promote rooting of cuttings for plant propagation, and preventing fruit and leaf drop.
2. **Gibberellins** — stimulate cell elongation, cell division and many other plant responses similar to auxins. However, gibberellins are chemically different from auxins and act in a different manner. *Example:* gibberellic acid. Used commercially to increase stalk length of grapes, speed malting process of barley, and increase sugarcane yield.
3. **Cytokinins (Kinins)** — stimulate cell division (cytokinesis), cell differentiation, and many other plant responses. *Example:* zeatin. Used commercially to delay leaf senescence.
4. **Growth Inhibitors** — inhibit growth and development and induce dormancy in seeds and plants. *Example:* abscisic acid (ABA), and phosphon.
5. **Ethylene** — a gaseous substance that may also be considered a growth inhibitor. Hastens fruit ripening and inhibits many other plant responses. Used commercially to accelerate abscission of flowering and fruits, and hasten ripening of several fruits including apples, bananas and tomatoes.

It is difficult to attribute a particular plant response to just one type of plant hormone. Growth and development is frequently adjusted due to the interaction of 2 or more plant hormones. One hormone may enhance or inhibit the action of another. The amounts and balance of plant hormones within the plant are important regulatory factors. Synthetic hormones have been used for a variety of purposes ranging from weed killers (herbicides), producing seedless grapes, cloning plants, retarding vegetative growth, and stimulating uniform ripening in fruit crops.

C. Measuring Growth Rate

Growth rates of plants or plant parts can be estimated by measuring the progression of length or weight over time. To illustrate differences in growth rates, an experiment using plant growth regulators is shown:

Experimental Objective: To determine the effect of growth regulators on the rate of legume plant growth.

Method and Materials: Twenty-four legume plants were planted and grown in the greenhouse for a 21-day period. The plants were divided into 3 groups of 8 plants each, As the epicotyls began to elongate, minute concentrations of growth regulators were applied in a lanolin paste to leaf axils of plants in each group. Treatments were labeled A, B, or C, and consisted of:

Treatment A — control (lanolin paste only).
Treatment B — lanolin paste with a synthetic growth inhibitor.
Treatment C — lanolin paste with gibberellic acid (a plant hormone that stimulates cell elongation).

Measurements: The lengths of the unifoliate leaves (in mm) and the first internode (in cm) were measured at the intervals indicated in the table which follows. To obtain measurements for day 0, three soaked seeds were split open. The lengths of the first two true leaves were measured. The lengths of the internode between the cotyledons and the unifoliolate leaves were also measured.

Results: The growth of the plants was recorded in Table 1.

TABLE 1

		Average Length of Selected Plant Parts Day					
		0	9	12	15	18	21
Unifoliolate Leaves					—mm—		
Treatment	A	1	10	22	34	35	36
	B	1	9	20	27	28	29
	C	I	11	26	37	39	40
Internodes					—cm—		
Treatment	A	0	2	7	12	13	14
	B	0	1	5	9	10	11
	C	0	3	11	17	19	20

The above data should now be plotted in Figures 2 and 3.

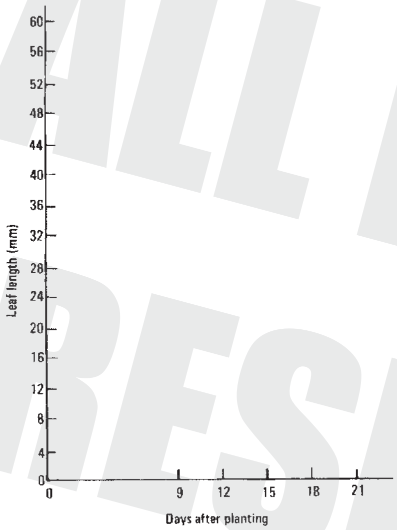


FIGURE 2. Growth Curves of Leaf Length for A, B, and C Treatments

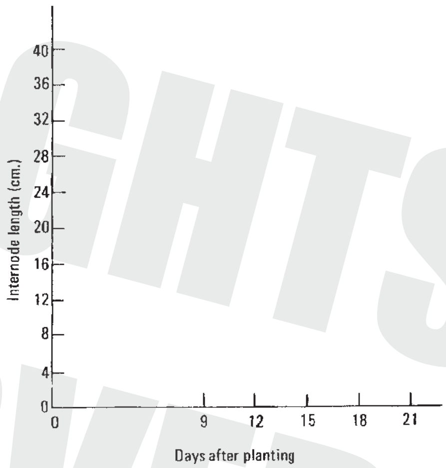


FIGURE 3. Growth Curves of Internode Length for A, B, and C Treatments

Draw smooth lines through the data points plotted in Figures 2 and 3. These lines represent the growth curves for the unifoliolate leaf and for the first internode or epicotyl. The same kind of curve could be obtained for each internode and leaf and also for the whole plant.

Conclusions: The leaves and internode receiving the gibberellic acid had the longest and steepest logarithmic phase. The control or untreated plants had a shorter and less steep logarithmic phase than the gibberellic treatment. The synthetic growth inhibitor treatment produced less growth than the control. Gibberellic acid increased cell elongation and the growth rate, while growth inhibitor decreased cell elongation and the growth rate.

Results of the dry weight comparison: The plants in each of the three treatments were clipped (on day 21) at the soil surface. The wet and dry weights of the plants with cotyledons detached were recorded in Table 2. (Calculate the % dry weight using the formula in the table.)

TABLE 2. Record of Plant Response

	TREATMENT		
	A (Control)	**B (Growth Inhibitor)**	**C (Gibberellic Acid)**
Wet Weight (gm)	4.59	3.88	5.81
Dry Weight (gm)	.64	.61	.65
Percent Dry Weight			
[% D.W. = (D.W. ÷ W.W.) × 100]			

Conclusions: The plants treated with growth inhibitor have the lowest wet and dry weights, the darkest green color, and the highest percent dry weight. Plants treated with gibberellic acid have about the same dry weight as the untreated plants but have a higher wet weight, and the lowest percent dry matter.

NOTE: Temperature, moisture, light and perhaps other environmental factors may interact to accentuate or nullify the anticipated results of biochemical reactions.

D. Regrowth

Plant growth and regrowth occurs from meristematic tissue at the apical (tip) and axillary (lateral) buds, and for some plants, such as grasses, meristematic tissue located at the base (crown) area of the plant. Frost, hail, wind, insects, animals, and machines can cause field plants to lose anatomical parts. The species, size, or age of the plant plays a major role in determining the ability of the plant to survive and to regenerate new growth. In cereal crops, growth of a stem and its leaves is largely determined by the growing point (apical bud). The cereal crop stem has no lateral buds. In grasses, each stem has an apical bud, and if the apical bud is destroyed or removed, the stem will not produce new growth and will eventually die. Most grass plants however, can survive and produce new stems from nodes in the basal area (crown area) of the plant.

Stems of legumes, however, have lateral buds and an apical bud, which can produce new growth if not damaged or removed. Vegetative regrowth can occur as long as one or more meristematic buds remain and remaining leaf tissue and/or stored carbohydrates in the plant can sustain regrowth. When crops are in the seedling stage, the risk of plant death by removing the growing point and all lateral buds is greater because of the low total number of meristematic buds on a young plant. If the growing point of the young plant is removed or injured, regrowth can be completely blocked or reduced. It is important to know where the growing points of the plant are located at all times during the life of the plant. The following demonstrations illustrate the regrowth capacity of young maize and soybean seedlings:

Demonstrations

Twenty-five soybean and corn (maize) seeds were planted and grown in a greenhouse sandbench for twenty-one days. The following treatments were applied to each group of five plants:

1. **Soybeans**

Treatments:

1. Removed one cotyledon (day 9)
2. Removed two cotyledons (day 9)
3. Epicotyls removed; cotyledons left intact (day 9)
4. Hypocotyls clipped below the cotyledons (day 9)
5. Normal untreated plants

On day 21, the growth of the treated soybean plants was recorded in Table 3. Try to explain the reasons for the various treatment responses.

TABLE 3. Growth of Soybeans

Treatment Number	1	2	3	4	5
Average stem length (mm) (above cotyledonary node)	62	39	41	0	70

As shown in Table 3, the first 3 treatments stunted the plants to varying degrees but did not kill them. However, clipping stems of soybean seedlings below the cotyledons resulted in plant death.

Why does the removal of soybean cotyledons greatly reduce the amount of seedling growth?

Why were soybean seedlings killed when the hypocotyls were clipped?

2. **Corn (maize)**

Treatments:

1. Clipped off at day 9 (clipped at 1.25 cm above the soil surface)
2. Clipped off at day 14
3. Clipped off at day 19
4. Normal untreated plants

On day 21, the growth of the maize plants in the above treatments was measured. The average height was recorded in Table 4.

TABLE 4. Height of Corn Plants

	TREATMENTS			
	1	2	3	4
Extended height above ground (cm)	12	7	0	23

The maize plants clipped on days 9 and 14 should continue to live and resume growth after the clipping treatment. Those clipped on day 19 may or may not regrow depending on whether or not the growing point was clipped off. Under field conditions the growing point will be above the soil surface in three to six weeks, depending upon the temperature and general growing conditions. In the laboratory, under ideal growing conditions, the growing point will likely be above the soil line in less than three weeks, thus the 19-day clipping treatment should have killed the plants.

If frost, hail, insects, or wind cut young grass plants off at the soil level, the plants will likely be stunted but they will not be killed. If these crop hazards occur later on in the life cycle when the growing point is above the soil surface, the plants will be killed and no regrowth will occur.

IV. PHOTOSYNTHESIS AND RESPIRATION IN CROP PLANTS

Over 90% of all plant dry matter yield is the result of photosynthesis. Therefore, it is important to understand how photosynthesis occurs, and even more important, to learn how photosynthesis can be controlled for efficient crop production. The basic energy and chemical reactions in photosynthesis are shown in Figure 4.

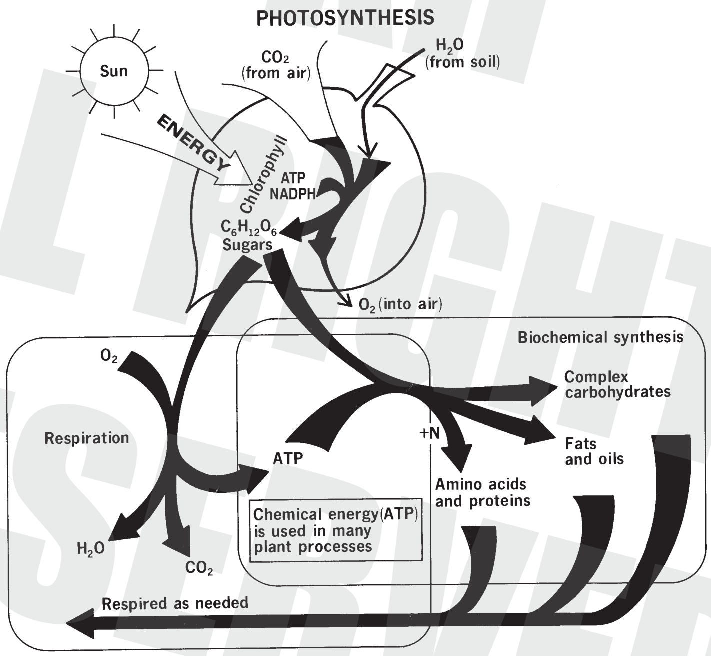


FIGURE 4. Diagram of Plant Metabolism

A. Terms and Definitions

1. Photosynthesis

a. The use of light energy to convert non-nutritious inorganic compounds (CO_2 and H_2O) into essential or nutritious foodstuffs for use by plants, animals and humans; occurs in the chloroplasts of plant cells.

b. Solar energy is captured in the chlorophyll of green leaves and is temporarily stored in adenosine triphosphate (ATP) and nicotinamide adenine dinucleotide phosphate (NADPH). CO_2 enters the stomata from the air and H_2O is delivered to the leaf from the soil through the xylem. Using ATP and NADPH, CO_2 and H_2O, enzymes manufacture sugars and oxygen (O_2) is released. The photosynthetic process fixes CO_2 into organic compounds. Photosynthetic formula: $6CO_2 + 6H_2O$ + light energy = $C_6H_{12}O_6$ (sugar) + $6O_2$

c. Plants can use sugars for energy or as structural materials for growth. They may store the sugars for future growth or store them for the next generation in the seed.

2. Respiration

- **a.** The oxidative breakdown of organic substances. Occurs in the mitochondria of plant cells. Respiration formula: $C_6H_{12}O6 + 6O_2 = 6CO_2 + 6H_2O$ + ATP (energy)
- **b.** Sugars are usually the raw material and carbon dioxide, water and energy are most often the end products.
- **c.** Energy is the most important product of respiration.
- **d.** The energy is stored in the high energy bonds of ATP and used to carry out many energy-requiring reactions in the cell.

TABLE 5. Photosynthesis and Respiration Compared

Photosynthesis	Respiration
1. Occurs in the green cells of plants.	1. Occurs in every active living cell of both plants and animals.
2. Takes place only in the presence of light.	2. Takes place at all times during the life of the cell, both in the light and in the dark.
3. Uses water and carbon dioxide.	3. Uses the products of photosynthesis.
4. Releases oxygen.	4. Releases water and carbon dioxide to the atmosphere.
5. Solar (radiant) energy is converted into chemical energy which may be used for manufacturing carbohydrates or protein.	5. Energy is released by breakdown of carbohydrates and proteins.
6. Results in an increase in weight.	6. Results in a decrease in weight.
7. Food is accumulated.	7. Food is broken down.

3. Synthesis

- **a.** Energy released in respiration is used to synthesize more complex materials. Synthesis occurs in different cell parts, such as chloroplasts (carbohydrates), cytoplasm (fats and oils), ribosomes (proteins), and nucleus (DNA).
- **b.** Some of this energy is stored in complex molecules that can be subsequently respired when additional energy is needed.

4. Net photosynthesis (Pn)

Energy stored in photosynthesis minus the energy released in the respiration process. May also be called net assimilation rate (NAR). Can be increased by genotype, leaf area and leaf orientation — but is limited by shading and deficiencies of water and minerals.

$$\text{Pn} = \text{Photosynthesis} - \text{Respiration}$$

5. Leaf area index (LAI)

The ratio of the total leaf area of crop plants to (divided by) the soil surface area occupied by the plants measured. A crop with a LAI of 3 indicates that there would be 3 ha of crop leaf surface above an hectare of ground.

6. Canopy

The space above the ground surface that is occupied by the aerial portion of plants. Canopy photosynthesis is the rate of photosynthesis of the canopy above a unit of ground area.

How does LAI affect NAR?
What is another term for CO_2 fixation?
What % of plant dry matter yield is directly due to photosynthesis?
What is the LAI of a plant with a leaf surface of 1 sq. meter occupying a space of ¼ sq. meter?

B. Photosynthetic Efficiency

Photosynthesis is an energy conversion process. Solar energy is converted to chemical energy in the leaves of green plants. This process is not completely efficient. Leaves fail to utilize all the solar energy they intercept and not all of the CO_2 absorbed by the leaf is converted into sugar. Crop species, environment, and management practices influence the plant's photosynthetic efficiency. People who grow plants on an area basis (i.e., fields, gardens, greenhouses) are managers of photosynthesis and therefore, try to maximize photosynthetic production per unit area.

1. Light Quality

The quality of light refers to the wavelengths that are most effective in photosynthesis, which represent only a fraction of the total solar radiation reaching the earth's surface. Leaf pigments absorb light between 400 and 700 nm, which represents about 40% of the total solar radiation hitting the leaf. Of this 40%, some is lost as heat, some is reflected or transmitted, and some is consumed in photosynthetic and other metabolic processes. Even for a photosynthetically efficient species, only about 5% of the radiation striking the leaf is used in carbohydrate formation. The wavelength characteristics of the radiant energy spectrum emitted by the sun, ranging from cosmic and gamma rays with short wavelengths to the long radio and electric rays, are shown in Figure 5.

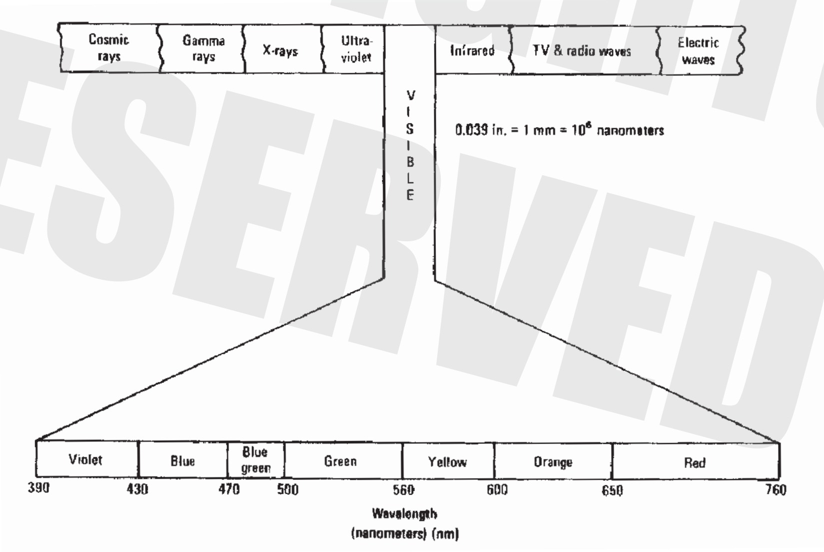


FIGURE 5. The Radiant Energy Spectrum

The visible portion makes up a very small part of the spectrum. Yet it is most important in terms of plant response. The absorption spectrum of a plant leaf is shown in Figure 6. Absorption is quite efficient between 400 and 500 nanometers (nm) and also between 650 and 700 nm. Wavelengths in the green range are not effectively absorbed by chlorophyll and are reflected, thus healthy leaves appear green to the human eye.

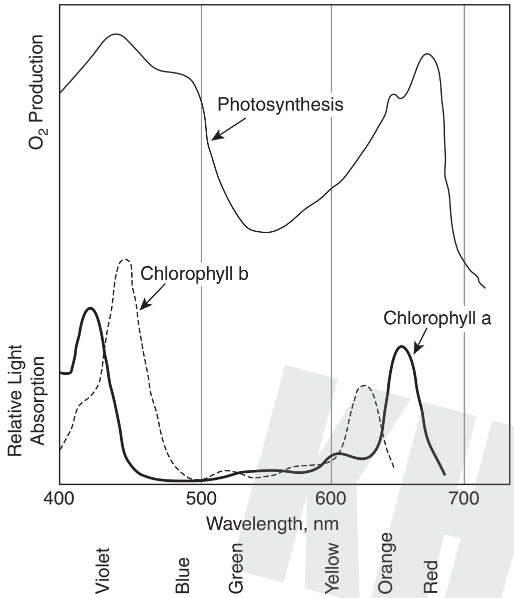


FIGURE 6. Absorption Spectra for Leaf Chlorophyll

What is the range of radiant energy wavelengths that is important in photosynthesis?

1. Light Interception

a. Plant Spacing

Yield can be increased by increasing photosynthesis or decreasing respiration. In the field, photosynthesis can be increased by arranging plants in a pattern that will intercept more light. This can be accomplished by adjusting the row width, plant population (LAI), or changing the shape or orientation of the plant leaves. Table 6 shows how soybean yields may be increased by using narrow rows which intercept more light.

TABLE 6. Light Interception and Soybean Yields

Row Width (cm)	% Light Intercepted	% Yield Index
51 (20 in.)	84	115
102 (40 in.)	75	100

From R. M. Shibles and C. R. Weber, "Biological Efficiencies in Soybean Production," Plant Food Review Vol. 12(4): 8–10, Winter, 1966. The Fertilizer Institute, Washington. D.C.

In Table 7, the effect of row spacing on the yield of two soybean varieties is shown. The yield increase for 30.5 cm over 102 cm rows was 30% for Hark and 19% for Wayne. The variety Hark has a more erect type of growth and does not fill in the middle of the 102 cm rows (40 inch) like the bigger, bushier Wayne variety. Because of this, there is considerable sunlight that reaches the ground and is not absorbed by leaves of the smaller, more upright varieties. However, in narrow rows 51 cm (20 inches) or less the varieties are more efficient and usually give higher yields than the bushier varieties. The smaller, more upright leafed varieties may not have as much total leaf area per plant as the wider leafed, bushier varieties but more sunlight can penetrate to lower leaves and thus increase the photosynthetic efficiency of the crop. The upright leaf pattern of varieties also increases the light interception of the lower leaves.

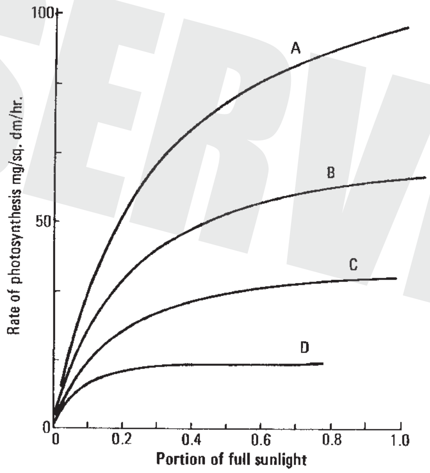
TABLE 7. Yield (kg/ha) of Two Soybean Varieties in 30.5 (12 in.) and 102 (40 in.) cm Rows

	ROW SPACING, CM	
Variety	**30.5 (12 in.)**	**102 (40 in.)**
Hark	3584 (53.3 bu/ac)	2757 (41.0 bu/ac)
Wayne	3383 (50.3 bu/ac)	2845 (42.3 bu/ac)

From G. O. Benson and J. P. Shroyer, "Soybean Row Spacing," Iowa State Univ. Extension Publication PM 864, Feb. 1980.

b. Leaf Angle

For many crops the midday intensity of full sunlight often is greater than is needed for a single leaf to reach maximum photosynthesis rate. A soybean leaf attains a maximum rate of photosynthesis at approximately one-half of full sunlight. Increasing light intensity above this level on a single leaf does not contribute as significantly to dry matter production as allowing about 50% of full sunlight to fall on several leaves down through the leaf canopy. In Figure 7, you will note the relationship between sunlight intensity and the rate of photosynthesis of several field crops and ornamentals.



Examples of species which fit the above curves:
A. Corn, sorghum, sugarcane, bermudagrass (C4 species)
B. Soybean, alfalfa, cotton (C3 species)
C. Orchard grass, red clover, tobacco (C3 species)
D. Oak, maple, and most house plants

FIGURE 7. Light Utilization by Plants

For all plants, the low intensity light is utilized more efficiently than the high light intensities. This is why two leaves receiving 50 percent of full sunlight can fix more carbon dioxide than one leaf receiving full sunlight. Leaves with a more upright orientation will permit more light to penetrate further into the canopy. Figure 8 shows how leaf orientation affects light penetration.

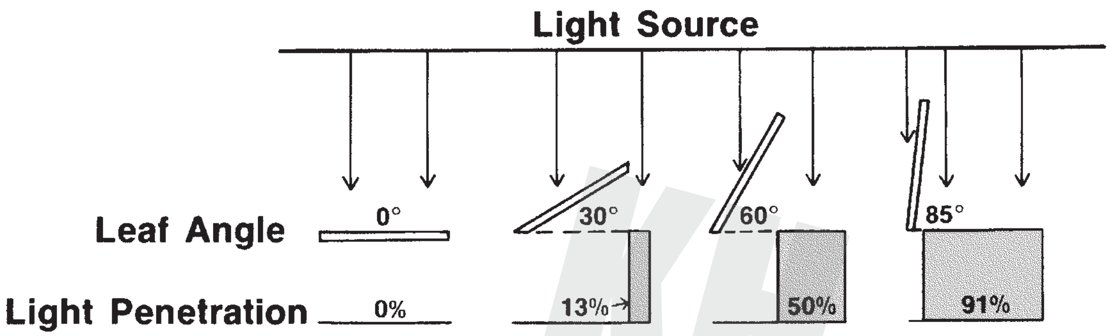


FIGURE 8. Leaf Angle and Light Penetration

With increasing light intensity, a unit area of a maize leaf shows an increasing photosynthetic capacity over the same area of a soybean leaf. Maize is one of the most photosynthetically efficient crop species. These relative efficiencies can be altered by such things as leaf angle and leaf shape.

The upright leaf angle of maize is used as a means of increasing yields by permitting the use of narrow rows and high plant populations that utilize more sunlight. Table 8 shows that an upright leaf can increase the yield of corn by 40 percent and reduce barrenness (plants producing no seed) by 50 percent.

TABLE 8. Corn Grain Yields and Barren Plants with Differing Leaf Angle*

Leaf Angle	Yield kg/ha	% Barren Plants
Normal leaf	6,202 (99 bu/ac)	28
Upright leaf	8,769 (139 bu/ac)	14

*Population = 59,300 plants per hectare (24,000 per acre)

From W. Pendleton et al., "Field Investigations of the Relationships of Leaf Angle in Corn to Grain Yield and Apparent Photosynthesis," *Agronomy Journal* 60:422,1968.

3. CO_2 Concentration

The efficiency of photosynthesis is also influenced by the low CO_2 concentration of the air and the plant's ability to utilize it in photosynthesis. Air contains about 0.04% (400 ppm) of CO_2, which limits the photosynthetic potential of most crops. Crops differ in their capacity to fix CO_2 into sugars depending on their photosynthetic pathway. There are two major photosynthetic pathways called C3 and C4, based on the first stable product (3-carbon or 4-carbon) of the pathway. Thus, crop plants are often referred to as "C3" or "C4" species. The C4 pathway is believed to have evolved most recently and is considerably more efficient in CO_2 fixation than the C3 pathway under the currently low atmospheric CO_2 concentrations (Table 9).

TABLE 9. Comparisons of C3 and C4 Plants

C3 Plants	C4 Plants
Primarily cool season crops; cooler photosynthetic maximum (15–25°C)	Primarily warm season crops; warmer photosynthetic maximum (30–47°C)
Utilizes 60% or less of maximum solar intensity; leaves light saturate (see Figure 7)	Utilizes up to 100% solar intensity; leaves do not light saturate (see Figure 7)
Inefficient leaf anatomy and enzyme that fixes CO_2; low CO_2 uptake rates; lower yield potential	Evolved a specialized leaf anatomy and enzyme that more effectively fixes CO_2; high CO_2 uptake rates; higher yield potential
Typically less efficient user of water	More efficient user of water
Crops include: Alfalfa, barley, cotton, Kentucky bluegrass, oats, potatoes, rice, rye, soybean, tall fescue, tobacco, wheat, banana, peanuts, many vegetables and fruit trees	Crops include: Bermudagrass, cassava, indiangrass, little bluestem, millet, maize, sorghum, sugarcane

The photosynthetic pathway of a crop or weed will often affect its adaptation, competitiveness or agronomic utility. *Examples:*

a. A C4 crop such as sorghum or pearl millet will use water more efficiently than a C3 crop such as soybean or perennial ryegrass, and will be better adapted and more productive in warmer and drier conditions.

b. A C3 crop such as oats will grow rapidly in cool temperatures, become established early and compete effectively with warm season C4 weeds such as pigweed.

c. Typically, C4 weeds are a greater problem in warmer climates and C3 weeds more of a problem in cooler climates.

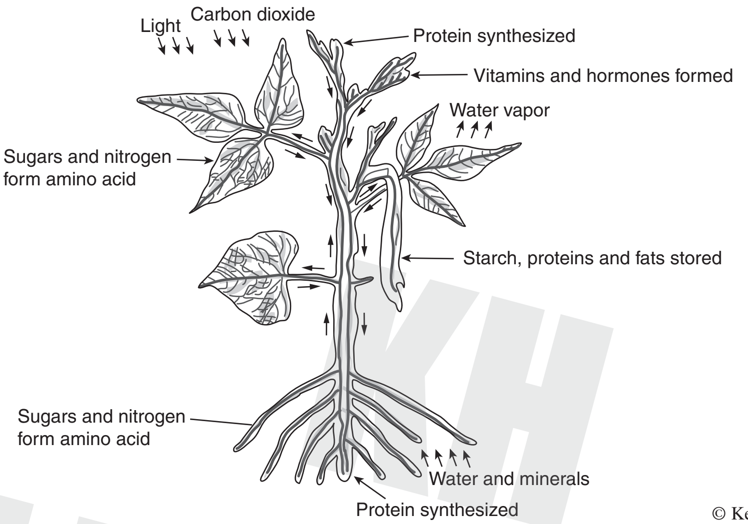
> The atmospheric CO_2 concentration in the earth's atmosphere is increasing from the burning of fossil fuels. Would you expect C3 or C4 weeds to become more competitive? Why?

V. TRANSPORT AND UPTAKE IN CROP PLANTS

A. Translocation

1. **Definition:** The movement of organic and inorganic solutes from one part of the plant to another.

In Figure 9, observe the following sites of synthesis and the role of translocation in the metabolism of the plant.



Adapted from "The Circulatory System of Plants," Susann and Orlin Biddulph. Scientific American Reprints #53. February, 1959. Copyright © 1959 by Scientific American, Inc. All rights reserved.

FIGURE 9. Plant Translocation

a. When light, CO_2 and water are available, sugars are formed in the leaf (photosynthesis).
b. Amino acids are also formed in the leaves and roots from sugars and nitrogen.
c. Amino acids and carbohydrates are translocated to other parts of the plant in the phloem tissue.
d. Proteins are synthesized from amino acids in the growing point of the shoots and roots.
e. Water and minerals are absorbed by the roots and translocated upward in the xylem tissue.

In what forms may nitrogen be translocated in the plant?
What are the major storage areas for protein, starch and fats?

B. Transpiration

1. **Definition:** The loss of water from plant tissues in the form of vapor.
   a. It is an evaporative process.
   b. It is a cooling process.
2. **Evapotranspiration:** The total water loss in a crop canopy that equals the sum of the water lost from crops by transpiration and from soil by evaporation.
3. In Figure 10, observe the following leaf structures and their function.
   a. The stoma is the entrance to a large intercellular space.
   b. The cells surrounding this space act as evaporative surfaces.
   c. The stoma provides an easy exit for water vapor.
   d. When the stomata are open, the amount of transpired water greatly increases.
   e. Stomata also provide for the gaseous exchange of carbon dioxide and oxygen.
   f. Translocation tissues are located near the evaporative surfaces.

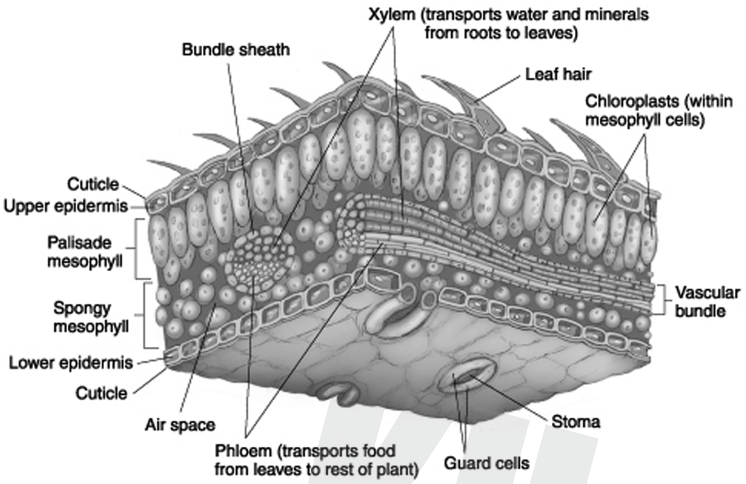


FIGURE 10. Diagram of Leaf Section

4. **Water requirement (evapotranspiration ratio)** — The units of water required to produce a unit of plant dry matter. Or, in equation form:

$$\text{Water Requirement (WR)} = \text{kg } H_2O \text{ evapotranspired/kg dry matter.}$$

   a. The WR varies for a given crop from one climate to another and usually decreases with increased fertility and weed control.
   b. Drought tolerance is not always increased by using plants with a low evapotranspiration ratio.
      1. For instance, alfalfa with a relatively high WR of approximately 800 may be a productive crop under drought conditions because its deep root system is able to tap water supplies deep in the soil.
      2. Oats and other small grains are also grown in drier climates regardless of their higher WR because they mature early and miss much of the hot summer weather (escape crops).
   c. Generally the species with low WR will withstand water shortages better than species with high WR.
   d. Table 10 shows the average water requirements for different climates, management, and crop species.

TABLE 10. Water Requirements

Climate	Evapotranspiration Ratio
Hot, dry	High
Cool, humid	Low
Management	
Poor fertility	High
Good fertility	Low
Poor weed control	High
Good weed control	Low
Crop Species	
Alfalfa	High (800+)
Cotton, Wheat, Soybeans	Medium (600–700)
Maize, Sorghum	Low (300–400)

Why are stomata in crops generally open in the daylight and closed at night?
What causes a plant to require less moisture than another plant?

C. Mineral Uptake

1. Methods of nutrient uptake by crop roots

Roots must be in contact with soil nutrients in order for the root to absorb them. This root-nutrient contact can occur in different ways (Figure 11):

a. By root growth and interception of nutrients
b. By nutrient flow in soil water
c. By diffusion of nutrients from a high concentration zone to a low concentration zone

Once the root-nutrient contact is made, roots can "absorb" the nutrient in two ways (Figure 11):

a. *Passive Uptake* — nutrient ions move with the water into roots. Transpiration is the essential driving force for passive uptake of water and nutrients.
b. *Active Uptake* — nutrient ions are "pumped" into the root requiring ATP energy.

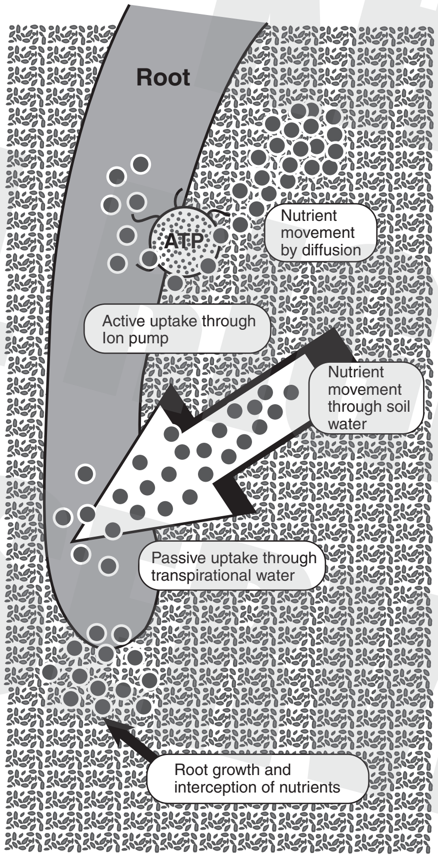


FIGURE 11. Nutrient Uptake by Crop Roots

2. Factors affecting nutrient uptake

a. Factors that reduce root growth also reduce nutrient uptake.
b. Nutrient uptake is greater when nutrient concentrations in the root zone are high.
c. Adequate soil aeration and soil moisture improve nutrient uptake.
d. Nutrient uptake rate is generally greatest in the root hair zone and in newly formed roots than in older roots.
e. The soil and plant must maintain a balance of cation (positive) and anion (negative) nutrients to avoid a flow of electrical current. Proper soil pH improves cation-anion balance and nutrient availability.

How would soil temperature affect the nutrient uptake potential of young roots?

D. Biological Nitrogen Fixation

For plant proteins to be formed, nitrogen must be combined with carbohydrates. The atmosphere contains about 80% nitrogen. However, the plant cannot use this nitrogen directly from the air. The application of nitrogen fertilizer to the soil is one way to get nitrogen into the plant, but nitrogen fertilizer is an expensive input.

In addition to root uptake of mineral nitrogen, legumes have an important way to get atmospheric (gaseous) nitrogen into the plant through biological nitrogen fixation utilizing *Rhizobium* or *Bradyrhizobium* bacteria. These are the genus names of important nitrogen-fixing bacteria. For the bacteria to accomplish this fixation of gaseous nitrogen, they must infect a host plant (usually a legume). This relationship between the bacteria and the host plant, for the mutual benefit of both organisms, is called symbiosis. The plant provides carbohydrates as an energy source for the bacteria. The bacteria convert atmospheric nitrogen from the air in the soil into a form that is essential to the plant's metabolism and growth. The bacteria may be naturally present in the soil or placed on seeds as an inoculant and enter the roots of specific host plants and form nodules on the roots of these host plants.

The magnitude of the fixation process in soybeans is shown in Table 11. Nitrogen-fixing and non nitrogen-fixing lines are varieties that nodulate and do not nodulate, respectively. Notice with 0 kilograms of fertilizer nitrogen, the nitrogen-fixing bacteria produced a 531 kg/ha (8 bu/acre) increase with 40% of the seed nitrogen coming from nitrogen fixation. Also note that over 224 kilograms of nitrogen fertilizer was required to permit the non-nodulating line to yield as much as the nodulating line. At these high levels of fertilizer nitrogen, a lower percentage (13%) of the seed nitrogen was provided by the fixation process.

There are several species of grasses which in association with the symbiotic bacteria *Azospirillium,* fix small amounts of nitrogen. The genus *Azotobacter* and *Clostridium* are the two major nonsymbiotic nitrogen-fixing bacteria. Some blue-green algae also fix atmospheric nitrogen.

Why do biological nitrogen-fixation processes receive more attention during periods of high petroleum prices?

TABLE 11. Analysis of Soybean Nitrogen Fixation

Soybean Line	Nitrogen Applied kg/ha	Seed Yield kg/ha	% Increase	N_2 Fixed kg/ha	% of Total N
Nodulating	0	2688	24.6	80	40
Non-nodulating	0	2157			
Nodulating	224	3024	2.8	34	13
Non-nodulating	224	2943			

Adapted from G. E. Ham, et al. Yield and Composition of Soybean Seed as Affected by N and S Fertilization. *Agron. Jour.* 67(3): 293–297.

VI. CROP PLANT RESPONSES TO PRODUCTION ENVIRONMENTS

A. Germination

One of the primary goals in seeding is to obtain rapid, uniform germination of crop seeds. In order for this to occur, the environmental conditions required for germination must be met. Seed germination is a growth process: therefore, many of the environmental requirements for germination are similar to those required for plant growth.

Environment required for germination:

1. Water
2. Suitable temperature (varies with species — see Figure 12)
3. Oxygen
4. Light (in some species, not required for most crops)

Seeds must imbibe water to begin the germination process. After the imbibition of water, the seed reserve substances such as fats, carbohydrates and proteins are enzymatically converted to simple sugars and amino acids that are transported to the embryo where some are utilized in the synthesis of protein, starch and cellulose while others are respired to provide energy. Water and oxygen are essential for the enzymes to function in the breakdown of the seed reserves. The proper temperature is needed to permit the biochemical reactions of synthesis to occur. The ability of the soil to supply the necessary environmental factors for germination can vary among soils, times of the year, and growing regions.

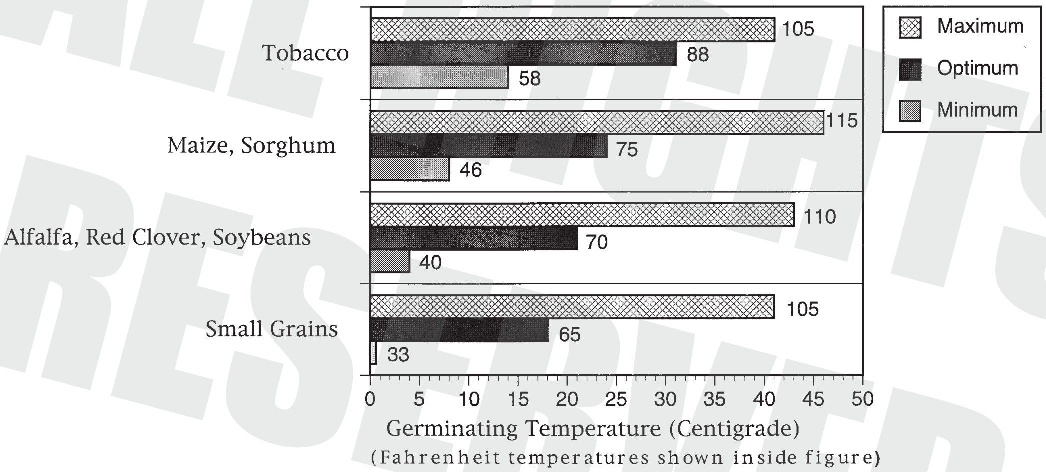


FIGURE 12. Approximate Germinating Temperatures C (F)

How might one manage the soil environment to control weed seed germination?

B. Etiolation

1. **Definition:** The elongation of plants grown in the dark or in light of very low intensity.
2. **Causes of Etiolation**
   - **a.** It is usually caused when plants are grown in shaded or darkened conditions.
   - **b.** It occurs under field conditions when crops are grown at very high plant populations.

c. The shaded condition increases the level of auxins (plant growth hormones), especially indoleacetic acid (IAA).
d. Sunlight destroys IAA. Shaded or darkened conditions increase IAA in the plants.
e. Too high plant population increases shading, increases IAA, increases elongation of stems and increases stalk lodging (stem breakage and falling over of plants).

C. Tillering, Branching, and Barrenness

1. Causes

a. A plant will not tiller (produce secondary stems from the crown area), branch or produce seed unless the IAA level in the plant is reduced below the optimum level for vegetative elongation.
b. Tillering is increased by cool temperatures, adequate soil fertility and soil moisture.
c. None of the factors in (b) will cause tillering, branching or seed production. The IAA concentration is the critical factor and triggers the response.
d. Some varieties have higher optimum levels of IAA and are more population tolerant.

NOTE: Table 8 shows how barrenness (failing to produce seed) was reduced by using an upright leaf variety that permits more sunlight into the canopy to reduce the IAA level.

What is the significance of the rapid etiolation response of many weeds to shaded conditions?
What causes plants to be barren (without seed)?

D. Crop Development

1. Reproductive development

Crop plant development proceeds from vegetative growth to reproductive growth, but this transition differs among crop species. Crop species are often categorized into determinate and indeterminate growth types, based on the nature of the vegetative-reproductive growth transition.

a. Growth types

1. Determinate Growth Type — Develops most of the vegetative growth before flowering. The transition from vegetative to reproductive growth is relatively rapid and the plant terminates growth with a large reproductive structure.

   Examples: wheat, oats, barley, maize, sugarcane, tobacco and most species of field crops.

2. Indeterminate Growth Type — Vegetative and reproductive periods overlap for a longer period. The transition period from vegetative to reproductive growth is slower and less distinct. The plant may terminate growth with a smaller reproductive structure.

   Examples: alfalfa and other forage legumes, cotton, trees and many other perennials.

   Soybeans are an example of an annual crop with both determinate and indeterminate growth types.

   Determinate soybeans — Used primarily in the southern U.S.A.
   — Develops most of the vegetative growth before flowering.
   — Terminal growth is a raceme usually with many pods.
   — Is more susceptible to stress.

Indeterminate soybeans — Used primarily in the northern U.S.A.
— Vegetative and reproductive periods overlap for a longer period.
— Usually grows taller, has a thinner stem, and is more susceptible to lodging.
— More drought tolerant during the reproductive period.
— Has a small terminal raceme, has fewer pods on upper stem.

Taller plants, whether determinate or indeterminate, are more susceptible to lodging (falling over). Consequently, plant breeders select and breed for shorter plants that will reduce lodging while maximizing yield.

2. Time of flowering and photoperiodism

The time that reproductive growth begins in plants is greatly influenced by growth temperature and photoperiod (the length of daylight in a 24-hour period). Reproductive development occurs when a particular growth stage is reached by crop plants; thus, moderate increases in growth temperature generally hasten the time to flowering. The flowering response may also be modified by the crop's response to photoperiod (photoperiodism). When some plants reach a certain age, reproductive growth may be induced by certain daylengths. Once these plants have been induced, warmer temperatures generally hasten the reproductive progression.

a. Photoperiodism: The effect of photoperiod on flowering and plant maturity.

b. Classifications of photoperiodism

Long Day Plants — plants that flower when some critical minimum period of daylength is exceeded (this critical minimum photoperiod may vary with species and environment)
— plants flower under continuous light
— includes most cool season crops

Short Day Plants — plants that flower when daylengths are shorter than some critical maximum (this critical maximum photoperiod may vary with species and environment)
— plants will not flower under continuous light
— includes most warm season crops

Day Neutral Plants — plants whose flowering response is insensitive to daylength
— flowering generally begins when plants reach a certain age or size

Table 13 shows some of the major crops in each daylength category.

TABLE 13. Plant Photoperiod Classification

Short Day Plants	Day Neutral	Long Day Plants
Maize	Apple	Alfalfa
Lespedeza	Buckwheat	Barley
Rice	Cotton	Bromegrass
Sorghum	K. Bluegrass	All clovers
Soybeans	Sunflower	Oats
Sugarcane	Tobacco	Rye
Peanut	Tomato	Sugar Beet
		Wheat

c. Photoperiodic response and phytochrome

The flowering response of plants to daylength occurs through a special plant pigment called phytochrome. Phytochrome is a single pigment that can exist in two interchangeable forms. One form (PFR or Phytochrome Far Red) is formed during the day. The other form (PR or Phytochrome Red) is formed during the night by the slow conversion of PFR to PR. Thus, the length of days and nights regulate the amounts (ratio) of PFR and PR in the leaves and consequently, the photoperiodic response. It is through this phytochrome mechanism that plants appear to "sense" the seasons and long or short days.

Photoperiod	Phytochrome Forms	Flowering Response
1. Shorter days (longer nights)	Less PFR; more PR	Stimulates short day plants to flower
2. Longer days (shorter nights)	More PFR; less PR	Stimulates long day plants to flower

What effect do long days and short nights have on phytochrome?

d. Photoperiodic response and latitude

Figure 13 shows the effects of latitude and resulting daylength on plant growth, flowering and developmental characteristics of a soybean (short day plant) variety adapted to Central Iowa. Note the following relationships when the variety is planted at three locations.

1. The three locations are at about the same longitude.
2. The length of the longest day varies from 14.4 hours to 15.8 hours as latitude increases from 35°N to 47°N.
3. The shorter daylength and warmer temperature at Little Rock stimulates the flowering process earlier than at Ames or Duluth.
4. The plants are ready for harvest on Sept. 21 in Little Rock but are still producing leaves, stem growth and pods at Duluth.
5. This short-day plant grows taller in areas of increased daylength. The same would be true for corn, sorghum and other short-day plants when grown under longer day regimes.

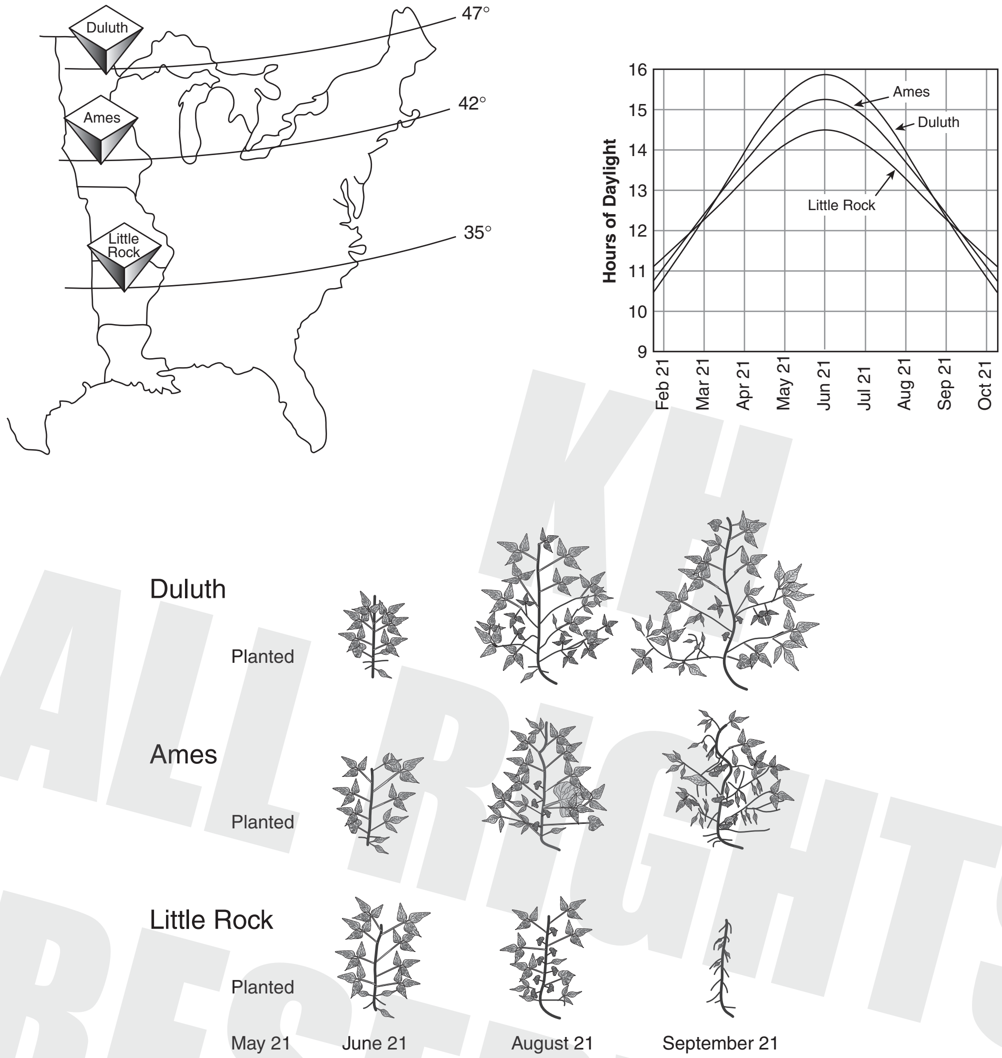


FIGURE 13. The Effect of Daylength on Plant Growth

Would a short day plant grow taller in Mexico than in Canada?
If the critical photoperiod is 14 hours for soybeans, would soybeans flower when daylength is 13 hours?

SELF-EVALUATION TEST

Circle letter corresponding to one best answer.

1. The ratio of the total leaf area of plants to land occupied by the plants is called the

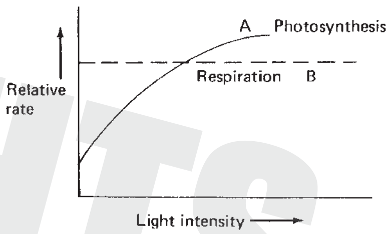
   a. NAR
   b. IAA
   c. LATLA
   d. LAI
   e. Auxin

2. C4 plants:

   a. have lower maximum temperatures for photosynthesis than C3 species
   b. have leaves that light saturate
   c. have lower yield potential than C3 species
   d. have higher CO_2 fixation rates
   e. include most cool season crops

3. At any light intensity the difference between line A and line B in the figure below equals

   a. PR
   b. NAR
   c. compensation point
   d. IAA
   e. assimilation rate



4. Which of the following is not true of the plant process called respiration?

   a. uses the products of photosynthesis
   b. occurs in all living cells
   c. releases energy
   d. releases water and carbon dioxide
   e. releases oxygen through stomata

5. The visible spectrum of light is indicated by the distance between which letters?

   a. A to I
   b. C to F
   c. F to H
   d. D to G
   e. B to F

A	B	C	D	E	F	G	H	I
360	390	450	630	690	760	820	960	1000 nm

6. High light intensity on the stalks of plants would result in

   a. shorter plants
   b. taller plants
   c. more indole acetic acid
   d. barren plants
   e. weaker stalks

7. If a leaf respires at a rate of 14 mg CO_2 per hour and the photosynthetic rate is 27 mg CO_2/hr, the Pn for the leaf is

   a. 41 mg CO_2/hr.
   b. 15 mg CO_2/hr.
   c. 23 mg CO_2/hr.
   d. 13 mg CO_2/hr.
   e. 20.5 mg CO_2/hr.

8. Soybean nodulation

   a. proceeds better at pH 4 than at pH 7
   b. provides the plant with usable nitrogen
   c. is caused by the same species of bacteria for all legumes
   d. increases the amount of nitrogen used from the soil
   e. is always adequate

9. The efficiency of photosynthesis in corn leaves is

   a. less than that of soybeans
   b. less than that of oak trees but greater than that of soybeans
   c. less than that of soybeans but greater than that of oak trees
   d. less than that of alfalfa, but greater than that of soybeans
   e. greater than that of soybeans, alfalfa, and oak trees

10. The following statement most nearly describes transpiration

   a. It is always helpful to the plant
   b. It causes the plant's temperature to be lower
   c. It is mostly due to water loss through the cuticle
   d. It is through the mitochondria
   e. It does not occur from the upper surface of corn plant leaves

11. Which of the following is not an important aspect of sunlight as it affects plant growth?

   a. quality
   b. intensity
   c. wavelength
   d. day length
   e. humidity

12. Pick the group of factors that will most strongly promote etiolation in corn plants.
    a. high light intensity; low fertility; low population
    b. high light intensity; high fertility; low population
    c. low light intensity; high fertility; high population
    d. low light intensity; high fertility; low population
    e. low light intensity; low fertility; low population

13. Select the correct statement concerning the flowering process.
    a. Most warm-season plants require long days for flowering.
    b. Phytochrome reversibility is regulated by temperature.
    c. Long-day plants require less PFR phytochrome than short-day plants to promote flowering.
    d. Plants exposed to daylight will have more PFR phytochrome than plants left in the dark.
    e. Rice is a day-neutral plant.

14. Translocation of amino acids
    a. is in the phloem tissue
    b. is only from the roots to the leaves
    c. is in the xylem tissue
    d. is in the same tissue as water and minerals moving from the roots

15. The raw material for photosynthesis that enters through the stomata is
    a. nitrogen
    b. water
    c. carbon dioxide
    d. oxygen
    e. magnesium

16. Roots absorb nutrients
    a. through stomata
    b. by translocation
    c. by the C4 pathway
    d. by ion pumps requiring ATP
    e. in the canopy

17. Plant auxins include
    a. gibberellic acid
    b. phosphon
    c. phytochrome
    d. NAR
    e. IAA

18. The evapotranspiration ratio of a plant is the
    a. water transpired in 24 hours
    b. units of water required to produce a unit of dry matter
    c. water used per growing season
    d. water used per plant per day
    e. units of water required to produce one unit of seed