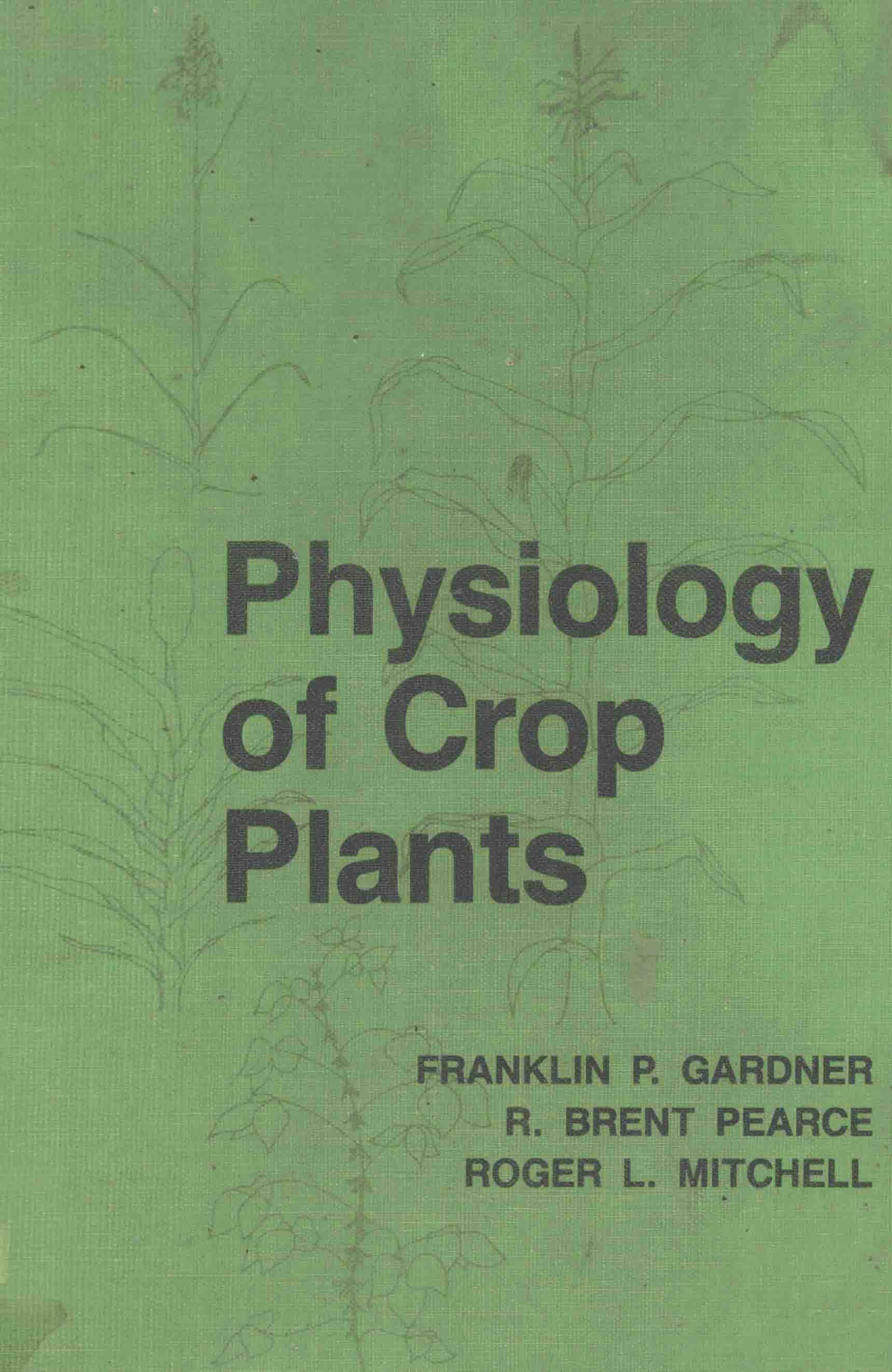

Physiology of Crop Plants

FRANKLIN P. GARDNER
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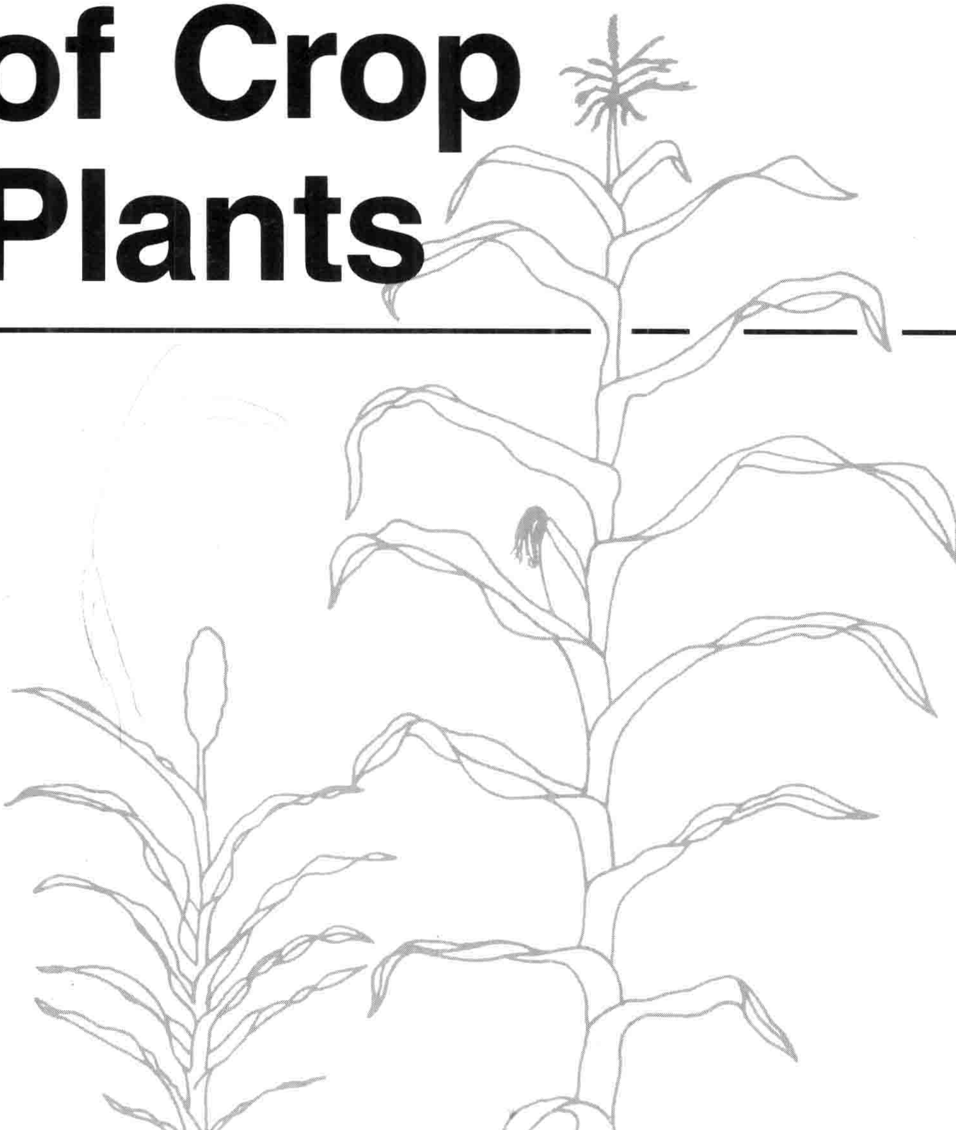

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Physiology of Crop Plants

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FOREWORD

THIS SECOND EDITION of a textbook focused on crop physiology reflects the many changes and expanded efforts occurring since the first edition was published in 1970, at which time it was acceptable for agronomists to use only a broad title like *Crop Growth and Culture.* In the ensuing years, the discipline of crop physiology has become widely recognized; thus this second edition can be titled *Physiology of Crop Plants.*

As noted in the first edition, the unique contribution of agronomy as a discipline, represented by the subdivisions crops, soils, and climatology, is the integration of biological, chemical, and physical phenomena into useful crop management systems. With the basic biological scientist's continuing emphasis on molecular biology (the reductionist approach), it remains imperative for the agronomist and the crop physiologist to integrate information, synthesize new levels of knowledge, and develop systems for problem solving, all the while interfacing with biologists, chemists, physicists, and researchers in other basic areas of science.

Our treatment continues to break from the tradition of organization on a crop basis; the emphasis is on physiological concepts and the factors influencing metabolism, growth, and reproduction. While crop plant examples are a key part of the discussion, the first order of business is to identify the basic principles that apply across species. As in the first edition, specialized terminology has been kept at a moderate level and illustrations have been used liberally in order to enhance readability and understanding for undergraduates in advanced crop science courses and to provide a text or reference for introductory graduate courses in crop physiology. Crop physiology peers have indicated the desirability of such a dual-level approach.

This discussion thus has two major purposes: to develop an understanding of the important principles underlying the practices used in the culture of crop plants and to develop the ability to apply these principles in production strategies.

The second edition expands on crop physiology and omits specific chapters on seeding; winter and drought survival; weed, insect and disease problems; and harvest and storage. We concluded these topics were more appropriately treated in other courses.

This approach to crop physiology was developed in outline form by Frank Gardner and Roger Mitchell in 1963 and prepared as a first edition by Roger Mitchell. In this second edition, Frank Gardner took a primary role in a major rewriting and Brent Pearce contributed extensively to the expanded focus on crop physiology.

Roger L. Mitchell

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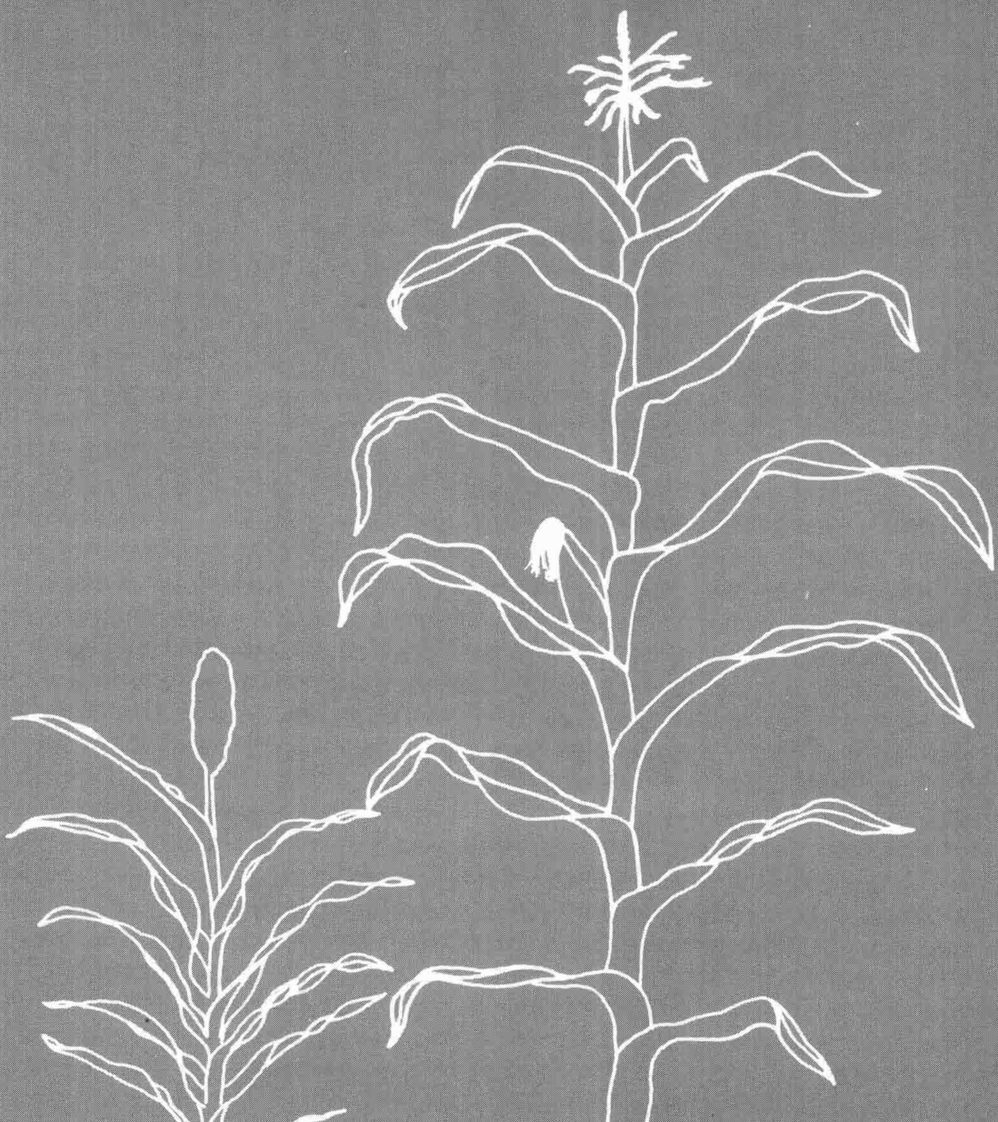

1 Photosynthesis

AGRICULTURE is basically a system of exploiting solar energy through *photosynthesis*. The primary source of energy for humans, photosynthesis has supplied the energy for food, feed, and the fossil fuels that power electrical generating plants and many machines. A study of crop physiology soon leads to the discovery that the yield of crop plants ultimately depends on the size and efficiency of this photosynthetic system. Crop management practices proceed from this assumption. Because photosynthesis is the cornerstone of crop production, it is important to be aware of the energy available to drive photosynthesis and to consider how the anatomical features and biochemical processes in the plant interact to capture and store radiant energy.

Light Used in Photosynthesis

PROPERTIES

Visible light, the source of energy used by the plant for photosynthesis, is part of the radiant energy spectrum (Fig. 1.1). Radiant energy has unique characteristics that can be explained by using two related theories, the electromagnetic wave theory and the quantum theory. The *electromagnetic wave theory* states that light travels through space as a wave. The number of waves passing a given point in a certain interval of time is a *frequency*.

$$\upsilon = c/\lambda$$

where υ = frequency (wavelengths/sec), c = speed of light (3×10^{10} cm/sec), and λ = wavelength. If we divide the speed of light by the frequency, we obtain the *wavelength*.

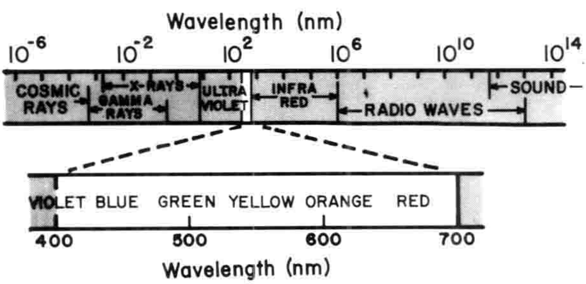

Fig. 1.1. Radiant energy spectrum. Photons in the 400- to 700-nm range are used in photosynthesis.

The *quantum theory* states that light travels in a stream of particles called *photons*. The energy present in one photon is called a *quantum*. Because the energy present in one photon is proportional to the frequency, the quantum can be expressed in terms of wavelength and the energy per photon is inversely proportional to the wavelength (Fig. 1.2).

$$E = h\upsilon = c/\lambda$$

where E = photon energy (quantum), h = Planck's constant (662×10^{-7} erg/s), c = speed of light (3×10^{10} cm/sec), and λ = wavelength. The light reaction of photosynthesis is a direct result of photon absorption by pigment molecules such as chlorophyll. Not all photons have the proper energy level to excite leaf pigments. Above 760 nm the photons do not have enough energy; below 390 nm, the photons (if absorbed by leaf pigments) have too much energy, causing ionization and pigment degradation. Only the photons with wavelengths between 390 and 760 nm (corresponding to visible light) have the proper energy level for photosynthesis.

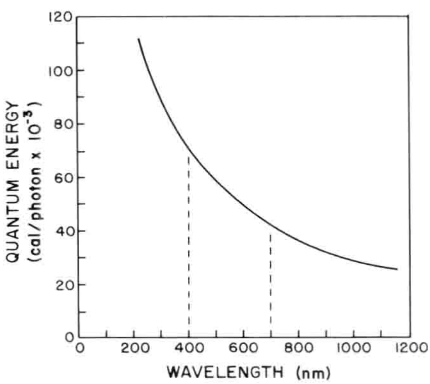

Fig. 1.2. Energy of photons at different wavelengths. Dashed lines show the lower and upper limits of wavelengths that can cause photosynthesis.

Because pigment excitation is a direct result of interaction between a photon and the pigment, a measure of light used in photosynthesis is often based on photon flux density rather than on energy. *Photon flux density* is the number of photons striking a given surface area per unit of time. Since wavelengths between 400 and 700 nm are most efficiently used in photosynthesis, light measurement for photosynthesis is usually based on photon flux density within those wavelengths. These measurements are called photosynthetically active radiation (PAR) or photosynthetic photon flux density (PPFD). The term *Einstein* (E) is defined as one mole of photons, so PAR is often listed in terms of $\mu E \bullet m^{-2} \bullet sec^{-1}$, or under the international system of units as simply $\mu mol \bullet m^{-2} \bullet s^{-1}$.

SOLAR RADIATION

The radiant energy available for photosynthesis on earth comes from the sun. Every energy source used by humans, directly or indirectly, results from solar radiation, with the exception of atomic energy and possibly geothermal energy. For crop growth and development, the sun is the only source of energy.

The sun is a blackbody radiator, and according to Wein's law, the maximum wavelength is inversely proportional to the heat of the body and

$$\max \lambda = 2.88 \times 10^6/K$$

where 2.88×10^6 is Wein's displacement constant and K is the temperature. For example, the temperature of the sun is believed to be 5750 K, so

$$\max \text{ of sun} = (2.88 \times 10^6)/5750 = 500 \text{ nm (green)}$$

Thus, the solar radiation spectrum has a peak at λ of 500 nm (Fig. 1.3). Plants have apparently adapted to solar radiation because the visible light of λ between 400 and 700 nm corresponds to 44 to 50% of the total solar radiation entering the earth's atmosphere.

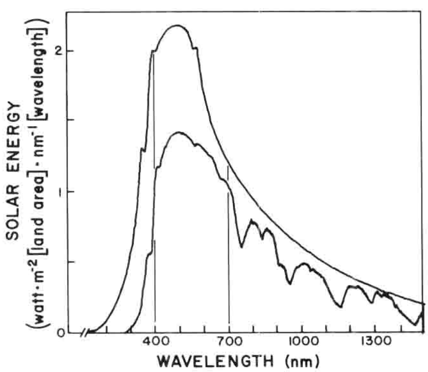

Fig. 1.3. Energy at different wavelengths of solar radiation at solar noon. The top line is the energy just outside the earth's atmosphere, the lower line is the solar energy hitting the earth's surface.

The *solar constant* is 2.00 cal • cm^{-2} • min^{-1} (1395 W • m^{-2}). It is the amount of energy received on a flat surface that is perpendicular to the sun's rays and immediately outside the earth's atmosphere. The solar radiation level decreases as it passes through the earth's atmosphere due to absorption and scattering. The solar radiation at the earth's surface, when that surface is perpendicular to the sun's rays, is reduced from 2.0 to between 1.4 and 1.7 cal • cm^{-2} • min^{-1} on a clear day.

Figure 1.4 illustrates that the axis the earth spins around is tilted in rela-

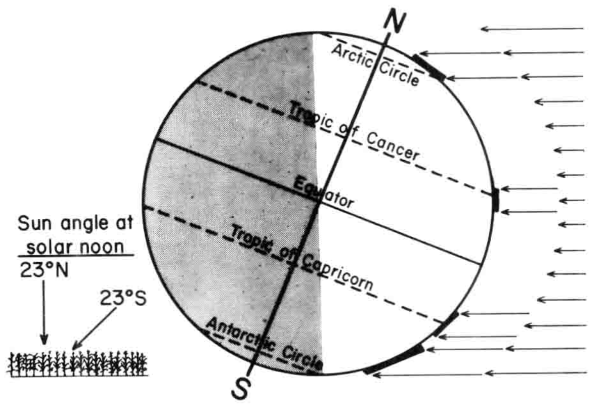

Fig. 1.4. Earth's relationship to the sun on June 22. Earth is angled 23° toward the sun, so the northern hemisphere has days longer than and the southern hemisphere days shorter than 12 hr. The Arctic has constant sunlight (mainly from the horizon), and Antarctic has no direct sun rays. The sun's angle at solar noon is 90° from horizontal at the Tropic of Cancer but only 46° at the Tropic of Capricorn. The situation is reversed on Dec. 22, when the South Pole is oriented 23° toward the sun.

tion to the sun. Therefore annual cycles (Fig. 1.5) and diurnal (daily) cycles (Fig. 1.6) of solar radiation are governed primarily by latitude. Because of this latitude effect, the following factors influence the amount of solar radiation received in one day:

1. Angle of the sun's rays directed on that spot. When solar radiation comes in at smaller and smaller angles from perpendicular to the earth's surface, the light spreads out over a larger ground area, reducing the light level per unit of ground area.

2. Day length.

3. The amount of atmosphere the radiation passed through as a function of the angle of the sun's rays. If the sun is 90° overhead, the number of atmospheres light must pass through equals one; at 60° it is equal to two atmospheres, and at 30° it is equal to five atmospheres.

4. The number of particles (e.g., dust or condensed water particles such as fog or clouds) in the atmosphere. In many tropical regions much less light hits the earth's surface in the cloudy monsoon season than in the cloudless dry season.

5. Other minor factors, such as fluctuations of solar output, distance of the earth from the sun, and the earth's reflecting ability.

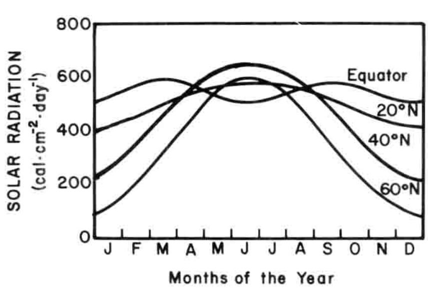

Fig. 1.5. Annual variation in solar radiation energy at different latitudes on cloudless days.

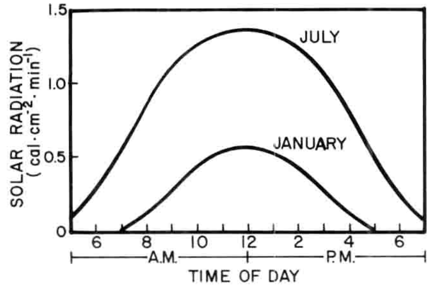

Fig. 1.6. Diurnal (daily) variation in solar radiation energy on cloudless days at 42° N latitude for summer and winter.

Of the solar radiation absorbed during the daytime by a crop surface, 75 to 85% is used to evaporate water; 5 to 10% goes into sensible heat storage in the soil; 5 to 10% goes into sensible heat exchange with the atmosphere by convection processes; and 1 to 5% goes into photosynthesis.

Since the maximum solar radiation level occurs in June and July for the northern hemisphere, the untutored observer might expect agriculturalists to always have their crops ready to make their peak growth at that time (e.g., to have sorghum at the grain-filling stage). However, the opportunity to utilize this radiation peak is limited by seasonal temperature boundaries and the fact that most crops must develop from small seeds or other small organs before the *economic yield* (the harvested portion of the dry matter) can be produced. The challenge to crop physiologists and plant breeders is to develop crops and crop management practices that will place the crop in the appropriate growth cycle to take maximum advantage of this radiation peak.

The Photosynthetic Apparatus

LIGHT REACTION

Electron microscopy has made it possible to look more closely at the chloroplast, which is the photosynthetic apparatus of the plant. The chloroplast, a lens-shaped organelle 1 to 10 μm across, displays two key areas: (1) the *lamellae* (membranes), consisting of stroma lamellae (a double lamella) and grana lamellae (stacked lamella), both of which are concentrated areas of photosynthetic pigments, and (2) the *stroma*, a less dense, fluid area where the reduction of carbon dioxide (dark reaction) occurs (Fig. 1.7). The transformation of light energy to chemical energy (photophosphorylation) occurs in lamellae and consists of the oxidation of water and production of chemical potential, or reduced nicotinamide adenine dinucleotide phosphate (NADPH) and the phosphorylation of adenosine diphosphate (ADP) to adenosine triphosphate (ATP) (Fig. 1.8). The NADPH is one of the most powerful *reductants* (acceptors of electrons and suppliers of hydrogen ions) known in biological systems. ATP is synonymous with available energy in the biological

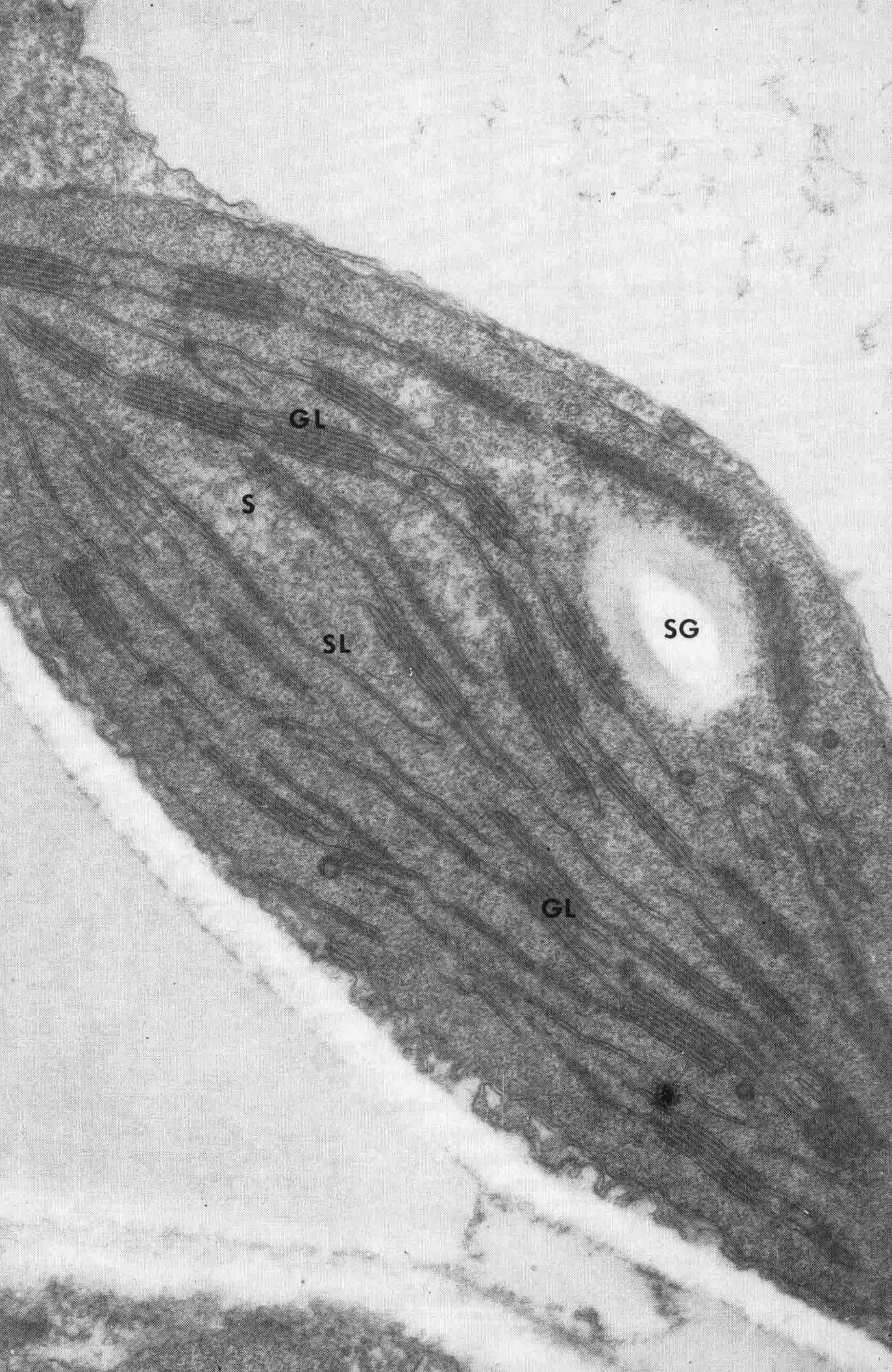
GL
S
SL
SG
GL

Fig. 1.7. Photomicrograph of an alfalfa chloroplast enlarged 64,500 times (Stifel et al. 1968): stroma (*S*), grana lamella (*GL*), stroma lamella (*SL*), starch granule (*SG*).

system; when a phosphate group is released from ATP, energy is also released. The released phosphate, attaching to some molecule (*phosphorylation*) by an energy input, raises the energy of the molecule and allows it to undergo even more chemical reactions. Both NADPH and ATP are needed to convert carbon dioxide (CO_2) to organic molecules.

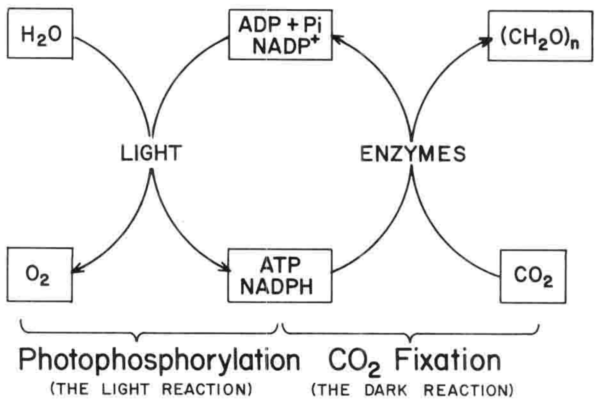

Fig. 1.8. The light and dark reactions that make up photosynthesis. The energy flows from light (irradiance) to high-energy intermediate compounds (ATP and NADPH) and then to long-term energy in bonds connecting carbon atoms of organic molecules.

The electron transport system is fairly well understood (Fig. 1.9). There are two reaction centers where energy from absorbed photons are used to drive the system. These reaction centers have many pigment molecules. When a pigment like chlorophyll or a carotenoid absorbs a photon, the energy lifts an electron (e^-) from a lower (ground) energy state to a higher (excited) state. While in this excited state the pigment molecule can donate and accept electrons from other molecules. Photosystem II catalyzes the removal of electrons from water molecules, and these electrons are accepted by a substance labeled Q. Photosystem I, using more energy from absorbed photons, catalyzes the removal of electrons from Q. This sets up the energy needed for *photophosphorylation* (ATP formation) and the reduction of $NADP^+$ (Fig. 1.9). The chloroplast lamellae are specialized membranes containing the pigments, proteins, and lipid materials that facilitate electron transport (Fig. 1.10).