Chapter 12

Energy Transfer and Energy Migration in Photosynthesis

In Chapter 11, we discussed the effectiveness of different pigments in contributing energy to photosynthesis and suggested that pigments other than chlorophyll *a* cooperate by transferring their excitation energy to the latter pigment. This transfer probably takes place by a resonance mechanism, similar to the one familiar from acoustic experience, but properly describable only in terms of quantum mechanics. There are reasons to believe that most chlorophyll *a* molecules also do not participate directly in the primary photochemical process in photosynthesis, but transfer their excitation energy (by a somewhat different mechanism) to the few chlorophyll *a* molecules directly associated with the enzymatic reaction centers.

We shall deal in this chapter with energy transfer between different pigments ("heterogeneous" transfer), as well as with transfer between identical molecules ("homogeneous" transfer). The latter can be repeated many times, giving rise to energy *migration*.

Direct evidence of energy transfer between different pigments is provided by *sensitized fluorescence*. Light quanta absorbed by molecules of one pigment (for example, chlorophyll *b*) are transferred to molecules of another pigment (for example, chlorophyll *a*); when the first pigment is excited, only fluorescence of the second is observed. This phenomenon is well known from studies on gases and solutions. The occurrence of

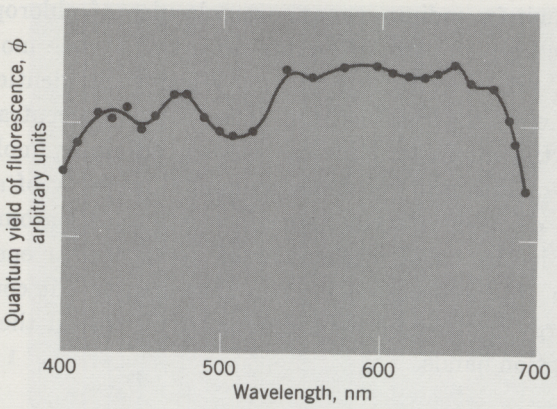

FIG. 12.1 Action spectrum of fluorescence excitation in *Chlorella pyrenoidosa;* fluorescence observed at 740 nm. (P. Williams.)

heterogeneous energy transfer between plant pigments is indicated by the action spectra (or "excitation spectra") of chlorophyll *a* fluorescence in vivo.

In Chapter 11, we described the action spectra of photosynthesis, showing that various accessory pigments contribute excitation energy to photosynthesis with different efficiency. If, instead of the yield of photosynthesis, we plot, as function of wavelength of the exciting light, the yield of chlorophyll *a* fluorescence (measured in the long-wave region where fluorescence is not reabsorbed), we obtain curves that approximately parallel the action spectra of photosynthesis (compare, for example, Fig. 12.1 with Fig. 11.1).[1] This suggests that accessory pigments sensitize photosynthesis by transferring their excitation energy to chlorophyll *a*.

In dealing with excitation energy transfer we have to distinguish between two mechanisms—the "first order" mechanism operative in "homogeneous" energy transfer (and perhaps in some cases of heterogeneous transfer as well!), and the "second order" mechanism operative in heterogeneous energy transfer.

In the first case, that of "ideal" resonance, such as exists between

[1] The reason for discrepancy between the two curves in the 400–450 nm region remains to be elucidated. Fluorescence measurements in the blue-violet excitation region can be made with much narrower bands than those of photosynthesis, thus permitting a more detailed determination of the action spectrum.

atoms of sodium in sodium vapor, or molecules of chlorophyll *a* in a photosynthetic unit, the size of quanta absorbed by one molecule equals precisely that absorbed by the others. When such identical atoms or molecules are close together, as in a dense vapor, concentrated solution, or a crystal, the interaction forces between adjoining molecules cause the excitation quantum to become a communal property of all of them—just as a free electron is a communal property of all atoms in a metal crystal. This is the basic mechanism of *homogeneous* energy transfer and migration (to be discussed later in this chapter); it could also contribute to energy transfer between different molecules if they have overlapping absorption bands.

HETEROGENEOUS ENERGY TRANSFER

The mechanism of resonance transfer of energy between unlike molecules without overlapping absorption bands was analyzed in 1948 by

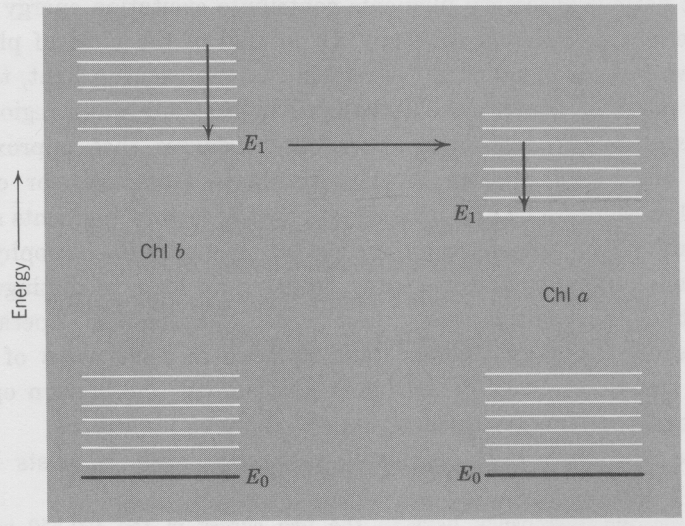

FIG. 12.2 Energy level diagrams of Chl *b* and Chl *a*, indicating why energy transfer is possible from the lowest excited state of Chl *b* to Chl *a*.

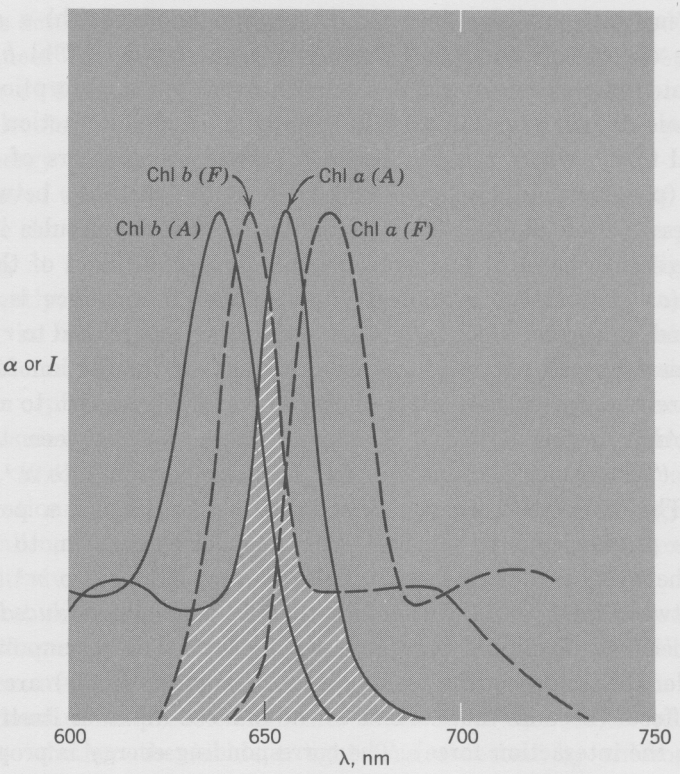

FIG. 12.3 Overlapping of absorption band (*A*) of Chl *a* with fluorescence band (*F*) of Chl *b* (shaded area), and of the absorption bands of the two pigments.

the German physicist Theodor Förster. In this case, "resonance" does not operate *during* the absorption process itself. The absorbed quantum belongs, at first, to one pigment molecule only. However, in the process of vibrational energy dissipation in the excited electronic state of the "donor" pigment (say Chl *b*), states are reached that are in resonance with certain (strongly vibrating) states of the "acceptor" chlorophyll *a* (Fig. 12-2). This "delayed" resonance is what makes energy transfer possible. According to Förster, one measure of probability of such a transfer is the overlapping of the fluorescence band of the donor and the absorption band of the acceptor, indicated by shading in Fig. 12.3. (These two figures refer to the pair Chl *b* + Chl *a* in which *both*

mechanisms are possible, since the absorption band of Chl *a* overlaps both the absorption band and the fluorescence band of Chl *b*.)

The interaction between molecules with overlapping absorption bands is a dipole-dipole interaction.[2] The energy of such interaction is proportional to r^{-3}, where r is the distance between the centers of the two dipoles (presumed to be large compared to the distance between the two poles in each dipole). The interaction between molecules in which the fluorescence band of one overlaps the absorption band of the other, caused (as previously mentioned) by "delayed" resonance is, on the other hand, a "second order" effect; as such, it is proportional to r^{-6}.

The hierarchy of potential energies, E (and of interaction forces, F, which are the derivatives of potential energies in respect to distance, $F = dE/dr$), begins with the Coulomb interaction between two free charges ("monopoles"). In this case, E is proportional to r^{-1}, and F to r^{-2}. The interaction energy between a monopole and a permanent dipole is proportional to r^{-2}, and the force between them, to r^{-3}. The energy between two permanent dipoles is proportional to r^{-3} and the force between them to r^{-4}. The interactions involving an *induced* (rather than a permanent) dipole (that is, a dipole formed in a nonpolar molecule under the influence of a monopole, or of another dipole) are "second order" effects (because the moment of the induced dipole is itself proportional to the interaction force). The corresponding energy is proportional to $(r^{-2})^2$, or r^{-4} in the case of monopole-induced dipole interaction, while the interaction energy of two mutually induced dipoles is proportional to $(r^{-3})^2$ or r^{-6}. This is the type of interaction that quantum mechanics suggests exists between unlike molecules resonating in the above-described "delayed" way.

Förster's calculations suggested that, if the overlapping between the fluorescence band of an excited "donor" molecule and the absorption band of a nonexcited "acceptor" molecule is substantial (as in Fig. 12.3), the time needed for energy transfer may become equal to the natural lifetime of the excited state when the distance between two approaching molecules still is considerably larger than the sum of their "kinetic" radii (that is, radii determined by gas-kinetic methods). In other words, the probability of energy transfer can reach 50% long before the two

[2] The dipoles being the "virtual" dipoles corresponding, in quantum-mechanical treatment of light absorption and emission, to coexistence of the excited state with the ground state (no dipole corresponds to each state separately).

molecules actually collide. The calculated (and actually observed) "critical distances" over which the transfer probability equals 50%, are of the order of 5 nm. In a chloroplast, the distance between different pigment molecules is likely to be much less than 5 nm, so that the probability of energy transfer must be quite high.

Because of the Stokes shift, the fluorescence band of a pigment absorbing at the shorter waves often overlaps the absorption band of a pigment absorbing at somewhat longer waves, but not vice versa (Fig. 12.3). Consequently, energy transfer usually can go in one direction only. For example, in red algae, energy transfer goes from pigments absorbing in the blue region of the spectrum (carotenoids) to those absorbing in the green (phycoerythrin); thence to those absorbing in the orange (phycocyanin); and ultimately to those absorbing in the red (chlorophyll *a*) (Fig. 12.4). In each transfer, some electronic energy is converted into vibrational energy (and then dissipated into thermal energy).

We shall now consider experimental evidence of this kind of excitation transfer in vivo.

The first relevant observation was made in 1943 by H. J. Dutton, W. M. Manning, and B. M. Duggar at the University of Wisconsin. They measured the yield of fluorescence of chlorophyll *a* in a diatom, using monochromatic excitation, and found that this yield was almost the same whether the incident light was absorbed by chlorophyll *a*, or by fucoxanthol. This suggested that most light quanta taken up by fucoxanthol were transferred, by resonance, to chlorophyll *a*. Subsequently, C. S. French and co-workers in California, and L. N. M.

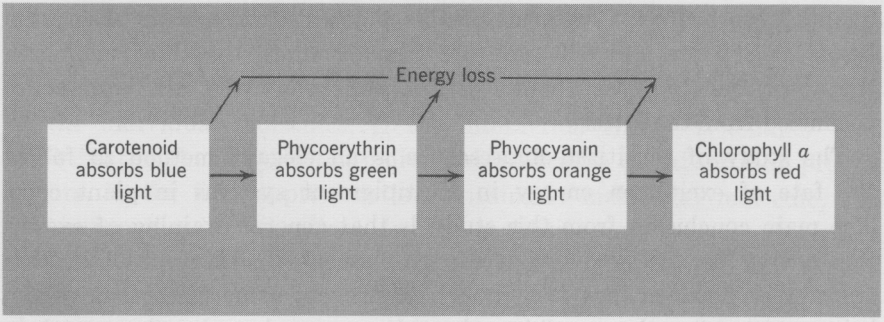

FIG. 12.4 Energy transfer from accessory pigments to chlorophyll *a*.

Duysens in Utrecht in the Netherlands, found that a similar transfer goes on, with varying effectiveness, between all accessory pigments in photosynthesizing cells and chlorophyll *a* as the final energy acceptor. Least efficient is the transfer from the yellow carotenoids; only 20–50 percent of the quanta absorbed by carotenoids find their way to chlorophyll *a*. Much more effective—of the order of 80–90%—is the transfer from phycoerythrin to chlorophyll *a* in red algae. In our laboratory, first S. Brody and then G. Tomita determined directly the time lag of emission of chlorophyll *a* fluorescence after absorption in phycoerythrin (or phycocyanin) as compared to its emission after absorption in chlorophyll *a* itself. The transfer times were found to lie between 0.3 and 0.5 nsec. In other words, they are considerably shorter than the average emission times of phycoerythrin fluorescence (7.1 nsec) or phycocyanin fluorescence (1.8 nsec). Consequently, only a small amount of phycoerythrin or phycocyanin fluorescence is emitted in competition with energy transfer from these pigments to chlorophyll *a*.

Still more efficient is the transfer from chlorophyll *b* to chlorophyll *a*—probably close to 100 percent; the same must be true for transfers from one form of Chl *a* to another in the same photosynthesis unit. ("First order" transfer may contribute to this efficiency.) Because of the smallness of energy differences, the transfer between the different chlorophylls will not be entirely in one direction. An equilibrium distribution of excitation energy will be established between the different forms of chlorophyll, such as Chl *b*, Chl *a* 670, Chl *a* 680, Chl *a* 690. Most of the fluorescence emitted from this system appears, however, to originate in Chl *a* 680 (see Chapter 15).

In the case of bacteriochlorophyll in photosynthetic bacteria, the light quanta absorbed by two forms of this pigment (those with absorption bands at 800 nm and 850 nm) are transferred to the third one, with the absorption band at about 890 nm, and practically all fluorescence is emitted from the latter.

The study of sensitized fluorescence is an elegant method to follow the fate of excitation energy in multipigment systems in plant cells. The main conclusion from this study is that general draining of excitation energy occurs from the accessory pigments to chlorophyll *a*. This transfer is, however, not fast enough to prevent some fluorescence from being emitted "on the way," in red or blue-green algae, by phycoerythrin

and phycocyanin. If (see Chapter 13) the chloroplast pigments are divided into two "systems," energy migration should be analyzed separately for each of them; but this has not yet been attempted.

HOMOGENEOUS ENERGY TRANSFER

We now return to energy transfer between identical pigment molecules, particularly between chlorophyll *a* molecules in "photosynthetic units." These units may contain about three hundred chlorophyll *a* molecules. Energy transfer is known to occur in such dense assemblies; but, unfortunately, we have no simple way to demonstrate it (as sensitized fluorescence permits us to demonstrate the occurrence of heterogeneous transfer).

Since the molecules in the unit are identical, conditions in it are appropriate for a "first order" resonance interaction, with a transfer rate proportional to r^{-3}.

The consequences of this resonance interaction depend on its strength. In one extreme case—that of "weak coupling"—a proper approximation may be the picture of excitation energy migrating by a sequence of "jumps" between adjoining molecules—a kind of "random walk" of the excitation quantum. On the opposite end, that of "strong coupling," one must instead imagine a simultaneous, "communal" excitation of all pigment molecules involved in the exchange (forming, as it were, a single "supermolecule"). The latter case is well known from the study of certain dye polymers, in which strands of several hundred molecules behave like a single giant molecule. In the excited state, the electron sweeps through the whole strand. "Weak" and "strong" interaction are defined by comparison of the interaction energy with the vibrational energy in the individual molecules. If the interaction energy is smaller than the vibrational energy in the individual molecules, the absorption process occurs, in the first approximation, within an individual molecule, and the intramolecular vibrations (whose excitation converts an absorption line into an absorption band, as described in Chapter 10) are excited in the same way as in an isolated molecule. In the second case, when the interaction energy is much larger than the vibrational quantum,

the excitation exchange frequency, ν_e, is (according to the basic law of quantum mechanisms, $E = h\nu$) higher than the vibration frequency, so that numerous energy transfers can take place during a single vibration. Under these conditions, electronic excitation becomes a "communal" phenomenon, and intramolecular vibrations are uncoupled from electronic excitation, with consequent far-reaching change in the shape of the absorption band.

In the case of chlorophyll *a* in vivo, the similarity of the absorption spectrum of the pigment in vivo with its spectrum in solution (in which absorption occurs in isolated molecules), clearly indicates that conditions in photosynthetic units are *not* those of "strong interaction" in which individual molecules are combined into a supermolecule. Rather, the situation approaches the case of "weak interaction," in which excitation moves around from molecule to molecule in a random walk.*

The random walk of excitation in the photosynthetic unit energy ends when the quantum is either reemitted as fluorescence by one of the molecules it visits on the way, or is dissipated by internal conversion in one of them, or reaches a "trap" (a spot where its energy is used to bring about a chemical reaction).

We believe this is what actually happens in the photosynthetic units in chloroplasts; but nobody has been able to devise an experiment directly demonstrating the random walk of the quantum in them. One indirect evidence is almost complete depolarization of chlorophyll *a* fluorescence in vivo (see below).

Simple arguments can be adduced in favor of migration of the excitation quantum as an indispensable step in photosynthesis. In order to utilize efficiently solar radiation, plant cells must strongly absorb it (compare p. 102). A leaf, containing a few layers of green cells, in fact absorbs red and blue-violet light almost completely. Even a single Chlorella cell, about 5×10^{-4} cm thick, absorbs up to 60% of incident light in the maximum of the red absorption band—this is why it appears distinctly green under the microscope. To achieve such absorption, it is not enough for the cells to contain a strongly absorbing organic pigments, such as chlorophyll (or a phycobilin); these pigments have to be present in large amounts. A French proverb says, "the most beautiful girl cannot give more than what she has"; and the most intensely colored pigment cannot absorb more quanta than its absorption coefficient permits!

* Weak first order coupling should not be confused with the still weaker second order coupling.

The highest absorption coefficients of organic pigments are of the order of 10^5 (See[3]). Typical green plant cells have linear dimensions of the order of 10^{-3} cm. To produce a 50% absorption in the band maximum ($I = 0.5I_0$), the pigment concentration in such a cell must be of the order of 3×10^{-3} mole/liter, as the following simple application of Beer's law proves. If I is equal to $0.5I_0$, we can write.

$$\log (I_0/I) = \log 2 = 0.3 = \alpha cx = 10^5 c 10^{-3}; \text{ or,}$$
$$c = 3 \times 10^{-3} \text{ mole/l} \qquad (12.1)$$

Actually, fully green leaves do contain up to five percent of chlorophyll *a* in relation to dry weight, corresponding to a cellular concentration of the order of 10^{-2} mole per liter.

The purpose of this estimate was to make clear that by the very nature of the task placed before photosynthesizing cells, they must be densely packed with pigment molecules. Now, having absorbed the light quanta, the cell must use the absorbed energy to set in motion chains of enzymatic reactions, by which the unstable primary photochemical products are converted into the final products, O_2 and (CH_2O). For this, at least a dozen, if not more, specific enzymes are needed (see Chapter 17). An enzyme molecule is a protein with a molecular weight (and thus also space requirement) a hundred or thousand times larger than that of a chlorophyll molecule. There is not enough space in the cell for a separate "enzymatic assortment" to be assigned to each pigment molecule! A large number of pigment molecules simply *must* share a common enzymatic "conveyor belt."

Fortunately, the catalytic capacity of enzymes is quite sufficient for this purpose. It is easy to calculate, from Beer's law, that a single pigment molecule, with an absorption coefficient α will absorb, in a second, out of a light flux $I_{h\nu}$, (measured in number of quanta falling each second upon one cm^2), a number, n, of quanta determined by the following equation:

$$n = 4 \times 10^{-21} \alpha I_{h\nu} \qquad (12.2)$$

[3] A molar absorption coefficient of 10^5 means that 6×10^{23} molecules have a total "opaque" cross section of $10^5 \times 10^2$ cm the factor 10^2 appears because concentration is measured in moles/liter). This means $10^7/6 \times 10^{23} = 1.6 \times 10^{-17}$ cm^2, or 15 A^2, per molecule—which is close to the "kinetic" cross section of a medium-sized organic molecule, such as chlorophyll, as determined, for example, from its diffusion coefficient. In other words, pigment molecules are practically "black" to light in the peak of their absorption band.

The strongest flux to which plants are exposed in nature is that of full sunlight at noon, which corresponds to $10^{16} - 10^{17}$ (visible) quanta per sec per cm^2. This means according to Eq. 12.2 that each pigment molecule will absorb, under natural conditions, only a few quanta ($n = 4 - 40$) each second. This is very little by standards of enzymatic efficiency; many enzyme molecules can handle tens of thousands of substrate molecules per second. One "enzymatic conveyor belt" is, therefore, quite sufficient to handle the photochemical production of hundreds, if not thousands, of pigment molecules.

We have already reviewed in earlier chapters (Chapters 6 and 8) evidence suggesting the presence in chloroplasts of one "reaction center" for about 300 chlorophyll molecules. A mechanism is required by which light quanta absorbed by several hundred chlorophyll molecules can be put to work on a single enzymatic conveyor belt—a system of "messengers" connecting the many pigment molecules in a unit with a single reaction center. These messengers could conceivably be material particles, for example, the primary oxidation or reduction products, diffusing from the many pigment molecule where the quantum had generated them, to a single "reception point" of the enzyme system. A more compact, safer, and faster mechanism is, however, physically possible: instead of a messenger with a letter, the communication can be by a telegram! This is what resonance energy migration amounts to. In it, only excitation energy, in the form of "excitons"—in other words, only the light electrons and not the heavy atoms or molecules, need to move.

It is the nature of a quantum phenomenon that the energy of a migrating "exciton" is not dissipated during migration, but kept in one piece. The *course* of migration can be represented by a spreading *wave,* but the whole energy of the "exciton" can be found, at a given moment, in one or the other of the many resonating molecules. The wave describes merely the spread of the *probability* of finding the quantum in different locations. (In ordinary mechanical resonance, on the other hand, the vibrational energy actually spreads over the assembly of resonating forks or bells, and is unlikely to be found assembled again in a single one of them.)

One can visualize the exciton as consisting of an excited electron and an "electron hole" left in an atom or molecule. In "random walk" of energy—the case we consider here—the electron and the hole move together, always remaining in the same atom or molecule (Fig. 12.5).

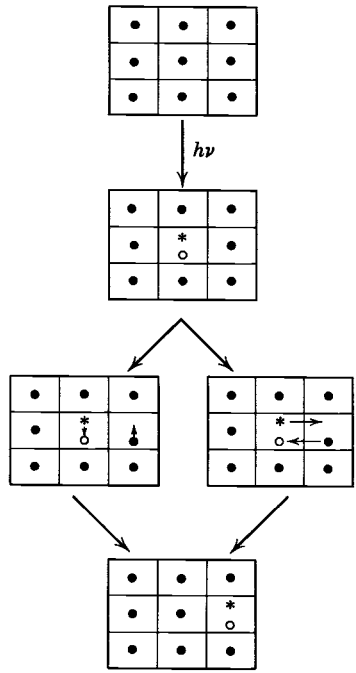

FIG. 12.5 Two mechanisms of exciton migration in a crystal lattice. *Left:* Heller-Marcus mechanism; *right:* Wannier mechanism. Dots represent unexcited molecules, asterisks, excited electrons, and circles, positive cores left after excitation.

In other words, this type of migration involves no separation of positive and negative charges.

The random walk picture of energy migration reminds one of a pinball machine, into which a steel ball had been shot; the different bulbs light up one after another, as the ball runs around on the board, until it either falls to the bottom (which corresponds to reemission of the quantum by fluorescence), or falls into a "pay hole," that is, its energy is utilized for a photochemical process.

It is worth mentioning here that resonance energy migration does not in itself affect the natural lifetime of excitation. A man could not extend his natural life expectancy by sleeping each night in a different bed! However, in practice, the random walk of the "exciton" involves risks. Some "beds" on its way may be infected, or have to be shared with dangerous companions. A migrating quantum has a greater chance

of getting into such a dangerous situation than a stationary one, and this may lead to its premature death. More specifically, some molecules in the array may be engaged in chemical interactions. This can create a "trap" (or "sink") into which the migrating quantum stumbles. In other words, resonance energy migration can lead to the abbreviation of the lifetime of the exciton, and thus to the *quenching of fluorescence.* In photosynthesis, the trap may be identical with the "reaction center," where the migrating quantum is caught and put to useful work.

Resonance migration accounts, at least in part, for the well-known phenomenon of *concentration quenching* of fluorescence: strong solutions of fluorescent pigments fluoresce weaker than the more dilute ones. An even more sensitive index of resonance energy migration is *depolarization* of fluorescence—weakening or disappearance of polarization normally present in fluorescence excited by polarized light. If fluorescence is excited by plane-polarized light, that is, light that vibrates (and causes, upon absorption, the electrons in the molecule to vibrate) preferentially in a certain plane, the emitted fluorescence also is polarized. This is so because in the interval between absorbing a quantum and reemitting it, the molecule does not have enough time to forget the orientation it has had at the time of absorption. But if the energy quantum undergoes, between absorption and emission, a series of resonance transfers, each molecule in the resonance chain will be oriented somewhat differently, and after a few transfers, the original preference for a certain direction will be lost. It has been observed, for example, that the fluorescence of phycobilins, excited by polarized light, is completely depolarized. This can be considered as evidence that a quantum absorbed by one of many phycobilin molecules contained in the pigment-protein complex, moves, by resonance, from one of them to another and becomes completely "disoriented" by the time of reemission.

ELECTRON MIGRATION

A few words should be said about another possible mechanism of energy migration: the migration of *electrons.* This is a phenomenon well known from the study of crystals.

In *metallic* crystals, the electrons move freely even without external

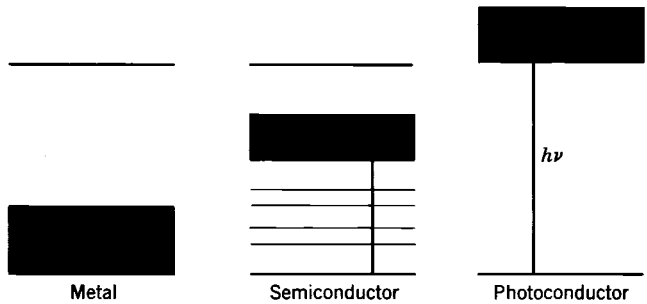

FIG. 12.6 Conductance levels (shaded areas) in a metal, a semiconductor, and a photoconductor.

excitation. The sharp energy levels of individual atoms are replaced, in metals, by so-called "conductance levels," which are not sharp, but form broad bands (Fig. 12.6). This sharing of electrons by all atoms in a piece of metal is the reason for its electrical conductivity. If we apply a potential difference to the two sides of a metallic piece, all free electrons rush in the direction of the applied force, toward the positive electrode, like kids left by their mothers to play in a park will run towards the street where a band is passing.

In *semiconductors,* such electron migration becomes possible only after thermal excitation. The conductance levels in them are higher than the energy levels in which the electrons belong to individual atoms; but the difference is small, so that moderate heating is enough to send some electrons into conductance bands. Finally, in *photoconducting* crystals, the separation between the "atomic" and the "conductance" levels is much larger than kT at room temperature (k is the Boltzman constant and T, the absolute temperature); this gap cannot be bridged by thermal excitation, but only by absorption of a light quantum. A normally insulating crystal thus becomes a conductor when exposed to light (Fig. 12.6). Such "photoconductivity" is found in many organic crystals.

In addition to conductivity based on free movement of electrons (which are negatively charged), there exists a second mechanism of photoconductivity: the migration of (positively charged) holes, left in the lattice by electrons raised into conductance levels. Migration of holes is, in essence, still a migration of *electrons:* a hole in an atom, left by excitation of an electron, is filled up by an electron supplied by

a neighboring atom, and so on, in a chain. The net result is that the positive hole migrates through the crystal. If an electric potential is applied, this migration becomes directed preferentially toward the negative electrode, and the hole emerges from the crystal at this electrode. The hole migration may become more significant than the migration of the excited electrons if the latter get stuck—as electrons often do—in some traps in the lattice (provided by lattice irregularities).

The arrangement of chlorophyll molecules in the chloroplasts is *not* crystalline, as proven by its absorption spectrum. It was suggested that light absorption could nevertheless make the chlorophyll layer "photoconducting." The migration of an electron (or of a corresponding hole) could serve then as a "quantum gathering" mechanism, instead of a migration of excitons. An "enzymatic center" could represent a "sink" or "trap" catching the migrating electron (or hole).

We recall that taking up an electron is *reduction*, and losing one, *oxidation*. An electron "trap," surrounded by closely packed pigment molecules, could catch electrons produced by light absorption anywhere in the pigment body, while holes, migrating in their turn, could be trapped somewhere else, in "reducing" (that is, electron-donating) traps. This view is advocated particularly by William Arnold at Oak Ridge, who described a number of experiments suggesting photoconductive behavior of chloroplasts.

A combination of the two mechanisms—exciton migration and electron migration—has also been suggested: An exciton, produced by the absorption of a quantum, migrates through the photosynthetic unit, until it meets an oxidizing (electron-catching) or a reducing (electron-donating) enzymatic center. There, the excited electron is trapped (or the hole is filled up), and an enzymatic conveyor belt is set into motion. The exciton is now reduced to a free electron (or a free hole), which, in turn, migrates through the units until it reaches an electron-donating (or electron-catching) center. The primary photochemical oxidation-reduction process is thus completed, the oxidation product being formed in one enzymatic center, and the reduction product in another center.

This indirect mechanism of charge separation is more plausible than a direct one for the following reason: Whenever charge separation and photoconductance are a direct result of the absorption of a quantum, the absorption spectrum of the material shows that sharp excited electronic levels, characteristic of isolated molecules, have been replaced by

broad conductance bands. No evidence of such transformation appears in the spectrum of chlorophyll in vivo; the absorption bands of chlorophyll in the living cell are similar to those of chlorophyll in a molecular solution. This objection does not apply to the above-described indirect mechanism of charge separation.

It is useful to realize that the difference between the "pure" exciton migration mechanism, and a combined exciton-electron (or exciton-hole) migration mechanism consists in spatial separation of the loci of primary reduction and primary oxidation in the second mechanism; while in the first one, the two processes must follow each other in the same place.

Much further experimental and theoretical work remains to be done before the role (and the mechanisms) of energy migration and electron migration in photosynthesis will be completely understood.