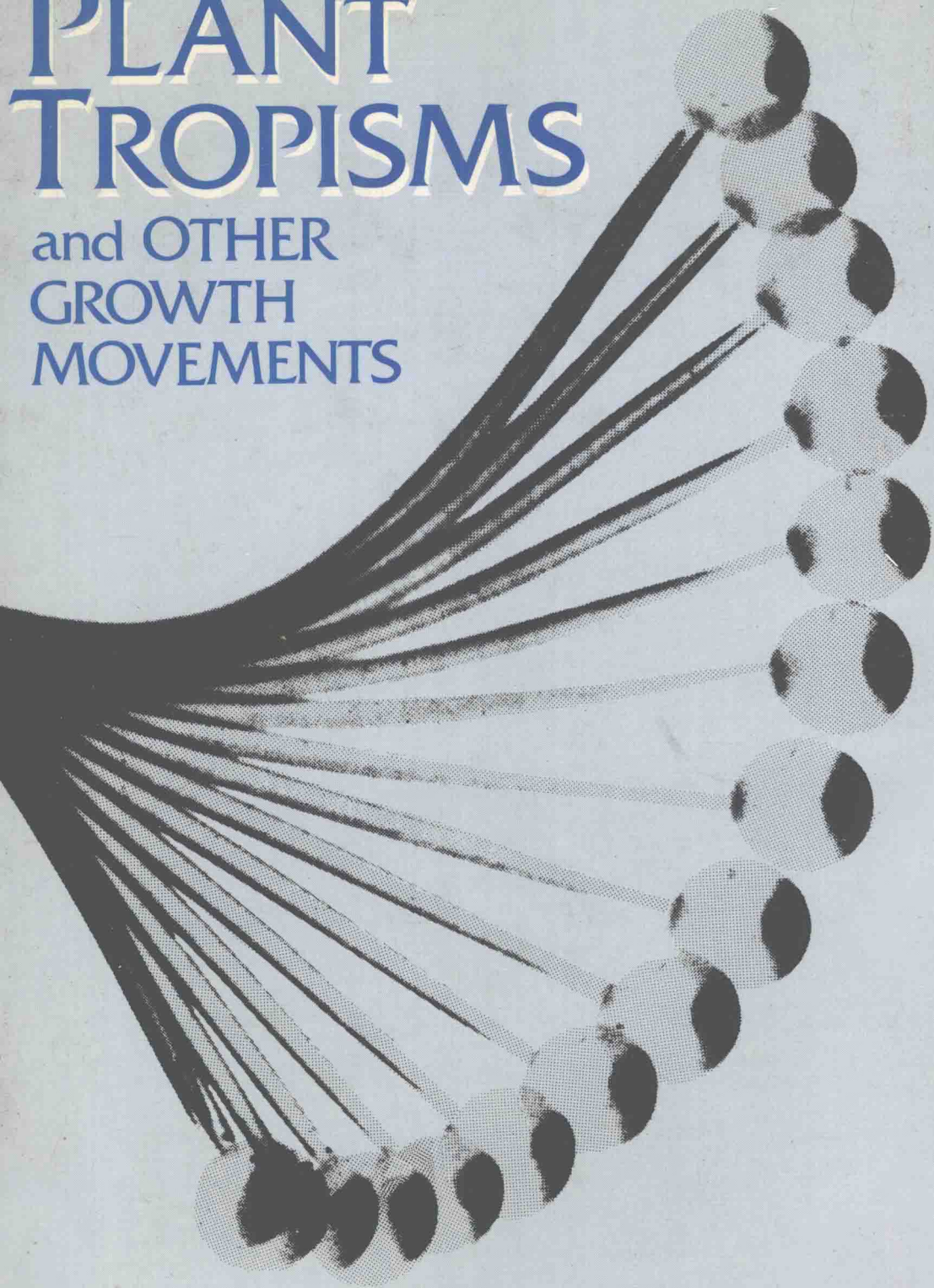


PLANT TROPISMS

and OTHER
GROWTH
MOVEMENTS



James W. Hart

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If we look, for instance, at a great acacia tree, we may feel assured that every one of the innumerable growing shoots is constantly describing small ellipses; as is each petiole, sub-petiole, and leaflet . . . The flower peduncles are likewise continually circumnutating . . . All this astonishing amount of movement has been going on year after year since the time when, as a seedling, the tree first emerged from the ground.

Charles Darwin (1880)
The power of movement in plants

No plant is entirely without the power of movement . . . The fact that in large plants the power of growth and movement are not strikingly evident has caused plants to be popularly regarded as 'still life'. If mankind . . . were accustomed to view nature under a magnification of 100 to 1,000 times, or to perceive the activities of weeks or months performed in a minute, as is possible by the aid of a kinematograph, this erroneous idea would be entirely dispelled.

Wilhelm Pfeffer (1906)
The physiology of plants

Preface

Life involves movement. Plants are no exception to this generality, although their mechanisms of movement are markedly different from those of animals. One way in which even sedentary higher plants move is through changes in the rates or patterns of growth within their organs, often directly in response to stimulation by some environmental factor. Tropisms are one such form of plant movement, and represent a major means by which a plant senses, responds, and adjusts to its surroundings. This book attempts to give an account of this area, and to demonstrate that the beauty, and sensitivity, of plants extends beyond any static 'still-life' picture.

Chapters 1 and 2 are introductory, dealing respectively with plant movements in general and tropisms in particular. The next three chapters deal with responses to the major types of tropic stimuli, i.e. gravity, light, and mechanical factors. And the final chapter considers other types of stimuli, such as chemicals, water, and injury, which are of most significance only to particular plants, particular stages of development, or particular situations. Throughout the text there are also special topic 'boxes' consisting of squared off sections of text. These are simply devices for presenting explanatory background information, or for considering related aspects that I myself find particularly intriguing.

In the interests of space and readability no attempt is made to produce an exhaustive literature review, particularly with regard to the older literature. In many cases, of course, some specificity or priority is required and original sources are given, but in general, access to the older literature can be obtained through the reviews that are cited in the text in relation to particular areas.

I would like to thank Norman Little for his expert assistance with many of the illustrations and photographs, and my typist, Mrs Betty Smith, for expertly disentangling and dealing with my manuscript.

J. W. Hart
Aberdeen, 1989

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CHAPTER ONE

Tropisms and other forms of plant movement

Tropisms constitute one particular form of directional movement shown by plants. Before the detail of later chapters, it may be useful to consider them within this general context of plant movement in order to get some idea of their overall significance in the life of the plant.

This approach also provides the opportunity to introduce turgor responses, another major form of plant movements that are sometimes closely associated with tropisms.

1.1 PLANTS AND MOVEMENT

If asked to distinguish between plants and animals, perhaps most people would sooner or later offer the observation that 'animals move and plants do not'. But in fact, movement pervades all aspects of plant behaviour, though not always in the restricted sense of locomotion of the whole organism.

In the plant kingdom, controlled voluntary locomotion is seen only in the streaming (slime moulds), gliding (diatoms), and free-swimming movements (flagellated algae) of lower plants and certain kinds of reproductive cells. The types of protein-based mechanisms that are responsible for these movements are restricted in higher plants to driving intra-cellular movements, such as occur in cell division, cytoplasmic streaming, and so forth.

In higher plants, movement of the whole organism does occur in one sense, through the dispersal of reproductive units such as seeds, spores, and vegetative propagules. However, in all the wide variety of mechanisms used in this area, whether based on some form of explosive dehiscence or on passive transport by wind, water, or animals, the energy for the actual movement itself does not come directly from the plant's own metabolic activity, but is supplied by some other agency or

organism. Therefore, although reproductive dispersal can result in the movement of plants over vast distances, it represents an involuntary form of movement that is neither under the direct control of the plant nor necessarily related to immediate environmental problems or pressures.

All higher plants move, however, in the sense that they are continually carrying out controlled changes in the orientations and juxtapositions of their various parts. Such movements, directly analogous to changes of posture in animals, are brought about by two distinct types of mechanisms in plants. *Turgor movements* are due to reversible changes in the sizes of special cells which bring about the movement of a lever arm, such as a leaf blade or a reproductive structure. *Growth movements* result from particular patterns of differential growth within or between organs, and, although necessarily slow, are no less dramatic or crucial to the life of the plant.

Each of these forms of movement, by change in turgor or by change in growth, can be controlled endogenously or exogenously. Endogenously regulated movements are initiated or controlled by some factor within the plant, although factors in the external environment may have an indirect effect on the movement. In most cases, the exact nature of the internal regulatory factor is not clear. Endogenously regulated turgor movements generally occur in some kind of periodic repeating pattern or rhythm. When the rhythm is approximately the length of a day, the movements are considered to be controlled by, or to be a manifestation of, the circadian clock (Koukkari & Warde 1985). Movements showing much shorter rhythms are known, but in these the regulatory mechanism is completely obscure. Endogenously regulated growth movements are generally part of the normal pattern of development of an organ and, as such, are considered to derive from some preprogrammed physiological asymmetry within the tissues, perhaps, for example, involving some sort of differential behaviour of a growth-regulating chemical or some sort of differential sensitivity of the tissues towards a growth regulator.

In exogenously regulated movements some environmental factor *directly* initiates or controls the change in turgor or growth rate that is responsible for the movement. Turgor movements are generally initiated either by light or by physical contact, depending on the type of movement. Directed growth movements are most generally controlled by light or by gravity. However, it is becoming increasingly apparent that other forms of mechanical stimulation, such as contact, flexure, vibration, and pressure, also play a major role in regulating growth movements. And, particularly in lower plants, specific chemical signals often stimulate growth movements. Temperature, of course, also exerts major effects on plant growth. Thus, the range and types of environmental factors that initiate or control plant movements are directly comparable to those

PLANTS AND MOVEMENT

Table 1.1 Summary of the major forms of movement responsible for changes in the orientation of plant organs.

Type of stimulus	Type of mechanism	
	Turgor change	Growth
endogenous	nyctinasty* (leaves) ultradian rhythms (leaves) flower movement* (sunflower)	nutations (all organs) epinasty (petioles, shoots) autotropism (see Ch. 2)
temperature		thermonasty (petals)
light	photonasty (leaves) heliotropism (leaves)	photonasty† (flowers) phototropism† (aerial organs)
gravity		gravitropism (most organs)
mechanical	seismonasty (<i>Mimosa</i> leaves) thigmonasty (floral parts) (insect traps)	thigmonasty (most tendrils) thigmotropism (some tendrils)
chemical		epinasty (petioles, shoots) chemotropism (fungal hyphae, pollen tube?)
injury		traumatropism (all organs?)

* The rhythms of these movements are entrained by light.

† In a nastic movement the direction of response is determined by features of the tissue; in a tropic movement, the direction of response is determined by the stimulus.

provoking sensory responses in animals and, indeed, in many instances the sensitivity of a plant or plant part towards any one of these environmental factors is of the same order of magnitude as that of many animals (Shropshire 1979). (It is only in regard to their responsiveness towards external electrical stimulation that the sensory ranges of plants and animals seem to show any appreciable difference, although even in this respect it is now clear that, internally, electrical signals are important within the plant (see Ch. 2), and, externally, in some responses (Miller *et al.* 1986) electrical signals may act as important sources of directional information to certain types of plant.)

All of these regulatory environmental factors initiate and control plant movements by acting through catenary events, which involve processes of stimulus reception, physiological mediation of the signal, and regulation of the eventual biological response. These aspects are discussed in Chapter 2.

In the nomenclature of plant movements, the two terms 'nastic' and 'tropic' (or 'tropistic') are commonly used. It should be noted that these terms do not relate to the particular mechanism of movement (turgor change or growth response), nor specify the means of regulation (endogenous or exogenous). They simply refer to the directionality of the

movement. A nastic response is one in which the direction of the movement is determined by features of the tissue, rather than by the stimulus; thus, nastic movements can be initiated by endogenous or exogenous factors; and they can also result from turgor changes or from growth. A tropic response, on the other hand, is one in which the direction of movement is strongly related to the direction of some environmental factor; thus tropic responses are always initiated by exogenous stimuli; they usually result from changes in growth, though some (e.g. tendril movements) may also involve turgor responses and at least one (i.e. heliotropism) seems to result wholly from turgor changes.

The various types of turgor and growth movements are summarized in Table 1.1, and a general account of each of them is given in the rest of this chapter.

Box 1.1 Movement and life's problems.

All organisms, including plants, animals, and humans, must overcome problems in three general areas in order to be biologically successful. These are:

- (a) *Self-protection*, which involves protection against climatic conditions and against other organisms.
- (b) *Food collection*, which in its widest sense includes processes involved in reaching (or creating) an environment that provides adequate levels of resources, as well as processes involved in the actual uptake of food into the organism.
- (c) *Reproduction*, which, to be wholly successful, involves not only fertilization and the production of offspring, but also the dispersal and establishment of the offspring in suitable environments.

Of course, most animals utilize some form of voluntary locomotion or movement in all of these areas, but sedentary higher plants must depend largely upon other means. These are often based upon the elaboration of specialized metabolic pathways, e.g. chemical methods of protection (against other organisms by means of toxins, or against high light intensities by means of pigments), and chemical enhancement of reproductive efficiency (by the production of visual or olfactory attractants). And they are also often based upon specialized modes of development, e.g. protection against the rigours of climate by means of dormancy, and regulation of reproductive events by means of photoperiodism.

However, as should become apparent from the discussion throughout this and subsequent chapters, plants do use movement in various forms and to different extents in each of these biological 'problem areas'. For example, the relative rapidity of turgor movements means that they are often involved in aspects of protection and reproduction. On the other hand, the slower growth movements; and in particular the directionally controlled tropisms, are more generally involved in 'moving' plant parts towards the most favourable environment.

1.2 PLANT TURGOR MOVEMENTS

1.2.1 *General nature of the mechanism*

Turgor movements are brought about by osmotically driven changes in the volume of special cells, or of cells in special regions (Hill & Findlay 1981, Findlay 1984). That is, the osmotic potential of the cells is increased, usually by the uptake of potassium and balancing anions such as Cl^- ; water is therefore taken in and the cells increase in size. When potassium is lost from the cells, water is also lost and the cells decrease in size. The uptake of potassium is generally considered to be an active, energy-requiring process, perhaps coupled to proton extrusion through a membrane ATP-ase, but its efflux is thought to be passive (Satter 1979, Galston 1983). However, in some extremely rapid turgor movements, such as occur in certain pollination mechanisms, the phase of cell shrinkage is so fast that some contractile mechanism is also thought to be involved in the active expulsion of water (Findlay 1984).

The volume changes of the guard cells during opening and closing of stomata represent a structurally simple form of turgor movement, but the same type of osmotic engine is also used to drive movements that are more elaborately structured and more obvious. For example, in many species the base of the leaf petiole consists of a bulbous region, the *pulvinus*, which contains special, structurally distinct 'motor cells', with very thin walls. Turgor changes in the motor cells bring about changes in the angle of the leaf petiole, i.e. the pulvinus functions as a kind of active hinge. The anisotropic changes in volume of the motor cells in *Phaseolus coccineus* seem to be due to the hoop-like arrangement of cellulose microfibrils in their longitudinal walls (Mayer *et al.* 1985).

In many types of turgor movements, however, the arrangement and appearance of the motor cells are not so anatomically distinct as in the leaf pulvinus.

1.2.2 *Types of turgor movements*

Turgor movements can be somewhat arbitrarily categorized according to whether the major factor that is directly responsible for their initiation is of endogenous origin or is some exogenous environmental stimulus.

Endogenously regulated turgor movements

The leaves of many plants, including all legumes, show daily changes in orientation known as 'sleep movements' or *nyctinastic* movements (literally, 'night-folding'). In these movements (Fig. 1.1a) the leaves are opened out during the day and folded in along the stem axis at night, upwards or downwards depending on the species. (The adaptive sig-



(b)

Key
 F flexor cells (swell during closure)
 E extensor cells (swell during opening)
 → directions of K^+ movement

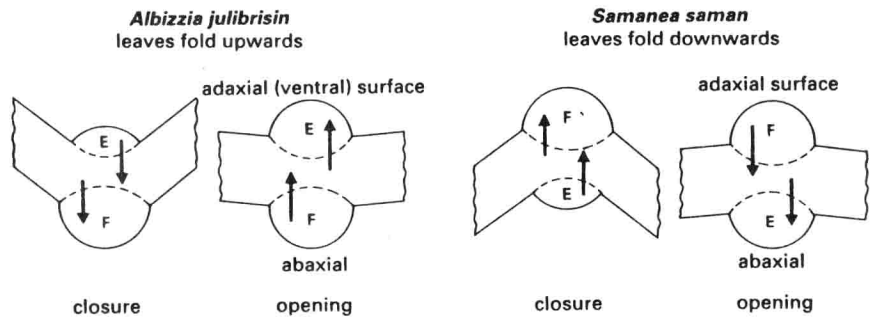


Figure 1.1 Nyctinastic sleep movements in leaves. (a) Leaf orientation in *Desmodium gyrans* (the 'telegraph plant') during the day (left) and at night (from Darwin 1880). (b) Summary of events during sleep movements in two species of legume, viewed through idealized sections of rachis and leaflets (from Hart 1988).

nificance of these movements is not too clear, but they may minimize radiative heat loss from the plant at night.) In some cases, these leaf movements may be due to changes in growth rate (Yin 1941), but they more generally result from rhythmic turgor changes in the pulvinar motor cells (Satter 1979, Galston 1983). In many species these motor cells consist of two functionally distinct types (Fig. 1.1b): during leaf opening, those designated as 'extensor' cells take up potassium and swell, and the 'flexor' cells lose potassium and decrease in size; during leaf folding, the directions of potassium movement are reversed and the extensors shrink while the flexors swell.

Nyctinastic leaf movements show a strong circadian rhythm, i.e. they continue in a cycle of approximately 24 hours even under constant environmental conditions and continuous darkness. The actual basis of circadian timing, the so-called biological clock, is not yet clear, although several models have proposed a central role for the cell membrane in the timing mechanism (reviewed in Engelman & Schrempf 1980). For example, one such model (Njus *et al.* 1974) suggests that the timing system involves the active pumping of potassium into some cell compartment until at saturation the pump is switched off by feedback inhibition; the circadian timing period then results from the time taken for potassium to passively leak out of the compartment and the pump to become switched on again. Such events may be involved in the turgor changes of nyctinasty.

However, a certain class of chemicals has also been shown to specifically regulate leaf turgor movements in a wide range of species (Schildknecht 1984). These chemicals, derivatives of organic acids such as gallic acid and catechuic acid, have received the general names 'turgorins' or 'leaf movement factors' (LMFs) and are thought to bring about water loss from the motor cells by binding to the cell membrane. The turgorin LMF1, from *Robinia pseudoacacia*, has also been shown to induce stomatal closure in *Commelina communis* (Paterson *et al.* 1987). It has been suggested that rhythmic cycling of turgorins between active and inactive forms may be involved in circadian timing (Schildknecht 1984).

Circadian leaf movements can also be influenced by factors in the external environment, particularly light. The actions of two separate photoreceptors seem to be involved (Galston 1983). Blue light, given at the appropriate stage of the circadian rhythm, generally stimulates leaf opening, and in some species this effect completely overrides the rhythm, to result in photonastic and heliotropic leaf movements (discussed in the next section). The effects of red light, acting through phytochrome are less straightforward and seem to involve effects on the entrainment of the circadian rhythm as well as effects on the actual rates and extents of leaf opening (Galston 1983). In a few species, mechanical