Chapter 1

ECOLOGICAL ADAPTATIONS OF GOSSYPIUM SPECIES

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INTRODUCTION

Gossypium is a large genus, comprising almost 40 species, that encompass a notably wide range of diversity. Several species are well known in cultivation as the world's commercial cotton crop. The majority, however, are less well known and occur as elements of the indigenous vegetation in various parts of the world. Among these wild species (from Australia, Africa, Mexico, and elsewhere) a great range of ecological variation is found, including various morphological and physiological adaptations to the diverse habitats in which they occur.

It may be argued that an understanding of the physiology of the (cultivated) cotton plant is not complete without a knowledge of the range of variation exhibited by these (wild) related species. This is true in a dual sense: (1) that an understanding of the phylogenetic milieu from which the cultivated species originated in a historico-evolutionary sense is important; and (2) that a knowledge of the physiological spectrum of variation that is inherently available in the genus and therefore potentially available in the cultivated species through selective breeding and germplasm manipulation is also important. The present chapter is offered in such a context.

Many detailed physiological studies of the cultivated cottons have been made (witness this volume), whereas relatively few such studies have been made of their wild relatives. Consequently, a comparative presentation at this level is essentially impossible. Instead, attention will focus here on their ecology and particularly on their adaptations to ecological factors from which physiological inferences may be drawn. There is, of course, an evolutionary dimension to such a study, evolution not only of the plants themselves but also of the climatic situations in which they occur.

HABITATS

The wild cottons are generally confined to subtropical and tropical regions, although there are some instructive exceptions. They tend to occur in relatively arid habitats, sometimes in extremely arid habitats. These climatic factors, coupled with edaphic factors, have a controlling effect on the entire vegetation of a given region, and in turn the associated vegetation (or vegetation type) is itself a significant ecological factor for each of the wild species of *Gossypium*.

Climate is generally regarded as an integrated expression of temperature, moisture, prevailing winds, and amount of sunshine for a given locality, including cyclical aspects of the changing seasons. These (and other) variables are interrelated in complex ways and, in fact, are not independent of the vegetational cover itself. Therefore, it must be understood that statements about the relation of a particular climatic variable to the ecology of the plants of the region are generally oversimplifications to a greater or lesser degree.

TEMPERATURE

Temperature is, of course, a key climatic factor. As already noted, the wild cottons generally occur in the tropics and subtropics, that is to say in frost-free areas. There are exceptions to this statement (to be discussed below), but the general fact is that the protoplast in most species of *Gossypium* is sensitive to, and is killed by, freezing temperatures.

A second observation to be made about temperature in the habitats where the wild species of *Gossypium* occur is that maximum temperatures are often very high, especially in the relatively arid regions where insolation rates are very high. For example, maximum temperatures in excess of 45C are characteristic of the shores of the Gulf of California (Rzedowski, 1978) where four species of *Gossypium* are indigenous. Similar extremes presumably occur in such areas as the Arabian peninsula and the deserts of southwestern Africa, where other species occur.

In addition to extremes of temperature, attention should also be given to fluctuations of temperature, whether diurnal or seasonal. In certain maritime climates (e.g. Hawaii), wild cottons are adapted to highly stable temperature regimes, with diurnal and seasonal fluctuations of only a few degrees. In other regions (e.g. western Mexico) average diurnal fluctuations of 20C are the rule. This variation no doubt has implications for physiological responses such as floral induction (See Chapter 4), and the unique ways in which particular species are adapted to the particular regions where they occur. Similarly, annual temperature fluctuations are quite variable and are to some extent a function of latitude. Such fluctuations may be measured in various ways, one of which is the difference between the monthly mean temperatures for the hottest and the coldest months. Using this metric, values as high as 20C are characteristic of a high-latitude (for *Gossypium*) area like Arizona, whereas a fluctuation of 4-5C characterizes a tropical area like Oaxaca.

PRECIPITATION

Rainfall patterns of wild *Gossypium* habitats vary in their total amount and in their seasonal distribution. Certain extremely arid regions (the Arabian peninsula, central Australia, Baja California) have such restricted amounts of annual rainfall (often less than 50 mm annually) that patterns of seasonal distribution are of minimal ecological significance. More commonly, wild cottons grow in areas of less extreme aridity, but the annual rainfall is still less than 500 mm in most cases. However, where the total amount of rainfall is higher, the seasonality becomes of greater significance. Many parts of the tropics are characterized by wet-season, dry-season cycles, often with an extreme contrast between the two seasons. In such regions, the total amount of rainfall is an imperfect index to the climatic impact of precipitation on vegetation. The wild cottons have adopted different strategies to enable them to survive the aridity and to evolve in the different regions in which they occur, as will be discussed subsequently.

SUNLIGHT

Prevailing wind patterns are rarely a significant factor in the ecology of species of *Gossypium*, but the amount of insolation, on the other hand, appears to be a very important factor. It is, of course, closely (and inversely) related to the precipitation patterns. Those species that grow where rain rarely falls are exposed to high incidences of sunlight. Most of the regions where wild cottons are indigenous have relatively high rates of insolation. Moreover, *Gossypium* species either grow in very open types of vegetation or have arborescent growth habits that rise above the associated vegetation. They typically grow fully exposed to the incident light and not in the shade of other plants, with the exception of *G. longicalyx* from East Africa and several species from northern Australia.

SOILS

General statements about the soil types typical of *Gossypium* habitats are difficult to make because few data are available. Apparently a majority of the species grow on well-drained soils, however, often on relatively steep slopes with excellent drainage. Some desert species show a preference for growing in dry or intermittent stream beds (arroyos), often in nearly pure sand, where water is preferentially available on the relatively rare occasions when rain falls (often flash floods), but where water nevertheless quickly drains away.

BIOTIC FACTORS

The place of biotic factors in the ecological milieu is clear enough but dealing with them in any depth becomes too complex for present purposes. It will suffice to enumerate some of the more important factors. Reference has already been made to the influence of the associated vegetation on the ecology of individual species. This influence involves such obvious factors as crowding and shading and such less obvious factors as mycorrhizal association or parasitism by mistletoes, about which little is known at the present time. Allelopathic interactions with other species may exist, but have not been studied in *Gossypium* to my knowledge. Also important are biotic interactions with various pests and diseases such as nematodes, chewing and sucking insects, fungal and other pathogens, etc.

Where host-specificity is relatively precise (as in the cotton rust disease, for example) the interactions can have considerable ecological significance.

ADAPTATIONS

Ecological adaptations of the various species of *Gossypium* (or of any other plants) may be discussed in either of two different ways. On the one hand, a reductionist approach may be adopted, and individual morphological, physiological, or other factors may be conceptually isolated and emphasized. Alternatively, a holistic approach may be used, discussing individual species or groups of similar species in terms of the integrated constellations of adaptations they possess. In view of the complexity of these adaptational phenomena and relationships, and in view of the limited knowledge we have for the wild species of *Gossypium*, I believe the subject can be more profitably approached here from the latter (holistic) point of view. Accordingly, I will discuss species or species-groups in terms of the more outstanding adaptational patterns they exhibit.

The first group I wish to discuss comprises three Mexican species, *G. aridum* (Rose & Standl.) Skov., *G. lobatum* Gentry, and *G. laxum* Phil. & Clem. These three arborescent species are closely related and occur principally along the west-central coast of Mexico in the short-tree forest that is subject to extreme wet-season, dry-season fluctuation. The wet season extends from about May to September and the dry season from about September to May. The life cycles of these trees are closely adapted to this climatic cycle. When the wet season begins and moisture again becomes available, the plants leaf out and begin active vegetative growth, which continues as long as moisture is available. When the rains cease and residual soil moisture begins to decline at the beginning of the dry season, the leaves senesce and abscise, and blossoming occurs. Flowering thus reaches a peak when the plants are leafless. Fruit maturation follows during the height of the dry season, when the plants are otherwise dormant, and indeed when the vegetation of the area generally is dormant as a result of the severity of the drouth at this season.

The flowering cycle of *G. aridum* is described by Mauney (1968) as follows: It is photoperiodic and begins initiating flower buds when the photoperiod is shorter than 12 hours. The first squares are borne in short, one-node fruiting branches, and are dormant.The buds become progressively less dormant as the season progresses. Thus, the first blossom to expand, at about the time of severe drought and defoliation, is the top-most bud. Subsequently, the buds break dormancy and blossom from the top downwards on the stems.

Interestingly, the adaptation to severe drouth in these species does not involve morphological factors for limiting water loss. Instead, these plants have adapted their life cycles to take advantage of the wet season with typical mesomorphic growth but to endure or escape the dry season with dormancy. The flowering and fruiting pattern is deferred until the onset of the dry season.

A second group of species includes three shrubby species, *G. harknessii* Brandg., *G. armourianum* Kearn., and *G. turneri* Fryx., from extremely xeric habitats around the Gulf of California in western Mexico. These species are subject to high temperatures, high insolation, and low rainfall through most of the year. They have evolved adaptations of xeromorphic nature than permit them to withstand these extreme conditions. These adaptations include a compact growth habit, the shrubs being broader than tall and the branching pattern intertwining; small leaves with a suberized epidermis to minimize water loss; a double palisade layer (with spongy mesophyll in between) to retain photosynthetic capacity while minimizing water loss; and deciduous involucre bracts, which possibly are also an adaptation for minimizing water loss. Contrary to the preceding group, this group does not have a dichotomy between its vegetative and reproductive phases, but flowers and fruits when in leaf and metabolically active.

Species such as *Gossypium populifolium* (Benth.) von Muell. ex Tod. from the northwestern part of Australia also have relatively small leathery leaves. Its nearest relatives from the same general area, *G. pilosum* Fryx., *G. costulatum* Tod., and *G. cunninghamii* Tod., *G. pulchellum* (Gard.) Fryx., and several undescribed species have similar though less extreme morphology. All of these species die back more or less to ground level during the dry season and then resprout from the perennial rootstock during the subsequent wet season.

Two species from central and western Australia, *G. sturtianum* J.H. Willis and *G. robinsonii* von Muell. have evolved glaucous, heavily suberized foliage as a means of limiting water loss. This feature is more fully developed in the former species, which also has the capacity to fold its leaves inward when subjected to water stress. *G. robinsonii*, on the other hand, is less xeromorphic but apparently grows preferentially directly in the beds of the intermittent watercourses of its desert habitat and thus has direct access to available moisture during the brief season (December-February) when rain falls. This tendency to prefer dry stream beds subject to flash floods is also characteristic of *G. raimondii* Ulbr. (coastal Peru), *G. thurberi* Tod. (southern Arizona and Sonora), *G. incanum* (Schwarz) Hillcoat and *G. areysianum* Defl. (southern Yemen; cf. Hearn, 1968), to some extent *G. gossypioides* (Ulbr.) Standl. (Oaxaca), and probably also *G. somalense* (Gurke) Hutch. and *G. anomalum* Wawr. & Peyr. (Somalia and Sudan). These species show few xeromorphic adaptations (except for dense pubescence in some species) but manifest their xerophytism principally in their choice of microhabitat and presumably also in an aggressive root system.

Gossypium triphyllum (Harv.) Hochr. occurs in the severe deserts of southwestern Africa. It has evolved a deeply divided (trifoliolate) leaf that limits transpirational water loss, a feature presumably enhanced by its fine close tomentum. Little ecological information is available for this species, however, other than the knowledge that it is adapted to one of the more extreme deserts of the world.

Gossypium longicalyx Hutch. & Lee is unusual in being an understory shrub (trailing or scandent), growing in shady situations with *Acacia, Terminalia, Combretum,* and similar vegetation. It occurs in East Africa (Uganda, Tanzania) in a region of more than 500 mm annual rainfall. Its preference for shaded habitats is unusual for *Gossypium,* although this preference is shared with some of the northern Australian species, as previously noted.

Two species show extreme expressions for *Gossypium* in tolerating low temperatures, but in two different ways. *Gossypium thurberi* is the northernmost species of *Gossypium,* reaching southern Arizona. Since it occurs at elevations as high as 2000 meters, it is growing in a temperate zone climate, the only *Gossypium* to do so. It achieves this adaptation by undergoing leaf senescence and abscission (simultaneously with fruit maturation) in the autumn, and becoming fully dormant by the winter months. In this case, the move toward dormancy is not triggered by declining moisture supplies in the soil, but rather by the advancing season (daylength, temperature regime, or some combination of factors). The dormant plants are fully capable of withstanding hard freezes, and do so regularly, resprouting the following year (when moisture permits) from old stems several feet above ground level. This hardiness is a physiological capacity that no other *Gossypium* possesses.

The other type of cold tolerance is exhibited by *Gossypium sturtianum,* the southernmost species of the genus, from central and southern Australia. This species cannot withstand hard freezes, but has the capacity, when in full leaf, to tolerate temperatures at freezing or a few degrees below freezing, without adverse effect. The protoplast of this species thus has some physiological characteristic not shared with other species of the genus. Hexaploids involving *G. sturtianum* and *G. hirsutum* L. (Muramoto, 1969) retain at least some of the cold tolerance of the *G. sturtianum* parent.

Most of the world's species of *Gossypium* occur in relatively arid habitats, as discussed previously. In general, these habitats tend to be inland habitats or, if near the coast, not a part of the littoral vegetation (Fryxell, 1965, 1979). Some of the wild tetraploid species, on the other hand, are principally found in the littoral vegetation or derived from it, most notable the indigenous forms of *G. hirsutum* found in coastal habitats around the Gulf of Mexico, the Caribbean Sea, and in parts of the South Pacific. Such localities are habitats of relatively high salinity, resulting in part from the continuous bombardment by salt spray characteristic of coastlines, and from the results of occasional severe storms that inundate and drench the soil with sea water, thereby increasing soil salinity. There are, of course, strong physiological parallels between aridity and salinity, both being agents of water stress. The point to emphasize here is that these coastal cottons are adapted physiologically to relatively saline habitats, and that this adaptation is one of their distinctive characteristics.

The preceding discussion of ecological adaptations of *Gossypium* spp. is largely anecdotal and inferential in nature, because ecological knowledge of these species and of their habitats is quite limited, since field studies have been made of relatively few of them.

SUMMARY

The almost 40 species of *Gossypium* occur in many parts of the world and are adapted to a variety of habitats, many of them arid. The present study considers this ecological spectrum from a holistic point of view, discussing individual species or species groups in terms of the integrated constellations of adaptations they possess. This viewpoint is considered important in two respects: (a) It is important to understand the evolutionary origins of the cultivated species; and (b) it is important to understand the spectrum of variation that exists in the genus which may be exploited in the cultivated species through germplasm manipulation.