Macmillan's Science Monographs

THE COTTON PLANT IN EGYPT

W. LAWRENCE BALLS

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TORONTO

THE "SHORT-STYLE" FLOWER OF COTTON.

THE
COTTON PLANT
IN EGYPT

Studies in Physiology and Genetics

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PREFACE

THIS book has been written with the purpose of abstracting the results of a series of researches made upon cotton plants in Egypt, which investigations, though diverse, were connected by the desire to know all that could be learned about the plant itself. Portions of these inquiries have appeared in various journals, but most of the material here utilised has not yet been published. Where it may appear to the reader that a conclusion necessitates much fuller data than is placed before him, I can only ask his clemency until such time as a fuller monograph shall be written.

Primarily, I have written for those few Economic Botanists who are more botanical than economic, but I have found so much genuine interest displayed by the pure botanist, and by the pure economist, as well as by the cotton spinner and the irrigation engineer, that in the hope of giving them some explanation of the relation between my inquiries and their interests, I have written with divided attention. The result is avowedly unsatisfactory, but the difficulty is inherent in any application of natural science to economic material.

While the subject is parochial in its origin, having been studied almost entirely at Cairo, I venture to think that its interest is not purely Egyptian, if only from the fact that American Upland cottons have been employed extensively; the chapters on Heredity apply equally to the American crop.

Some of the data are not without suggestiveness to students of even human physiology and genetics.

The views expressed are purely personal, except where specific reference is made to the contrary. To any who may recognise their assistance inadequately acknowledged I herewith proffer my regrets, with the assurance that such plagiarism has not been conscious.

The botanist may find, I fear, that the treatment is far from thorough in its consideration of recent work, and it may be that in many matters which I have regarded as original the priority rests elsewhere. For such mistakes it may be fairly pleaded that Egypt has been a lonely place for a botanist until the current year. Even the card index reproduced as the bibliography is rather casual than systematic.

The economic importance of any contribution to our knowledge of the cotton plant needs no explanation. The industry is one of the largest in England, with almost unlimited influence. In Egypt itself the cotton crop is the prime factor in the finance of the country; other crops and industries are relatively insignificant, and a partial failure of the cotton crop may cause a financial crisis.

It might be thought that such an important crop would have been one of the first to which scientific investigation should have been applied by the world in general, so soon as the profitable nature of such inquiries became obvious to the financier. Unfortunately, the trail of the "practical man" was followed somewhat too closely in the investigations which were made before the end of last century, with the result that many field experiments have expressed the net result of many conflicting factors, and have given but little indication as to the components.

On my appointment to the staff of the Khedivial Agricultural Society at the end of 1904, as Cryptogamic Botanist, and hence specialising on heredity and physiology in cotton—on account of the innate perversity of things Egyptian—I decided to abandon the accepted method of crop-inspection on a large scale, and to substitute detailed examination of a few plants. The literature then extant gave scarcely any assistance to such heterodox procedure, and the story of the researches which followed from this decision has been written on a tolerably clean sheet.

The work began as Genetics, but necessarily extended into Physiology. This mental transition was accelerated by the pronounced deterioration of the Egyptian crop, both in yield and quality, which began to be obvious in 1905, and culminated in the catastrophic failure of the 1909 crop. The physiological researches necessitated by demands for information as to the possible effects of unsuitable soil-water conditions have given results of more immediate interest, and of greater novelty, than the weary routine accumulation of critical data for Mendelian analysis, though the latter are probably of higher intrinsic value.

For years it had been intended to establish a suitable field laboratory in which the work could be conducted efficiently, but, owing to various causes, this establishment was delayed, and it has taken from December 13th, 1907, when the resolution was passed, till March, 1912, to realise intentions in this respect. The scope and utility of the work has been limited to a regrettable extent by the absence of this provision, and more particularly on the economic side.

My acknowledgments for assistance rendered must of necessity be incomplete. In the first place, my thanks are due to the Khedivial Agricultural Society, which for six years gave me freedom to conduct researches as I choose; for this exceptional treatment I am indebted to H.H. Prince Hussein Pasha Kamel, President of the Society, to Mr. G. P. Foaden, and to Abdel Hamid Bey Abaza, successively Secretary-General thereof, while my colleagues on the staff have given every assistance. Since my transfer to the new Department of Agriculture the work has been continued, the Mendelian laboratory projected by the Society has been established by the Egyptian Government, and a pure-strain system of seed-supply is in process of adoption.

Many of the records utilised would not have been obtainable without the steady co-operation after 1909 of my assistant, Mr. Francis S. Holton, to whom I am especially indebted. The members of the Cairo Scientific Society, and of the Botany School at Cambridge have displayed an encouraging interest in the work.

To specify individual assistance among so many would be invidious, but on looking back over the train of ideas involved, I find that the most illuminating of these have come from the late Mr. J. R. Gibson, English Commissioner for the State Domains, from Mr. F. F. Blackman, F.R.S., Reader in Botany in the University of Cambridge, and from Mr. J. A. Todd, Professor of Economics at the Khedivial School of Law, Cairo, while the data on the hydrology of sub-soil water garnered by Mr. H. T. Ferrar, of the local Survey Department, have provided a foundation for discussions on this most important topic.

I should like also to acknowledge the pains which Prof. R. A. Gregory, the Editor of this series, has taken, under all the disadvantages involved by my absence in Egypt.

The greater part of the work would not have been executed had it not been for the assistance of my wife, who has also helped me in preparing the present volume, and in working up the records on which it is based.

W. Lawrence Balls.

Gezira House,
Cairo.

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THE COTTON PLANT IN EGYPT

SECTION I

HISTORICAL[15] *

The history of civilisation in the Nile Valley can be followed into the past for half a hundred centuries. Textile fabrics have been found among the earliest remains of Ancient Egypt, but in none of these can we recognise any fragment of the plant upon which is based the latter-day prosperity of the country.

The cloth found in the ancient remains, notably as mummy-wrappings, was invariably made of linen, and though a watch is being kept by the Antiquities Department for traces of the cotton plant, none have yet been discovered. Still there is a strong presumption that the genus *Gossypium* is no modern upstart in Egypt, for in spite of philological confusion it seems clear that cotton was in common use during Ptolemaic times, though flax was exclusively employed for funereal purposes. Pliny gives an unmistakable description of a cotton plant which grew in the upper part of Egypt, from which garments were made for the priests, Herodotus describes how Amasis sent a cotton corselet of wonderful fineness to the Lacedæmonians, and the famous tri-lingual "Rosetta

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* Reference numbers appearing in the text denote publications by the Author, as enumerated in the Bibliography. References to other authors therein enumerated are made in the usual manner, with a number in brackets where more than one paper is given.

Stone," which solved the riddle of the hieroglyphs, bears a reference to cotton.

These and similar data, however, do not enable us to trace the existence of cotton in the Nile Valley beyond an earlier date than about B.C. 200, and such antiquity is trivial in Egypt. There are, however, several wild cottons in the Sudan, some of which were recorded by explorers in the early nineteenth century; whether they are truly indigenous, in view of the extensive movements of Arab traders all over Africa, may well be doubted, but their existence leads one to think that some lucky excavation, or perhaps a casual glance through a microscope, will suddenly extend the known history of cotton in Egypt by two or three thousand years.

The geographical position of Egypt, on the overland commercial route to the East, makes the recognition of indigenous cotton a difficult matter for mediæval times. Later, at the end of the sixteenth century, we have records by Arabic writers which describe the cultural operations pursued in Egypt itself, and mention the principal localities in which weaving was practised. At the same epoch we have the first botanical record of an Egyptian cotton plant, by Prosper Alpino and by Vesling. Although the plant they figure was merely an ornamental garden shrub, and apparently distinct from the cultivated one, the record is not without interest, as it seems to describe the same Peruvian-type tree cotton which was taken from a garden and extended into a field crop by Jumel, some two centuries later, and from which the present stock has developed.

When Napoleon Buonaparte effected his famous invasion of the country at the end of the eighteenth century, he brought in his train a peaceful force of *savants*, whose labours are fully recorded in the unique "Description de l'Egypte." From this we obtain much detailed information, with the added advantage that the herbaria then collected are still extant. Two entirely different species of cotton were then under cultivation. One was a tree, grown in Upper Egypt, and apparently identical with Alpino's plant. The other, an annual, peculiar to the Delta, was possibly the same as the cultivated form which Alpino did not describe; in any case it belonged to the Asiatic group of cottons, still found on the other shore of the Levant, but now extinct in Egypt, and only represented in the Nile Valley by a tree-cotton found in Sennaar, two thousand miles away.

The cultivation of this short-stapled Asiatic cotton died out in consequence of the economic development of Jumel's plant, and the last trace we find is a record in 1840 stating that it was almost extinct.

The tree-cotton from Upper Egypt, probably identical with Alpino's garden plant, possibly even with that of Pliny, was next brought forward under the ægis of Mohammed Ali, founder of the Khedivate, at the suggestion of M. Jumel, a Franco-Swiss engineer. Taken from the garden of Maho Bey, in Cairo, it was propagated rapidly from the year 1820 under a system of State-control, and soon displaced the Asiatic type. The brown, long, strong lint, readily ginned from the almost naked seed, quickly made its reputation with the spinners, and this type of lint has been typical of the Egyptian product ever since.

To trace the origin of the present cultivated varieties from this stock is almost impossible. Still, the following interpretation meets all the facts at present known.

The success of Jumel's tree-cotton led to the importation and trial of other cottons, notably Sea Island. Importations of this latter strain, an annual in habit, have continued to the present day. It is not very successful in Egypt, yielding lightly, and suffering unduly from "shedding," but the lint is often of good quality, equal to that of Georgia's and Florida's. The state control of the seed-supply became disorganised after a time, partly in consequence of Mohammed Ali's military activities, and the inevitable mixing of the two seed stocks was accelerated. This mixing, combined with natural crossing, led to the formation of splitting-forms, some of which were annual but brown-linted, and these gave rise to the Ashmouni stock, or old "Brown Egyptian," which dominated the fields up to 1887. The tree-type disappeared in consequence of its greater liability to damage from insect pests such as the Boll-worm (*Earias insulana*) which was definitely recorded in Egypt as early as 1876, and also on account of the better cultivation obtained with plants of annual habit. The only remaining trace of its influence is the presence of abnormally tall rogues—up to four metres in height—in the field. The Hamouli variety was possibly an intermediate stage in this process of extinction by artificial and natural selection.

From the Ashmouni stock came the Afifi, in 1887, by selection, probably natural in part, and from this now degenerate complex of sub-varieties and splitting-forms other varieties have been selected. The Ashmouni stock was driven into Upper Egypt, and has there improved itself until it is now making a reputation anew.

The relatively white lint of the Sea Island stock has always been a feature of at least one Egyptian variety, such as Abyad and Gallini, both extinct, and the modern Abbassi. Gallini in particular, while possessing the bigger boll, higher yield, and "climatic suitability" of its Peruvian-type ancestor, was a very fine cotton, which controlled the fine-spinning market for years until it deteriorated through mixture and crossing and was driven into oblivion by competition with Georgia's and Florida's, its own ancestors. Gallini has been revenged of late years on its unnatural ancestors by the modern Yannovitch, itself a single plant selection from the Afifi complex.

The apparent identity of all the modern varieties of

Egyptian cotton in external appearance—for even when grown side by side they are scarcely distinguishable—is the natural result of their origin from two related stocks. This absence of differentiating characters, excepting for the lint itself, has been responsible for a fund of fatalistic ideas about deterioration, which, though possibly appropriate to the near East, are nevertheless untenable. The "running-out" of varieties, miscalled inevitable, need no longer be the bogey of the cultivator. A recognition of the incontrovertible fact that the nominal varieties are more or less heterogeneous complexes of heterozygotes, even when first introduced to commerce, should enable us in the future to dictate the history of Egyptian cotton with greater definition than Mohammed Ali could ensure.

Systematy.—In this brief summary of the few available historical facts, it has seemed advisable to evade systematy, and the pitfalls thereof, by referring to *G. vitifolium* (Cav.) as the "Peruvian type," and to *G. herbaceum annuum* as the "Asiatic type." For further details the reader should consult Mr. Fletcher's article * and Sir George Watt's monograph. Though opinions may differ as to the real importance of some of these classifications, the latter book nevertheless forms a standard and permanent record of specimens and synonyms.

The three main phyla of *Gossypium* are all represented in the Nile Valley, for the weed "Hindi" cotton now found in the fields is certainly on the same phylogenetic line as the "American Upland stock," or *G. hirsutum.* The author's inclination is to believe it to be a smooth-seeded sport from *G. hirsutum,* since parallel cases are well known in both the other phyla.† In any case, the Egyptian "Hindi" is not homogeneous, but consists of at least two forms, one hirsute, the other glabrous.

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* Fletcher (2).

† Allard, H. A. (1), Fyson, P. F.

SECTION II

THE INDIVIDUAL PLANT

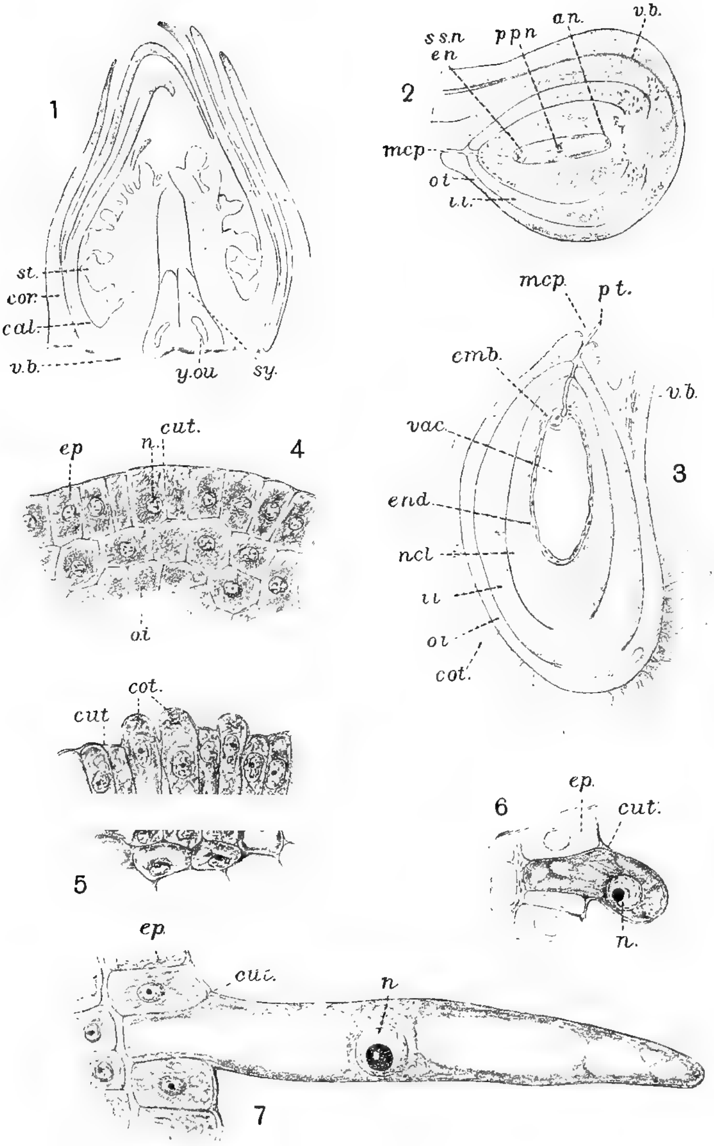
CHAPTER I

FERTILISATION, CYTOLOGY, AND EMBRYOLOGY

THE development of the sexual cells[1] in the cotton flower bud is not marked by many special features, but the intrinsic importance of the gametes is such that the main characteristics of their microscopic history should be examined, if only to facilitate their visualisation when matters relating to heredity are under discussion.

The life-story of the individual begins at the moment of fusion between the male and female gametes, viz., between the generative nucleus of the pollen grain and the egg-cell of the ovule. The unicellular zygote thus formed develops by repeated division into an embryo enclosed in the seed-coats, and the germination of this seed is the stage commonly regarded as beginning the life-story. For reasons both of precision and of ultimate convenience, we shall commence the study of an individual plant at the union of the gametes, first, however, describing the genesis of the latter.

The Gamete-mother Cells.—The young flower-bud (Fig. 1) develops centripetally from the primordia of involucral bracts, calyx, corolla with staminal column, and lastly ovary. The latter is composed of two to six carpels, which originate as separate ring-primordia, developing



W.L.B. del.

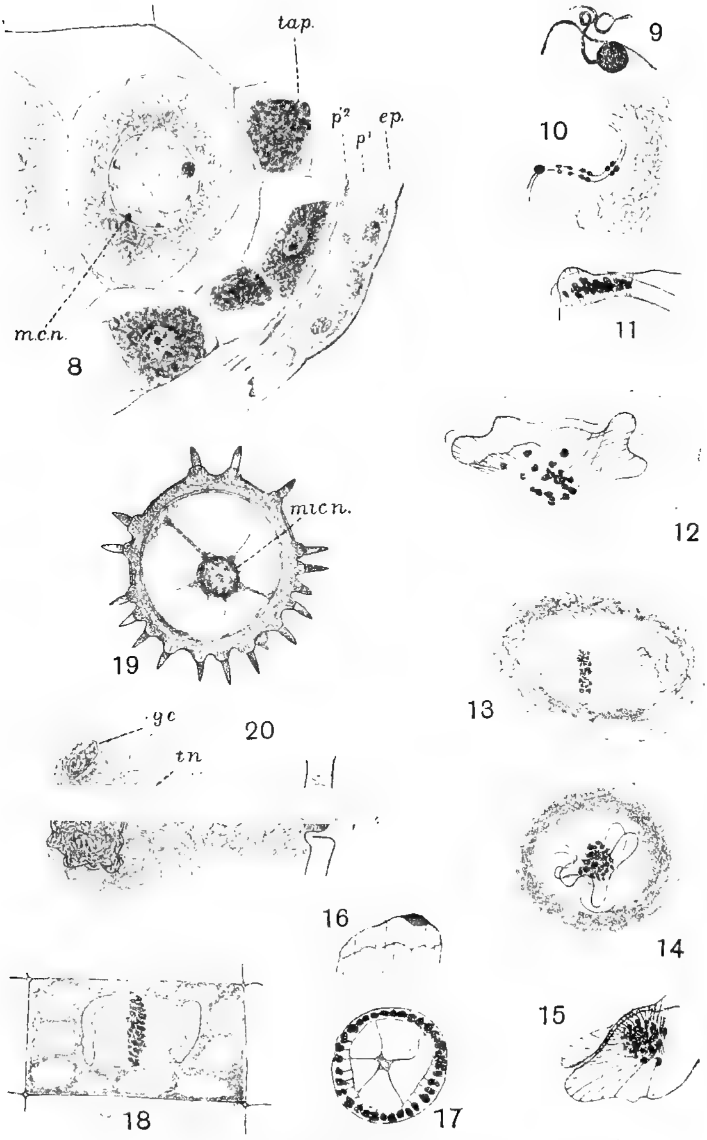
FIGS. 1 to 7.—OVULE, SEED, AND LINT.

into hollow cones. These unite laterally to form the 2- to 6-locular ovary, while the combined apices of the cones elongate to form the style (*sy.*). Large-celled conducting tissue is formed at the base of the style and in the radial walls, which afterwards facilitates transit for the burrowing pollen-tube. On the inner side of these hollow cones (*y. ov.*) there arise the ovules with their double integuments; a single cell in the centre of the nucellus enlarges into the single megaspore mother-cell.

The microspore mother-cells are formed in plates below the epidermis of the embryo anthers (*st.*) on the staminal column. They arise from the cell-layer immediately below the epidermis, but soon separate themselves from it by two layers of cells, and then enlarge till their diameter is about 40 μ, when they pass into the synapsis stage. Meanwhile (Fig. 8), the cells which surround them on all sides divide once, and thus give rise to a tapetum, which is ultimately disintegrated.

The mechanism of nuclear division in reduction.[28]—This division has not been captured for observation in the megaspore mother-cell; it appears to take place very rapidly, judging by the ease with which the stages immediately precedent and antecedent can be found. The same applies to the microspore mother-cell, where the stage is easily observed about ten days before the flower is due to open.

The extraordinary minuteness of the chromosomes of *Gossypium* is very obvious in this division, where they are inconspicuous in comparison with the linin threads, which have actually been figured in error as the chromosomes themselves. The latter appear to consist of twenty groups of pseudo-tetrads, each unit of the group being about 0·6 μ in diameter, arranged in prophase along one side of the somewhat tangled close spireme of linin. This spireme splits longitudinally and the two halves separate like loops of cotton in a broken soap-bubble, retaining



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Figs. 8 to 18.—The Mechanism of Nuclear Division.
Figs. 19, 20.—Development of Pollen.

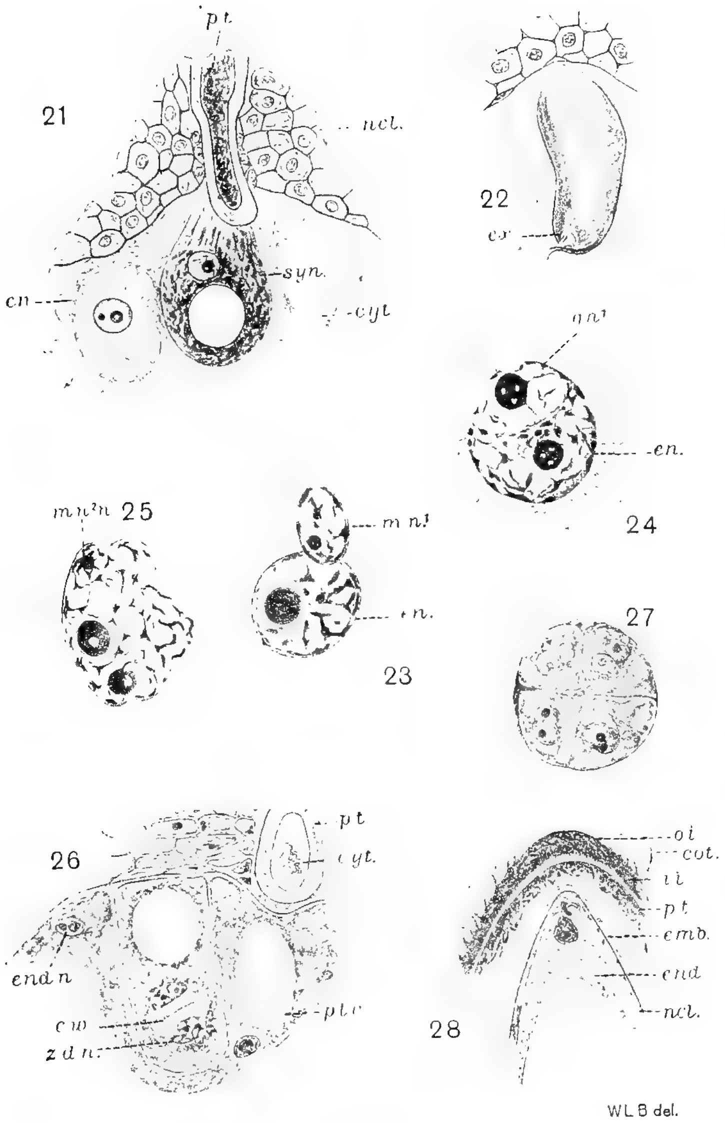
connection with the chromosome groups by fine fibres (Fig. 11), which become the spindle fibres. The pseudo-tetrads are then halved into groups of pairs, the inter-chromosome fibre disappears in the cytoplasm, and the two daughter nuclei rapidly divide again (Figs. 14, 15) in the same way, never breaking the thread-rings, and thus distribute one minute chromosome from each pseudo-tetrad to each of the four microspores.

The prominence of the non-chromatic linin structures in this remarkable division has enabled these changes to be examined thoroughly. The main features are summarised above, and the possibility of providing a physical explanation for nuclear division on these lines makes the observation one of general interest. The same thread-rings are found in the somatic nuclei (Figs. 16, 17, 18), where the chromosomes number forty, and the same scheme is followed.[28]

The spores.—The microspores, or pollen-grains, are thus formed in groups of four. Each member of the group enlarges (Fig. 19), develops spiny sculpturings on its outer wall, colouring matter—golden in the case of Egyptian cotton—and finally floats free in the liquefied residuum of the tapetum. Some three days before the flower opens, the single nucleus divides into a moruloid vegetative nucleus and a smaller ellipsoid generative nucleus (Fig. 20). The latter again divides into two, the male gametes, and the pollen grain is then ready to fertilise the ovary.

The megaspores are also formed in groups of four, but the three nearest the base of the ovule abort, and only the fourth member becomes a megaspore. The usual nuclear changes then take place: the three antipodals abort before the flower opens, while the two polar nuclei have met in the centre of the spore, though without fusion, and two typical synergids support the egg-cell or female gamete.

Fertilisation.—We shall have ample occasion later to



Figs. 21 to 28.—Fertilisation and Embryology.

discuss the methods by which the pollen-grain reaches the style, whether of its own, or of another flower, and also to inquire into the pseudo-parasitic nature of the pollen tube, which attacks some styles more easily than others. For the present we will examine a normal case.

The sugar solution excreted by hairs on the style retains the pollen-grain, and causes it to germinate. The single pollen tube traverses the tissue of the style and the conducting tissues till its end enters one of the loculi, along the wall of which it passes till it finds (Fig. 3) the micropyle of an ovule. Traces of branching may be seen at this point. Passing through the micropyle channel to the nucellus, it bores through the tissues of the latter, and after literally squeezing its way through the firmer wall of the megaspore, the end of the tube swells up and bursts (Figs. 21, 22). From the torn end escape the two male gametes, one of which passes to and fuses with the egg-cell (Figs. 23, 24), forming a zygote, and thus beginning a new life-history. The other male fuses with the two polar nuclei, and the triple nucleus thus formed (Fig. 25) serves later to provide the endosperm.

The process is exceptionally rapid. Fertilisation is normally completed within thirty hours after the first opening of the flower, *i.e.* by the afternoon of the following day.

The embryo.—From the date on which the flower opens until the boll cracks, some forty to sixty days later, according to the weather and the kind of plant, the embryo is developing inside the fertilised ovule, or seed.

On the third day of this period the unicellular zygote divides along a plane at right angles to the axis of the ovule, its forty chromosomes, formed by the addition of two twenties from each gamete, being each halved and distributed to the daughter-cells (Fig. 26). Two more divisions produce an octant (Fig. 27), and by the end of the week the embryo is just visible to the naked eye, consisting of some hundreds of cells, and exhibiting a cordate form under the microscope (Fig. 28). The pointed end becomes the radicle, and the two lobes develop into two cotyledons, marked with black dots caused by the presence of the resin-glands which are characteristic of all portions of the cotton plant other than the root. The adult cotyledons are folded in a complex way, being considerably broader than the seed in which they are contained, and they envelop the straight radicle. Their cells contain much of the food reserves in the form of oil, which is an important commercial product. The endosperm, formed by rapid division of the triple nucleus, is destroyed during the growth of the embryo, so that the ripe seed is ex-albuminous.

We shall postpone consideration of the seed coat, and of the development of the lint upon it, to its proper place at the end of the story of the individual.

CHAPTER II

DEVELOPMENT AND ENVIRONMENT—I.

THE physiology of a cotton plant growing under the field conditions which obtain in Egypt may be conveniently considered in two stages. During the first stage, which includes the period from sowing to flowering, the plant is mainly under the control of aërial conditions. After flowering, in the middle of June (near Cairo), a critical period ensues, during and after which the soil conditions commonly provide the limiting factors.

The subject is one of great interest, on account of the stringent environmental conditions which prevail during a great part of the Egyptian cotton-season. (See Figs. 30 and 33, Environment.) Thus, in the month of June at Cairo the meteorological conditions are somewhat as follows:—Sun temperature maximum, 75° C.; Clouds, rare; Shade temperature maximum, usually 34° C., at 2 p.m.: occasionally 42° C.: minimum about 20° C., at 6 a.m.; Humidity, dropping to 20 per cent. of saturation, or even less, during the day, and rising above 90 per cent. at night; Wind, strongest by day.

Such conditions result in xerophytic adaptions, unless an ample water-supply is available, as it is in Egypt through irrigation; but we shall see later that even under conditions of field cultivation, the cotton plant virtually becomes a xerophyte every afternoon. After the month of June, however, the increasing size of the plants automatically modifies the severity of the environment, in so far as the lower portions are concerned, by producing a "surface climate" with higher humidities and less wind, consequently less evaporation, and affording at least intermittent shade to any given portion of plant tissue.

Germination.—The sowing of the Egyptian crop takes place at different times, varying with the locality and with the weather, from the end of February until May. The habit of sowing on ridges running east and west secures a higher soil-temperature on the south face. The temperature of the seed bed before, during, and after optimum sowing-time was recorded electrically in 1911 (Fig. 29); the sudden rise shown at the moment of sowing (a) is due to the scorched surface soil which fell into the hole, showing how effective is the heat insulation of dry soil, since the depth of the hole was only 4 cm. The heat absorptivity and conductivity of the soil after irrigation (b)

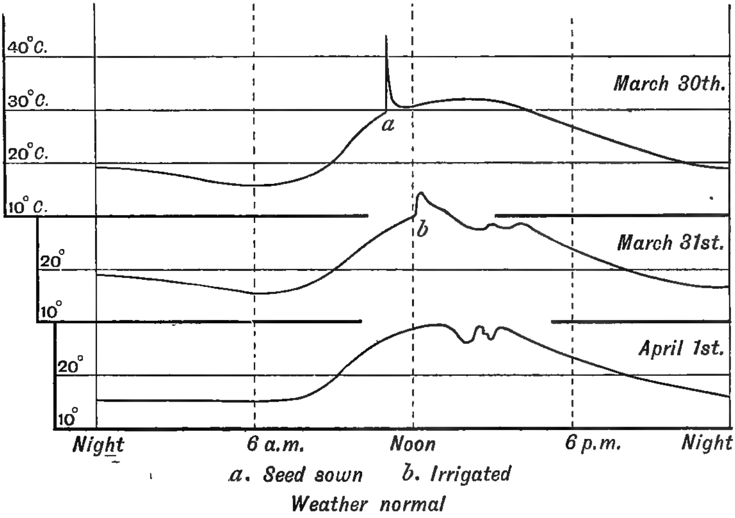


FIG. 29.—TEMPERATURE OF THE SEED BED.

Recorded by thermo-electric junction placed 5 cm. below surface on south side of ridge.

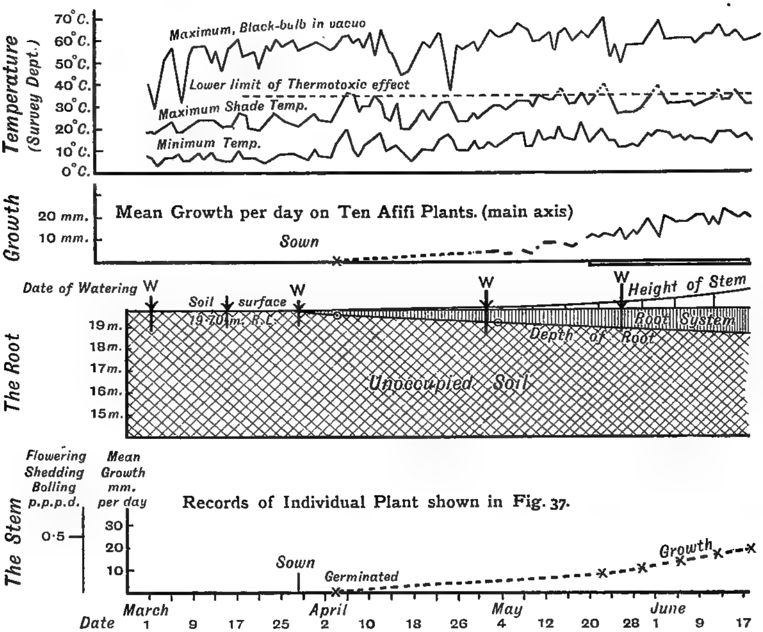
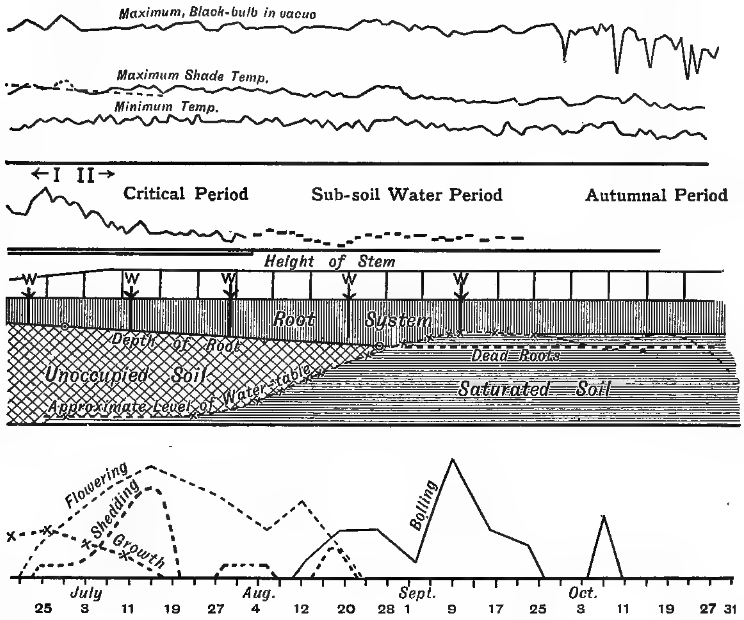


FIG. 30.—THE PLANT AND THE

are both obviously greater than that of the dry soil. The magnitude of this daily change in soil-temperature diminishes with increasing depth, and is negligible below 50 cm. Thus the root-tip in the early stages of germination is subject to great variations in temperature, but after the root has grown some 15 cm., the temperature is constant, except for the annual change. At a depth of 50 cm. the temperature is approximately 17° C. at the beginning of March, rising to about 25° C. in the summer.

The localisation of the optimum sowing-date will be discussed later, in connection with the date of the first flower. For the present it suffices to notice that sowings in the middle of February near Cairo will take twelve days to show the cotyledons above ground, while identical sowings made in the middle of April may appear in five days, temperature being the limiting factor. The sowings



ENVIRONMENT. GEZIRA, CAIRO. 1911.

on intermediate dates take intermediate times, varying, of course, with the particular weather which they experience.

The proportion of seeds which successfully complete their "field-germination" also varies—other things being equal—with the sowing-date. The lowest proportions are found in the very early and very late sowings, though for totally dissimilar reasons. The failures in the first instance are almost entirely due to a damping-off fungus, known as "Sore-shin," which we must consider in further detail, not merely because it is the only serious fungoid disease of cotton in Egypt, but rather because certain conclusions drawn from the study of its relations to temperature will be used extensively for interpreting the growth-processes of its host.

The "Sore-shin" fungus.[2 & 6]— This facultative parasite was first described in 1895 by Mr. G. F. Atkinson in the United States. It is practically omnivorous, and is the only damping-off fungus which seriously attacks cotton-seedlings in the Egyptian fields. The organism is an extremely simple one, probably a degenerate Basidiomycete, but devoid of any spore-forms. A resting-stage is produced by free branching of hyphæ into clusters of short swollen cells, which turn brown, forming irregular hard black spots on the mycelium. Such resting-cell formation precedes the staling or exhaustion of an ample food supply. The mycelium containing these cell-clusters has been kept over calcium chloride for nearly two years, and sent out abundant hyphæ when moistened at the end of the period. The hyphæ are all equivalent, in the absence of any sexual process, and are diagnosed by a curious septum which is formed in each lateral branch immediately above the point of origin.

When a cotton seedling has been completely decomposed by the fungus in a somewhat dry site, the hyphæ which grow away from it form branching brown rhizomorphs, seeking fresh sources of food. The fungus is ubiquitous in Egypt, and its sterile mycelium must be regarded as a gigantic network, stretching through the soils of all the country.

It is strictly aërobic, grows freely on most culture media, though with difficulty when the nitrogen is presented as urea, and forms resting cells very quickly on asparagin media, while it can infect cotton seedlings under perfectly sterile conditions. The cotton plant is immune when cork layers have been formed, though even then it can be infected at wounds, but without any notable injury.

The chief interest of the disease lies in its absolute dependence on temperature, and the consequent misapprehension existing as to the effect of cold on cotton seed. If germinating seeds, or seedlings, are kept damp at a temperature of 20° C. with a fragment of "sore-shin" culture, they are visibly infected in three hours, and completely destroyed in a few days. Repetition of the experiment at 33° C. produces slight superficial brown scars, and nothing more, while at 37° C. the seedlings remain without injury. Moreover, if an infection has been well established at 20° C., and is then transferred to a temperature of 37° C. for an hour or two, or for several hours to 33° C., the infection is arrested. The hyphæ cease to advance, and the host proceeds to delimit the damaged portion by means of a cork cambium.[2]

The effect of high temperature can be modified in one way. If the tissue to be infected is partially immersed in water and kept at 33° C., the fungus will destroy all the cells on the water-line, though merely scarring the epidermis above, as before, and leaving the immersed portions untouched, on account of deficient aëration.

The results of infections in the field depend on the age of the plant. The brown skin of seedling roots is commonly regarded as normal to the cotton plant, whereas it is actually due to abortive attacks by this fungus and possibly by a *Rhizopus*. Very late sown seedlings have pure white roots. The seed is doomed if the attack takes place as soon as the tip of the radicle emerges from the seed-coat; its growing point is destroyed, while the fungus enters the seed-coats and rots the cotyledons; such seed is commonly said to have been "killed by the cold." When the attack is made on an established root or hypocotyl, the infection has to be sufficiently extensive to reach the phloem tissues; such destruction of the phloem limits the supply of synthesised food from the leaves to the root, and may check root-growth; this check in its turn limits aërial growth, and so produces stunted plants, which flower late and make the crop irregular. If much phloem tissue is destroyed, the seedling may die through indirect water shortage during the day, but though seedlings which have wilted from this cause are common in the field, the most serious attack is the inconspicuous one which occurs at the beginning of germination.

A treatment of the seed with 2½ per cent. of its weight of naphthalene, mixed with gypsum as a cement, effectually prevents this primary attack, though leaving the seedling unprotected by the time of secondary infection.

A notable example of secondary infection was observed in May, 1906, on a piece of land at Giza, which had become very foul with weeds, and was consequently a hot-bed of "sore-shin," so that a third sowing had been necessary. The clusters of seedlings from this were perfectly clean, under the protection of the summer temperature, till two abnormally cool and cloudy days arrived. When these were over, every tenth cluster had been completely destroyed,[6] and the clean white roots had deliquesced into a sodden brown mass.

The facts here related led the author to a conviction that further investigation would be profitable, and after some experimental difficulty, a method for studying the relation of this fungus to temperature was devised. Since the results appear to be capable of general application, their description may be considered under a general title, and supplemented by less precise data from cotton itself.

Temperature and growth.[9]—The effects of temperature on the growth of the "sore-shin" fungus were studied with special apparatus. A moist-chamber was devised in which the concentration of the "hanging drop" containing the fungus remained constant, however quickly the temperature was changed. This change was effected through a double jacket of liquid in which the chamber was completely immersed. The measurements of elongation of the observed hypha were made every minute through a water-immersion objective with a micrometer eyepiece, while the actual temperature of the hanging-drop itself was recorded to 0·1° C. by means of a delicate thermo-electric junction in the field of the microscope, balanced on a similar couple in a water-bath of known temperature.

Consequently, the two variables under examination were recorded with unusually high precision, and relatively rapid temperature changes could be employed with safety.

The general arrangement of the initial work was such as to ensure that temperature, and temperature alone, should be the factor which limited the growth. The rate of temperature-change was usually about 1° C. in three minutes, so as partially to avoid errors from prolonged exposure to high temperatures, and the air space of the chamber was filled with pure oxygen. Under these conditions growth-curves like Fig. 31 were obtained from fresh cultures, recently renewed, and kept at low temperatures, so as to be free from any suspicion of staleness. These curves indicated that growth followed chemico-physical laws, being accelerated by increased temperature, and approximately doubled in velocity by a rise of 10° C. This acceleration began to fail in the neighbourhood of 36° C., and growth ceased altogether at a mean temperature of 37·5° C., the maximum. A value of ±0·5° C. covered departures from normal in the position of this maximum. Obviously, a second factor was coming into play, antagonistic to the normal acceleration, and probably itself accelerated by rise of temperature.

Slower rates of heating, down to the maintenance of culture-flasks at various constant high temperatures, showed that the time of exposure had an influence on this factor. The more rapid the heating, the nearer the growth-curve approached to its hypothetical form, *i.e.*, a sudden arrest at 37·5° C. when in full swing. The slower the heating, the lower was the temperature at which the slowing of the growth-rate appeared on the curve, and the lower the temperature at which growth ceased.

Following this graduated series of conditions down to the stage at which the change of temperature is infinitely

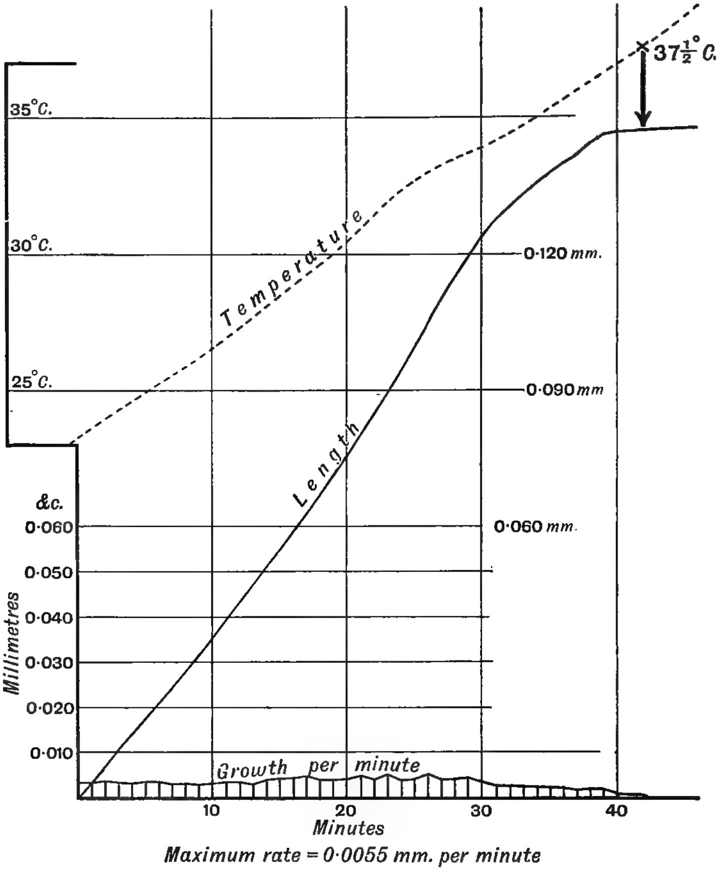
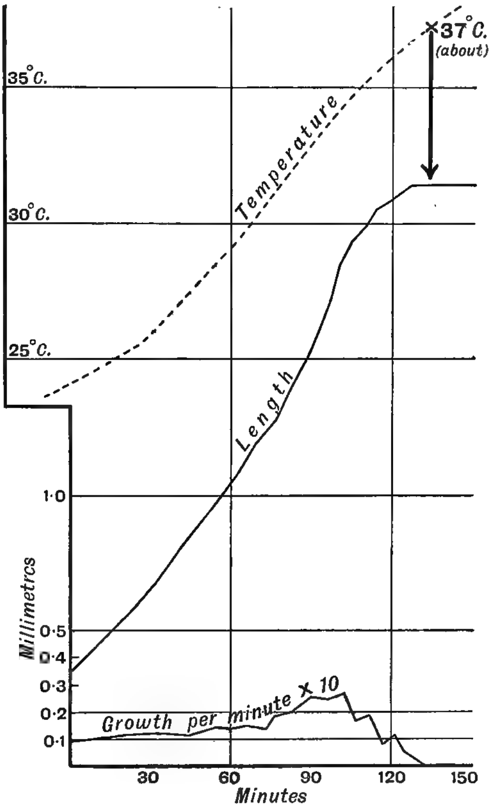


FIG. 31.—GROWTH AND TEMPERATURE OF A FUNGUS.
Hypha of "Sore-shin."

slow, we find that growth stops even in a culture kept constantly at 20° C., if kept long enough. Such cessation of growth is not necessarily due to exhaustion of food from the culture, for all the food-ingredients may still be present. Further, it takes place, for any given temperature, after a lapse of time which is directly proportional to the volume of the culture media. Lastly, such "stale cultures" will resume their growth if they are diluted with pure water.

Plainly, then, the staling of cultures is due to excretion of a toxic substance by the fungus into the surrounding medium. Such excretion takes place more rapidly at high temperatures than at low ones. Lastly, retracing our series of conditions, the cessation of growth in fresh cultures raised rapidly to a temperature of 37·5° C. is due to poisoning of the protoplasm by the toxin, which is produced most rapidly at this temperature. We shall denote this hypothetical substance, or mixture of substances, by the symbol "*x*," for convenience.



Maximum rate = 0·025 mm. per minute

FIG. 32.—GROWTH AND TEMPERATURE OF A ROOT.

Cotton seedling.

The chemical nature of "*x*" is obscure. It is not an enzyme, however. On prolonged boiling, or on exposure to air in thin films of water, it is decomposed, and by either of these methods we can rejuvenate a stale culture medium. Since "*x*" is thus unstable, and its chemical nature unknown, we are thrown back upon the growth-curve as a test for its presence. Denoting completely stale culture media as 100 per cent "*x*," we find that the depression of our growth stopping-point from the normal

37·5° C. is apparently proportional to the percentage of "x" which we add to the culture medium. Thus, a 50 per cent. solution has a stopping point in the neighbourhood of 32·0° C., however quickly the temperature be raised.

Were it not for the accumulation of "x" in the cells, the growth-rate would go on doubling with every ten degrees until the death-point was reached at about 49° C.

This substance is formed only in growing cells of the fungus, and unless the formation is very rapid it diffuses out into the surrounding medium before an injurious concentration can accumulate. Stale mycelium can therefore be rejuvenated by washing with fresh culture medium, or with water. Conversely, when the volume of the surrounding culture medium is of microscopic dimensions, as in a cell of the host plant, staling takes place rapidly.

We are now in a position to comprehend the peculiar relationship to temperature of the "sore-shin" disease. Owing to the minuteness of the cells of the host, a very short exposure to temperatures above 30° C. will completely inhibit the parasite's growth—unless the tissue is washed by water—and the host-plant is thus given time in which to form the protecting barrier of corky cell-walls.

It would seem natural to assume that the host-plant itself had a different temperature-relationship, since its cells would otherwise become stale at the same time as those of the fungus, and high temperatures would have no protecting effect. This assumption is not correct, however, and a different explanation has to be tried, in view of the following experimental work.

In parallel with the experiments on the fungus, a few similar measurements were made with the root of germinating cotton-seeds. The seedling was immersed in a double-jacketed water bath with a glass side, through which the elongation of the root-tip was observed by a Comparator measuring to 0·01 mm. The reserves in the seed formed a sufficient food supply, and aëration was maintained by a stream of bubbles of oxygen through the water. The rate of heating had to be reduced to about 1° C. in five minutes, in order to obtain accurate measurements, but even so, the growth-curve (Fig. 32) was identical with that given by the fungus, showing the same acceleration, and also stopping at about 37·5° C. Slower rates of heating were employed in the form of germination trials in the incubator, when it became clear that some similar "*x*-substance" was again operative. The germination of samples of seed stored at higher temperatures is much quicker, though the ultimate germinating percentage is unaffected. Moreover, a 37° C. sample is surpassed in four days by a 25° C. sample, not only in the mean length of the radicles, but also in mean weight. The sample at 37° C. is, in other words, stale, and needs a prolonged exposure to lower temperatures if it is to be restored to health.

It should be noticed that a shade temperature of 40° C. is frequently reached during the early summer, so that some manifestation of this process, which the author has denoted as "Thermotoxy," may be expected to occur during the growth of the crop in the field. We shall see later that such is actually the case.

Meanwhile, one other point needs to be considered. The heat-poisoned fungus is cured through removal of "*x*," whether physically by washing, or chemically by decomposition. The first method is impossible in the higher plants, so that chemical decomposition must be invoked; the effect of overheating in one afternoon, though plain during the following night, has disappeared by the second night.

Now it has long been a truism that every plant has an "optimum temperature" for growth.* We have just seen,

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* See various writings by Mr. F. F. Blackman for critique of these terms.

however, that two such dissimilar organisms as a cotton plant and a sore-shin fungus possess identical growth-curves with no true optimum. On the other hand, the cotton plant certainly grows best at temperatures near 32° C.; we are therefore led to a final conclusion, namely, that the general "growth-optimum" of any higher plant is that temperature at which, after prolonged exposure, the equilibrium of growth-acceleration with "x-production" allows the maximum sustained value to the former. The "x-production" factor is itself compound, being the balance of "x-production" against "x-decomposition," for the latter of which there appear to be special facilities in the higher plants.

Summarising this section, we have found that, in the absence of other limiting factors, growth is accelerated by rise in temperature along a logarithmic curve, while a time factor ("thermotoxy") acts against this acceleration, unless the toxic katabolites are removed as fast as they are formed. The "optimum" is essentially a variable, but the "maximum" is normally constant, though it can be depressed by suitable treatment. Tissue temperatures which exceed 38° C. reduce the subsequent growth-rate of the cotton plant to a marked extent, while prolonged exposures above 35° C. are proportionately harmful. Exposure to temperatures below 30° C. for a long time appears to produce no injurious effect on the cotton plant.

The effect of sunshine.—The conclusions of the preceding discussion would lead us to expect that strong sunlight might conceivably have a prejudicial effect on the growth of the plant-stem, by over-heating the growing-point, but thermo-electric measurements of tissue-temperatures indicate that the young leaves and buds rarely exceed the shade temperature during early summer, owing to the regulation of their temperature by transpiration.

Actual measurements of growth, on the other hand, show that direct sunshine inhibits it completely.[26] [29] (Figs. 33 and 34).

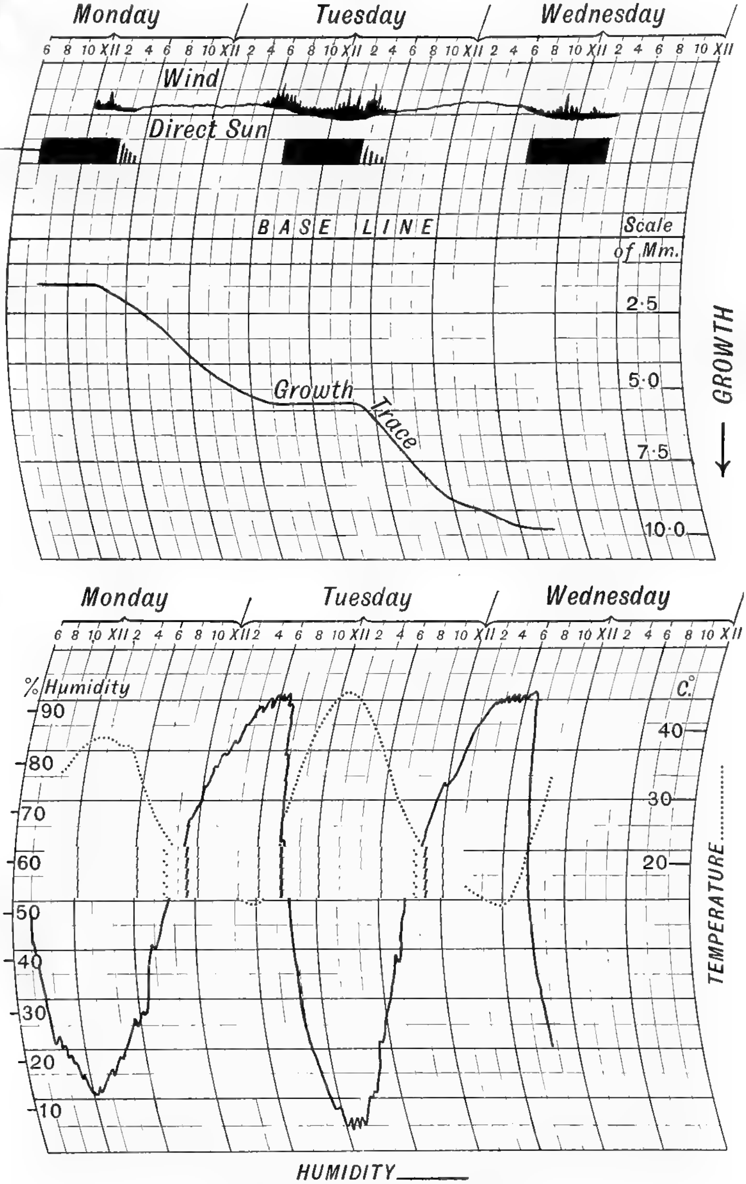
This simple discovery has had an almost revolutionary effect on our study of plant physiology in Cotton. The phenomenon, though almost unprecedented outside Egypt, is exhibited by many other plants in Egypt, notably by *Helianthus.*

The "sunshine effect" was first recognised in May, 1910, and has since been found to be usual from the first appearance of the seedling till the autumn, if not throughout the season. The elongation of the stem is checked immediately the sun strikes upon it, and a slight shrinkage usually follows. A cloud passing across the sun is immediately effective in permitting growth, which ceases again directly the cloud has passed.

The contraction of the stem in sunshine indicates that loss of water is the direct cause of growth cessation. That this explanation is the true one can be shown in many ways; thus plants covered by a glass bell-jar so as to surround them with an atmosphere of high humidity, will grow rapidly in the sun during May. Similar conditions occur in the field for a day or two after watering, when the plants are large. The most striking proof is provided, however, by leaf-removal; if the total leaf-area is reduced about one quarter, by simply cutting off the lower leaves, growth is almost instantly resumed, since the water-loss of the stem is reduced. This last experiment shows in a striking manner the delicacy of the water equilibrium between root-supply and stem-loss.

Disturbances of this equilibrium are normally effected by variations in the weather, such as abnormally high sun or shade-temperatures, hot dry winds, etc. It should be noticed that the equilibrium-point is probably determined by the worst normal conditions, namely, at 1 p.m. to 2 p.m.

Artificial disturbances of this equilibrium can be effected



period of sun

Fig. 33.—Growth of Stem.

Showing the environment on June 6–8, 1910.
June 7th was abnormally hot.
Last watering on May 28th.

Fold out

by limited defoliation, or by root-pruning, or by cultivation in limited quantities of soil, as in flower pots. All these methods give similar results as regards the "sunshine effect."

The qualification "limited" is added to the mention of defoliation methods because of the interference with photosynthesis which follows if too many leaves are removed, or if they are removed from near the terminal bud.

The positive effect of day temperatures on growth is thus almost non-existent, and the modicum of truth which attaches to "accumulated-temperature" approximations is still further diminished. The only effect of day-temperature is the prejudicial one of "thermotoxy," excepting on the rare occasions when the sky is overcast. Such days are remarkably interesting; usually the clouds take the form of a dust-storm, accompanied by high temperatures, and so long as the temperature does not reach the "thermotoxic" limit, or 35° C., they cause abnormal growths to be recorded, since elongation of the stem is continuous throughout the twenty-four hours.

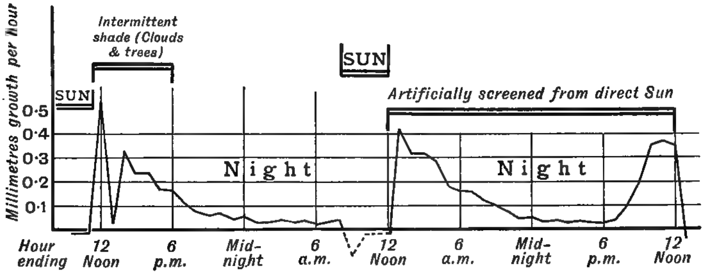


FIG. 34.—THE SUNSHINE EFFECT.

Growth-rate per hour in hypocotyl of an Assili seedling sown on March 7th, during March 19th to 21st. Compare screened portion with temperature in Fig. 33.

In view of the rarity of such weather we are justified in deducing the conclusion that night-temperature is the prime factor in growth during the first half of the growing-season, provided only that no limiting factor other than temperature operates during the night. On this latter point, unfortunately, we are unable to generalise with safety. The curve of growth—after sunset—leaps from zero to a maximum, and thereafter follows the temperature curve* till the small hours of the morning (Fig. 34). It is not clear whether there is any limitation through exhaustion of the photosynthetic food supply before sunrise. On the whole, the evidence is against this view, except in rare cases, and in any case such limitation would take place at the period of minimum growth-rate.

Night-temperatures.—Combining our knowledge of temperature control with the elimination of day-temperatures provided by the "sunshine effect" we are enabled to interpret the growth-rates obtained under field-conditions with fair exactitude.

The curve shown in Fig. 30 was obtained by daily measurements of the axial shoots of ten cotton plants, thus summarising the mean growth of the twenty-four hours. The correlation between minimum night-temperature and the growth rate up to July 1st is very close ($r = 0{\cdot}7843 \pm 0{\cdot}0459$) if those daily periods are excluded in which the maximum temperature had risen above 35° C. The correlation sinks to a value of $0{\cdot}5236 \pm 0{\cdot}0755$ when these are included, owing to thermotoxic effects.

At this stage of the plant's existence there can be no question as to the economic interest of stem-growth. The faster the growth of the stem and branches, the sooner will the first flowers open, and the period which we are now considering ends with the appearance of these.

Thus, the date of "arrival" of the crop depends first on the night-temperatures which have been experienced, secondly, on the date of sowing, and thirdly, on the clouds. We shall return to this subject later, in connection with the date of the first flower.

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* Except after heat-poisoning, when it remains constant, or rises slowly until cut by the falling temperature.

Meanwhile, we must not forget that the night-temperature is commonly recorded as a minimum only, and that the true mean night-temperature may be somewhat different. Moreover, the internal temperature of the tissues is appreciably affected by clouds, which check radiation.

Having now discussed the main factors which control growth during the first half of the season, we can turn to the examination of the water factor in more detail, since its importance will be considerable at a later date. Before so doing, an example may be studied which will remind us that the idiosyncrasies of the plant have to be taken as the base-line for all environmental effects.

Length of the seedling stem.—That portion of the stem known as the hypocotyl, situated between the true root and the seed leaves, forms the greater part of the "root" which emerges from the seed-coats on germination. It is distinguished from the true root by the black speckling of resin glands. The length to which it attains after raising the cotyledons out of the soil would appear to be a matter of pure chance. Seed buried under clods of earth, or deeply sown, develops a stouter hypocotyl in reaction against the mechanical resistance; much of the reserve food having been exhausted in the effort, the aërial portion of the hypocotyl is shorter, and the cotyledons smaller.

A series of seedlings grown under uniform conditions showed that specific foundations were discernible in such a trivial character even as this. The strains employed were derived from an American Upland (King), and an Egyptian (Sultani). Having been soaked for a night at 30° C. they were planted at a uniform depth of 2 cm., at uniform distances of 5 cm., in finely sifted soil which had been uniformly damped, and the hole which had been dibbled for each seed was filled by more fine soil without compression. The box containing the soil was kept in the open air. Daily measurements of height were made, and the final length of the hypocotyl when growth in this region had ceased showed that the Upland exceeded the Egyptian by 50 per cent. under the field conditions of an Egyptian April. This excess was the more striking, in that the Upland seed was much smaller than the Egyptian, and a large seed usually displays a stronger "field germination" than a small one.[23]

This difference became still more remarkable when the first internode developed above the cotyledons had also attained to its full length, for it completely reversed the hypocotyl length, being 50 per cent. longer in the Egyptian than in the Upland. The length of subsequent internodes is correlated with that of the first one, and since the internodes are developed at about the same time, the height of the plant is determined by the internode length unless other factors intervene, which we shall consider later.

A repetition of this experiment in a cool greenhouse in England threw some light on the specific temperature-relationships. Under these conditions the Egyptian seedlings exceeded the American in all their dimensions, including the hypocotyl length.

More detailed examination of the water-relationships which we have already encountered in the "sunshine effect" are now necessary, dividing the same into the two components, namely, absorption by the root and loss by the stem.

The root.—The root first makes its appearance in germination at the end of the emerging hypocotyl as a zone of embryonic tissue about three millimetres in length. The growing zone is remarkably small throughout root-development.

The primary root is positively geotropic, and its elongation is indefinite. The plant is consequently tap-rooted, and the depth to which the root system extends is determined by external conditions alone. The greatest depth to which an unbroken tap-root has actually been followed is two metres and twenty centimetres. This depth had been attained between March 28th and September 1st, in soil where the sub-soil water level is four metres below the surface until September (Fig. 30).

The growth of the tap-root is arrested or diverted horizontally upon arrival at saturated soil, and plants grown in land with a constant high sub-soil water level consequently possess insignificant tap-roots,* with a greater development of laterals.

In case of injury to the growing point of the tap-root one or more of the lateral roots nearest the tip turns downward and replaces it.

The resistance offered to root-growth by soils of normal texture appears to be negligible, both from the indirect evidence of growth-rates, and from actual observation in glass-sided boxes.

The secondary roots normally begin to develop when the tap-root has attained a length of some 12 cm. Their original diameter is about half that of the tap-root, and roots of higher orders arise from them. Their rate of growth under the same environmental conditions is slower than that of their tap-root; this phenomenon is one of those commonplaces of observation which have never received a satisfactory explanation. In spite of their slower growth, they produce an enormous increase in root area, on account of their numbers, and if the soil is carefully washed away from a cluster of cotton seedlings about six weeks after sowing (Fig. 35), the root system appears as a tangled white gossamer web. Only a few of the rays of this web survive (Fig. 37).

Before discussing the factors controlling root growth, we may advert to the general form of the root-system, which, beginning as a vertical line, rapidly becomes an inverted

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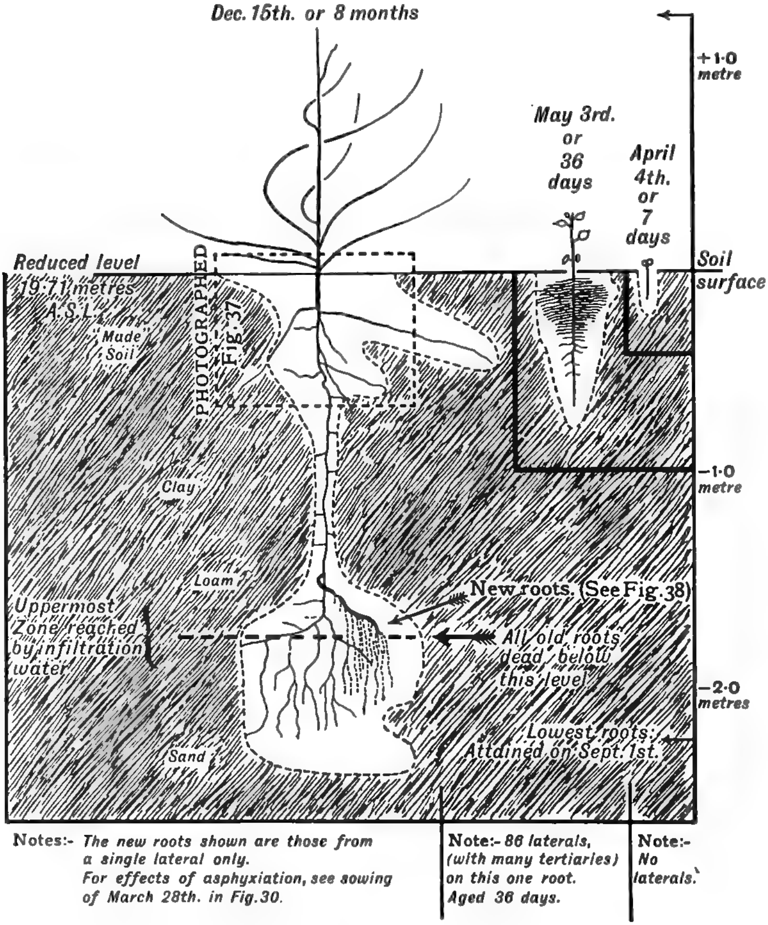
* Audebeau.

cone. When plants are sown at wide intervals, this conical form is maintained, the principal laterals extending radially by the autumn to distances of over two metres (Fig. 37); the irregular base of the inverted cone thus becomes about five metres in diameter, while its depth may exceed two metres. When the plants are closely



Notes:- *The new roots shown are those from a single lateral only. For effects of asphyxiation, see sowing of March 28th. in Fig. 30.*

Note:- *86 laterals, (with many tertiaries) on this one root. Aged 36 days.*

Note:- *No laterals.*

Fig. 35.—The Root: Development, Asphyxiation, and Regeneration.

Scale drawings from measurements.

sown, as in the field crop, the uppermost laterals from adjacent plants begin to encroach on each other's territory, within three months from the date of sowing; although interlacing takes place, the form of the effective root-system is modified by this lateral limitation into a cylindrical upper portion ending below in a cone. The depth of the cylindrical portion increases as lower and lower laterals come progressively into contact. If the downward extension of the tap-root is checked, the conical portion is overgrown, and the whole root-system becomes a cylinder. The interest of this "root-interference" will become apparent later, when we find that plants in field crop behave as if they were "pot-bound."

That the total volume of soil occupied by an adult cotton root must be enormous is shown by the examination of pot plants. The photograph of Fig. 36 represents an average plant from sowings in six-litre pots after fourteen days; the tap-root had attained a length of 16 cm. and was diverted by the floor of the pot after seven days only. Having been exposed to higher temperatures during the day than it would have experienced in the soil, the absolute size of the root is somewhat abnormally large, but the ratio of increase is interesting. After seven days the total root-length was 20 cm.; after fourteen days, two metres; after three weeks, four and a half metres. Yet the growth-curves from the plants during this last week showed that their root system was insufficient for the needs of the stem, though the total leaf area amounted to less than 30 sq. cm.

On account of the more obvious importance of the root system at a later stage, we shall at present omit further discussion of its functions, but one experimental result might be mentioned. With plants growing in pots where the water content of the soil can be determined with certainty, we find no obvious relation between this factor of the environment and the growth of the stem during the night until the water content has sunk below a certain limit. Since deficient water-absorption is the real limiting factor of the sunshine effect, it follows that the *size* of the root-system is the true limiting factor of water-absorption, and that the humidity of the soil may vary between wide limits without affecting it. Much more work needs to be conducted on this question, in view of its importance in irrigation practice.

Fig. 36.—Seedling.
Fourteen days old.

The rate of growth of the roots under field conditions is primarily controlled by temperature. Once the tap-root has passed into soil at constant temperature, containing perhaps 70 per cent. of the saturation quantity of water, the growth rate can safely be predicted. We have already examined the effect of temperature on root growth, and it suffices to add that the mean growth rate of many roots growing in soil in the laboratory works out at approximately 0·9 mm. per hour at 18° C., and 1·25 mm. per hour at 22° C. When the seedlings under examination are placed out of doors, the total growth of the roots in twenty-four hours is considerably less than the calculated amount (see also Fig. 35), and it seems probable, although a complete experimental proof has not yet been obtained, that this diminution is due to the "sunshine effect," which disturbs the water-equilibrium of the root conjointly with that of the stem.

The rate of growth under field conditions is not easily ascertained. Small plants can be grown in boxes or tubes with glass sides, which are buried flush with the soil surface, and pulled up as often as may be necessary for examination of the root, which grows down the inclined glass side. For checks on such plants, and for examination of all large plants, we have no method other than the primitive and muddy one of excavation with a jet of water and a trowel till the end of an unbroken root is reached. Measurements made by these methods have given data of which the following series is representative :—

		Length of true root.
Sown	March 28	0
Measured	April 2	6 cm.
,,	,, 4	14 cm.
,,	May 15	55 cm.
,,	July 1	140 cm. (abt.)
,,	September 1	220 cm. +

From these it follows that the root-depth in well-drained soil certainly reaches two metres by the end of August.*

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* The lower soil-temperature in the Northern Delta should diminish the root-extension considerably. The point needs investigation on account of its intimate relation to drainage projects.

Lastly we have to consider an abnormal limiting factor of root-growth, namely deficiency of soil-oxygen, usually due to water-logging of the minute interstices which the soil contains. Owing to the fact that its anatomical structure does not include an elaborate system of intercellular air-spaces, such as aquatic plants possess, the cotton root is locally asphyxiated in water-logged soil, and in a few weeks even the stout, woody roots are not merely dead, but decomposed. Here also we require precise information as to the degree of soil saturation which produces these effects under field conditions, but the main facts are perfectly clear, and we shall meet with the serious economic effects of this root-asphyxiation at frequent intervals.

Fig. 37.—Water Jet Excavation of Roots.

See Fig. 35 on which the area of this photograph is marked. Lateral from neighbouring plant on right is marked with an **X**. Length, 170 cm. +.

The stomata.—Certain plant physiologists have expressed doubts as to the importance of the stomata in regulating transpiration, but such is certainly their function in the cotton plant. Consequently, an examination of the stomatal movements, so far as they are at present known, is necessary to an understanding of the way in which the stem loses water.

The stomata of Egyptian cotton plants are found on both surfaces of the cotyledons; on the hypocotyl and stem, and on both surfaces of the foliage leaves.

A full grown stoma is about 0·04 mm. in length, and the mean frequency of these organs in each square millimetre has been found to be as follows.

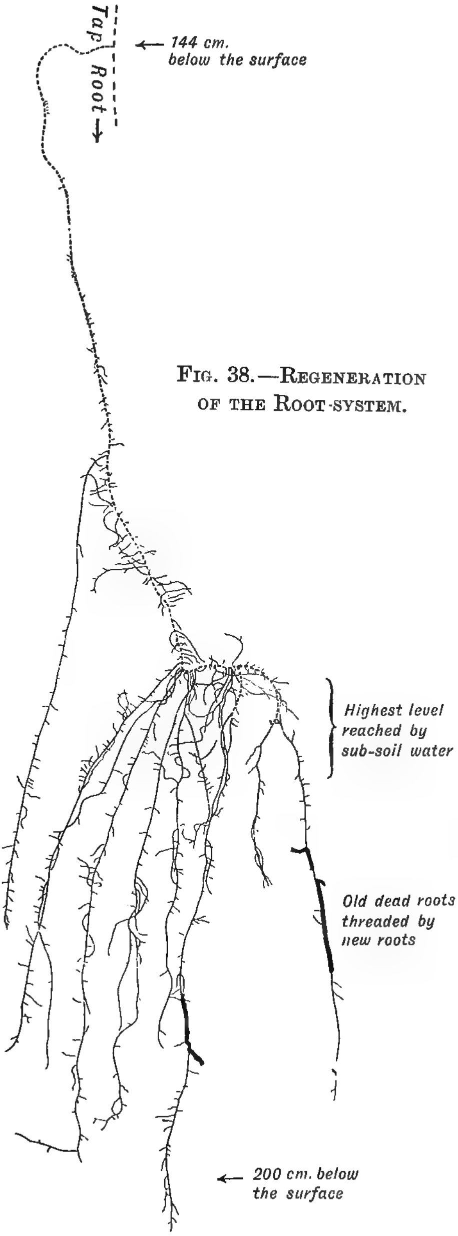

Fig. 38.—Regeneration of the Root-system.

Showing crop of new roots developed in six weeks from merely one uninjured lateral (the dotted line). Tracing from a blue-print of the root itself, after floating it upon a sheet of glass. See Fig. 35 and also 30.

Cotyledon: Lower epidermis	275
Upper ,,	200
Hypocotyl and stem	20, &c.
Leaf: Lower epidermis	176 to 116
Upper ,,	97 to 44

The total number of these apertures is consequently enormous. Such a seedling as that portrayed in Fig. 36, already possesses about half a million. Nevertheless, the cotton plant is not abnormally rich in stomata, though the fact that they are found on both sides of the leaf should be remembered.

The functional capability of the immature stomata found in very young leaves is not clear. The cuticle of such leaves is yet thin, and in all probability it allows some evaporation to take place. The density of the stomata on such developing leaves is about the same as on adults, so that fresh stomata are continually being differentiated as the leaf expands.

Further, with changes in the age of the leaf we find changes taking place in the degree of those reactions which the stomata exhibit towards environmental changes. These are by no means fully understood, and for the present we must confine our attention to the normal leaves, fully grown, but as yet showing no signs of senescence, which constitute the greater part of the leaf area. The principal observations upon which this account is based were made during May, June, and July.

The study of changes in stomatal aperture under field conditions has formerly been impracticable except by personal observation, which almost precludes continuity in the records. The author succeeded, however, in adapting Mr. Francis Darwin's Porometer method,* to a self-recording system, and the first continuous automatic records of stomatal aperture were thus obtained.

In the Porometer, the leaf is made to seal an air-tight

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* Darwin and Pertz.

chamber, within which the pressure is higher or lower than that of the atmosphere. The air-flow, restoring equilibrium of pressure, can thus take place only through the stomata and mesophyll tissues, while the square root of the velocity of this flow is approximately directly proportional to the stomatal aperture.

The author's Stomatograph[31] consists of a sensitive electric air-pump, which maintains a constant pressure gradient between the chamber and the outside air, signalling the time of completion of every stroke—and hence the stomatal aperture—on a chronograph drum. The pump, with its operating battery and a relay, is contained in a small dust-proof box, placed below the plant under examination. From this box issues the tube leading to the leaf-chamber, and also a telegraph wire which leads from the relay to the chronograph; the latter may be at any convenient distance, preferably in the field laboratory. The instrument is independent of any meteorological change or disturbance.

In the usual simple experiments, we find that desiccation, darkness, and poisons cause closure, while sunlight causes the stomata to open to their maximum aperture.

The records obtained from normal leaves in field conditions, which in one case extended over five consecutive days with the same leaf (Fig. 39), reveal a most fascinating interplay of factors. During the night the stomata are completely closed; they begin to open slowly at dawn, and continue to do so until a moderate aperture has been attained, even in diffuse light. When direct sunlight strikes the leaf, the aperture is rapidly increased, till maximum is reached at about 9 a.m. This maximum aperture is maintained for a varying period, the length of which is undoubtedly determined by the water-absorption of the root, provided that sunshine be continuous. Immediately after irrigation it may last two or three hours, while on hot, dry, windy days, with a soil approaching to physiological dryness, the full aperture has scarcely been attained before closure sets in. Such facts indicate that the closure which follows must be due to "water-supply shortage," and that its utility is to check the excessive water-loss involved by free transpiration. By noon, on most summer days, this closure is almost complete, and we shall revert to its effects on transpiration and photo-synthesis when considering these functions.

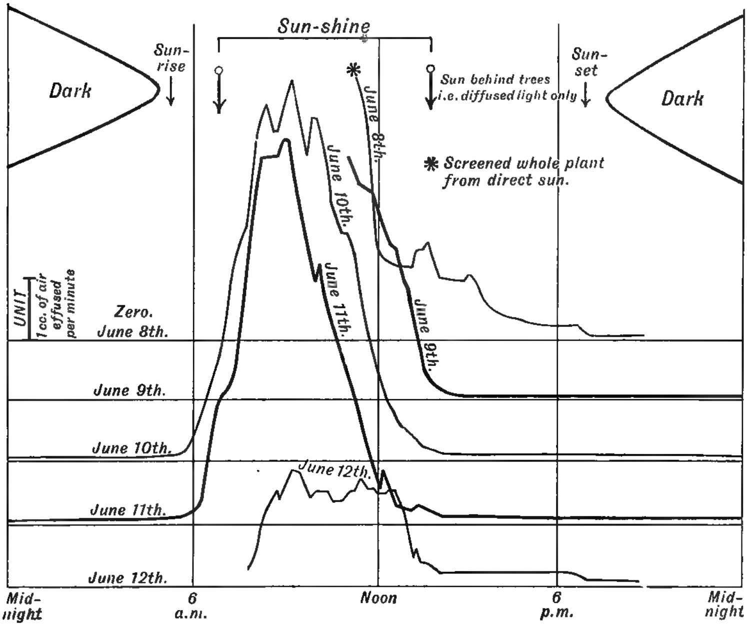

Fig. 39.—Stomatograph Records.

Curves show volume of air driven through an area of 80 sq. mm. of leaf per minute, under a pressure of 1 mm. of mercury.

Five-day record on the same leaf without alteration of apparatus. Fifth day is abnormal.

On cloudy days, or when a screen is placed across the plane of the ecliptic so as to cut off all direct sun from the whole plant, the maximum aperture is not attained, but a moderate aperture persists throughout the day, followed (Fig. 39, June 8th, from noon onwards) by slow closure in the late afternoon, and complete closure at sunset. In such circumstance the illumination is the controlling factor, and there is no water-shortage; this might be expected from consideration of the fact that the existing root-system has been developed to cope with the demands of sunny weather.

If this very plausible hypothesis of diurnal water-shortage be correct, it must mean that the water-content of the soil which is in juxtaposition with the roots has been reduced at a greater rate than that at which water can be restored by capillarity. During the night there must be a purely physical movement of water into these semi-desiccated portions of soil, since the water-shortage is not apparent on the following morning. We thus obtain from the Stomatograph some conception of the severe strain which the plant undergoes during the torrid weather of a summer in Egypt.

The verb "to vegetate" is frequently misused as a description of inert torpidity, but the daily experiences of a cotton plant in Egypt almost justify this libellous employment of the word. From noon onwards, this long-suffering plant is neither growing, nor feeding, nor transpiring beyond the necessary minimum, and possibly not even breathing properly.

The supremely injurious effect of fogs has long been an article of the cotton grower's faith. It is difficult to see any reason for this conviction, apart from the continued low temperature which morning fogs entail, but it is possible that the blocking of the stomata by condensed water may have a prejudicial effect. Even so, a fog should merely postpone the brief period of general activity of the plant by a few hours, and not actually curtail that period. On the whole it seems safer to adhere for the present to the cynical explanation that most "fog" is boll-worm, while the rest is either mere spoiling of the seed-cotton in the open boll, or else a simple reduction of temperature.

Transpiration.—We have examined the principal machinery by which the water-loss of the plant is controlled and it now remains to ascertain what the amount of this loss may be under field conditions.

On this subject we are profoundly ignorant, owing to the experimental difficulties, and the present section is intended rather to indicate the possible lines of attack than to attempt a statement.

The usual methods of investigation are divided into gravimetric and volumetric determinations, which may be used to summarise the net result of a long period, such as a day, or to investigate the effects of a particular set of factors at a given moment. Direct weighings of the plant are feasible in the earliest stages, but we have seen that a plant aged three weeks, growing in a six-litre pot, is already abnormal. Further, we shall come later to evidence which shows that two plants growing in an iron cylinder 2 metres high and 80 cm. in diameter, are suffering from root limitation by the middle of July; since similar signs are shown by close-sown plants in field crop, the objection is not fatal, but the conditions cannot be regarded as normal. Furthermore, such isolated plants have room to develop all the branches they produce, and their leaf area is consequently much larger than that of a field plant. Lastly, being isolated, they are freely exposed to wind, and this rapid removal of saturated air must increase transpiration enormously. The only serious attempt at determinations by weighing large tanks was carried out by M. Audebeau. The objections just mentioned apply to this excellent series of observations, especially after June, when the field plants are beginning to produce a "surface climate." The discrepancy between M. Audebeau's total transpiration and the actual state of affairs was strikingly shown to the author by Mr. J. I. Craig, who computed that on this basis the whole Nile flood would be lost through the transpiration of the cotton crop alone !

It may be possible, however, to obtain data from plants growing under nearly normal field conditions, by underpinning large masses of earth to form concrete tanks in the middle of a field of cotton, and determining the fall of the water-table in these tanks from day to day. The method is open to many objections, but it lends itself to automatic recording, and if regarded in part as a problem in soil physics, the results should form a near approximation to the truth. It is not however suitable for examination of the diurnal variation.

For the problems of diurnal change it is usual to employ the Potometer, which compares the velocities of intake of water by means of a tube intercalated in the cut stem. This method has not been persuaded to work in Egypt owing to the severity of the sunshine effect, which promptly kills the severed stem.

The only method which holds out any prospect of utility is the least obviously practical of any. It consists in cutting off portions of plant tissue of known area, and weighing them repeatedly on a Joly spring balance as soon as possible after cutting. The weighing is done in the field, usually under difficulties due to the wind, and the balance is set up so that the tissue shall remain in the same position which it occupied before being cut off. Even whole plants may be treated in this way and measured up with a planimeter afterwards. The curve of weight-diminution in time is then plotted backwards to the moment of cutting, and its value at that moment is assumed to be the true transpiration rate. This is then converted for purposes of comparison into milligrammes per square centimetre per minute.

The few determinations yet made in this way have given consistent results, four of which have been plotted in Fig. 40. They show that transpiration is practically in abeyance at night, slow in the early morning. By 9 a.m. in sunshine it has reached a maximum which is maintained till past noon. The last result is perhaps rather unexpected, seeing that the stomata are nearly closed, but it is easily explained when we remember the increase in stringency of the environment which has taken place during these four hours: Sun-temperature has risen from about 50° C. to 75° C., shade-temperature from about 25° C. to 35° C., and humidity has fallen from about 60 per cent. to 20 per cent. of saturation. During the afternoon the transpiration rate appears to fall

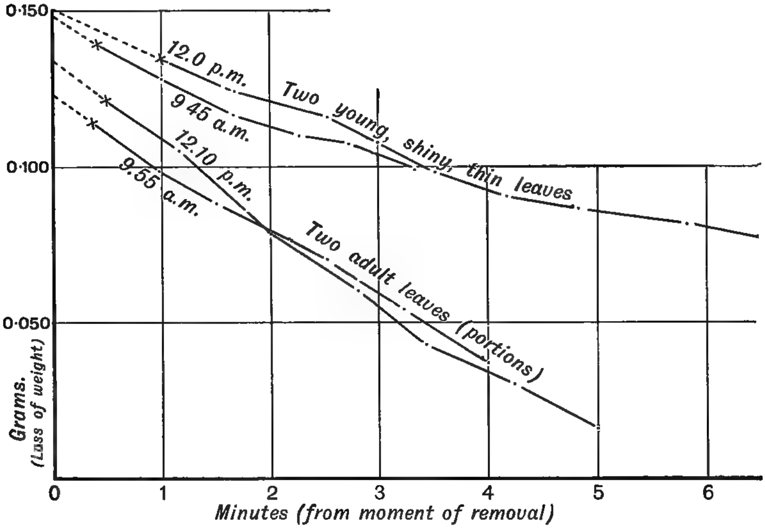

FIG. 40.—TRANSPIRATION IN FIELD CROP.

Rate of water-loss from detached leaves, plotted backwards to instant of removal.

Initial weight of all four was about 0·85 gram ; areas, 30–40 sq. cm.

Time.	*Wet Bulb.*	*Dry Bulb.*
9·50 a.m.	25·6°	28·4°
12·5 p.m.	23·9	32·8

steadily, but the shape of the curve is only known approximately as yet.

The rate of mean maximum transpiration obtained in these trials was 0·00076 g. per sq. cm. per minute, which seems to be within the order of probability. A trial with an entire plant in the same way indicated a rate of 0·0003 at midday on June 15th, many of the leaves being shaded by others; there were twelve leaves, with a total area of 585 sq. cm., the wet and dry bulbs reading 24° C. and 33° C. respectively.

Tissue temperatures.—A number of records of the internal temperatures of various tissues have been taken by inserting a thin copper-constant in thermo-electric couple in the tissues;* it is then balanced upon a similar couple bedded in a rod of paraffin wax, which is kept at shade temperature behind a screen close to the plant. The actual shade temperature is simultaneously recorded by means of a thermograph near the control couple.

Since the shade temperatures form the standard of comparison between various sites, this method is preferable to direct determinations of absolute tissue temperature. The difference between the two couples is automatically recorded by a "Thread Galvanometer," a zero line being first traced in order to show when the couples are at the same temperature.

The results obtained in this way present a few features of exceptional interest. Variations of ±1·0° C. are shown even by large bolls, while the stem within five millimetres of the terminal bud varies in the same way as the younger leaves, though with less amplitude. Young leaves, which have not attained to a third of their ultimate length, rarely exceed the shade temperature, but frequently fall below it, their extreme variation being about +0° to

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* Blackman & Matthaei.

– 6° (Fig. 41A). Old leaves, on the other hand, rarely fall below air-temperature but frequently rise above it, varying from – 3° to + 10° (Fig. 41C). These oscillations in leaf-temperature are extremely rapid, differences of 10° C. being recorded often at intervals of only a minute.

The thermo-regulation of the leaf seems to diminish with age, and it is not inconceivable that the senescence of a leaf may thus be hastened by thermotoxic effects. In general terms, the old leaf follows the sun-temperature, but the younger leaf follows the wet-bulb temperature. Puffs of wind, whether natural or artificial, produce no notable effect on the old leaf, but reduce the temperature of young leaves.

Thus it follows that in considering the effect of maximum day-temperatures on growing tissues, we were justified in taking the shade-temperatures as the maximum tissue temperatures.

That thermo-regulation is real may be seen by comparison of Fig. 41A and Fig. 41B. The two records were taken from the same tissue, at an interval of twelve days, during which the vascular tissue had been destroyed by a "boll-worm." The top of the stem wilted in the usual way and became dry, and the recording couple inside showed most erratic oscillations of temperature, due solely to the intermittent cloudiness of the sky.

The night-temperature of tissues is practically identical with the air-temperature, excepting for variations of about 2° C., which have been shown to be caused by clouds, checking radiation. The effect is not an important one.

Fogs cause no noticeable alteration in leaf-temperature, so that any chilling effect they may have is directly recorded by the thermometer.

The most important result obtained from these records is one which relates to the effect of water-shortage on the temperatures, through reduction of transpiration, and consequent loss of thermo-regulation. On account of the

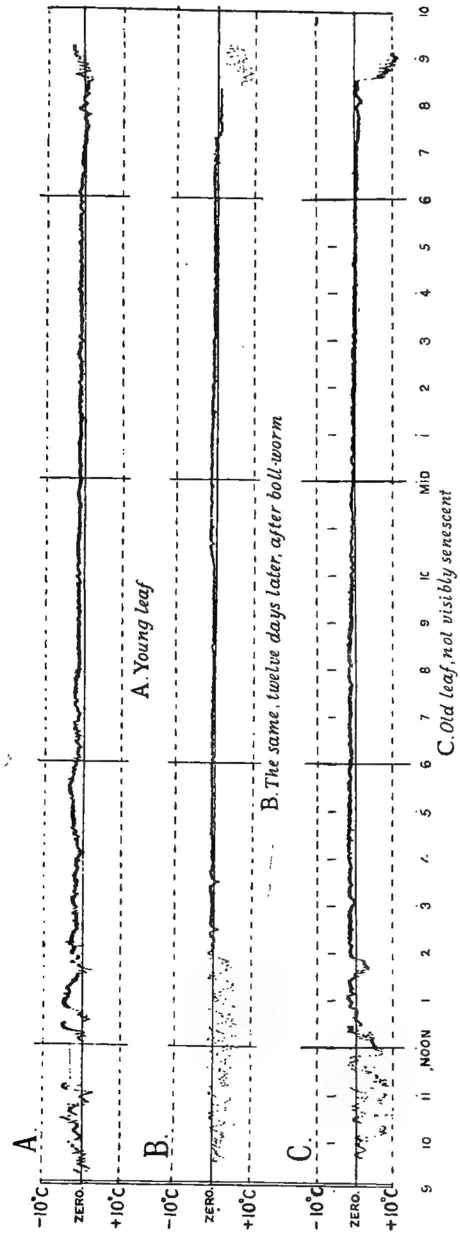

Fig. 41.—Internal Temperature of Leaves.

Balanced upon the shade temperature of adjacent air (zero), by means of Blackman thermo-electric couples and a C.S.I. thread galvanometer.

Site exposed to full sun from 8.20 a.m. till 12.20 p.m. Intermittent sun afterwards through trees until 4 p.m.

varying nature of such controlling factors as clouds and sun-temperature and the age of the leaf, it is not very easy to demonstrate the progressive effect produced by desiccation of the soil over a period of many days. Mimicry of this progressive change by sudden root-pruning may be regarded as tolerably just, and the effect of such pruning is to cause all but the youngest leaves to behave like old ones; they are easily over-heated, and where they had formerly held their temperature down below that of the air, they now exceed the air temperature by several degrees. Hence nearly all the plant tissues suffer from over-heating during the day. The bearing of this fact on our interpretation of the fall in growth-rate which follows water-shortage in July will shortly be mentioned.

Another method of demonstrating this loss of thermo-regulation is simply to examine the tissue-temperature record of a young leaf during a day when the stomata had closed at an early hour. This temperature-trace starts below the air-temperature line and slowly rises up to it, or above it. Differences of not less than 5° C. in mean relative tissue-temperature may thus be produced by stomatal closure.

Photosynthesis.—We can scarcely leave the general physiology of the cotton plant without some reference to this prime function, but a critical and exhaustive series of data has yet to be obtained.

The first attempts at obtaining such a series by the Sachs-Thoday* dry-weight method were rendered fruitless by the unexpected high error of a-symmetry in cotton leaves. The probable error of difference between nominally identical areas of 15 sq. cm., cut from the right and left sides of the central segment, amounts to ± 4 per cent. of the mean weight of each pair. Hence at least sixteen pairs have to be examined in each

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* Thoday, D.

experiment if a result with a probable error of ± 1·0 per cent. is to be obtained.

The evidence to hand indicates that photosynthesis takes place largely in the early morning, the subsequent closure of the stomata preventing free access of CO_2 to the chloroplasts. The curve of increase in dry-weight follows the temperature curve till nine o'clock, and then the stomatograph record, with differences in detail between old leaves and young ones during the afternoon.

The increase in dry-weight in hourly series of observations, without correction for loss by translocation, has given record values at the highest point of the curve, namely 25 (± 4) mg. per sq. decim. per hour. This rate is reached in June, between 8 a.m. and 11 a.m., when the stomata are at their maximum dilatation, and the temperature is above 30° C. There is reason to believe that values of about 30 mg. may yet be obtained under certain conditions, thus reaching the absorption of a surface of KOH when exposed freely to the wind.

It is improbable that the intensity of illumination should ever be a limiting factor in the process, except before sunrise.

No definite signs of growth-limitation by deficient photosynthesis have yet been discovered, unless in such circumstances as the last three hours of Fig. 34, though here again we ultimately may find some such effect in the autumn.

The first flower.—The date of appearance of the first flower on any individual plant deserves consideration in a separate section; being the ultimate result of a long series of interacting factors, morphological and physiological, it is in itself an automatic summary of their effects and it possesses the additional distinction of being commercially important. The "date of arrival of the crop" is almost entirely dependent on the "first-flower date," but the grower does not seem to realise that he is given nearly two months' clear warning as to whether his crop will be late or early. Specific differences between various strains of cotton depend in the first instance on the method of branching. If the first branches of the young plant are sympodial flowering shoots, the flowering will probably be early. Sometimes, however, strains have been noticed which ought to have been early but were actually late, owing to a propensity for shedding the unopened flower buds. Again, specific differences due to branching may take the form of irregularity; all the plants of some strains in the author's possession (notably King Upland), come into flower almost simultaneously, even if some are stunted; other strains show a wide scatter among plants which appear to be equally healthy. Other, and more subtle, differences can only be relegated to the protoplasm itself for ultimate explanation, some strains developing identical flowering branches at a much slower rate than their neighbours, just as the lateral roots grow more slowly than the tap-root under the same environmental conditions.

A point of importance, which is still obscure, relates to the influence of the environment upon the nature of the branch arising from a bud. In certain circumstances, not yet clearly understood, but apparently including excessively high night-temperatures, the plant delays its formation of flowering branches. In many cases the delay is only apparent, the flower buds being formed but soon shed. In others it is real; "Nyam-nyam Kidney" cotton grown at Giza, though otherwise healthy and growing strongly, forms very few flowering branches.

When dealing with most pure strains we find considerable uniformity in the date of the first flower. The stunted plants, if any, flower late, so that a close correlation here exists between the height of the young stem and the flowering-date. Curiously enough, however, this correlation vanishes when we reach the normal plants, which all flower at about the same time in spite of noticeable fluctuations in height.

Another form of the same phenomenon is presented when we examine data for plants sown at varying times. This was first recognised by the author when plotting data for sowing and picking-dates in a series of years, provided from various large estates in Egypt. The graph was interesting as showing the influence of district on sowing-date, and on picking-date in consequence, but more especially so because it indicated—in spite of the many sources of error—that it is useless to sow before a certain critical date in any given district. However early or late the sowing may be, the crop "arrives" at the same mean time until this limiting date is exceeded, after which a delay in "arrival" results, following the delay in sowing. Ultimately, of course, the paraboloid "arrival-curve" will leave the "sowing-curve," since plants sown absurdly late will not flower at all.

The same phenomenon was shown on a smaller scale, though with greater precision, by weekly sowings on a single site in a single season. The mean date of the first flower was actually slightly later in the earliest sowing, on account of the larger number of stunted plants. Three Upland sowings indicated the same behaviour as the Egyptians, but within a shorter period. Sowings made on the critical date were not merely superior in arrival, but also in height, in yield, and in all respects.

We cannot, of course, lay down rigid rules as to the date on which to sow in any place, since the weather varies a little from year to year. Nevertheless it seems clear that the tendency in Egypt is towards sowing too soon. Thus, March 24 was the critical date for Giza in 1911.

The variations in night-temperature from year to year during the six weeks before flowering probably constitute the chief cause of variations in first-flower date, and hence in crop arrival, since the growth-rates of all the branches are closely correlated until June. There have recently been two striking examples of this in the early crop of 1910 and the late one of 1911.

CHAPTER III

DEVELOPMENT AND ENVIRONMENT—II

The second half of the development of the cotton plant in Egypt may be conveniently subdivided into three stages, though none of these have any definite boundaries. They are, successively, the critical period, the water-table period, and the autumnal period. The first of these three is little more than an abstract term which has been found useful in discussion, while the other two explain themselves.

The chief feature of all three, though especially of the first two, is that the main control of the environment has been transformed from the air to the soil (Fig. 30). This change can be seen clearly in the growth curve. During the first period, under the modern conditions of Egyptian irrigation, the plant can always be supplied with sufficient water, but the adjustment of the water-supply becomes a very delicate matter during the critical period, owing to root-interference; while excess of water is likely to be present during the next period, partly from natural causes, and hence reduction in the effective root-system follows. When the sub-soil water period is very early, and consequently overlays the critical period, the combination of the two produces disastrous effects, of which the 1909 crop was our worst example, through an early and high flood.

During these three periods the maturation of the crop takes place. We are chiefly concerned with the flower, and with the boll which ripens from it, though also with the boll which does not ripen. We should also be able to discuss the growth phenomena shown by the lint in the boll, but the experimental difficulties of such investigation have not yet been overcome, and this section of the development, which is of prime interest to the spinner, must be left almost blank.

Methods of observation.—So far as this part of the research has at present been carried, the author has had to devise methods in which the accuracy of the individual observation is low, while the ultimate precision of the result is due to multiplication of such observations. Thus, averages are worked out for a large number of plants and expressed in terms of "per plant per day" (abbreviated for convenience to "p.p.p.d."), with respect to such characters as the opening of flowers, the ripening of bolls, the shedding of flowers, and the growth rate.

The results are usually plotted in graphic form for convenience in examination.

The lack of moderately trustworthy assistance in Egypt often makes it necessary to arrange the time-table of work so as to have daily observations on special plants and groups for three days, then for three days more on another series, and to take those families where the number of plants is large, such as variety-rows, only once a week, depending on the greater number of component individuals to compensate for the scarcity of observations. All these observations can be plotted down to the same "p.p.p.d." basis, and are directly comparable with the results obtained by daily observation, or from large areas.

The task of working data up at any stage is lessened by tabulating note-books at the beginning of the season, though the balance between minimum discomfort in the field, and facility at the writing-desk, is not always easy to strike. The speed of desk-work can often be greatly increased by preparing nomographs to take the place of the slide-rule.

A natural outcome of these methods of observation has been the employment of some of the simpler tools of the statistician. The author having for some years depended on detailed observation of random rows whereby to obtain expressions for the behaviour of plots in ordinary cultivation, was particularly interested when Prof. Wood and Mr. Stratton combined data and treatment in a critical discussion of field experiment methods. The appearance of their article implies that science has at last been introduced into agricultural field experiments, and an examination of the available data respecting cotton should therefore be profitable. The figures for the yield of nominally identical plots in Egypt are too scanty to provide a definite statement of the probable error; those available work out to a probable error of ± 6 per cent. of the mean yield for the total yield of half acre plots; the same figure in the case of Wood and Stratton's investigations for English crops was ± 5 per cent.

The difficulty of obtaining identical plots of Egyptian cotton, even in the same field, is extreme, since great variations in the physical texture of the sub-soil are normal, which involve similar differences in the water-supply of the roots, when they have penetrated thereto, though the surface soil may appear to be uniform. Consequently, we are not justified in expecting the Probable Error (P.E.) of Egyptian cotton plots to be any lower than that of plots of English wheat and we may take ± 6 per cent. as a very liberal estimate of the accuracy of cotton plot experiments in Egypt. Taking odds of 30 : 1 as practical certainty it follows that two plots of different varieties grown for comparison side by side may show yields of four kantars and six kantars respectively, and will yet give us no justification for stating that the greater yield is due to the superiority of one variety over another.

This is a very unsatisfactory state of things, since much money has obviously been wasted in trying such useless experiments. If further application of Wood and Stratton's analysis can be made to enhance the precision of cotton experiments, the attempt is worth making.

The method of examining single rows and computing to single plants is capable of high precision. The examination can be carried out daily, weekly, or casually, and may be extended to any observable character, or restricted to mere pickings of the ripe cotton. In the latter case it is actually less laborious than the ordinary method, since smaller quantities have to be dealt with. Confining attention to total yield only, the author obtained a series of data from double rows of five varieties, badly cultivated on an extremely irregular strip of land (Fig. 42). Comparing two adjacent rows of the same variety, each comprising from 25 to 35 plants in the row, and expressing the differences in terms of the mean yield per plant for the two rows, the final figure for nineteen such pairs gave a P.E. of ± 5·5 per cent. for number of bolls, or 6·8 per cent. for weight of seed cotton. Two little rows growing side by side, of 30 plants each, may thus be made to give as good a comparison for the

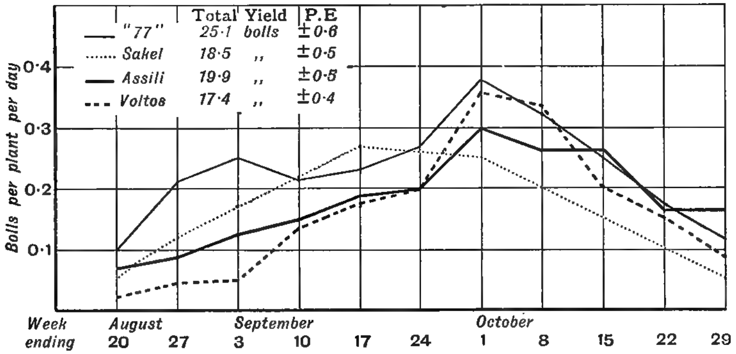

FIG. 42.—COMPARISON OF VARIETIES.

Yield expressed as bolling-curve per mean plant.
Six scattered groups of 30–40 plants per variety.

particular locality between, *e.g.*, two varieties, as can be obtained from plots of any dimensions whatever, while by taking more pairs we increase the precision of our comparison to such an extent that mean divergences of only 5 per cent. cannot be due to accident.

Having obtained from these and from similar small-scale records some definite expression of the precision of the "observation-row method," and knowing approximately the limitations of plot trials, we are in a position to arrange future tests of varieties, manures, waterings, sowing-distances, sowing-dates, &c., with a definite foreknowledge of the significance of our results.

The growth-curve.—Records of the growth of the main stem have already been discussed with respect to the controlling factors up to the end of June. After this date we begin to perceive remarkable differences between various strains of cotton plants. Thus, on the same piece of land, and in the same season, by weekly or fortnightly measurements of the height, made to the nearest five centimetres with a graduated rod, we obtain mean growth-curves like those of Fig. 43, plotted from families of King American Upland, Egyptian Afifi, Egyptian Sultani, and commercial Afifi. The first ceases to grow during June, the second during August, while the third continues at a fairly uniform growth-rate until October. In the third case we find on examination at the end of the season that the length of the internodes is uniform throughout the adult stem. In the case of American Upland only a few internodes of uniform length are produced, after which some half-dozen of decreasing length result in total cessation of growth from the terminal bud of the main stem. The Afifi strain behaves in the same way, but less suddenly, and at a later date. These compressed internodes contain abnormal quantities of calcium oxalate crystals.

Until more detailed investigation of the growth-rates of various portions of the same plant has been completed, there is little profit in discussion of the phenomenon. It should be mentioned, however, that—so far as the available data go—the cause seems certainly to be a form of Thermotoxy, local in, and peculiar to, the particular growing point. The differences between the various strains thus are reduced to a specific susceptibility to thermic effects, either in the form of increased "x-production," or deficient "x-destruction." The view does not claim to be an explanation, but it at least offers the prospect of an answer to the question.

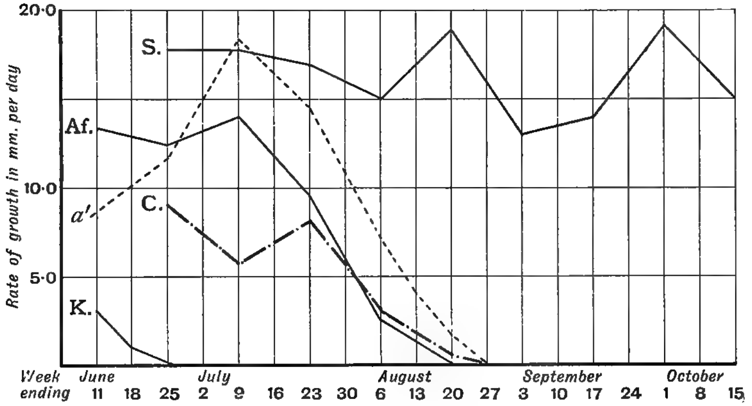

Fig. 43.—Specific Growth-habit.

Mean growth-curves for central axis from various families in same year and on same plot.

K. King Upland. S. Sultani. Af. Afifi. a'. Afifi, stunted plants only. C. Commercial Afifi in field crop.

Leaving these specific differences, and confining our attention to the Afifi type of growth-curve just figured, which is fairly representative of the Egyptian cottons, we can return to the effects of the environment proper. The curve showing the mean growth per day of the terminal bud of ten plants of Afifi (Fig. 30, growth), from which we have already demonstrated the effects of night-temperature, now becomes still more interesting. After June 15th there is a slight indication of a lag in the growth-rate behind the night-temperature control. After June 26th this lag develops rapidly into the dominant feature of the curve, and some factor is obviously at work which leads to a general and progressive falling off of the growth-rate. A part of this degrading is probably of the chemical nature indicated above, which results in a decreased range of sensitivity in the growing protoplasm; some such inferiority would account for the slower growth of lateral roots. To postulate such "deadening" of response is not inadmissible, since it has often been noted in the fungus studies,[9] where two hyphæ in the same field, with the same temperature relationships, were yet found to grow at proportionally different rates, whatever their temperature might be. In these same studies it was also found that such decrease in the growth-rate sometimes appeared as the result of short exposure to high temperatures, too short to affect the stopping-point.*

Such general slowing down of the growth-rate will not cover all the observed facts, for if we smooth the growth-records to the basis of such an assumption, we find that the formerly preponderant influence of night-temperatures on the daily growth is rapidly vanishing. On the other hand we find that the actual records show a long-period modality, corresponding to the intervals between the waterings; growth attains its maximum from two to five days after watering. Obviously the root-absorption is partially involved, probably indirectly through thermo-toxy, or auto-toxy of some other kind, and also through a partial and temporary suppression of the sunshine effect.

These soil-water effects disappear in their turn after the middle of September, when—in the particular series under discussion—the infiltration water from the river raised the water-table and smothered the roots. By this time, how-

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* *Loc. cit.*,[9] "Triple curve."

ever, the main axis had reduced its growth-rate below even that which was possible under these conditions, and the effects of root-asphyxiation are shown by the laterals only, as in the flowering-curve.

A peculiar confirmation of the interpretation just given as to the influence of the soil-water in July is shown by the growth-curves of families sown at different times. During the week ending on June 26th, 1911, a depression of the growth-rate was recorded in the oldest family, while the oldest but one showed it in a less marked form. The remaining families were unaffected. When we consider that the earlier the plant is sown, the larger its root-system must be, we see that the drying-effect of the early plants on the soil surrounding them will be more severe than in the case of the later plants, and hence they will show the soil-water limiting effect at an earlier date.

The flowering-curve.—As in the case of the growth-curve, we meet with specific differences in the manner of distribution of flower-production in time. The beginning of the curve, as the date of appearance of the first flower, has already been discussed.

The specific differences in growth-reaction to environment, which we have just discussed, affect the form of this curve also. Thus, owing to the habit of "early growth-cessation" taking place first in the oldest bud, namely, the terminal one, and then progressively in the younger ones, the growth of the flowering branches is checked in the strain of King Uplands by the end of July, and no flowers open during August or September. By the end of August a plant of King appears to be dead, but the flowering begins again in October, and a second crop of bolls may be produced from these flowers. The Egyptian Sultani strain already mentioned, with its continuous growth-habit, continues to flower throughout the season, while the usual Egyptian flowering-curve rises to a maximum in the beginning of August, and then descends steadily till the winter. The form of the later part of the curve is usually modified by subsoil water effects, either through root-asphyxiation, or by continuously shallow soil, which accentuates thermo-toxic effects through water-shortage.

The actual form of the curve is also determined by the branching-habit, since the flowers are produced by special branches. For our purpose it is not worth while to enter into detailed discussion of these branches and their effect on the utility of the plant; they have been closely investigated by Mr. Leake.* Their general effect on the flowering-curve may be seen best in second generation hybrids; continuous growth without lateral mynopodial branches, resulting in a straight stem bearing sympodial flowering branches only, produces a flowering-curve which remains low and without modes throughout the season. The substitution of discontinuous growth-habit in combination with the same habit of branching, cuts out a resting-period from this curve. Discontinuous growth with free vegetative monopodial branches at the base of the stem, which in their turn produce sympodia, causes the flowering-curve to run up to a high mode, then to fall rapidly to zero, and to rise again in the autumn. Similar branching to this, but combined with continuous growth-habit, builds up an enormous flowering-curve, which rises steadily to a maximun (not infrequently amounting to 25 p.p.p.d. flowers), and then descends to the winter. A total production of five hundred flowers in a month is common among plants possessing this last combination of habits.

Confining our attention again to the usual Egyptian type of flowering-curve, the normal form of this may be affected by the environment through the growth-processes, but it is frequently important to remember that a normal form exists, since these distortions often serve as useful

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* Leake ($^{2, 3}$).

indications of environmental changes, and especially of changes in the condition of the root-system. A concise example is provided by the flowering-curve of plants growing in the two-metre cylindrical tanks already mentioned, when compared with similar wide-sown plants growing in ordinary soil near by, and with others growing under the close-sown conditions of the field crop (Fig. 44). The curves shown were all taken in the same year, and all from an area of a quarter acre, cultivated in these various ways with the same pure strain. Taking the wide-sown plants as nearest to normal development, we see that field-planting reduces the number of flowers formed, presumably by the crowding of the flowering branches, and hence reduces the height of the maximum. Comparing these plants with the wide-sown ones grown in the tanks, we find that the ascending flowering-curve is checked under the latter conditions, and is not allowed to continue at the normal maximum. Obviously a limiting factor has supervened, and it is more than probable that this factor is the limitation of root-development through the confinement of the roots within the limited capacity of the tanks. An interesting side issue

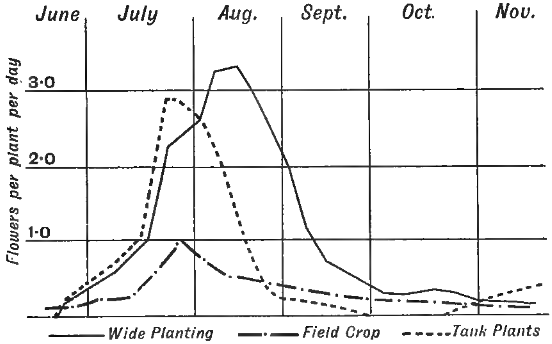

FIG. 44.—FLOWERING CURVES. GIZA. 1910.

Showing root-limitation of tank-plants equally with field-sowings. Note the smaller effect of root-asphyxiation in the wide-sowings.

of this result is the inevitable deduction that two cotton plants can occupy more than three tons of soil with their roots by the end of July. In making a further comparison of the tank-plants with those sown in field-conditions, we find in the latter a similar arrest of the rising curve, which is probably to be explained in the same way, as due to root-limitation, formerly discussed.

Such variations as those just mentioned may be produced within the same pure strain in at least two ways; either by checks upon the growth of the flowering branches, or by shedding of the flower-buds. The latter falls into the same category as the shedding of flowers or bolls, but should be mentioned here as a possible source of variation in the flowering-curve. With certain strains, notably one bred by the author from an Egypto-American cross, this effect is marked very strongly; some plants, otherwise identical with their neighbours, shed their flower-buds just before opening them, while their neighbours retain them. The first produce a scanty flowering-curve, the others a gigantic one. Neither, however, ripen any early bolls, and the distinction appears to be due entirely to accidental root-differences.

Another important factor which modifies the form of the later part of this curve is the water-table. The coincidence in time between the contact of the roots with the water, and the rapid cessation of flowering, is shown very clearly in records from families sown on different dates, the idiosyncrasies of each family being obliterated when this contact takes place; on continued rising of the water the flowering curves all coalesce at or near zero. The field-crop records taken at Giza show variations in this respect as between 1909 when the flood was very early, and the two following years when the flood was late (Fig. 45).

These last records are of exceptional interest, as they demonstrate for the first time the effect of increasing the head of water on the Delta Barrage and so immersing the lower roots sooner than would normally be the case, in the land lying up-stream.

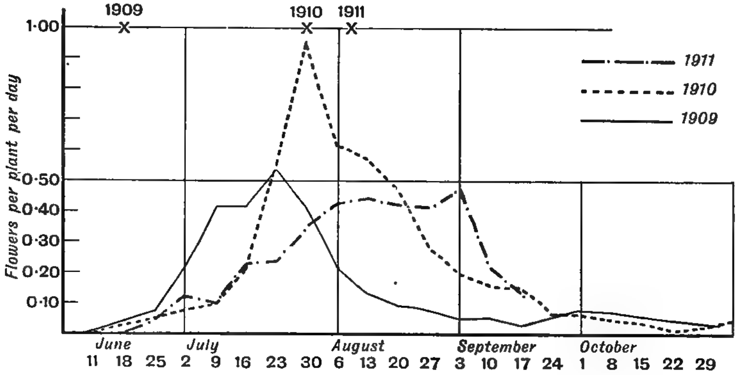

FIG. 45.—MEAN FLOWERING CURVES IN FIELD CROP.

On same land, with same variety, in three successive years, at Giza.
× = Date on which Roda Gauge reached 16 m. A.S.L.
Decaudation due to rise of sub-soil water over roots. See Figs. 30, 35, 38, and 47.

The bolling curve.—Curves plotted to show the number of bolls opening each day in the same way as for the flowering curve, should be identical with them, if all the flowers which opened were ripened into bolls. Such perfection has never been obtained by any of the author's plants. Some of the flowers are always shed, and the ratio of bolls formed to flowers opened has never exceeded 90 per cent., and has been known to fall almost to zero. To take an extreme example, a certain plant, otherwise quite healthy, in the year 1909, ripened three bolls out of a total of 746 flowers which opened before the middle of September.

The early part of the bolling curve, formed by flowers which have opened at the beginning of the Critical Period, is usually identical with the form of the originating flowering curve (Fig. 30), but after the first few weeks it frequently bears no relation whatever to the latter. Hence, the variations in form of the bolling curve have to be studied principally in terms of "shedding."

In order to ascertain the shedding-curve, unless sufficient assistance permits of direct measurement, we have to subtract the bolling curve from the flowering curve, allowing a certain interval for the maturation of the flower into a boll. This period is variable, its length being in the first instance specific. Thus, quoting again from the same three families, at Cairo, King Upland has a mean maturation period of forty-two days, Egyptian Sultani has a mean period of fifty-one days, while the Afifi strain takes forty-eight from the day when the flower opens till the day when the boll cracks and discloses the contents. The figures are determined by labelling single flowers with the date on which they open. Apart from these specific differences, which are, after all, only the mean expression of numerous environmental influences acting on specific organisms, we find variations in this period on individual plants. Flowers which open on the same day and on the same plant may differ by two or three days in their maturation-period; we must be content for the present to describe such differences as due to chance. Further, it was first pointed out by Allard that in the United States the maturation period became longer as the temperature fell, so that the late bolls took longer to develop; he pointed out, as a curious example of the practician's unreliability in practical matters, that the belief of the farmer holds to the exact converse. The maturation period is eight days longer in the middle Delta than at Cairo.

Since the mean for the standard Afifi strain at Cairo lies at forty-eight days ±3 per cent., we shall not introduce any serious error if we plot the mean shedding curves of this strain by subtracting bolling from the flowering of seven weeks previously. Such a subtraction-result is not precise, but it is very useful in cases where direct shedding-records have been impossible.

The shedding curve.—We have just seen that the bolling curve, which represents not only the distribution but also the size of the ultimate yield of the plant, and hence of the area, is in reality the flowering curve modified by shedding. This shedding process thus becomes a matter of great economic importance. More than this, the shedding of an organ of the plant is a phenomenon of great interest from the general scientific viewpoint. The fact that removal of a few roots should cause the abscission of leaves or flowers, quite automatically, leads directly to consideration of the complex interaction of stimuli necessary to produce such transmission and conversion of cause into effect.

The term in common use to describe the process under discussion is "boll-shedding." It is not altogether satisfactory, since the organs shed by the plant are chiefly flowers shed three or four days after opening, and hence only described as bolls by courtesy. Ripening bolls, up to two centimetres in diameter, may be shed, but this is less common. In addition, there may be extensive shedding of unopened flower-buds, and the fall of the leaves belongs to the same general category. Consequently, the general term "shedding," while sufficiently descriptive, is more truthful.

The composition of the sheddings actually gathered from the ground beneath a field plot of more than a thousand plants in 1910, at Giza, is shown in Fig. 46. Shed leaves were not counted, but the diagram shows that flower-buds may be shed even before the opening of the first flower, that the majority of the sheddings are flowers which have been cut off before they had definitely "set" their ovaries, while the percentage of true bolls of various ages up to three weeks old is only noticeable in the autumn.

The act of shedding is, of course, under the control of the plant, its immediate cause being the formation of a special tissue across the base of the stalk of the leaf, bud, or flower. The facultative position of this tissue, or "absciss-layer," is marked by a slight groove on the stalk. When the determining stimulus has been received by the cells of this layer, which are otherwise indistinguishable from their neighbours, they proceed to divide, and the daughter-cells separate from one another, thus destroying the continuity of the stalk except in such tissues as the wood. The phloem being among the severed tissues, synthesised food supplies are cut off, the organ dies, sooner or later the stalk breaks, and the organ is shed. Even before any sign of unhealthiness becomes visible, the stalk may break at a light touch, being retained merely by the wood-vessels, bast fibres, and cuticle.

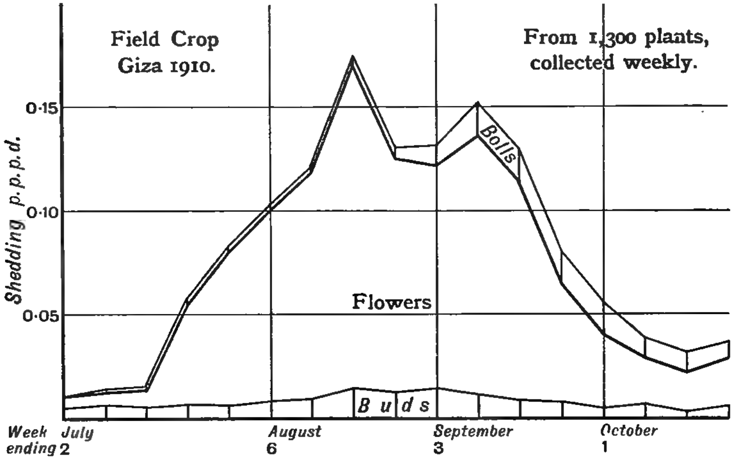

FIG. 46.—COMPOSITION OF SHEDDINGS.

The reaction to the determining stimulus is very rapid in cotton, on account of the extreme simplicity of the absciss-layer. A convenient way of provoking this unknown stimulus is to cut off a few roots. Within four days after such treatment, we find that complete severance of the tissues of the absciss-layer has taken place. Microscopic examination at intermediate stages shows that the plate of dividing cells is only one cell thick, that the divisions begin at the periphery, and extend towards the centre, and that the dividing wall between the daughter cells splits immediately along its middle lamella. The daughter cells which are left on the face of the scar, after the stalk has broken away, bulge outwards, and form a simple callus.

In many plants this stimulus is also provoked by non-pollination, so that unfertilised flowers are shed. This occurs in cotton, of course, but it does not seem to be common under ordinary conditions.

For the present we are unable to form any clear conception of the chain which extends from the severed root to the absciss layer. It is certain that the main factor, if not the only one, is the water-content of the plant. Mere severance of the root does not provoke shedding as a traumatic stimulus ; thus, plants which are screened from direct sun after the root has been damaged, show little or no shedding. Consequent on such root-damage we find a general closure of the stomata, and it seems at least probable that this abnormal closure reacts first of all on the absciss layer, by bringing about abnormal internal temperatures. Much more experimental work is required before further discussion can be profitable.

Though the primary cause of shedding in Egypt is a deficient root-absorption, it follows that an excessive transpiration rate must produce the same result, since the terms "deficient" and "excessive" are relative. A very dry hot day may provoke shedding, but such weather is infrequent at the time when shedding is important. The heavy shedding of wide-sown plants as compared with that of plants in field crop is probably caused by excessive transpiration, or rather, by too great irregularity in this function, since wide-sown plants are freely exposed to wind, and do not create a humid "surface climate." In the Sudan, however, spells of hot dry wind are generally recognised as being the precursors of shedding epidemics.

Before considering a few typical shedding-curves it may be well to insist once more on the economic importance of these records. Plants whose flowering curves are identical may give entirely different bolling curves ; in other words, entirely different crops.

The record of the behaviour of families sown on various dates in the same year may be reconsidered in this connection. We have already mentioned a decrease in the growth-rate caused in the older families by water-shortage, but by the time when boll-shedding is becoming notable, all the plants are suffering from root-interference, which in a light soil results in periodic water-shortage. As the result, of this we find successive modes in the shedding curves, common to all the families. Following these modes we have periods of less shedding, which immediately follow irrigation. Some of these records show three such modes in each family, followed by a fourth one.

This fourth mode is apparently due to a distinct cause. Firstly, it comes a week sooner than one would expect; secondly, it is followed by a general cessation of flowering ; and lastly, it coincides with the intersection of the root-depth line by the level of the infiltrated sub-soil water (Fig. 30).

Thus we have two ways of producing a mode in the shedding-curve, relatively to the number of flowers available for shedding. One acts through decrease of the amount of available water in the soil, while the other way is through increase of the soil-water-content to saturation-point, thereby excluding air, causing root-asphyxiation, and so reducing the size of the root-system; this root-system, having been developed to cope with a certain mean maximum demand for water from the aërial portions, or, more correctly, having controlled the development of aërial organs of a certain size, is now insufficient to cope with the normal water-loss of those organs. They in their turn reduce their water-loss to meet the new conditions by stomatal closure, but the general metabolic disturbance, due to demolition of the delicate balance between root and shoot, produces shedding. We have already seen how delicate that balance is, when noting that plants would grow in sunshine if a few leaves were removed. Here we are dealing with the converse.

Much more experimental work is needed on such points as the permissible degree of desiccation or of saturation in various types of soil, on the rate of renewal of soil water to a root-dried zone, and so forth, but the main principles of the matter are now fairly clear.

In light soil, which has a low power of water retention, it would seem from consideration of the shedding curve that frequent light waterings are necessary. This practice might, on the other hand, be unnecessary, if not injurious, in a heavier soil, with a higher capacity for holding water.

A mode in the bolling curve may actually originate from a falling flowering curve, if all the flowers had been held during one week, so that a heavy crop of bolls is picked seven weeks later (Fig. 30).

Some interesting shedding curves have been obtained by the author from land arranged * in three terraces, at half-metre differences of level. The purpose of this arrangement was to ensure differences in the time and intensity of the effect of rising subsoil water; the lowest terrace was first affected, the highest last; the water-table in the lowest one almost reached the surface of the soil, while in the highest it left a metre of normal soil. The method is not ideal, on account of the soil disturbances entailed, even when the top half-metre of soil is carefully replaced on each terrace; the remainder of the

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* In collaboration with Mr. Hughes.

plot was not disturbed and always produced superior plants during the three years over which the experiment lasted, but the three terraces were quite comparable. Each terrace carried not less than 300 plants per annum, sown in ten ridges, under conditions which were otherwise those of the field crop. The water-table in this site was chiefly controlled by changes in the level of the Nile, at a distance of nearly a kilometre, though there were variations due to impervious patches of soil, even within this small area.

In the year 1909 the Nile rose abnormally early; in 1910 it rose late; 1911 was rather later than 1910. The curves of flowering and bolling in 1909 were taken from daily observations of three ridges in each plot.* They are plotted in Fig. 47, which shows that while the flowering curves were identical within the probable error on terraces A, B, and C, the later portions of the bolling curves were dissimilar, and that this dissimilarity was due to the shedding curve. The steady progression from terrace C—the lowest—to terrace A, becomes still more apparent when the curve of shedding is plotted in the form of percentage of flowers shed to flowers open. The amount of shedding thus appears to be proportional to the depth of root-system which is submerged by the rising water-table. In 1910 the same set of observations gave no result which could be discerned by the methods of observation employed; this was not unexpected, since the rise of the Nile shown by the water-table on these plots began forty days later than in 1909; as also in 1911 (Fig. 45).

It is noticeable that the 1909 curves show two maxima of shedding; one is coincident with the "critical" period of maximum evaporation, the other with root-reduction. The first maximum was very clearly shown by M. Audebeau,

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* Report 1910 Cotton Commission.

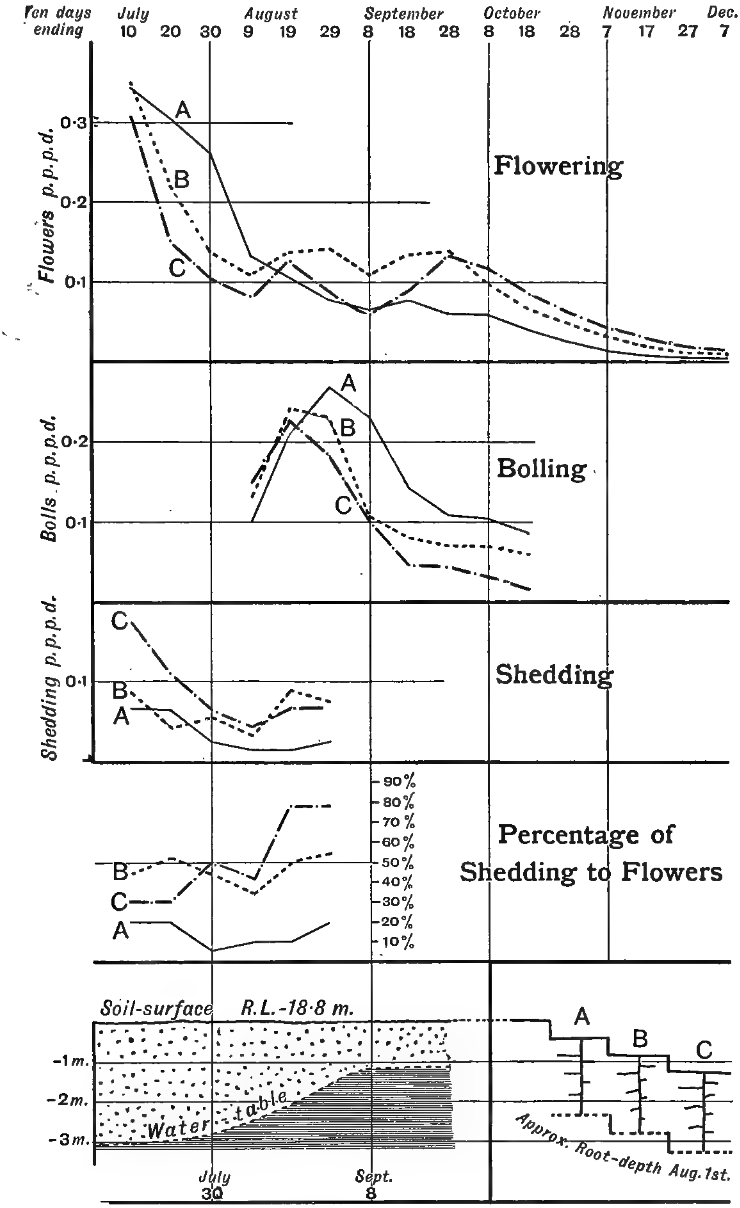

FIG. 47.—TERRACED LAND. GIZA. 1909.

Three terraces, each 40 cm. lower than predecessor.
Observations on 100 plants in each terrace; flowers counted every day, bolls every tenth day, shedding by subtraction.

who cultivated plots of cotton in small cement tanks, with the water-table fixed at definite depths in each tank throughout the season; his data showed that even the absolute shedding, and much more the relative shedding, was greatest in soil with a water-table only half a metre below the surface, while it became proportionately smaller in deeper soils, down to a two-metre water-table. In his experiments there was no second mode, since no change took place in the water level. We shall appreciate the bearing of these data better at a later stage. In general, they imply that a sufficiently large volume of soil must be occupied by the roots to ensure a uniform water-supply for the stem.

Since the "terraces" were open to agricultural criticism on account of the soil-disturbance involved by their construction, a set of six cylindrical iron tanks, each 80 cm. in diameter, and two metres in height, were sunk in a pit in the ground, until their tops were flush with the surface. Each was fitted with an inlet pipe at the bottom, protected by a loose brick arch, rubble, and sand, and was finally filled with good uniform soil. A rubber tube leading from this inlet pipe, and connected to an adjustable reservoir of water, allowed the level of the water-table in each tank to be maintained or adjusted to any required level. Various combinations have been employed with these tanks, but the results have only substantiated those already described. Fixed high water-tables cause undue shedding, so that the early part of the bolling curve is abnormally small; changing water-tables cause temporary shedding, so that a wedge is cut out of the bolling-curve about seven weeks after the change has been initiated.[29]

Such small tanks are, however, open to many objections, and the ideal method of study would be to encase an undisturbed mass of soil with armoured concrete by underpinning, so as to convert it into a large tank. A set of at east six such tanks should be arranged at intervals in a large cultivated field, with their rims just buried beneath the surface; cultivation could then be normal, and the water-level in each tank could be exactly controlled by pumps and tube wells.

The amount of space which we have devoted to the subject of shedding may appear disproportionate, but the Egyptian reader will realise its relation to recent problems concerning deterioration of yield.

The centre of gravity of the root system.—A metaphorical term is often of use in discussion, and the words "centre of gravity" are here used in a metaphorical sense.

The C.G. of the root system may be considered in two respects; either structurally, or functionally. The structural C.G. is first situated in the radicle of the germinating seed, from which it moves steadily down the tap-root so long as the latter continues to grow. Unequal development of laterals would displace the C.G. from the axis of the root-system, but we shall assume that root-development is perfectly symmetrical in its radial distribution. The position of this structural C.G. is the resultant of the length of the tap-root with the length, number, and position of the lateral roots. A plant growing in shallow soil, whose tap-root has consequently been arrested, and whose laterals have developed uniformly over all parts of the stumpy axis, will thus have a structural C.G. situated mid-way between the surface of the soil and the limiting lower stratum; this stratum may be a rock or a water-table. If this limiting stratum is removed, the tap-root will descend further, and the C.G. will be lowered.

The mere structural C.G. is of less importance than the functional C.G., which must obviously change its position from day to day, even when the structural C.G. is constant. The magnitude of these changes depends on various factors, most of which we have already discussed, and although much tedious analysis of soil samples will be required before we can plot a curve to show this diurnal change, yet the conception of a variable centre of gravity for the water-absorption of the root seems so to clarify our ideas on certain points that we will discuss it in more detail than it probably deserves.

As a basis for discussion we may take four series of soil-water determinations made at intervals of 20 cm. downwards for a depth of two metres, in the soil occupied by the plants on which the daily growth (Fig. 30) was measured. The bores were made within a few feet of each other, among these plants which—it will be remembered—were growing under field-crop conditions. The soil contained 25 per cent. of water when completely saturated, and the water-determinations, made by drying in the steam oven, are expressed in terms of the saturation amount.

The determinations were made under the following circumstances :—

June 27th :—Four days after irrigation, when the maximum growth-rate of the whole year had just been recorded during the previous twenty-four hours. The precedent watering had arrested the symptoms of water-shortage yet shown by the plant. We may safely conclude that the water-distribution shown on this date was nearly ideal.

July 11th :—The day before the next subsequent watering, when severe water-shortage was being exhibited by all plants, and the growth curve had been falling fairly steadily since the last determination. The water-distribution here was decidedly typical of insufficiency of water.

July 15th :—On the third day after watering, when the growth of the main axis, having been accelerated for two days, had again begun to decrease. The water conditions were probably very good, though no growth-measurements were being taken on lateral branches by which this statement could be corroborated, but comparison with the growth after the previous watering indicates that the water-distribution in the soil had not yet reached its optimum.

July 30th :—These determinations were made just before the next watering. Water shortage was again apparent, and the period elapsing since the last watering was the same as in the case of the determination of July 11th.

The actual changes in saturation-percentage under these various conditions are shown in the following table. The values shown are significant to plus or minus three per cent.

Date.	July 27th.		July 11th.	July 15th.		July 30th.
Depth.		Difference.			Difference.	
20 cm.	43	−18	25	57	−43	14
40 cm.	58	−17	41	73	−54	19
60 cm.	62	−17	45	56	−22	34
80 cm.	84	− 9	75	77	− 2	75
100 cm.	80	−11	69	82	− 6	76
120 cm.	84	−10	74	86	−22	64
140 cm.	90	− 3	87	84	− 3	81
160 cm.	90	+ 1	91	87	− 9	78
180 cm.	86	+ 3	89	93	− 6	87

Firstly, we seem to have found a way of ascertaining the depth of the root-system. The depth of the roots had been measured by excavation at the end of May, and the mean depth for the end of June calculated from this was approximately 140 cm. ; this depth was the last at which a loss of water was shown. A month later, at the end of July, when the roots had grown another 50 cm. at least, the samples from 160 cm. and 180 cm. also showed a definite loss of water. This is not recommended as a trustworthy way of finding mean root-depths, but it at least adds an extra method to the scanty stock available for root-investigation.

For further interpretation of these data we obviously need to intercalate observations at intermediate dates. Certain points may however be deduced from them as they stand. Thus, root-growth is not inhibited by soil-water amounting to 80–90 per cent. of saturation. Again, it would seem that less than 50 per cent. of saturation in the soil is sufficient to produce water-shortage; on the other hand, the pot experiments on this subject have indicated that a lower value, perhaps 20 per cent., does not usually limit growth at night; the difference must be due to the fact that a large plant with a " limited " root-system, having dried up the soil particles near its root hairs, has to wait for the incoming of water from adjacent particles as reinforcements, so that the plant is injured during the day. The greater severity of the water-strain during July, due partly to the higher evaporimeter readings, and more to the greater leaf-area, is shown by the greater water-loss during similar intervals, resulting in more severe desiccation of the soil on July 30th as compared with July 11th.

The water-loss is more severe in the upper layers of soil, partly on account of surface evaporation, but more from the complete occupation of such soil by the lateral roots. The extent of this desiccation becomes more severe as the plant becomes larger, and it extends to a greater depth in the same time. In other words, the centre of gravity of the absorbing root-system shifts downwards as the root grows larger, along with the structural C.G. Moreover, even on the narrowest assumption, the top 40 cm. of soil could have been providing little or no water to the roots it contained on July 30th, whereas it had been making free provision on July 15th. Thus, on July 15th the functional C.G. and the structural C.G. probably coincided, whereas on July 30th the functional C.G. has descended far below the structural.

The extent of this displacement obviously increases as the root grows larger, and as root-interference between adjacent plants extends to greater depths. Thus, in the germinating seed there can be no displacement; structure and function have a common centre of gravity. In seedlings with a ten-centimetre root there is a slight change as the surface soil dries up after watering, but the displacement is slight. So, as we progress to older and older plants, the amplitude of the displacement increases, its duration being bounded by successive waterings, till we reach a maximum amplitude probably in early August.

Using a different method of expression, we may state that the plant becomes more and more dependent, for longer and longer periods, upon deeper and deeper layers of soil for its steady water-supply.

If now we decrease the depth of available soil by raising the water-table, and at the same time asphyxiate, or ultimately kill, the lower part of the root-system, we are throwing more strain on the surface roots, and reducing the deep-seated reserve. If this reduction is effected in July or August, when the amplitude of displacement of the functional C.G. is at its maximum, the effects—shedding, for instance—will be much more severe than if the reduction is effected at a later date, when the leaf-surface has increased but little more, when the surface climate is damper, and the sun-temperature is lower; all these alterations tend to relieve the water-strain on the roots, by reducing the evaporation from the stem.

In this interpretation we find a reasonable explanation for the otherwise disproportionate severity of the effects produced by an early Nile flood, shown in the shedding-curve and flowering-curve on the terraces in 1909, and—according to the author's interpretation and forecast [16, 17, 18] —by the whole of Egypt in the same year, with disastrous results.

Root regeneration.—The appearance of a root-system in December is most remarkable, if it has been partially immersed in the sub-soil water. The fullest examination which the author has made was effected on the Gezira at Cairo, where the sub-soil water-level is controlled entirely by the river. By excavating a trench of three metres' depth near the side of the plants, washing away the soil with a jet of water from a force-pump, and using the Ancient Egyptian method of reflecting mirrors to illuminate the deeper portions, it was shown that the tap-roots had descended to a depth of not less than 220 cm. Below the depth of 160 to 170 cm., however, all the original tap-roots and their branches were dead (Figs. 35, with 37 and 38).

This level coincided with the maximum height of the water-table, which had been maintained for ten days at the end of September, and again for a day or two about October 20th. Side by side with these brown and partly decomposed roots, which had been traced unbroken from the surface of the ground, there were clean, white, new roots in abundance, which terminated at various depths up to 210 cm. On following these new roots upwards they were found to arise from those laterals which had not been reached by the water-table. When the fall of the water-table began at the end of October, these healthy laterals had broken out into hundreds of tertiaries of all sizes (Figs. 35, 38), which all turned downwards, following the flight of the water-table, and reconquered the invaded territory. The effect of this reconquest is shown above ground by renewed growth of the stems in November on a falling temperature-curve.

CHAPTER IV

THE COTTON FIBRE

When the "sunshine effect" was first announced, a somewhat smiling denial came from many cotton experts. When some of them had been converted to a belief in the fact, they objected that it could not apply to the growth of the lint. Substituting "may" for "could" this criticism is still valid; yet if the reader has succeeded in gathering some conception of the fate of cotton plants under Egyptian field conditions, he will probably expect this criticism to yield before further experimental work.

We are, in point of fact, profoundly ignorant as to the bearing of the two preceding chapters upon the final commercial result, owing in the main to difficulties in the technique of investigation. Methods for determining the strength of small samples of fibre, for instance, are non-existent; true, it is possible to determine breaking-strains, but the labour involved is enormous * if sufficient results are to be obtained to give a reasonable probable error for only a single seed. When not merely a single seed, but a thousand, have to be examined, the method becomes hopeless. The author is experimenting with indirect methods such as determinations of weight, specific gravity, etc., which can be made on single fibres by suitable appliances, but as yet we are dependent on the rule of

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* *Vide e.g.* Yves Henry.

thumb, and finger, of the expert, who objects to handling even single-plant samples. Probably a combination of all these methods with a minimum of microscopic observation, which is undesirable on account of its high subjective error, will give us a line of attack, and we may be able in the future to explain why a fibre has become strong or weak, and how such weakness or strength is affected by the environment.

Even such an obvious character as length of fibre is very difficult to examine during development. The tangle of lint hairs on the seed is almost inextricable, especially in the early stages, when the individual fibres are too weak to endure combing. Further, as in the excavation of roots, a fruit once dissected for examination can be no longer observed, and averages must be struck.

The little which we know may be summarised under the microscopical evidence, with the evidence derived from fluctuation and correlation.

Cytology of the fibre.—The development of the fibre begins before fertilisation is accomplished, by radial growth (Figs. 3, 5) of a large number of the epidermal cells of the seed coat. These cells (Fig. 4) differ in no respect from their neighbours, and it seems possible that the density of the coating may be determined by the external conditions during a day or two after flowering. Possibly irregularity in length may arise from distribution of the normal simultaneous "sprouting" of these cells over several days.

The young fibre (Figs. 6, 7) at once assumes its final diameter, which is about twice that of the unaltered cell. It remains unicellular throughout its career, and is always covered by the cuticle which protected the original cell. The familiar "beading" which follows treatment with ammoniacal copper hydroxide is simply due to constriction of the swelling cellulose by the cuticular remains. For the first day the nucleus lies at the tip of the swelling, but after the third day it takes its place in the middle of the cell axis, and there remains, either slung in cytoplasmic bridles, or at the side. The cytoplasm, of course, lines the whole cell-wall, and appears to remain alive until the boll cracks.

The growth of the fibre is at first confined to linear extension. In fact, it seems that the boll attains almost to its full size before any secondary thickening of the fibre wall begins. By this time the fibre has reached to rather more than its final ripe length. This period embraces about half the total maturation period, being some twenty-five days. Presumably it is during this period that unfavourable environment, such as is made manifest by a mode in the Shedding Curve, could produce irregularity in length from boll to boll. The final length is of course constitutional, and can only be deflected from this constitutional basis to a relatively slight extent. Even seeds which have not been fertilised, and consist of empty, undeveloped seed-coats alone, possess hairs of nearly normal length, though abnormally weak. The best evidence in respect of this constitutional basis for length is given by measurements on the ripe seed. Thus, a random selection of data for maximum lint-lengths, in five seeds per plant in a pure strain grown under conditions favouring maximum fluctuation, has given the following figures on a total of 210 seeds.

Mean length	33·50 mm.
Extremes	27 and 39 mm.
Standard deviation	2·14 mm.
Probable error	1·44 mm.

Probable error as percentage of mean = ±4·3 per cent.

Comparison of one strain with another in this way shows that the mean lint-length is an inherited characteristic. The final attainment of the lint cell in the matter of length is effected by intercalary growth, the form of the tip and of the base being determined at an early stage.

The cessation of this growth is thus the result of internal constitution, though environmental changes exercise a limited effect. (Fig. 50 also, "310" and "77".)

It appears, though this point is not quite clear as yet, that linear extension has ceased before thickening of the wall commences. It is this thickening which determines the strength of the individual fibre. The strength of the commercial sample depends not only on thickness, but also on uniformity of strength as between different fibres. Moreover, commercial strength does not merely result from the thickness of the cell-wall, but also from the uniformity of that thickness over the whole length of the cell, and possibly is also affected by the "texture" of the thickening layers.

Even as regards the simple fact of thickening, we find many curious delusions in the extant literature of the subject. Confining ourselves to the known data, the matter is a simple one; concentric layers of cellulose, probably delimited from night to night, are laid down on the interior of the delicate cellulose-cuticle wall, until a certain thickness is reached. This deposition is not uniform, but results in the formation of simple pits at intervals, elongated obliquely.

In consequence of this pitting we find that fibres devoid of secondary thickening show no twisting when extricated from the unripe boll and dried, while fibres taken from a boll which is nearly ripe exhibit rapid and uniform twisting as they dry, owing to the closure of the solid portions of the cell-wall into the minute spaces formerly occupied by the pits.

Strength.—In respect of the strength of the lint, we have some evidence to show that the causes which provoke shedding are simultaneously effective in weakening the lint.

The lint from the terraces (Fig. 47) in 1909 was submitted to an expert* for grading. The first pickings from all were classified as uniform. The second pickings, ripened during the rise of the water-table, were progressively graded; the top terrace gave the strongest lint, and each step down was a stage weaker. These second pickings came from the bolls which had ripened during the rise of the water-table.

Another set of data came from an F_2 of Egyptian × American. The lints were classified by the grader into groups, according to their strength. The amount of shedding per plant in this family had been computed up to a certain date and found to range from 100 per cent. to 19 per cent. of the flowers opened, with a mean at 70 per cent. Grouping those plants which possessed Egyptian lint according to their strength, the following figures were obtained:

Strength.	Mean Shedding.
Weak	70·2 per cent.
Medium	68·7 ,,
Strong	60·6 ,,

In this case the cause of variation in shedding is constitutional, and the correlation is hence more striking than when the variations were due to environment only.

This same family was dissected in the same manner for other characters, but no other correlations were obtained, except with regard to lint-weight (mean weight of lint per seed). This ranged from 0·021 g. to 0·060 g. with the mean at 0·036 g. Classifying the Egyptians again by strength we found:—

Strength.	Mean Lint weight.
Weak	0·0348 g.
Medium	0·0358
Strong	0·0373

Thus the heavier lint is the stronger. Further, since lint-weight and seed-weight are closely correlated, we find

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* Mr. H. C. Thomas, of the National Bank of Egypt.

that the "ginning out-turn" is highest in the strong lints. This ranged from 48 to 111; mean at 75 about.

Strength.	Mean Out-turn.
Weak	69·90
Medium	72·96
Strong	74·67

The last result gives a partial clue to the preference for high "out-turn" which the buyer—independently of the grower—displays. A few notes on this matter should be made.

Ginning out-turn.—The out-turn of lint from seed cotton at the gin is expressed in Egypt as rotls of lint per 315 rotls of seed-cotton. The extreme means recorded for a whole factory throughout a season are 113·3 (Abbassi, Qalioubia, 1899) and 88·0 (Ashmouni, Sharkia, 1888). Variations in this figure occur from place to place, but when the mean out-turns of large ginning factories are considered, we find that the variation-graphs for a number of years are closely similar in different places.[15] Thus 1903 showed a sudden rise of out-turn almost everywhere in Egypt.

These variations are as yet inexplicable. Wide-sown plants give much lower out-turns than those which are sown in field crop,* and nitrogenous manures in field crop also depress the out-turn, through increase in the seed-weight.† The variation is due, of course, to imperfect correlation of lint-weight with seed-weight.[12] This correlation had a value of $r = 0{\cdot}810 \pm 0{\cdot}035$ in a set of forty-five commercial samples of one variety examined by the author. It has been shown by Mr. J. I. Craig ‡ that there has been also a slight correlation between mean out-turn and the total Egyptian crop in any given year; $r = 0{\cdot}3899 \pm 0{\cdot}182$ for fourteen years.

The study of variations in ginning out-turn is thus dissected into separate studies of fluctuation in lint-weight and in seed-weight.

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* *E.g.* Fig. 50. "Varieties." † Hughes, 3. ‡ Craig, 3.

Lint length.—The "length" of the lint is also a complex of several factors. Chief amongst these are the mean maximum length, and the regularity.

Some strains of cotton produce lint-hairs of the same length on all parts of the seed-coat. Most kinds, however, make shorter hairs at the micropylar end.* [5] Fluctuation in this respect does not seem to be very noticeable, and we can restrict our present remarks to the mean maximum length; this is ascertained by combing the lint on the seed, and measuring from the seed to the edge of its halo of lint.

Fluctuation in the mean maximum length is described later, and the relation of such fluctuation to the conditions under which the fibre develops has already been discussed. Briefly summarised, this length is determined primarily by the constitution of the individual plant; secondarily, by the experiences of the particular seed and boll during the first four weeks after flowering.

The second determinant necessarily varies greatly when we are dealing with a commercial sample which includes seed from bolls of various ages; the particular experiences of each boll may be so different that on the average we may consider the effects from year to year as being almost uniform. Consequently, though it is possible to depress a 40 mm. lint to 30 mm., we find that the practician draws a sharp distinction between 30 mm. and 40 mm. varieties.

We have now completed an outline sketch of the principal factors which are yet known to control the development of a cotton plant in Egypt, and certain hypotheses have been propounded which serve for the present as interpreters of the author's data.

It might seem that too much stress has been laid,

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* Photos.

whenever and wherever possible, on physico-chemical possibilities. The author's own opinion favours such readings of the experimental text, if only as a refuge from disguised vitalism. Lest such opinion be made an accusation, it may be well to point out that many recorded phenomena will not yet yield to the point of such hypotheses. One irreconcilable of this order is the striking "sleep-movement," which is exhibited by all leaves throughout the year, and even by the seed-leaves.

The organic factors of the environment, such as fungoid and insect pests, together with the flora and fauna of the soil, cannot be discussed within these limits. The fungi, excepting "Sore-shin," are of negligible importance in Egypt, though *Colletotrichium gossypii*, *Mycosphærella gossypina*, and *Meliola spp.* are extremely common. The insects, conversely, are of great economic importance, though the blame for many of their reputed crimes really lies at the feet of the plant, particularly in respect to the boll-worm. Some such confusions have already been noted in passing, and it is curious to note that a mild attack of cotton-worm, through diminishing the water-strain, may actually increase the yield by prolonging the flowering-period.

The soil flora, imperfectly understood, must be left untouched by us. In soils of the Nile Valley the geological aspect is superior to the chemical one; texture, and hence water-content (frequently complicated by "salting") is more important than manurial mixtures. The author's colleague, Mr. F. Hughes, has shown conclusively that the cotton-crop of latter-day Egypt is rarely limited—in Blackman's sense—by the chemical composition of the soil. Water, always sufficient, but never excessive, is the principal need of the crop;[21] and the desired balance between deficit and surplus is struck only by accident as yet.

SECTION III

THE RACE

At intervals throughout the preceding pages we have had to resort to evidence drawn from the average behaviour of groups of plants, in default of precise data from individuals. In other words, we have considered a group as representing an average individual. These groups have now to be considered for their intrinsic interest.

Such groups may be derived from a "pure strain," being all of identical gametic composition; in this case we find material to study in the fluctuation, which is the result of slight irregularities in a normally uniform environment. Again, the groups may be derived from the crossing of two pure strains, in which case their gametic composition may not be uniform; we have then to apply corrections for fluctuation, and having done this we search in the residuum for evidence of gametic differences wherewith to formulate expressions for the inheritance of each characteristic.

Lastly—though it will be more convenient to discuss this subject in the second place—the group may consist of many different pure strains, mingled with hybrids between them of every generation imaginable. Such is the composition of the commercial "varieties." Within limits, and for certain purposes, we may consider such varieties as uniform, since the inequalities smooth themselves out when a sufficiently large number of plants is taken.

These group limits have been drawn for convenience, and they are perfectly genuine. Nevertheless, the phenomena are mutually interdependent, so that the humblest plot of cotton cannot be understood without a knowledge of Physiology and of Genetics. The subject of Fluctuation forms a neutral ground between these two relative branches of science; it belongs to both; physiology explains it, genetics cannot be explained without it.

The author frequently had occasion to regret the lack of significance in his older heredity experiments, due to lack of fluctuation data as standards, and when these began to accumulate they were found meaningless until the physiology had been studied.

CHAPTER V

FLUCTUATION

When we desire to compare different sets of data, we must either admit of no observational error, or ascertain separately what error exists in each set, or else employ standard methods of known probable error. The last is the most convenient method, since the yearly programme of work can be standardised, and comparisons are easily effected. The particular method employed for any one characteristic, such as the form of the leaf, is a compromise between the probable error and the facilities for observation.

The slide rule and nomographs, measuring dividers, glass plates graduated in angles and lengths, the planimeter and pantograph, adding machine and Joly balance, with a string of simpler appliances stretching down to the oldest of all—a small-tooth comb—have been successfully pressed into service with the object of economising time in these researches.

The pure strains on which these observations have been made were derived from single plants of various kinds. A few of the offspring in every year during periods of three to six years have been covered with mosquito netting[15] to prevent natural crossing; the resulting strains are not visibly impure, so far as our present knowledge can ascertain.

Whenever a family is henceforth mentioned, it should be understood to be one of these strains. Commercial "varieties" will be specifically designated as such.

Since the fluctuation-graphs for parents will necessarily be consulted when dealing later with genetics proper, the reader is referred to these, except where some special point requires to be illustrated by a special figure.

For the expression of fluctuation in statistical terms, we shall take the percentage probable error, and not the "coefficient of variation." The latter is the "standard deviation" expressed in percentage of the mean. The former is roughly two-thirds of the latter, *i.e.*, $PE = 0{\cdot}67\sqrt{\frac{\Sigma d^2}{n-1}}$, and our particular expression is $\frac{P.E \times 100}{\text{Mean}}$. This form is convenient, since half the observed cases must lie within the limits given. The maximum possible true fluctuation may be taken as odds of about 30 : 1, or 3·2 times the probable error.

Whenever a specific figure is given for a family it should be understood as having been checked by comparison with other families, and therefore considered by the author as being fairly representative of the data available.

Colour characters.—Such characters as the colour of the petal anthers are devoid of appreciable fluctuation. This uniformity is probably apparent rather than real, since a difference of less than 10 per cent. in the intensity of a colour cannot be perceived by the ordinary eye.

When colours have to be classified, as in hybrid populations, standard flowers, &c. are always used, and the unknowns are matched to them.

Characters which depend on the presence of anthocyanin in the tissues, such as the red spot at the junction of petiole with lamina, fluctuate widely. Comparisons can only be made with safety when the plants are equally healthy.

The stem.—The branching habit of the stem has not received from the author the attention it merits. Some evidence may be gleaned indirectly from the flowering-curves, but systematic study of fluctuation in branching is difficult,* unless a high subjective error is risked.

The height of the central axis is easily examined. The plants are measured to the nearest 5 cm. every week or fortnight, taking the soil-surface and the terminal bud as the approximate extremes. A portion of the fullest series of height determinations obtained as yet is plotted in Fig. 48. This series represents an extreme case, some plants being badly stunted. The height determinations in this family can be compared with similar series from a very uniform lot of seedlings belonging to family "307," and also with rows of commercial Afifi plants in field crop. These last were measured to bench-marks with a water-level. The statistical statement is as follows :

Family.	Number of Plants.	July 4th.		August 29th.	
		Mean.	*P. E.*	Mean.	*P. E.*
			Per cent.		Per cent.
307. Wide-sown, uniform	17	52½ cm.	±12·0	115 cm.	± 9·2
77. ,, irregular	45	61 cm.	±18·3	114 cm.	±12·0
Commercial Field - crop ; fairly uniform	98	52½ cm.	±15·2	89 cm.	±15·4

The fluctuation in a wide-sown pure strain decreases as the plants grow older, stunts overtaking the normals. This is partly the case in field sowing, though to a less extent owing to competition, and it is further masked in commercial varieties by their non-uniform composition.

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* See, however, Leake, H.M., 2 and 3.

The same figure (Fig. 48) also shows the fluctuation in the growth curve, which can be obtained by following the same plant from date to date.

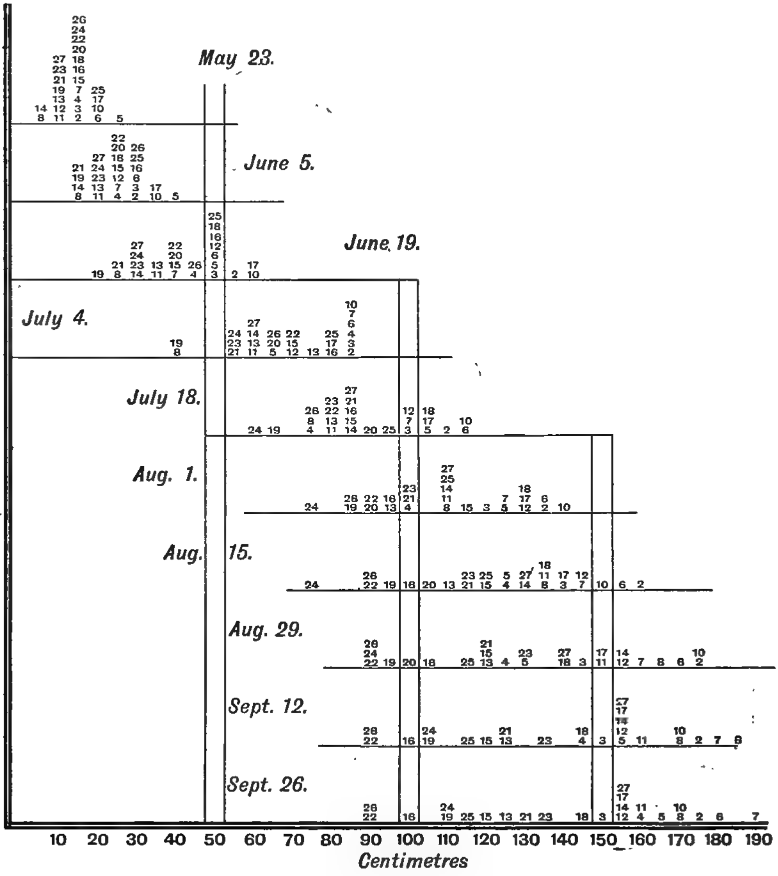

FIG. 48.—HEIGHT OF STEM.
Wide-sown, pure strain "77."
This figure is a reproduction of a page in the "Ledger" of this strain.

The correlation of fluctuations in height with the fluctuations of other characters has occasionally been interesting. The most curious result was obtained in this same family 77, with respect to the leaf-length. The latter was measured in the first week of September; plotted against height on July 4th, two months previously, there was a marked *negative* correlation; $r = -0·67$, on 31 pairs; plants which had been short in July possessed long leaves in September. The height on September 12th—at the time of leaf measurement—showed a small positive correlation, while August 1st gave a transition stage with no correlation at all. These data have obviously some bearing on the inter-play of root upon shoot, and conversely.

The correlation of height on July 4th with the data of the first flower—which varied in one series from June 19th to July 28—is definitely curvilinear. Plants which were stunted, and are therefore still short, flower proportionately late, but this correlation vanishes after passing the mean height, all the normal and super-normal plants flowering at approximately the same time. Here we are probably dealing with the data of initiation of the flowering-branch buds.

The correlation of early height with total flower- or boll-production is also close, and becomes less distinct as we pass to later height. This is effectively a statement that stunted plants, even if they grow up later to normal height, cannot produce a crop of normal size. This effect of stunting acts partly through the delayed first-flower.

The leaf.—Fluctuation in absolute size of the leaf, as expressed by measuring the length of the mid-rib, is obviously complex. The correlation with stem-height, previously mentioned, will serve to illustrate this. Still, even leaf-length is tolerably definite, the *P.E.* ranging from 6 per cent. to 3½ per cent. The discussion of leaf-form, however, introduces us to a new set of factors, of ontogenetic, or even phylogenetic nature. The first leaf of the seedling plant is entire, even when adult; later leaves became progressively more elaborate even when first unfolded, until the five segmented typical leaf is reached. The form assumed is nevertheless not independent of the environment, for later buds on old stems may develop leaves of juvenile form.

As regards the method of observation, we take three adult leaves from every plant during August–September. Each one is laid under a graduated glass plate, from which its length, and two angles, are read. From these we can complete any other constituents of the triangle thus recorded. This triangle gives us the form of the central segment, which is limited lengthways by the petiole and the central tip, and laterally by the sinus at which the leaf-margin bends sharply back on the lateral segment.

The position of this sinus is the essential feature. On examining growing leaves we find that the sinus moves outwards along a constant angle as the leaf enlarges, at a rate which is directly proportional to the growth of the leaf in length, consequently the sinus-angle relatively to the mid-rib, either from tip $(\angle^{t})$ or origin $(\angle^{s})$ shows the minimum fluctuation. More fluctuation is necessarily shown by the length of the line from petiole to sinus proportionately with the total length, but both are specific. If we neglect such additional factors as curvature of the segment-margin, plication of the lamina, &c., this method of expression is comprehensive. A check on the result is obtained by plotting sinus-positions in a pure strain, relatively to the tip or to the base. The resulting diagram resembles the side view of a choked shot-gun discharge, passing along the angle-lines, the centre of the pellets defining the mean sinus-length. The *P.E.* of these angles in Egyptian strains is about ±3·0 per cent.

The number of leaf-segments, or rather the development of the second pair of lateral segments, has been mentioned above as dependent on ontogeny. It is fairly definite under given conditions, same strains refusing to produce the extra pair.

Perhaps it is worth while to mention that such presumably primitive cottons as *G. Sturtii*, F.V.M.,* retain the entire leaf throughout their development.

The depth of the segmentation, when present, varies within the same sub-species, as in the two forms of "Nyam-nyam kidney cotton;" possibly the Okra-leaf sport in American Uplands is another example. Such facts are suggestive of mutation, but mutations in *Gossypium* ought not to be mentioned until we know much more about natural crossing and heredity than we are likely to acquire for several years to come.

The flower.—In the course of an attempt to breed an uncrossable flower, to be mentioned again later, the author had had occasion to measure the various floral organs, namely, petal, style, staminal column, and filaments. The sequence of development of these in the bud begins with the petal, followed by the column and filaments, and ends with the style.

The fluctuation does not follow this order. Fifty-one plants in "77" family gave the following typical results :—

Petal	Mean, 59 mm.	*P. E.* ±2·8 per cent.
Style	,, 33 ,,	*P. E.* ±3·5 ,,
Column	,, 19 ,,	*P. E.* ±5·6 ,,
Filament	,, 4·2 mm.	*P. E.* ±7·7 ,,

A portion of this increased fluctuation is probably apparent, being due to greater errors of measurement in the smaller organs, but much of the increase is certainly significant. One would rather expect the external organs to fluctuate most, but the reverse is the case.

The involucral bracts are intermediate in their fluctuation. Their width in the same family gave a *P.E.* of ± 4·0 per cent. The ratio of width to length also gives a 4·0 per cent. probable error.

The measurements are taken with dividing compasses

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* Watt, Sir G.

to the nearest millimetre exept in the filaments, where half-millimetres are attempted. Three flowers are examined on every plant, and the means for all three are taken.

First flower and maturation.—The obvious effect of early stunting is to provide a long tail of late-flowering plants upon a graph which shows the date of the first flower. If the originally stunted plants are excluded, the *P.E.* of this date works out at a little more than four days in most families, or 3½ per cent. of the time elapsing between sowing and flowering.

The maturation of the flowers opening during early July at Cairo has been directly recorded by marking the flowers. The results for, *e.g.*, family "77" in 1911 gave a mean of forty-eight days with a *P.E.* of ± 3·0 per cent. The period is longer in the Delta.

Flowering and bolling.—The limits of the present volume do not permit of detailed discussion of the fluctuation from plant to plant in flowering- and bolling-curves, beyond the account of the possible controlling factors already given.

The influence of sowing-distance is shown in Fig. 44, four times the number of flowers being found on wide-sown plants as against field sowing. The point is important with regard to propagation of new varieties;[32] by wide-sowing we can obtain 100 bolls per plant from a strain which will only produce 15 to 20 in field crop.

The influence of defoliation by cotton-worm is peculiar, the flowering being immediately arrested, but subsequently extended much later than usual, so that a warm autumn may enable the ultimate yield to reach the normal.

A few points of interest arise with regard to the total production of flowers up to a certain date, and the bolls developed from them. The correlation between these two quantities was worked out in the wide-sown, very irregular family of "77," for 1910, with the following results.

Total number of flowers per plant	Mean, 115	*P. E.* ±29 per cent.
,, ,, bolls ,, ,,	,, 50	*P. E.* ±34 ,,

Correlation between total flowers and bolls : r=0·85.
(Imperfection of correlation is mainly due to shedding.)
Percentage of retained flowers : Mean, 40·6 ; *P. E.* ±7·5 per cent.

These figures demonstrate the manner in which errors accumulate during field experiments. Comparison of two rows or plots of the same variety becomes more and more erroneous as the plants grow older ; comparison by the number of flowers has a lower *P.E.* than comparison by the number of bolls ; this in its turn has a lower *P.E.* than comparison by weight of seed-cotton picked ; this again is more precise than comparison by ginned lint. Fresh sources of error creep in at every stage, and the fact that field plots have a *P.E.* of ±6 per cent., at least, becomes quite comprehensible.

The boll.—The three chief characteristics of the boll are its diameter, the number of loculi, and the shape. The first and last are determined from three full-grown bolls per plant, measured with parallel-jaw callipers, the form being expressed as a diameter in percentage of length. The number of loculi is determined by examination of not less than twenty bolls of one kind on each plant; thus forty bolls may have to be examined to obtain the critical number, if half are trilocular and half quadrilocular ; such a plant receives the designating formula of 3·5. Plants whose bolls are all trilocular are designated 3·0 ; if all quadrilocular, 4·0, &c. For certain families the critical number has been raised to forty bolls of a kind (*e.g.*, Fig. 63).

Specimen data for these characters in Egyptian families are :—

Boll width	Mean, 25 mm.	*P. E.* ±3·6 per cent.
,, form	,, 64·6 ,,	*P. E.* ±3·8 ,,
,, Loculi	,, 2·81 ,,	*P. E.* ±2·6 ,,

The fluctuation of the last character is low, presumably because the number of loculi is differentiated at an early stage of bud-development, whereas the diameter of the boll is partly dependent on the environment in which it exists during the first thirty days after the flower opens.

It may possibly be owing to this division of boll-maturation into two periods that we find no correlation of seed weight with any of the boll-characters in pure strains, though such correlation is very evident in heterogeneous F_2 families.

Seed weight.—The mean weight of the seed is determined by weighing and counting samples of not less than 200 seeds. There is much to be done yet in determining the causes of fluctuation, by examining weekly pickings.

The highly irregular "77" family of 1911 had a mean at 0·097 gram, with a *P.E.* of ±8·3 per cent.

Another family, of twenty-three very uniform plants with a mean at 0·095, had almost as much fluctuation, viz., *P.E.* ±7·0 per cent.

The weight of a seed is completely determined by the mother plant, and not by the embryo. Thus the weights of single seeds of an F_1 plant show no modality, nor does the weight of the embryo. Forty such seeds, weighed singly, gave the following fragmentary result.

Mean seed weight ...	0·180 gram	*P. E.* ±5·9 per cent.
,, testa ,, ...	0·078 ,,	*P. E.* ±6·7 ,,
,, embryo weight...	0·102 ,,	*P. E.* ±5·3 ,,

Embryo weight = 57 per cent. of seed weight.

The difference between testa and embryo is slight, and both are equally important in causing fluctuation in seed-weight.

The causes of this fluctuation are obscure. Correlations have been plotted for all recorded characters, but with very few results. The values for "*r*" need not be given since a qualitative statement is sufficient for the available data. The only connections yet shown are: Leaf length, some, positive; Height, doubtful, positive; Lint-length, slight, negative; Lint-weight, high, positive; First flower, slight, negative.

None of these are very definite and the explanation lies in the fact that while height, leaf-length, and first-flower represent the mean result of a long period of environmental influence, the fluctuation in weight for any particular seed is probably fixed within a period of a few days.

The same explanation applies to the high *P.E.* of uniform families, which is nearly equal to that of the most irregular families.

Summarising, we may say that everything points to the root as the controller of fluctuation in seed-weight.

Lint weight and out-turn.—We have already dealt with the correlation between weight of lint and seed, in discussing ginning out-turns. The correlation is less close in pure strains, taken plant by plant (*e.g.*, $r = 0·72$) than for the crop-samples there mentioned ($r = 0·81$).

The fluctuation in lint-weight seems to be proportionally less than that in seed-weight, the *P.E.* being, *e.g.*, ± 7·5 per cent. as against 8·3 per cent. respectively in the same family. This statement probably requires revision for field crop conditions, since wide-sown plants give abnormally low ginning out-turns; the crop-samples gave a lower correlation between seed-weight and out-turn ($0·220 \pm 0·094$) than between lint-weight and out-turn ($0·316 \pm ·091$).*

The fluctuation in ginning out-turn for family "77" had a mean of 92 rotls, with a *P.E.* of ± 3·5 per cent. This is probably an excessively high figure, as the plants growing in the tanks gave much higher out-turns than the rest.

Seed fuzz.—Although this amount of "fuzz" on

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* See Craig, J. I. (3).

the seed scarcely admits of statistical expression, it is sufficiently important to merit a comment. The cytology of the "fuzz" hairs is as yet unknown. They are certainly different from the lint hairs, but the demarcation may not be very obvious in abnormal seeds.

The presumably primitive cottons * possess no lint, but abundant "fuzz" covers the seed-coat. Less "primitive" cottons have both fuzz and lint. In the cultivated cottons we find groups with "entire" fuzz like the primitive species, others with fuzz restricted to the hilum and raphe, and others with no fuzz whatsoever. The phylogenetic interest of the character is consequently high, especially since some evidence as to its factorial composition is available.

One of the chief features in this connection is the colour. Green, brown, and white fuzz are all known in most cultivated cottons, though—since the green is unstable—green and brown are not easily distinguished. The lint colour, on the other hand, ranges through browns and creams to white, while even the browns appear to be of various origins. There is, however, a green-linted cotton known as "Texas Wool" which appears sporadically in fields of American Upland, and breeds true to the green lint. This stock is of interest because it provides a suggestion of possible phylogenetic connection between lint and fuzz.

Apart from colour, however, we find a certain amount of fluctuation in the amount of fuzz. Within a pure strain this is very slight, but when severe constitutional changes are forced upon a semi-fuzzy stock by crossing or by a novel environment, the fluctuation may be conspicuous.

Lint-length.—Since data on fluctuation in lint-strength are not yet available, we can quote for lint-

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* Watt, Sir G.

length only of those characteristics which interest the consumer of the crop.

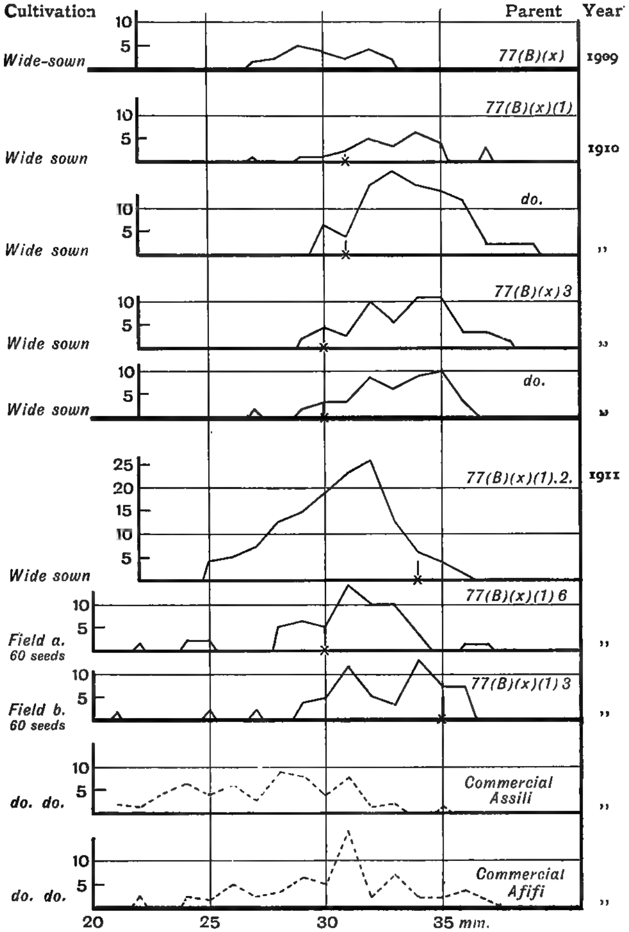

Fig. 49.—Maximum Lint-length of Single Seeds.

× Mean length of parent plant.
— Pure strain of Afifi.
... Commercial "varieties."

"Field *a* and *b*" were different field plots carrying alternating rows of various cottons.

Fluctuation in this respect has been shown to vary with the season and cultivation, with the sowing distance, &c.

The extent of this fluctuation is determined on the mean maximum lint-length of five seeds taken at random from the plant, and gives such results as a *P.E.* of ±2·9 per cent. on a mean of 33·5 mm.

Taking single seeds only, we obtain such results as those shown in Fig. 49. There is a definite bi-modality in some of these graphs; probably further investigation of such modes will show us how to persuade a plant into the production of abnormally long lint as a normal product.

CHAPTER VI

COMMERCIAL VARIETIES

THE probable origin of the type of cotton plant grown in modern Egypt has been discussed in the historical section of this volume. Many commercial varieties have been developed within this type. Some are extinct, and are only known to the author by name; such were Gallini, Abyad, Hariri, Bamia, Hamouli, Zafiri, and Ziftawi. Others which have been subjected to examination by the author, but which have not been able to make good their footing in the market, are Brown Yannovitch, Charara, Kerki, and Bolanachi. Others again are cultivated to a limited extent, such as Sea Island (both old stock and imported seed), Sultani, and Voltos.

The main varieties at present cultivated on a commercially important scale are Yannovitch and Sakellaridis in the "fine-spinning" group; Abbassi, as the white and moderately fine type; Ashmouni, Nubari,* Afifi and Assili in the "bread and cheese" group.

Ashmouni is the putative ancestor of all these, by way of Afifi. The origin of any one variety is most difficult to ascertain, but the majority probably arose as single-plant "selections." In the case of Yannovitch this is definitely known.

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* Nubari is not considered as a "bread and cheese" staple at present, but its future probably lies that way. The matter is discussed in as yet unpublished reports by the author on the Lancashire cotton demand.

Lastly we have the weed cotton, so-called "Hindi." It is not a cultivated variety, but sporadic as a weed mixed with other varieties. In general appearance it could easily be mistaken for American Uplands, but the seed is devoid of fuzz. Within the Hindi type there are various sub-types; thus, of some five hundred plants grown from Hindi seed of commercial origin, only about a third were very hirsute, while others were completely glabrous.

The seven important varieties mentioned differ in age. Ashmouni, or rather the name, dates back to the 'fifties of last century. Afifi was introduced commercially about 1887, Abbassi in 1893, Yannovitch in 1899, Nubari in 1907, Sakel in 1909, and Assili in 1910. These dates are, of course, approximate, being those years in which a conspicuous quantity of the lint reached the spinners.

Now with this multiplicity of varieties it might be imagined that their differentiation was easy. Such is by no means the case. All the varieties are similar in external appearance; even when grown side by side in field rows on the same plot, they cannot be distinguished with certainty. There may be far more difference between individual plants within the same variety than between two distinct varieties.

Certain physiological differences are found, however, but they are not very easily expressed in precise terms. Thus Ashmouni is the crop of Upper Egypt, Yannovitch is concentrated round a centre in the N.E. of the Delta, and Afifi gave the best results in the Southern Delta. Again, Yannovitch is credited with cropping lightly, about 10 per cent. below Afifi or Abbassi, and this opinion is supported by the scanty data available.

One of the cherished fables of the practician teaches that heavy crops and fine staple cannot co-exist. The inaccuracy of this belief, though long suspected, has only recently been proved by the Sakel variety. The bolling curves of Afifi, Sakel, Assili, Voltos, and the pure strain

"77" are shown in Fig. 42, determined from weekly pickings of five rows apiece, with a *P.E.* of ± 10 per cent. for any point in the curves.

The total yields of these curves work out as follows:

"77"	Yield = 25·1 bolls p.p.	*P.E.* ±0·6
Assili	,, = 19·9 ,,	*P.E.* ±0·5
Sakel	,, = 18·5 ,,	*P.E.* ±0·5
Voltos	,, = 17·4 ,,	*P.E.* ±0·4
(Afifi	,, = 20·0 ? ,,	*P.E.* ±1·5)

Thus the three commercial varieties included in the list are practically identical with regard to yield.

We have already figured the length of the lint of "77" under these conditions, and a comparison of this pure strain with similar rows of the two varieties Afifi and Assili should be of interest, one being old and notably irregular, the other new and presumably uncontaminated. The data are plotted in Fig. 49. The *P.E.* of random single seeds in respect of mean maximum lint-length being ±6·3 per cent., we find values of 7·8 per cent. for Assili and 7·5 per cent. for Afifi.

Thus, on the statistical evidence of lint-length, the newest "variety" is by no means uniform. This conclusion is abundantly confirmed by other evidence. Thus, the Sakel cotton contains at least two entirely distinct types of seed fuzz; the presence of these two types might possibly be unimportant, but in all probability it points to a heterogeneous origin for the original plant or plants. Such heterogeneity might occur even in the offspring of a single-plant selection, if the gametes of this plant were not uniform; in other words, if the plant was not pure-bred.

Such constitutional irregularity being manifest even in new varieties (see also Fig. 50), our next step must be to examine the cause. So soon as a family becomes heterogeneous, so soon does natural selection begin to operate. Once natural selection has begun, any sequence of alterations is possible. The usual result of such sequences is to stimulate the belief which lies dormant in the minds of most people—practical and otherwise—namely, that all man-made plant varieties suffer from an innate perversity, due to their "un-natural" origin, which causes them to "revert" at the first opportunity, and so to revenge themselves on human interference.

Up to the present point we have considered only the zygotic constitution of the "variety," and have merely laid emphasis on the fact that when a "variety" of cotton plants is inspected, plant by plant, the component individuals are not usually identical; we have seen, in addition, that the differences between nominal varieties are *mean* differences, which are negligible in most morphological characters, slight in physiological characters, and are definite only in respect to the nature of the commercial product—the lint hairs.

Our analysis has now to be driven much deeper. We have to investigate the origin of these zygotes, to ascertain whether they are derived from identical gametes or not, and to determine what effect their constitution may have on succeeding generations.

Gametic impurity.—In the older writings on plant-selection we find continual references to "transmitting power," coupled with advice to test this power by examining offspring. The reasons for this precaution are now better understood; "transmitting power" is not a mysterious vital function, but can be reduced to formulae. The causes of difference in this respect are two-fold.

In the first case, the plant originally selected may have been an extreme fluctuation and its offspring will therefore regress to the mean.

In the second case, with which we are now concerned, the original plant was heterozygous, derived from a natural or artificial hybridisation. Such hybridisation might have taken place in the previous year—the plant thus being an

F_1—or more probably several years before, in which case the plant may be denoted as F_x. In this second case we are dealing with an entirely different set of phenomena, superadded to fluctuation. The segregation of the character-bearing factors in sex-cell formation, with their reunion into new combinations at fertilisation, produces a set of offspring which differ constitutionally amongst themselves. The complexity of these differences will depend on the number of characters in which the original plant was heterozygous.

An example of such a plant may be quoted from the author's records. In 1909, while examining an old field-book of 1905, a note was found which gave the names of plants in flower at a very early date. They were all Uplands with one exception. This exception was a group of plants grown from a boll of Kerki, called No. 95. The few seeds available were taken from the files and sown in 1910, since an early-maturing Egyptian stock was much needed. Only five plants were raised, of which four were slightly stunted, while the best and earliest was found in the autumn to bear an inferior and quite distinct type of lint. Whether this plant was an F_1 from 1905, or an F_x from an earlier cross, our records could not disclose. The former is more probable. The remaining four were again fertilised naturally, and four families raised in 1911. They were fairly early, and—except for a few natural hybrids from crossing in 1910—were uniform in most respects excepting height. The original plants had been irregular in height, owing to stunting, but the offspring gave the following figures for height in October.

	Parent Height.	Offspring.		No. of Plants.
2	85 cm.	Mean, 117·7 cm.	*P.E.* ±12·0 per cent.	94
3	110 ,,	,, 138·4 ,,	*P.E.* ±11·8 ,,	118
4	145 ,,	,, 154·0 ,,	*P.E.* ±11·5 ,,	145
5	80 ,,	,, 138·2 ,,	*P.E.* ± 8·3 ,,	23

Inspection of the frequency curves showed that No. 95. C. 2 was breeding true to shortness, 95. C. 4 probably to tallness, while 95. C. 3 and 5 were throwing out shorts.

The uniformity of the deviation, which does not reflect the heterogeneity of 2 and 3, is due to the fact that the plants were growing in pairs, and had not been checked for stunting.

Such an experience is the rule rather than the exception. Thus, a series of 75 plants of various varieties were examined in four characters, and their offspring compared with them. The results were as follows :

a. Offspring like parent in thirty-eight cases ; some unlike in thirty-seven cases.

b. Alterations in each character, twenty-five, fifteen, sixteen, and fourteen cases respectively.

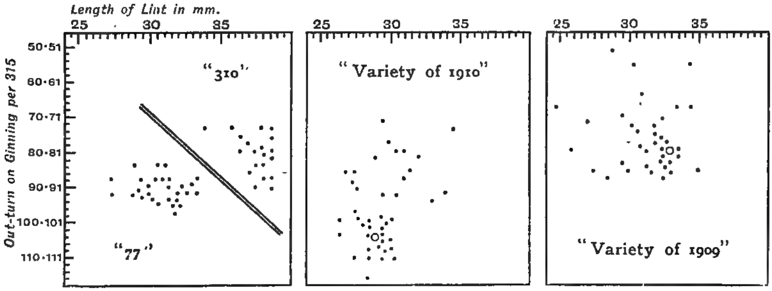
c. Alteration of all four characters took place in two cases, of three characters in seven cases, of two in fifteen, of only one in thirteen.

There is no recorded difference between the different commercial varieties in this respect. The newest are equally heterozygous with the oldest, though with less intensity of difference.

The cause of the impurity—which soon appears even when the original strain was pure—is to be found in the act of natural cross-fertilisation, or vicinism.

The effects of this double impurity need scarcely be elaborated. It is obvious that such a welter of unequal individuals must form an excellent medium in which natural selection can work. The transference of a "commercially pure" variety to a new district will be followed by "acclimatisation" ; such acclimatisation will be perfectly genuine, but it will not be due to any mysterious impress of the environment on the individuals.[11, 15]

Again, if such gametic contamination is continuous from year to year, and if our variety is not isolated upon an island in mid-ocean, we find a steady admixture taking place with other varieties. Such obvious contamination as takes place through seed mixture is relatively unimportant in comparison with contamination of the ovaries by foreign pollen. We have already laid emphasis on the external similarity of the different varieties, and its bearing now becomes apparent. A field grown under the name of Afifi might consist in reality of a mixture of five or six varieties with the original stock, together with all possible combinations and permutations of their multifarious gametes, but the difference would be almost invisible till the bolls opened. The mere fact that such a cotton as Yannovitch was a simple single-plant isolation from Afifi demonstrates this statement sufficiently without resort to our detailed tables of plant to plant differences (*e.g.*, Fig. 50).



Two Pure Strains. Two Commercial Varieties.

FIG. 50.—THE IMPURITY OF COMMERCIAL VARIETIES.

Target-diagram plotted from random single-plant samples in 1911.
Identical treatment, site, cultivation (wide-sown) and methods.
Compared in respect of only two important commercial characteristics.
o = Variety-type, under given conditions.

Further, although the author has quoted Egyptian illustrations, the same arguments apply to American Uplands, to Sea Islands, and to the few Indian cottons which he has studied. Mr. H. Martin Leake has demonstrated exactly similar heterogeneity in both zygotes and gametes for Indian varieties, but the Egyptian examples are perhaps more striking, on account of their higher economic value.

Even in a uniform environment, therefore, a commercial variety of cotton must change and may deteriorate. We might almost say that the change must be in the inferior direction, since a successful new variety is mostly superior to its parent stock, and will regress if contaminated by it. A plausible fiction declares that the life of a variety of Egyptian cotton is limited to fifteen years. The kernel of truth within this dogma should now be apparent to the reader, and it should further be self-evident that the life of a variety might be prolonged indefinitely by suitable precautions.

CHAPTER VII

NATURAL CROSSING

When the author first began his researches it was generally assumed that cotton was self-fertilised, and the only precise statement to the contrary was that of Webber, who had found 5 per cent. natural crossing between adjacent rows of distinct varieties. At the present day the seriousness of the crossing error has been demonstrated and admitted in many countries,* but the importance of the subject does not end with this conversion.

Field conditions.—The author's first concern was to investigate the amount of crossing which had taken place in field crop during 1904 by examining the offspring from random single bolls of that year.[5, 8] It was found that when a plant did not give uniform offspring, resembling itself, the difference of the offspring from the parent might be of two kinds.

In one case the offspring, or some of them, bore characters which were dominant over those of the parent; thus a 40 mm. lint might be derived from a 25 mm. lint; the presumption here was that all or some of the parent ovules had been crossed in the previous year by pollen from a long-linted plant. This was the rarer case, which in itself defines the amount of natural crossing, if we take

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* Notably Leake, H. M. (1), (4), and Allard, H. A.

the number of such cases in proportion to the total number of plants, or bolls, originally chosen for testing. This number was 5 in 75 in the original trials, but it must be remembered that not all the vicinistic pollen parents will have characters dominant over those of the mother plant; in any one character the chances will be even for or against such recognition. These chances can be reduced by taking more than one character, but when the two intercrossed characters are identical, or nearly so, the observational errors will prevent detection. Thus, we shall not be far wrong if we double the number of cases observed when working with two pairs of characters, so that our figure becomes 10 vicinists in 75, or 13·3 per cent.

In the other case we find that some offspring bear characters which are recessive to those of the parent. A lint of 40 mm. in this case gives rise to some plants with 20 mm. lint. The presumption here is that the parent was a heterozygote, produced by natural crossing in some year antecedent to the one in which the seed was taken from the field, having been simply self-fertilised in that particular year. The number of such F_x plants in the original total is nevertheless dependent on the amount of crossing which takes place every year, and should serve as a check upon the direct observation of the former case. If now we assume simple Mendelian segregation for the characters we employ, or prove it by growing further generations from these splitting forms, we see that the number of such F_x heterozygote plants depends not only on the renewal of that number each year by fresh crossing but also on its reduction each year by segregation of homozygotes from them.

If crossing to the extent of 10 per cent. per annum were naccompanied by segregation, we should find the number of vicinists increasing along a logarithmic curve, since some of the crossed strains would be re-crossed in subsequent years. Thus, the years would yield:— A, 0 per cent., B, 10 per cent., C, 19 per cent., D, 27·1 per cent., &c.

Again, if we start with F_1 plants, all being identical, allow no further crossing, and consider one allelomorphic pair only, we shall obtain the following series, P denoting homozygotes, and H denoting heterozygotes. A, 100 per cent. H. B, 50 per cent. H and 50 per cent. P. C, 25 per cent. H and 75 per cent. P., &c. In other words, assuming the productivity of H and P to be equal, the hybrid form will decrease to infinitely small proportions. When two pairs of characters are involved, the rate of decrease of H will be slower. Instead of a 1 : 2 : 1 ratio in the year B, or 2 H : 2 P, we shall have the ratio of 1 : 1 : 2 : 2 : 4 : 2 : 2 : 1 : 1, or 12 H : 4 P, being 25 per cent. instead of 50 per cent. of homozygote forms.

Combining these two antagonistic processes, crossing and segregation, we come to the following general algebraic statement.

For y pairs of simple allelomorphs involved in a cross we obtain in F_2:—

$2y$ homozygotes (P) from $4y$ individuals.

Since crossing is renewed every year we can consider this as a general value for purification.

In each generation let xP become H, by crossing, and yH become P, by segregation.

Then the composition of the crop will be :

$$\begin{array}{lll} \text{1st Year} & : & P \text{ only.} \\ \text{2nd ,,} & : & (1-x)P+xH. \\ \text{3rd ,,} & : & \{(1-x)^2+xy\}P+\{x(2-x-y)\}H. \\ \text{4th ,,} & : & \{(1-x)^3+xy(3-2x-y)\}P \\ & & \qquad +x\{3-3(x+y)+(x+y)^2\}H. \end{array}$$

Hence

$$n\text{th year}: \quad H=\frac{x\{1-(1-\overline{x+y})^{n-1}\}}{x+y}$$

When n is infinite (or practically in our case when it exceeds ten) :

$$x\{1-(1-\overline{x+y})^{n-1}\}=x$$

and
$$H=\frac{x}{x+y}$$

In the 75 cases already mentioned, we found, dealing with two pairs of characters, that there were twenty-six cases of recessives splitting out from dominants. Thus $H=\frac{26}{75}$ after n years.

With two pairs of characters

$$y=\frac{2^2}{4^2} \text{ or } \frac{1}{4}$$

And since

$$H=\frac{x}{x+y}=\frac{26}{75}$$
$$\therefore\ x=0{\cdot}132.$$

Thus there was 13·2 per cent. of natural crossing as the mean value for past years.

By direct observation we found five vicinists from the previous year, implying about ten altogether, or about 13·3 per cent. of natural crossing in 1904.

The two results agree.

The absence of facilities has prevented the author from carrying this analysis further by the use of pure strains planted under field conditions, but a value of 5 per cent. to 10 per cent. for natural crossing under field conditions in Egypt has been confirmed by numerous, though non-systematic, pieces of evidence.

This value is expressed in terms of flowers crossed to total flowers ripening. The possibility of mixed pollination should not be disregarded, since we shall see that hybrid and selfed embryos may be formed side by side in the same ovary. The expression of the value in terms of ovules crossed to ovules ripening would therefore be preferable.

Prevention.—The evidence as to the means by which the cross-pollination takes place is not yet as full as we should like it to be, but the greater part is performed by bees. Tests for wind-blown pollen made by the author with glycerine smears on glass plates have given negative results on the breeding plot, though a certain amount of pollen must be dislodged in this way in close-sown field crop.* The remedy, therefore, seems to lie in the exclusion of bees from the flower. In most countries this can be done by covering the flowers with paper bags, but the method fails in Egypt, since about 95 per cent. of the flowers thus treated are promptly shed; this shedding appears to be due to the local interference with transpiration, and consequent over-heating of the tissues. We have therefore employed mosquito-nets, which cover the whole plant, being supported over it on four posts. (Fig. 51). Practically no vicinism then takes place, though

Fig. 51.—Netted Plants.
First crosses and parents.

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* See Allard, H. A. (2).

one or two suspicious cases have been recorded. The method has its own disadvantages, however, the first being that of expense, while the second is that some strains resent the treatment, and refuse to hold their bolls. Rattoon plants, *i.e.*, plants which have been cut back and allowed to shoot again in subsequent years, usually grow well under the nets, as also do most American Uplands, but—though erratically—many Egyptians are failures. When the method was first employed we had yet to discover the sunshine effect; this effect is precluded from its full operation by the permanent veil of netting, and netted plants consequently grow during the day, becoming abnormally tall. Improvements are being made by substituting wire gauze for mosquito net, using larger cages, and so forth, since the perfection of some preventive method of this nature lies at the very foundation of all cotton-breeding and of seed-supply.[32]

Another obvious possibility is the discovery, or manufacture, of a cleistogamic flower, which shall obstinately refuse to admit foreign pollen to its style. At one stage of these researches the author seemed to be well on the road to success in this direction, and the story of the ultimate failure is not without suggestiveness.

The short-style flower.—At the time when it was being realised that natural crossing would be a permanent source of trouble, confusion, and error, the question of floral structure naturally came under consideration. No hint of the existence of uncrossable cotton flowers * could be found, but it seemed reasonable to expect that if we could decrease the opportunity for foreign pollen to reach the style, we might expect vicinism to diminish.[13]

✓ The cotton flower has a dense brush of anthers, borne on a cylindrical column, through the centre of which the style projects. The length of this style, and the extent

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* Compare Howard and Howard recently on the related genus *Hibiscus*.

to which it protrudes, varies in different strains and species. Most American Uplands have a much shorter style than Egyptians, and plants were noticed in F_2 of Upland Egyptian crosses, whose styles did not protrude beyond the column. The inheritance was therefore investigated statistically, and from a cross of 29 mm. style with 20 mm. column, upon 24 mm. style with 13 mm. column, we bred several strains with such flowers as the one shown in the frontispiece. The plant from which this flower was photographed was an F_2, and its descendants were grown up to F_5, still breeding true to this flower form. In F_4 they had a mean style length of 18½ mm. with a column of 14½ mm. : the anther filaments being 4½ mm. long made up the length of the brush to 19 mm., which sufficed to cover the style completely, so that it was visible only in end view, whereas the style of the Egyptian parent had projected for more than half a centimetre.

The short-style flower was thus at our disposal, but without avail. Four such plants from an F_3, similar to this respect, but otherwise differing, which had been growing close together in 1908, gave the following offspring in 1909 : A. 26 plants ; 7 rogues. B. 19 plants ; 5 rogues. C. 47 plants ; 16 rogues. D. 36 plants ; 12 rogues.

The percentage of rogues due to undoubted natural crossing in the four families was thus respectively 26, 26, 34, and 33. The control families grown from long-style brothers of these, gave the same range of variation, from 25 to 35 per cent. These figures have been extended since, but without improvement, and we are driven to the conclusion that the accessibility of the style is a minor factor in natural crossing, under the conditions of our breeding plot.

The figures for the breeding plot had always been so much higher than the 5 to 10 per cent. on which we decided for field conditions, that this last reverse led the author to reconsider the whole subject from a totally different point of view.

The breeding plot (Figs. 52*a* and 52*b*).—We have thus far found that floral structure has no protective effect. In addition it should be noted that the geographical position of any plant on the plot seems to make but little difference; in two cases we have found natural hybrids bearing a semi-red leaf, being first-crosses with a single plant of Willett's Red-Leaf, which was kept in a corner of the plot from year to year; these natural crosses had been made over a distance of 50 metres, the interval being occupied by dozens of other plants.* Further, we have found indications that different varieties, or even different plants, growing side by side, show differences in their

FIG. 52A.—THE BREEDING PLOT.

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* See, however, Leake, H. M. (4).

liability to natural crossing; we have just stated that such differences cannot be due to any obvious cause such as position or floral structure, so we are driven back upon a more abstruse explanation.

The hypothesis which has been framed to account for the facts observed is based upon an analogy drawn by Prof. Marshall Ward many years ago, between the pollen tube and the hypha of a parasitic fungus. We find in mycology that within the same strain of host-plant, different species and varieties of the same fungus possess different infection-capabilities. Conversely, the same fungus may be able to attack one strain of its host-plant with ease, while another strain may be practically immune.

Fig. 52b.—The Breeding Plot.
Irrigating Sudanese Tree-Cottons.

Using these facts to help us in forming conceptions as to the possible behaviour of pollen, we see at once that some such assumption as to differential susceptibility and infectivity between any style-pollen pair would lead us a long way. The method which has been employed by the author in testing this possibility, though on a very small scale as yet, is a method of mixed pollination. Equal quantities of foreign pollen and self pollen are placed on the style of a flower at the same time, as early as possible in the morning and the two sets of grains are allowed to compete with one another in the race down the style. The fact that artificial hybrids can easily be made between Upland and Egyptian in either direction shows that neither style is immune from the other pollen. Nevertheless it is quite possible that the tube from self pollen may grow faster in its own style than a foreign tube can do. Thus, on account of some effect, probably toxic, but as yet obscure, the foreign pollen-tube is beaten in the race down the style, and the majority of ovules are fertilised by the first arrivals, or self-tubes.

Using such a method, with all possible precautions to ensure equal opportunity to both sets of grains, we found that mixed pollinations of Egyptian by Upland, and the reverse, gave us ten natural hybrids in 330 ovules fertilised, or 3 per cent. of vicinism under the most favourable conditions for its manifestation. There was no significant difference between the reciprocal mixings. This figure is far below the minimum which we can possibly admit for field vicinism between plants of the same nominal variety. A new factor must therefore be involved, and we shall, in terms of our hypothesis, denote it as "relative immunity," regarding the pollen-tube of one kind as parasitic on the style of the other.

A curious side-light on this result is given by the Hindi cotton. Though the latter plant crosses readily with Egyptian under artificial treatment, and though it may amount in some fields to 15 per cent. of the crop, yet Hindi × Egyptian hybrids are merely frequent in the field. Certainly the error of natural crossing must be less between Hindi and Egyptian than between two Egyptians.

With a value of 3 per cent. for American and Egyptian, and of 10 per cent. for Egyptian and Egyptian, under the most favourable conditions, the occurrence of such values as 35 per cent., mentioned above, leads us to suspect that the story is not yet complete.

Before proceeding further we must define the value of our "percentage vicinism" with more exactitude. We are agreed that computation on the basis of the number of ovules is the most precise, but it remains to decide how we shall recognise those ovules. The difficulty which arises in recognition is due to the fact that all F_1 hybrids, and most F_x hybrids, germinate much more energetically than their parents. In this peculiarity lies the great weakness of simple "selection methods." The precise reasons for this difference are still not clear, but knowledge of the fact is very old. It is therefore not sufficient to count the number of vicinists in a population raised from contaminated seed; we shall be nearer to the truth if we take the ratio of vicinists to the number of seeds sown, thus assuming that all the seeds which did not establish themselves were pure-bred. In inter-Egyptian crossing this factor will be insignificant as compared with its importance in crosses of Egyptian with Upland. In the latter case the author has been the victim of such absurdities as the cultivation of a family which contained 100 per cent. of vicinists; the soil tilth was not good, the weather was cool, and between the two perils of mechanical resistance and "sore-shin" not a single selfed embryo survived.

When attempting to account for amounts of real vicinism which rise as high as 30 per cent., we must consider the nature of the pollen to be found on the breeding-plot. This plot has contained cottons from Egypt, from America, from India; indigenous cottons from Arizona, from the Sudan, etc. More than this, it has contained plants of F_1, F_2, F_3, F_4, F_5, and F_6, raised from crosses between American Uplands and Egyptian. Confining our discussion for the sake of simplicity to the F_1 of such crosses, it is obvious that we possess an infinite variety of pollen grains on an acre of land. To estimate the number of allelomorphic pairs involved in the cross of "38" (King) with "89" (Charara) at fifty would be very conservative. The number of possible combinations of these pairs works out at a figure which, for our present purpose, we may consider as infinite. Now, if Mendelism is not a delusion, this infinite number of combinations corresponds with an infinite variety of nuclear composition, on the part of the male gametes. It is true that these gamete-nuclei are devoted to sexual purposes, but their relations, the vegetative nuclei of the pollen grains, are generally admitted to control the growth of the pollen-tube, and these are of identical composition with the gamete nuclei. Consequently, we may reasonably expect to find some correlation, however indirect it may be, between the gametic differences and the physiological differences in growth-rate of the pollen-tube. Such relation would imply a greater "variability" in the growth processes of pollen tubes from an F_1 flower than that which we find in a pure strain. The standard deviation, or probable error, in the behaviour of F_1 pollen-tubes under a given set of conditions would necessarily be much greater than that of the pollen-tubes in a pure strain, whether Egyptian or American.

Regarded in another way, this conclusion may be stated thus. If 3 per cent. of the pollen-tubes from Upland pollen fluctuate sufficiently in a positive direction to enable them to beat 3 per cent. of the Egyptian pollen-tubes in a race down an Egyptian style, then we may expect—owing to greater variability—that much more than 3 per cent. of F_1 plant pollen-tubes will vary sufficiently in a positive direction. Hence, in mixed pollination of F_1 upon parent, we should find a higher percentage of vicinists.

The steps of the preceding argument were taken long before the experimental results were available. These results were as follows :—

Mixed pollination of F_1 upon Egyptian . . . 20/100 or 20 per cent.
Mixed pollination of F_1 upon Upland . . . 25/65 or 28 per cent.

Even allowing for all possible errors, and for the scanty numbers of ovules involved, the difference between 3 per cent. and 24 per cent. as values for the "prepotency" of mother-parent and of F_1 pollen, under the same experimental conditions, cannot be without significance.

Hence, we conclude that some part of the F_1 pollen from an inter-specific cross is prepotent over all other pollen; that self pollen is prepotent over pollen from some other species; and that pollen from other species only makes its way to the ovule with difficulty.

Gametic differentiation.—A conclusion which may be immediately drawn from these differences in prepotency of pollen is, that the error from natural crossing is likely to be less in the field—where it is difficult to avoid—than on the breeding plot, where it can be avoided by appropriate, though expensive methods.

Again, it is within the bounds of possibility that immune strains might be discovered or developed. Such discovery is scarcely probable, but it may as well be borne in mind.

The chief speculation in which we may legitimately indulge relates to gametic differentiation. If our postulate as to correlation between gametic composition of the microspore nucleus and growth-processes of the pollen tube can be substantiated, it follows that those tubes which succeed during mixed-pollination must possess certain gametic characteristics. A detailed statistical study of the composition of F_x plants resulting from such mixed pollinations has been begun, and if we can find any constant deflection of the frequency curves from expectation, we shall have a clue as to the nature of the winning pollen-grains.

In other words, our endeavour is to ascertain whether differences which are manifest before fertilisation exist between F_1 gametes. Further discussion[30] would be worthless at present, but any clue to gametic differentiation deserves to be followed up.

CHAPTER VIII

HEREDITY—I.

i. *General*

Having discussed physiology, fluctuation, and natural crossing, we are now in a position to examine the inheritance of characters in crosses between two strains of cotton derived from separate reputed species.*

The evidence to be adduced in the following pages is frequently most infirm beyond the second generation. Leaving out of account the inefficient conditions under which this part of the work has been done (Figs. 52*a* and 52*b*), the chief responsibility for this uncertainty lies with the difficulty of preparing self-fertilised seeds. When an F_2 of two hundred plants is to be studied, we desire to avoid the use of nets (Fig. 51) owing to their disturbing effect upon growth; yet, if nets are not employed, we necessarily raise F_3 families which are contaminated. Therefore it is better to dispense with the nets, and to rogue out the F_3 vicinists; very often, however, such decisions as to vicinistic origin are based on the appearance of abnormal characters which might very well be due in reality to some rare gametic combination following self-fertilisation; we thus argue in a circle; a plant shows an unexpected characteristic, therefore it is a rogue. We have endeavoured to reduce the probability of such unjust decisions by a system of voting, whereby no plant

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* The coming economic application of Mendel's Law to cotton will at first be made through crosses of much more nearly related forms, and hence of far greater simplicity than those which the author has chiefly investigated.

can be condemned unless it shows incredible abnormalities in several characters. Such treatment does not lend itself to precision.

A way out of the difficulty which has been employed several times has been to dispense with netting in F_2, growing the F_3 from natural seed, leaving the F_2 plants in the ground as rattoons, and netting any of them which appear to be important. The natural F_3 is thus used for indicative, while the selfed F_3 is used for critical confirmation in the following year. The method involves waste of a year, waste of labour, and waste of land, but it seems to be the only plan which gives trustworthy data.

The few crosses which have been made and studied were easily effected, taking the usual precautions.

The F_1 plant was invariably netted after 1906, and the experimental error of the F_2 data is therefore very low.

The F_3 results, on the other hand, which are of supreme importance in disentangling the complex F_2 data, are subject to the errors which we have just detailed. The same holds good for F_4 and F_5—which is the highest generation we have cultivated—though by this time we usually know what plants to net, so that the data are more likely to be trustworthy; on the other hand many such families have been grown but not studied critically, through insufficient opportunity.

The elucidation of inheritance in cotton is thus no light task, and should not be undertaken without a residential laboratory, ample skilled assistance, and financial resources.

The difficulty of obtaining accurate data beyond F_2 is so much the more regrettable in that the factorial analysis of cotton hybrids often requires the highest precision. We shall see that the composition of an F_2 is commonly very similar to a Gaussian curve of error; this similarity is usually—probably always—fictitious, and is due to the appression of several true modes, which blend into one another by fluctuation. Part of this blending, moreover, is not fluctuation in the ordinary sense, but rather an *autogenous fluctuation*,[30] provoked by correlation with other characters. Thus the modes of seed-weight in an F_2 are not only subject to a *P.E.* of 12 per cent., but before this allowance can be made they have to be corrected for correlation with diameter of the boll.

A simple way of applying such correction is to dissect the frequency polygon of the family, isolating the wide-boll and the narrow-boll forms, for example, and plotting their seed-weights separately (*e.g.*, Fig. 69). Unfortunately this method reduces the size of the groups under examination, which has never been excessive to begin with, so that the precision gained in one direction is lost in another.

Again, since correlation exists between certain characters, it might be thought that the slide-rule would give the necessary correction. The difficulty here is to find out the value and nature of the correlation. The simplest Mendelian combination, $AB \times ab$, where the characters are simply linear measurements, gives a correlation diagram in F_2, which consists of four groups, only separable with difficulty even when correlation is perfect and linear, which—worked out in the conventional way—gives a value for r from 0·6 downwards (Fig. 53). There does not seem to be any method at present extant by which a quantitative separation of these groups can be made.*

The difficulties enumerated, both of experiment and of computation, have prevented the author from making any exhaustive statement which can be considered as honest from the scientific viewpoint. The results are in the main indicative, and suggestive, often strongly so, but in all cases open to criticism.

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* W.L.B. 21, and reply by Craig, J. I., *Cairo Sci. Jour.*, August, 1910.

In rare cases we have been able to demonstrate the existence of Mendelian ratios in F_2, confirmed by the behaviour of later generations. In others we have failed to analyse the F_2 but have dissected the F_3, where the phenomena were simpler. In others, again, such analysis has been utterly impossible, and we have been obliged to rely on the bare fact that a certain character has "bred true" in the end, though we have been unable to trace the steps of its purification. As a last infirmity, and last resort, we have fallen back on comparisons from year to year in massed data: if the graph for seed-weight in F_2 shows certain modes, and if those modes reappear in the graph for all the F_3 plants in the following year, we have a claim to assume that the modes are at least due to a systematic cause and not to accident.

The data to be quoted are drawn largely from crosses of Egyptian with American Upland, especially from Afifi with Truitt Big Boll (No. 252),[15] and from Charara with King (No. 255). Other crosses which have been made, but only partially examined through lack of space and labour, are Hindi × Charara, King × Russell, Russell × Charara, and Sultani × King. In the early stages of the work many natural hybrids were examined, which had resulted from natural crossing between Egyptian cottons, while full analysis has been made up to F_2 in an inter-Egyptian cross between Afifi and another Sultani. The phylogenetic relationships of the various parents is doubtful, to say the least. The author has leaned to the designation "inter-specific," but this has been questioned, in view of the cultivated origin of the parents.* Perhaps a description of them as "reputedly inter-specific" would best meet the case.

The cross of Afifi × Sultani was made with the object of studying some simple examples in place of the com-

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* See references "Egypt," in Sir G. Watt's Monograph.

Computed.

P_1.

$\chi = 65$ or *a*.

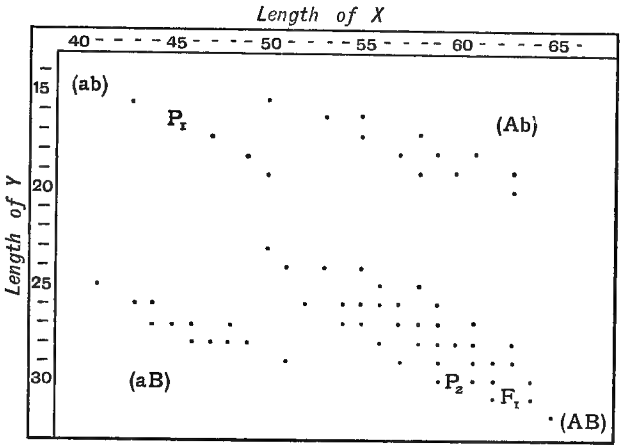
$\gamma = 15$ or *b*.

P_2.

$\chi = 60$ or *A*.

$\gamma = 30$ or *B*.

$\alpha = 0{\cdot}9$.



Experimental.—F_2 of King × Charara.

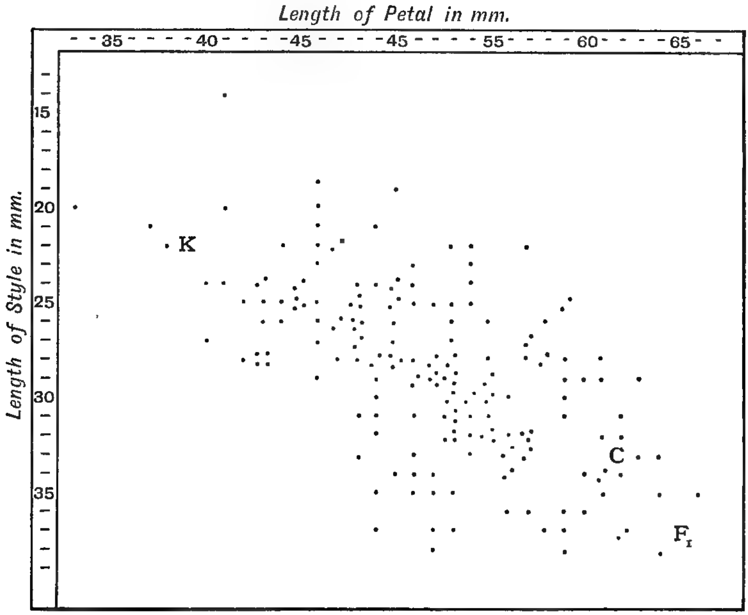


Fig. 53.—Correlation Diagram for Two Pairs of Allelomorphs.

plexities presented by the other crosses, but it is as complex in its own way as the Upland × Egyptian series. It seems to be quite probable that this cross was one between the old Peruvian and Sea Island stocks, and was hence not very much more intimate than the Upland × Ægypto-Peruvian crosses.

The author can only reiterate his conviction that all these hybrids are subject to Mendel's Law of segregation; often obscurely—on account of defective methods—but none the less certainly. The evidence available can all be interpreted in Mendelian terms, and it is very significant that most of it should appear at first glance to be completely dissociated from the classical ratios. Mendelian students of heredity have confined themselves to the more definable characters, such as colour, partly because statistical characters take up an excessive amount of time in mere determination, and partly because the use of statistical methods is prone to provoke irrelevant criticism from mathematicians with whom the mere biologist cannot fairly compete. At the same time it is clear that the frontier of Mendel's territory is not demarcated by any special character, and—with all their experimental disadvantages—the only characters which admit of complete treatment are those which can be measured with definable precision.

There are many features of these complex results which bear a tantalising resemblance to problems of human heredity.

Record system.—The examples to be quoted in these pages are drawn from a systematic set of records. These records are compiled from three sources, the Field-Books, Field-Cards, and the Laboratory-Books, in which the actual observations are entered. These are then worked up at the end of the year in two ways; first in the Files, and secondly in the Ledgers. The Files consist of printed forms, one to every plant, on which are entered all particulars available; the file-sheet of the plant shown in

Fig. 54 is reproduced in Fig. 55. The Ledgers collect the data from all plants of a family under the head of each character separately; this is conveniently done in the form of frequency polygons, in which the number of each individual is written; Fig. 48 reproduces a page of the ledger dealing with the height of the offspring of a plant which was brother to that shown in Figs. 54 and 55. The polygons elsewhere reproduced have had the component plant-numbers omitted in order to save space. Lastly, a Card Index of the completed ledgers enables any fact about any plant to be found immediately.

ii. *Qualitative Characters.*

Those characters which are not easily subjected to statistical expression are dealt with in this sub-chapter.

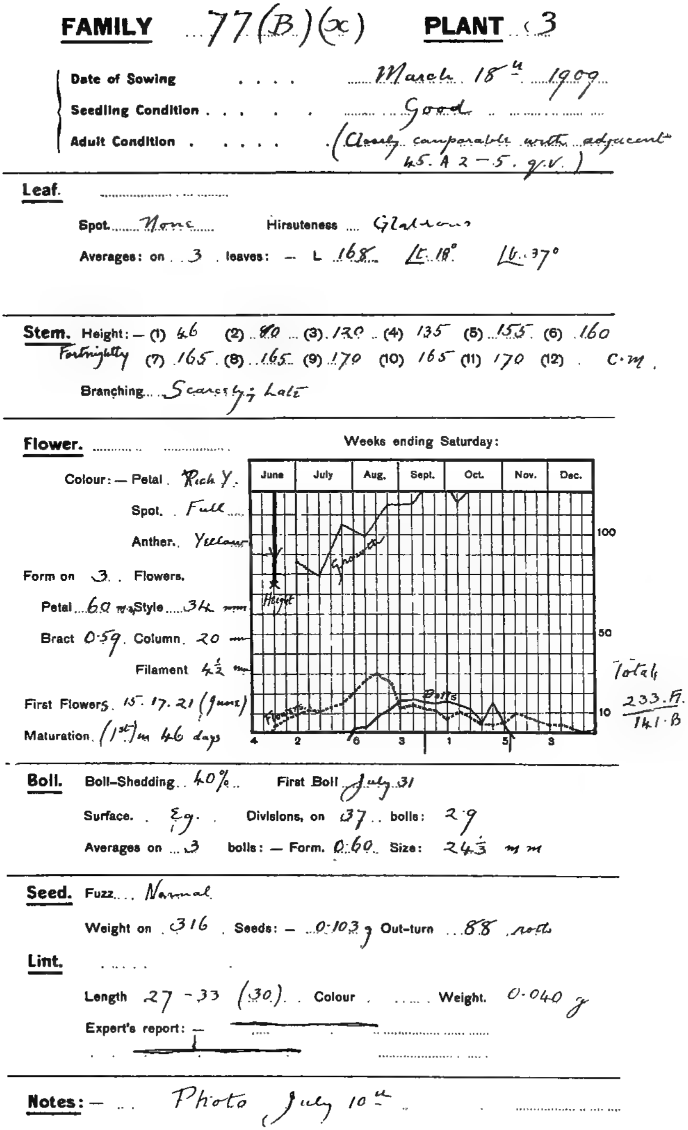
The Leaf-spot.—The development of anthocyanin in the leaf, which finds its fullest expression in the Red-Leaf sports, is usually noticeable at the point where the petiole begins to branch into the main veins. In Uplands, and in Hindi, this leaf-spot is conspicuous, and forms a useful diagnostic character in the seedlings for comparison with Egyptians, whose leaf-spot is fainter, smaller, and pink rather than crimson. The character varies with the water equilibrium and illumination of the plant, like all anthocyanin characters. The F_1 of the "spotted by relatively spotless" cross bears an intermediate spot. In F_2 the ratio of the three forms accords closely with 1 : 2 : 1. Extracted full-spot and spotless breed true, without known exceptions.

General colour of the leaf.—The Upland cottons possess a leaf lamina of much lighter hue than the Egyptians. This difference in colour is real, and independent of differences in hirsuteness, &c. The inheritance of the character, or character-complex, is unknown, except that large families have been found to breed true to one or the other colour after F_2.

The matter might be of importance with regard to photosynthesis.

Colour of petal.—The limb of the petal, apart from the colour of the basal spot, which we shall discuss shortly, ranges in colour from almost pure white to a rich golden yellow. Each pure strain of cotton has a definite petal colour, which is white to creamy in Uplands and Hindi, while in Egyptian families it ranges from lemon to golden.

Fig. 54.—Typical Plant of "77." July 10, 1909.



FAMILY 77(B)(x) **PLANT** 3

Date of Sowing . . . . March 18th 1909
Seedling Condition . . . . . Good
Adult Condition . . . . . (Closely comparable with adjacent 45. A 2–5. q.v.)

Leaf.

Spot. None Hirsuteness Glabrous
Averages: on 3 leaves: — L 168 ∠t. 18° ∠b. 37°

Stem. Height: — (1) 46 (2) 80 (3) 120 (4) 135 (5) 155 (6) 160
Fortnightly (7) 165 (8) 165 (9) 170 (10) 165 (11) 170 (12) c.m.
Branching Scarcely; Late

Flower.

Colour: — Petal Rich Y.
Spot. Full
Anther. Yellow
Form on 3 Flowers.
Petal 60 mm Style 34 mm
Bract 0·59 Column 20 mm
Filament 4½ mm
First Flowers 15. 17. 21 (June)
Maturation (1st) in 46 days

Boll. Boll-Shedding 40% First Boll July 31
Surface. Eg. Divisions, on 37 bolls: 2·9
Averages on 3 bolls: — Form. 0·60 Size: 24⅓ mm

Seed. Fuzz Normal
Weight on 316 Seeds: — 0·103 g Out-turn 88 seeds

Lint.

Length 27–33 (30) Colour Weight. 0·040 g
Expert's report: —

Notes: — Photo July 10th

FIG. 55.

White and creamy petals are not difficult to find in Egyptian field crop, but their ancestry is dubious; some may be true Egyptians, but most are splitting-forms from Hindi × Egyptian hybrids.

The hybridisation of these forms has not given a simple result in any cross yet made by the author. Mr. Fyson has published details from large families of Indian cottons, which indicate that the character was there controlled by a single pair of allelomorphs, but the data are not quite convincing as to this simplicity, and the same uncertainty is found by Mr. Leake (3).

The cross Afifi × Sultani was a cross of golden petal × lemon petal. The F_1 was intermediate. In F_2 we matched the offspring to the three forms, taking three flowers from each plant on different days. It should be remembered that the colour differences between these three forms are not very great, although the parents are quite distinct from one another. Many plants were matched to the same type-colour each time, but many others were matched first to one and then to another. The probability seems to be that there are more than three colour types in the F_2, just as in Tammes' work on hybrids of *Linum*, so that our matchings may mean very little.

On the simplest interpretation of the data we might imagine that the heterozygote was a simple intermediate, throwing out a 1 : 2 : 1 ratio in F_2. The figures are too discrepant to admit of this view. They tend more towards the interpretation based on two pairs of allelomorphs, giving a ratio of 9 : 3 : 3 : 1, where the last two are externally similar, making the ratio into 9 : 3 : 4.

The crosses of Egyptian with Upland have behaved in a similar way. The cross of yellow—whether lemon or golden—with white or cream has always given an intermediate F_1. In F_2 we have obtained ratios which approached very closely to 1 : 2 : 1, but with a constant excess of the paler parental colour-type. Testing this on the assumption of a 9 : 3 : 4 ratio, we obtained consistent results up to a certain point. Whites and some full yellows bred true, some intermediates threw out all colours like the F_1; other intermediates threw whites only, while yet others threw only the full parental yellow, giving approximate 3 : 1 ratios in both cases. It seemed at one stage that the double-pair hypothesis had met all contingencies, until the following test was applied.

A family raised from an F_3 plant which bore the intermediate colour had given twenty-two intermediates to seven full yellows. Six of these F_4 intermediates were grown into F_5; the obvious expectation was that four should throw out yellows, while two should breed true to the intermediate colour. The actual result was that none threw any yellows at all, but all threw whites. These whites were not, moreover, of the same colour as the parent white, but much nearer the intermediate itself. The figures for the six families, in ratio of "intermediate : new white" were (4 : 0), 21 : 5, 16 : 9, 26 : 1, 10 : 1, 11 : 3. The families were almost gametically pure in all other known respects, and all vicinists had been eradicated.

From this evidence it is plain that petal colour in crosses of Upland by Egyptian may be controlled by not less than *three* pairs of allelomorphs. The presumption is that our matching methods are not sufficiently precise, and that some form of colorimetric grading is needed. Even the inter-Egyptian cross shows the same peculiarities.

We shall see that similar evidence is to hand in the next character to be considered, together with a strong probability for gametic coupling. If the colour and marking of a flower's petal is controlled by at least five allelomorphic pairs, complicated by gametic interaction, it need not surprise us to find that the modes of seed-weight in F_2, for instance, are not very definite.

On the other hand, far more complex analyses of flower colour have been proved indisputably for such plants as *Antirrhinum*, *Matthiola*, *Lathyrus*, &c.,* so that the indications of our fragmentary evidence may be considered as quite probable, even in a simple sap-colour.

Petal spot.—The Egyptian flower is characterised by a rich crimson spot at the base of the petal. This spot is not so large as in *G. herbaceum*, where it occupies the whole of the petal claw, but it is conspicuous. The typical Upland cottons and Hindi have no such spot, the petal being self-coloured. The intensity of the spot may differ within commercial Egyptian varieties, like the petal colour. Similarly, commercial stocks of, *e.g.*, "King" Upland contain a notable proportion of plants with spots on their petals. Such differences are probably due to doubtful pedigree.

A cross between "full spot" Egyptian and "spotless" Upland gives an intermediate F_1. The F_1 spot is smaller, more vague in outline, and less noticeable than the spot of the Egyptian parent. In cases where the latter had a spot which was relatively small, the F_1 is proportionately inconspicuous.

In F_2 the ratios are very erratic. Taking them in the order "full : intermediate : none," we find two families from F_1 sister plants giving 11 : 22 : 18, and 23 : 42 : 31. In this case the ratio approximates to 1 : 2 : 1, but it is closer to 3 : 9 : 4, and the divergence from even this is more than can be explained by errors of observation. Probably, as in the case of petal colour, there are more classes than we have admitted. This view is substantiated by the fact that we have been unable to discriminate in many cases between "Full" and "Full ?". As in the case of petal colour we find that "spotless" breeds true, while "full" may either breed true or break, and inter-

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* See Bateson, Saunders, Baur, Wheldale, &c.

mediates break in at least two different ways. Probably there are again two allelomorphic pairs concerned.

Another series of crosses gave an entirely different set of ratios. One of these was derived from an Egyptian parent which possessed an inconspicuous petal spot, and the divergence from expectation was at first[8] attributed to fluctuation. The ratio in F_2 was 5 : 9 : 47. The other series was not open to this interpretation, since the Egyptian parent had a fully-developed petal spot, while the F_2 ratio was 27 : 41 : 112. If we assume that the petal spot in the latter cross was controlled by two allelomorphic pairs, with 3 : 1 : 1 : 3 gametic coupling, while the "full spot" class consisted of two groups which were practically indistinguishable, we obtain a theoretical ratio which is very close to actuality, viz., 25 : 40 : 115.

It is inadvisable to discuss the point more fully, since we require much larger series of numbers than those the author can present, before a decision can be taken as to the probability of this view. The consistently erratic behaviour of the spotted and intermediate forms in F_3 supports such interpretation, but the figures available are not sufficient to substantiate it.

The only decisions at which we can arrive with certainty are :—that the presence or absence of the petal spot in these Ægypto-American crosses is not determined by a single pair of allelomorphs, and that there is strong evidence for complication of this mechanism by gametic coupling in some cases.

Anther colour.—The colour of the central brush of stamens is an important feature in the general colour-effect of the cotton flower. In Egyptians it is bright golden-yellow, in Uplands and Hindi it is whitish, or rather buff in colour, and the F_1 is intermediate.

In F_2 we obtain ratios which appear to be genuinely 1 : 2 : 1, and no exceptions have yet been noted in subsequent generations. The characteristic thus appears to be under the control of a simple pair of allelomorphs, so far as evidence is available.

This presentment does not exhaust the possibilities, for a family of King Upland, grown from seed of a selected plant, showed itself to be a hybrid in this respect. The anther colour of the selected parent was pale lemon, which broke up on self-fertilisation into 24 lemon : 8 buff. The latter have since bred true, as have some of the lemons. In this case the pair was simple, with dominance of more colour over less colour.

Hirsuteness.—The hairiness of the plant involves a number of factors; one type of hair may be confined to the leaf-lamina, another to the veins, another to the stem, and so forth. During our studies of this character in cotton we have examined only the petiole of the leaf.

The Egyptian cottons have glabrous petioles, the American Upland petioles are more or less hirsute, and the F_1 petiole is almost glabrous. The author's first published mention of this character[5, 8] stated that the glabrous form was completely dominant. In almost all other plants the reverse is true, and further complications were expected when Mr. Holton discovered that a few long but scanty hairs were present on the F_1 petiole.

Early classifications of F_2 and F_3 in which glabrous and intermediate were grouped together as non-hirsute, gave ratios of "non-hirsute: hirsute" as 111 : 37, 58 : 17, 43 : 9, &c. On cultivating some extracted hirsutes in F_4 we found six out of seven breeding true to hirsuteness, while one broke up, giving 31 : 8, the eight being of the F_1 type. Moreover, we found that the extracted forms differed in the length and density of their hairs, and that segregation in this respect was indicated within the limits of the hirsute group.

A very careful classification was then made on the F_2 of another Upland-Egyptian cross, which gave the following results:

Like Egyptian parent	48
Doubtfully Egyptian	8
Doubtfully like F_1	1
Like F_1 (scanty hairs on dorsum)	71
Like F_1, but with more hairs	6
Like Upland, but shorter hairs	10
Like Upland parent	19
Like Upland, but denser	12
Total	175

Thirty-five of these plants were grown on to F_3, but their families were not sufficiently large. One notable feature was that an "F_1 type" plant gave thirteen offspring like itself, and no other forms. Other similar plants threw the glabrous type only, while others again behaved like the F_1 itself. Some of the differences which had been recorded between the F_2 plants seemed to be due to fluctuation, but the general trend of the evidence is to the same conclusion as in the characters already discussed, namely, gametic complexity, possibly with length and density as component factors.

It should be added that families of fifty plants have been grown in F_5, which bred true to new types of hirsuteness, such as the felty class described above "like Upland, but shorter."

Since the hirsuteness, or rather the glabrousness, of all Egyptians is practically the same, we have no data for simpler crosses. It might be well to investigate the character in a cross of glabrous Hindi with hirsute Hindi.

The stipule.—During examination of Afifi × Sultani F_1 it was noticed* that the form of the stipule was very different in the two parents. The Sultani parent had long narrow stipules, while the stipules of the Afifi parent were about four times as wide for the same length.

The F_1 stipule was long and narrow like the Sultani parent.

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* By Mr. F. S. Holton.

In F_2 we found, by simple matching, that 48 plants had stipules like the Afifi, 59 like the Sultani, while 27 were recorded as doubtful.

The evidence is inconclusive, but it again points to some slight complexity, possibly a ratio of 9 : 7.

The surface and glandulation of the boll.—All parts of the cotton plant, other than the root, contain abundant resin glands, which produce the characteristic black speckling externally. The depth at which these glands are situated in the ovary wall is characteristic of different kinds of cotton plants. In most Egyptian bolls they are near the epidermis, which is depressed above them, forming small craters. In American Uplands we find the glands situated much further below the epidermis, which is not depressed, so that the surface of the boll is smooth, and the speckling is scarcely visible. The F_1 of these two forms is intermediate, though more like the Egyptian parent.

A large number of bolls have been pickled and sectioned in the attempt to understand the inheritance of this character. It appears to be straightforward, but the evidence is not convincing. The appearance of the surface is not solely dependent on the glandulation; Egyptian bolls are bright green and shiny, while Upland bolls are of a dull, grey-green colour. Some structural differences are also shown by the microscope.

Thus the fact that an F_2 was matched into 17 Uplands : 33 F_1 type : 14 Egyptian type, must not be taken as evidence of simple segregation. The data from F_3, &c., lead to the same uncertain views as in the more definite characters of the flower colours.

The distribution of seed fuzz.—The differences between various strains of Egyptian cotton in this respect range from complete nakedness to a woolly coat which covers all but the back of the seed. The former are indistinguishable from Hindi seeds, but most of them give rise to plants which bear no sign of any Hindi ancestor.

Plants bearing seed with entire fuzz are occasionally found, but these appear to originate from crossing with Hindi.

Hindi cotton, on the other hand, always bears naked seeds, while typical American Uplands are entirely fuzzy. Naked-seeded sports occurring in the Upland crop have been discussed by Allard (1) and in the Indian crop by Fyson.

Several natural hybrids have been bred on from Egyptian cottons. In all cases they have given a simple 3 : 1 ratio, more fuzz being dominant over less fuzz, and expectation has been fulfilled in F_3. The cross of Afifi × Sultani behaved in the same way; some fluctuation was shown, but the groups were clearly 116 : 41 in F_2.

In crosses of any Egyptian with American Upland, we meet with complications. The entire fuzz is dominant, and the F_2 has given such 15 : 1 ratios of "entire : slight" as 97 : 6, 180 : 11, &c. The naked seed breeds true in F_3, and has continued to do so till F_6, while the entire fuzz either breeds true, or breaks up. There are indications that the latter process may give either a 3 : 1 ratio, or a 15 : 1 ratio, but the figures are too small. Further, there are indications of constant differences in the entire fuzz group, some being woolly, while others are felted; if a woolly seed does not breed true, it may throw out felted seeds in a 3 : 1 ratio. Felted seeds, which may be regarded as a step towards the Egyptian fuzz type, do not throw woolly ones.

It would seem that two pairs of allelomorphs are here implicated, giving a 15 : 1 ratio in F_2. The fifteen appear to consist of 12 woolly and 3 felted. In F_3 we find all the nakeds breeding true, some woollys throwing felted only, some throwing naked only, and some throwing both, while the felted forms either breed true or throw nakeds only.

An interesting proof of the tangibility of these gradations in fuzziness was afforded by a natural hybrid from Abbassi, bearing normal Egyptian slight fuzz on its seed. When selfed it threw recessive wholly naked seed derived from an unknown pollen parent. When it was crossed with American Upland we raised seven F_2 families, four of which contained the typical Egyptian seed as one plant in sixteen, while three contained the naked seed in the same proportion.

The behaviour of Hindi, the seed of which is devoid of fuzz, when crossed with Egyptian (Charara) has been somewhat remarkable. In the first generation the seed was entirely fuzzy, like an Upland. This was probably a case of reversion due to the meeting of cryptomeres, and it was naturally expected [12, 15] that the F_2 would show a ratio of 9 : 3 : 3 : 1, both the Egyptian fuzz and the Hindi fuzz reappearing. An unsuccessful sowing gave "14 entire : 3 Egyptian," which seemed to support this view. In the following year a family of 130 F_2 plants was raised, but without producing a single Hindi seed; the result was the same as if Uplands had been used instead of Hindi, namely, "123 entire : 7 Egyptian." The absence of the Hindi type in a family of this size can scarcely be accidental, and a few more crosses of this kind might throw light on the phylogeny of the Hindi cotton.

This complex inheritance is made even more interesting by the fact that a cross of the same Hindi strain with a natural hybrid of Hindi and Afifi yielded simple segregation of the naked Hindi seed in F_2.

Summarising the evidence with respect to this character we have tolerably convincing data as to the increasing complexity of inheritance when passing from varietal to reputedly inter-specific crosses, this complication taking the form of an additional pair of allelomorphs. In one case we have found reversion through the meeting of cryptomeres, and in general it would seem that the less fuzzy cottons have been evolved from primitive cottons with entire fuzz by the loss of factors. The particular factor lost has not been the same in certain strains of Egyptian as in others, nor as in Hindi; hence we obtain reversion in some crosses, though not in others. No case of reversion in inter-Egyptian crosses has yet been noted, but it is quite conceivable.

Colour of the seed-fuzz.—The presence and absence of colour in the fuzz-hairs appear to form a Mendelian pair. It is not easy to decide on the absence of colour, since the colouring matter is unstable, and in some cases fades very easily. There may be essential differences between green and brown fuzz, but the former fades very readily into the latter.

The quantity of fuzz on the parent is not coupled with colour. Thus, seeds which are practically naked, except for a most minute tuft of coloured hairs at the tip, will give rise, on crossing with white entire fuzz, to an F_1 possessing green entire fuzz. It is interesting to note that this phenomenon, together with the F_2 resulting, has been described * as an instance of the failure of Mendel's Law; it was expected that "black seed" should form an allelomorphic pair with "white seed."

Distribution of lint on the seed.—Parallel with the seed-fuzz distribution and colour, we find characters of lint distribution and colour.

The distribution of the lint is not easily recorded, there being a large subjective error involved by the combing which is required before it can be seen. Crosses of "irregular" with "regular" give a "regular" F_1, and segregation certainly seems to occur. The most convincing example of this was an F_3 from a "regular" F_2 plant. The irregularly covered seeds were clearly defined, so that the curve for weight of lint per seed showed a very

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* Cook, O. F. (1).

definite mode at the light end, consisting of eight plants as against twenty-two in the rest of the curve.[15] The extremes of the curve were 0·012 g. and 0·038 g. while the modes were situated at 0·018 g. and 0·032 g. respectively.

We may reason by analogy that the lint distribution will behave in much the same way as the fuzz-distribution, and may possibly be coupled with it in part.

Colour of the lint.—The first crosses made between Egyptians with brown lint, and Uplands with white lint, gave an intermediate F_1 of creamy hue, with simple 1 : 2 : 1 ratios in F_2 such as 12 : 21 : 11 ; the whites and browns bred true up to the F_5, while the creams broke up.

Even in these series there were manifest complications. Thus, while never transgressing the limits of "brownness," the extracted browns were by no means uniform, some being much darker than the Afifi parent, while others were lighter. We have not yet decided whether these differences were gametic, or whether they were due to "autogenous fluctuation" with other characters.

Another cross, that of Charara × King, where the parents were very light brown Egyptian, and white American, gave an intermediate F_1 as before, but the F_2 consisted of "9 brownish : 60 creamy : 109 white." This classification was made by a cotton expert, and not by the author. It is curiously reminiscent of the inheritance of petal spot, with its suggestion of gametic coupling.

The lint from F_3 of this family, and from all other families grown since, has never been examined by an expert, and since this is peculiarly a case where outside judgments are best, the author prefers to leave the discussion at this stage.

The "style" of the lint.—At present we are completely in the dark as to the real nature of the differences between such lints as Upland and Egyptian.

We know that the lint hair of the former is shorter and of greater diameter than the lint-hair of Egyptian, but there are other differences which the microscrope cannot as yet determine, though to the fingers of the expert grader of lint they are far more obvious than is the colour to his eye.

The F_1 of Ægypto-Upland crosses is always a superfine Egyptian. Thus, the mating of a "bread-and-cheese" Egyptian with a short-staple Upland gives a first cross bearing such lint as is required by the fine spinner. In the early stages of these researches we denoted this general peculiarity of these hybrids as "first-cross intensification," in the hope of explanation later. In many characters this explanation has been since obtained, but not in respect of the "style" of the lint. Until we know the component elements of "style" we cannot make much advance. It is safe to expect that such intensified characters will regress to the parental normal in later generations, but further knowledge might enable us to purify the particular combination of allelomorphs which leads to this immediate improvement. In point of fact we have raised families which breed true to an extremely fine and strong Sea Island type of lint, from the cross of King with Charara; the lint of the latter parent was of the Abbassi type.

From what has been said above it will be clear that the "style" of a lint sample is the resultant of an unknown number of unknown factors, both zygotic and gametic. When a set of F_2 samples is placed before an expert, this becomes obvious; the expert finds one lint which resembles Afifi, except that it has the colour of Yannovitch; he next meets another which has the colour of Afifi, but which he would unhesitatingly affirm to be American Upland if the room were darkened. The task of analysing an F_2 in this way is almost hopeless, however valuable the results may be for other purposes. The author is much indebted to three Alexandrian gentlemen,* who have assisted him in the past, by their expert opinion, given under all the difficulty involved by the smallness of the samples available, and their results, though open to these objections, are summarised thus :—

Afifi × Truitt :—F_1. Yannovitch ; F_2 composed of 7 Afifi, 24 Abbassi, 22 Yannovitch, together with 17 Hindi or Upland. Ratio, of Egyptian to non-Egyptian, being 53 : 17. The non-Egyptians bred true in F_3, while some Egyptians broke up. One plant from the F_2, the lint of which was described as being similar to that of the Afifi cotton when first introduced in 1887, gave a remarkable series in F_3 ; the limits of the brown Peruvian type of lint were never transgressed, but within these bounds we obtained almost every known modification ; the old Afifi, modern Afifi, Ashmouni of the Fayoum, Upper Egypt Ashmouni, and—most remarkable of all —the original Jumel cotton of Mohammed Ali's time. Within the limits of this one family there was plainly an opportunity for much research.

The examination of the King × Charara F_2 was complicated by the extreme range of lint length, which ran from 18 to 40 mm. Many plants were confessedly judged as non-Egyptian because of their shortness, and hence the fact that the ratio of Egyptian : non-Egyptian was 108 : 71, or almost 9 : 7, cannot be regarded as significant.

Summarising this and similar evidence, it would seem safe to affirm that some striking feature of the lint—possibly the diameter—is inherited as a simple factor. Complications may be introduced gametically, and also by "autogenous fluctuation." Until we can define the reasons which cause an expert to call one sample by one name and another by another, our investigation must be limited to rule of thumb.

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* Mr. E. A. Benachi, now Minister of Agriculture for Greece, and Messrs. Marco Nacamuli and H. C. Thomas, of the National Bank of Egypt.

We have now examined the nature of the problems which the non-measurable characters present. The general trend of the evidence is to show that inheritance becomes more complex as the crossed parents are less and less closely related. The amount of labour which the author has been able to apply to these problems, under the limitations imposed by natural crossing and accidental circumstances, has not been enough to produce one clean and indisputable proof for any character. Nevertheless, he believes that the preceding discussion will be found by later workers to represent the general position of a complex subject.

CHAPTER IX

HEREDITY—II.

ii. *Quantitative Characters.*

All possible characters have been investigated quantitatively, by the methods described in the previous chapter on "Fluctuation," including flowering, bolling, and shedding.

The same difficulties already enumerated have prevented conclusions from being drawn with certainty, the chief of these being the scanty F_3 data. On the other hand, we are no longer troubled by doubts as to the nature of our classification.

Presentment of all the data, the frequency polygons, correlation tables, and dissected curves, is not possible here, but it should be understood that one or more forms have been bred out pure in F_3 to F_6 for every character where a factorial analysis is suggested.

Height of stem.—The specific nature of the length of hypocotyl and first internode has already been mentioned. While the strains of Sultani and "King" Upland were being grown for this purpose, a set of F_2 seedlings from these two parents was raised in the same site and soil. Data for F_1 were unfortunately not available.

The plants were classified day by day, and the figures plotted from those plants only which had all germinated on the same day, being as exactly comparable as they could possibly be, show a very definite segregation of the two parental first-internode-lengths from one another, and from a central mode. Whether the segregation is simply in a ratio of 1 : 2 : 1, or whether it is more complex, we cannot pretend to say. It is clear, however, that in commencing to analyse the height of our hybrids, we have first to take into account the internode length.

This alone is not sufficient for us. If internode-length was the only factor, then the height of the Upland would be about half that of the Egyptian, whereas the early height of the former is rather greater than that of the latter. Again, on June 18th, in Fig. 56, the same Upland strain whose internodes we measured is equal in height to the same Sultani, both being grown side by side on the breeding plot. Hence the growth-rates must have been much the same, and the Upland merely produced more internodes in the same time. Comparing these heights with that of the F_1 on June 18th, we find that the latter is nearly twice as tall. The internodes are no longer, so that the great height of the F_1 must be due to a greater growth-rate.

The rate of growth, due to imperfectly known and constitutional causes, is thus the second factor in the height of the stem.

From these typical figures for June 20th, one hundred days after sowing, we might declare that tallness was dominant over shortness, whatever the components might be. If we follow the height-curve on to the end of September (Fig. 56) we shall see that this sweeping assertion would also be untrue, for the growth-rate of the F_1 has slowed down, though not as much as that of the Upland, while the Sultani parent is still growing steadily.

Hence the third factor in height of stem is the amount of change in growth-rate, or—as we have formerly interpreted this change—the liability to thermotoxy.

It was expected that a fourth factor would be found operative in F_2, &c., namely, the habit of branching, but all heights and growth-habits appear to be distributed evenly throughout all the branch-types, from plants without monopodial branches at all,* up to plants in which the main axis was scarcely recognisable.†

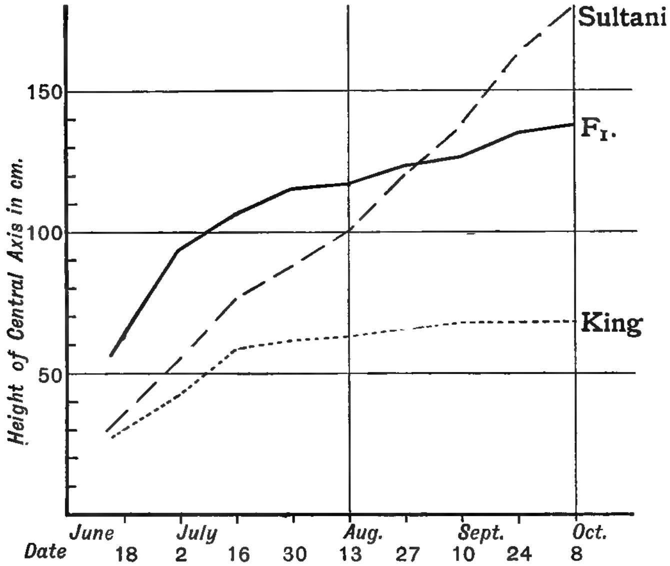

FIG. 56.—GROWTH OF STEM.

Parents F_1 of an Ægypto-Upland cross. Means of families.

The heights of the F_2 plants are therefore dependent on the three components first enumerated, but although we have described them as "factors," they may be each the resultant of more than one factor in the Mendelian sense, as is the colour of the petal. Within the limits of

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* See Leake, H. M., (2), (3), and W.L.B. (5) (8) (15).

† *Cf.* Bateson, W., in *Lathyrus*.

this book we cannot compress a full set of F_2 data, like the set given for fluctuation (Fig. 48), but the three main features are as follows :—

A. The internode-length of the parents reappears in F_2 forming modes in the curve.

B. The early rate of growth varies in normal plants, even if we dissect the curve of "growth-rate in June" into any component groups we may choose. Thus, taking only those plants which afterwards showed the habit of continuous growth, and omitting all but the normal seedlings, we find the growth-rate ranging symmetrically in thirty-five plants from 3·6 to 17·8 mm. per day. Moreover, on plotting these growth-rates against the ultimate height of these plants at the beginning of October—which is legitimate, since their growth curves were all "continuous"—we find a close correlation, with a value for "*r*"

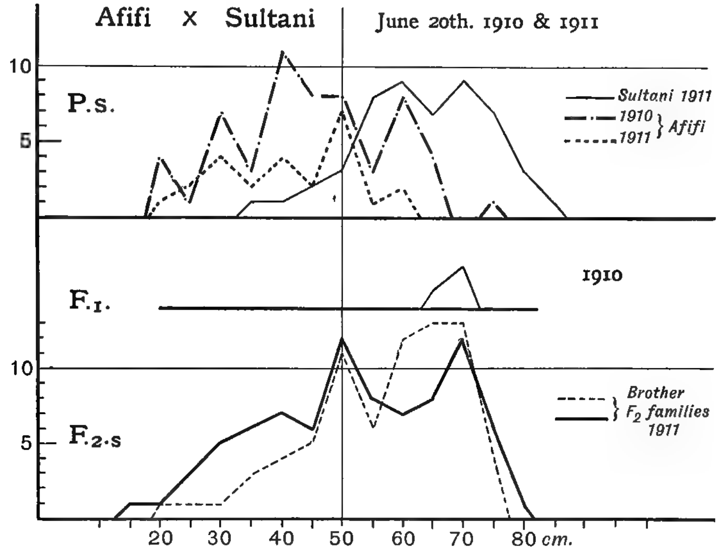

FIG. 57.—HEIGHT OF STEM IN JUNE.

Individual plants.

of not less than 0·622. The initial growth-rate of the F_2 plants therefore ranges at least as high as that of the F_1 and at least as low as that of either parent. (See also Fig. 57.)

C. Over and above this incomprehensible factor of "growth-rate," which needs the repetition of such experimental work as we have described under "the Individual" on every plant of a large F_2 before we can interpret it, we have also the change in growth-rate, affecting the height of the plants after the end of June, or earlier, which we have endeavoured to interpret in terms of specific liability to thermotoxy. On classifying the individual growth-curves in a family of 179 F_2 plants, we find that they were grouped as follows :

Continuous growth, like Egyptian parent	52
Doubtfully continuous	29
Doubtfully like F_1	27
Semi-continuous, like F_1	30
Doubtfully like F_1, being semi-discontinuous ...	30
Like American parent	9

Thus a small percentage of plants reappears in F_2 with the high thermotoxic susceptibility of the American Upland parent. It might be pointed out that the figures *could* be fitted to a 9 : 3 : 3 : 1 ratio, two pairs of allelomorphs being involved, namely, presence and partial absence of "x-production" and of "x-removal"!

There does not appear to be any necessary correlation between any of these factors in their distribution amongst individuals. A plant with a low initial growth-rate may have the habit of continuous growth and short internodes: strains of such plants have been bred out to F_4 and have remained pure. Such plants are short in the stem. Shorter still are those plants which have the discontinuous growth-habit, with short internodes and a low growth-rate. At the other extreme we meet plants with a high growth-rate, long internodes and continuous growth-habit. Consequently, it is not surprising that the curve showing the height of an F_2 at the end of the season exhibits continuous variation from one extreme to the other, especially since we have seen that the fluctuation in height is by no means

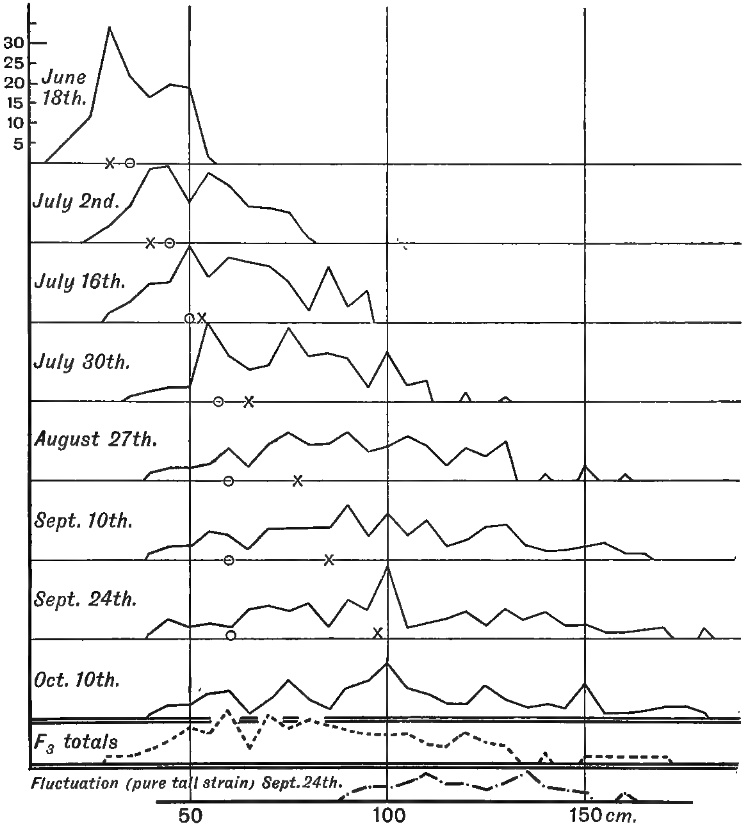

FIG. 58.—HEIGHT OF STEM IN F_2 OF KING (o) by CHARARA (×).
Stunted and damaged plants excluded. Ledger page, like Fig. 48.

inconsiderable in a pure strain. There are modes in this curve, nevertheless, and the following result shows that they are not due to accident.

The F_2, the heights of which in 1909 are shown in Fig. 58, was used to provide an F_3 from some thirty of its members in 1910. Most of the plants chosen for this purpose were—for subjective reasons—short in the stem. Plotting the aggregate height of all the normal F_3 plants in 1910 against the same date in 1909, we see the same modes reappearing, in spite of the differences of soil and season (Fig. 58). These modes become less markedly coincident amongst the taller F_3 plants, but the general result indicates that such modes are due to definite constitutional causes, inherent in the plants themselves.

The form of the leaf.*—The component characters of leaf-form appear to be the length of the mid-rib (*L*) the distance from sinus to petiole (*S*), and the angle of the sinus from the petiole relatively to the mid-rib (*/s*).

Two other components which we have not examined in detail for more than one family are, the angle made by the first lateral vein with the mid-rib, and the presence or absence of a second lateral vein and lobe.

The three first components are concerned with the form of the central segment alone, but even in this respect we find more problems than we can solve.

Taking the length (*L*) first, we have already seen that it is correlated with height of stem, in some obscure manner. King Upland, with a mean leaf-length of 75 mm., crossed with Charara, the mean leaf-length of which was about 135 mm., gave an F_1 with leaves rather shorter than Charara, and this by selfing produced an F_2 which ranged from 70 to 195 mm., with slight indications of modal grouping; most of the plants lay between the parental measurements (Fig. 59). This curve was dissected in various ways, thus, the plants with the "continuous" growth-habit had larger leaves than the rest, but although none of these plants had extremely small leaves, yet moderately small leaves were found as a detached group. Further dissection of this group never succeeded in

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* See Leake, H. M. (1) (3).

producing a group of plants with leaves of identical length (*i.e.*, identical within the *P.E.* of fluctuation). Thus it seems highly probable that the length of the leaf is inherited as a separate character, although it is distorted

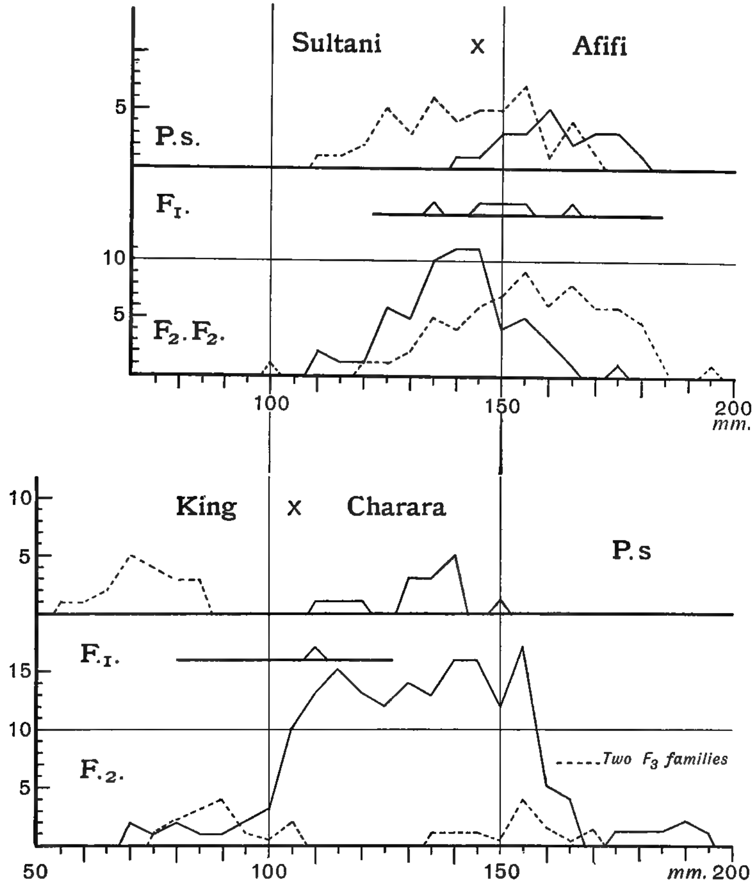


FIG. 59.—LENGTH OF THE LEAF.

from the parental length by autogenous fluctuation. The same probability is suggested by correlation diagrams for leaf-length with height, with petal length, &c.; such diagrams show a distinct indication of isolated groups, such as we shall inspect shortly in the flower measurements.

The next character "*S*," or distance from petiole to sinus, is inherited in much the same way as *L*. We can eliminate the diversities in absolute size by expressing *S* in terms of *L*, *i.e.*, plotting for the ratio S/L. We then find that an Upland leaf, in which *S* is relatively long when crossed with an Egyptian in which *S* is relatively short—or, in other words, slightly and deeply dissected leaves—give rise in F_1 to a leaf very like the Egyptian, but with a slightly longer *S*. In F_2 we obtain the same modal curve, stretching to the parental extremes. Correlation diagrams for *L* and *S* in F_2 show modal grouping and no general correlation. In other words, the length of the sinus is inherited independently of the length of the mid-rib. Now this sinus-measurement is determined by the plant at a very early stage in the primordia, since we find freshly expanded leaves showing the same form as adults; hence a factorial determination is highly probable. It is necessary to express *S* in terms of *L*, on account of the diversities of *L*. Thus, if we plot *S* simply, we find, *e.g.*, in the King × Charara cross, that the parents are identical, while the F_1 is 60 per cent. longer. It is, of course, quite possible that our use of *L* as the expression for mere size may be fallacious, but this would not affect the general argument for factorial inheritance of form.

The last component of the form of the central segment is $\angle s$. We have formerly seen that the position of the sinus fluctuates along the angle-lines, so that instead of using *S* and $\angle s$ we might employ $\angle s$ and $\angle t$, the latter being the angle made by the sinus with the mid-rib from the tip of the latter.

On crossing the narrow angle of Upland with the wide angle of Egyptian we obtain a wide angle in F_1. In F_2 we obtain the same wide and modal curve on plotting the angle values, with some indication of simple segregation of narrow angle from wide, which is probably fallacious.

The next point to consider is the inter-relationship of these angles, and whether a wide $\angle s$ is necessarily linked with a narrow $\angle t$ as in the Egyptian parent. The result of dissecting our curves in this way is very definite; there is no such linking. Thus, taking the 26 plants which had the narrowest $\angle t$ in an F_2 of 180 individuals, we find that while 24 had very wide $\angle s$, there were two with a very narrow $\angle s$, far removed from the rest. Conversely, taking out the 26 plants with the widest $\angle t$, we find from one to five possessing very wide $\angle s$, while the rest had narrow $\angle s$. Thus the two angles may definitely be said to be inherited factorially, and the origination of new leaf-forms in F_2 need no longer be surprising.

Flower form.—The characters studied in the flower were the length of the petal, style, and column, measured from the apex of the ovary cavity, the length of the filaments, and the width and length of the involucral bracts. The form of the corolla has not been examined; it ranges from an open cup to a long narrow one.

The story of the inheritance of all the first four characters is much the same. In the first cross studied we found that by correcting for fluctuation, taking the petal length as the standard because it has been the same in both parents, our graphs for the F_2 composition assumed the 3 : 1 form.[13, 15] Long was dominant over short, and all the extracted shorts tested bred true up to F_6. Here, in spite of the Ægypto-American crossing, the characters seemed to be under the control of a single pair of factors. In this way we bred out the "short-style flower" mentioned in connection with natural crossing (Frontispiece).

In the King × Charara cross we found indications of segregation in petal length also, and it was in this connection that we developed the correlation-diagram method of seeking for segregation (Figs. 53 and 60). The method is essentially the same as the use of the slide-rule, but it enables us to deal with two variables, without correction.

If long and short petals are represented by *A* and *a*, and the style lengths similarly by *B* and *b*, and there is no mutual interaction, then we obtain

9 Long petals with long style, *AB*.
3 Long petals with short style, *Ab*.
3 Short petals with long style, *aB*.
1 Short petal with short style, *ab*.

Now if the correlation of the two dimensions within any given flower is almost perfect, we shall obtain such a correlation diagram from the F_2 as that shown in Fig. 53 (upper). The *ab* group is almost continuous with the *AB* group, and is scarcely to be differentiated from it. The *aB* and *Ab* groups lie on either side of this diagonal compound scatter. Thus, on working out the value of "*r*" for the whole table we shall obtain quite a low value, whereas it is in reality a case of almost perfect correlation. Comparing this with the observed result obtained for the King and Charara F_2 as shown in the lower half of the figure, there can be no possible doubt that some such grouping is really present. The parents and the F_1 are marked on the diagram as A, E, and F. The F_3 data of the cross confirm this conclusion, so far as they go, and the probability is high in favour of the view that even the semi-smooth Gaussian curves of error shown by the length of petal, style, column, and filament in the F_2 of this cross are (Fig. 60) essentially nothing more than simple 3 : 1 curves, which have been deformed by fluctuation, both autogenous and ordinary.

With regard to the form of the bract and its width there is nothing definite to be said. Narrow bract is dominant over wide, just as narrow leaf segments are dominant over wide segments, and narrow bolls over wide bolls. The F_2 ranges from one extreme to the other in a modal curve, and pure strains have been extracted, but no details are available by which the stages of this segregation can be traced.

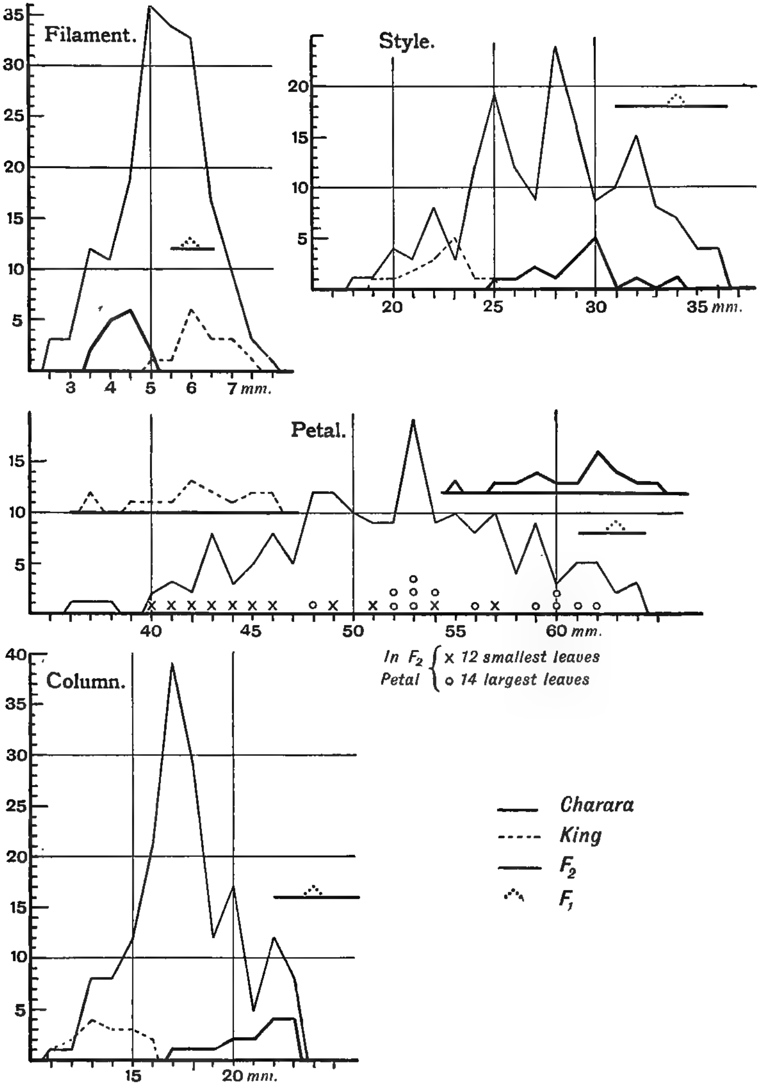


FIG. 60.—FORM OF THE FLOWER IN AN ÆGYPTO-UPLAND CROSS.

Width and form of the boll.—The Upland boll is usually wider and more nearly spherical than the Egyptian boll. Differences also exist within the Egyptian strains, some approaching the long narrow boll of the Sea Island type. The form is expressed as $\frac{\text{width}}{\text{length}}$. A cross of Upland with a mean form of 0·75 and a width of 31 mm., upon an Egyptian with a form of 0·58 and a width of 27 mm., gives an F_1 with a form of 0·60 and a width of 32 mm. In other words, the long narrow form is dominant though very much larger than the long narrow parent. (Figs. 61 and 62).

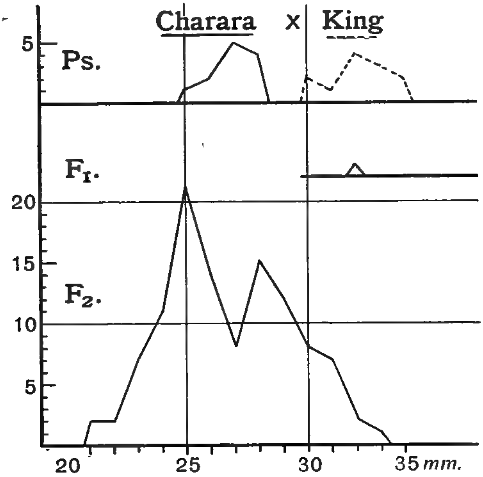


Fig. 61.—Width of the Boll.

The F_2 of such a cross ranges up to the F_1 width and form, but includes plants the bolls of which may be as narrow as 0·44 and 22 mm. So far as mere width is concerned, this might well be due to autogenous fluctuation, but the new form of the extremely narrow bolls cannot be attributed to this cause. As in the case of leaf-form, we are probably dealing with a compound inheritance, and the new forms are the result of recombinations of allelomorphs.

A side-light on this interpretation is provided by plotting the correlation table of form against width in F_2. While the general trend of the diagram indicates positive correlation between wider boll and more spherical boll, yet on comparing such a diagram with that from a pure strain, it becomes clear that the F_2 family is heterogeneous.

Again, families have been raised in F_4 which showed no more fluctuation in width than the parent strain, while the form varied over double the range which could be attributed to fluctuation.

One autogenetic factor in the width of the boll is the number of boll-loculi. Without attempting to correct for any possible modality in the diagram we found the value for correlation between these two characters in F_2 to be "r" = 0·331 (± 0·061). The explanation is presumably mechanical; the bolls with more loculi have more septa, and these occupy more space, hence the boll diameter is greater.

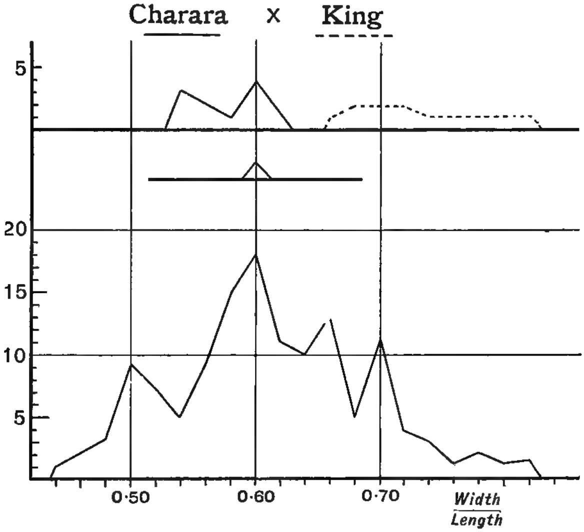
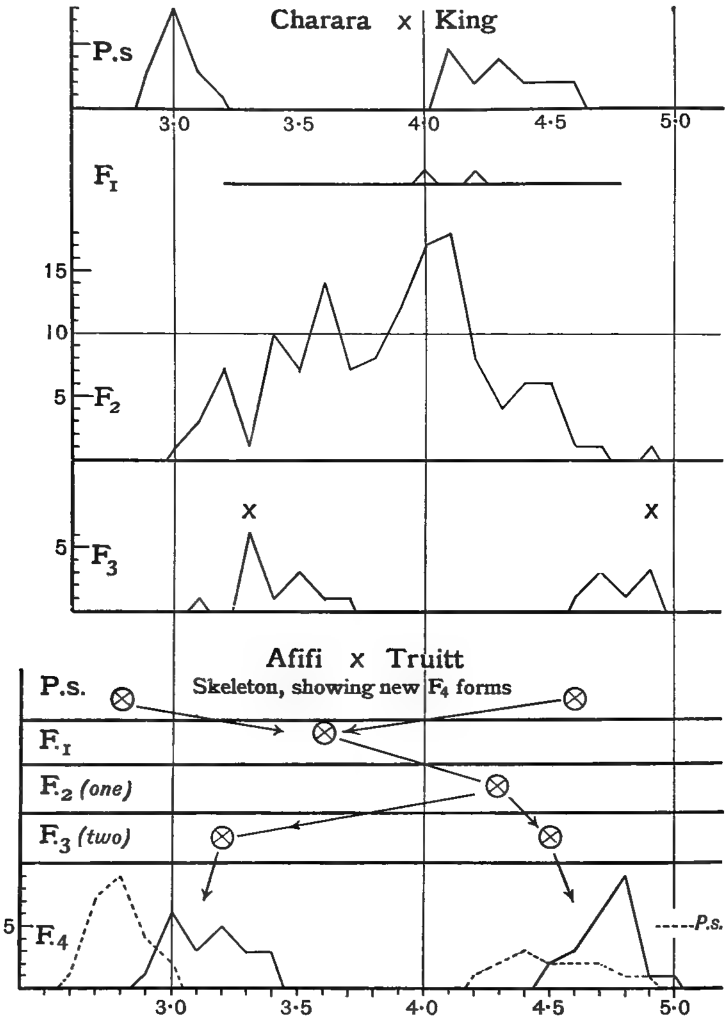


Fig. 62.—Form of the Boll.

More information on these two characters is highly desirable, because of their economic importance.

The loculi of the ovary.—The inheritance of this meristic character is of peculiar interest, since it is not a character of form, but of distribution, and analogous to such things as the number of ray-florets in the *Compositæ*.

A cross (Fig. 63) between an Upland with its mean at 4·3 and an Egyptian with a mean at 3·0 produced an intermediate F_1 with the formula 4·1. In F_2 this family gave a range of 3·0 to 4·7, with modes at 3·2, 3·6, 4·1, 4·4, and possibly elsewhere. In F_3 a 4·8 bred true to 4·8, and a 3·1 bred true to 3·2. On the other hand, 3·3 broke up into a scatter from 3·1 to 3·7, as did also a 3·6.



Figs. 63 and 64.—Loculi of the Ovary.

A 3·9 plant appeared to breed true round a mean of 4·1, while a 3·8 scattered from 3·8 to 3·3. Similarly, a 4·0 scattered from 3·9 to 3·2, and so on. On the data available it seemed clear that the parental forms could be extracted and bred true, while the intermediate forms represented new gametic combinations which broke up in new ways, giving new forms. No large family having been raised beyond F_2 in this cross, we may examine the data from another one.

The Afifi × Truitt cross had 2·8 and 4·5 as the parental values (Fig. 64). The figure 4·5 is uncertain, because there was every indication that the American parent was heterozygote in this respect. The F_1 had 3·6 loculi, and the F_2 spread from 2·9 to 4·8. Only five F_3 families were raised; one of these was derived from a 3·3 plant, and its twenty-one offspring ranged from 2·9 to 3·4, thus resembling the Egyptian parent closely but not exactly. Another 3·3 behaved in the same way, and repeated this behaviour in F_4. Conversely, a 4·8 gave only 4·6 to 4·9; while a 4·5 gave 4·2 to 4·6. The offspring of a 4·3 form broke up into a wide scatter from 3·3 to 4·9; several small families of these were bred on into F_4, but the largest and most interesting was one from a 4·5 plant, which consisted of twenty-nine plants, ranging only from 4·5 to 5·0, and giving a frequency polygon with the same probable error as the parent.

The inter-Egyptian cross was expected to unravel a portion of this tangle, but although the critical numbers were doubled, and the data classified to half-grades the result was much the same (Fig. 65). Sultani (3·20) crossed by Afifi (2·80) gave an F_1 at 3·00. The F_2 of this broke up with great symmetry over the parental extremes with a single mode at the F_1 value. The spread of this curve of the F_2 is too narrow to be the expression of a 1 : 2 : 1 ratio, so it is probable that at least two factors are involved even here. There is a slight indication of the possible nature of these factors, namely, differentiation and coalescence, but it is not worth further consideration until we possess the data from later generations.

This Afifi × Sultani cross was made principally in the hope of obtaining a simple inheritance of this particular character. Although it has failed to give the expected simplicity it is still less complex than the Ægypto-American crosses. The graphs are most strongly indicative, to the unbiased mind, of the formation of a new character in F_1, which subsequently breeds true; nevertheless, in the light of the other crosses, there can be little doubt that such is not the true interpretation.

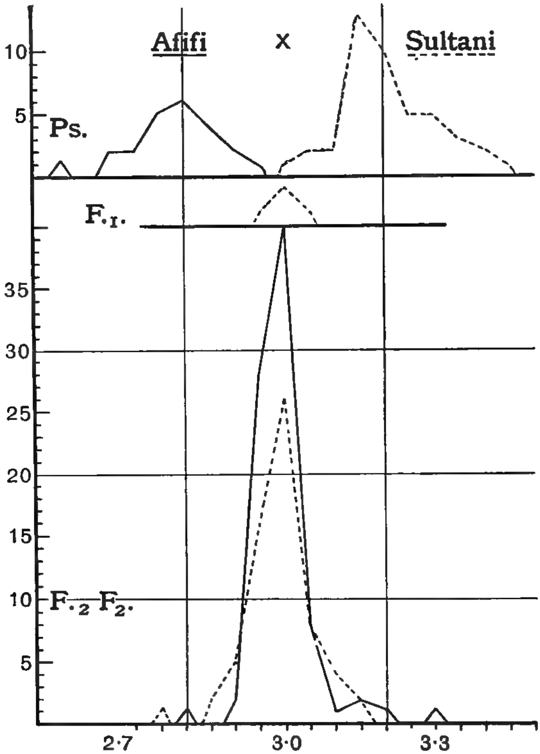


FIG. 65.—LOCULI OF THE OVARY.

The weight of the seed.—The inheritance of the mean seed-weight is particularly interesting. In the first place it fluctuates more than any other character, excepting the height, and it further shows clear evidence of autogenous fluctuation.

The first cross in which this character was carefully examined was Afifi × Truitt (Fig. 66), where the mean seed weights were 0·105 g. and 0·135 g. The seed weight in F_1 was 0·165 g. In F_2 the weights ranged from 0·08 to 0·175 g., with two marked modes at 0·095 and 0·115. The form of this F_2 graph suggested that light seed was segregating from heavy seed, and on testing this by breeding on, we found no reason to modify this conclusion; thus, a plant with seed weighing 0·100 regressed slightly in F_3 to a mean of 0·090, with a scatter from 0·070 to 0·110, and no higher probable error than the parent strain; and F_4 raised from a 0·090 plant of these gave the same result, ranging from 0·065 to 0·110. The plants of the F_4 had been extremely diversified in most other characters, such as height, while the F_4 was almost a pure strain.

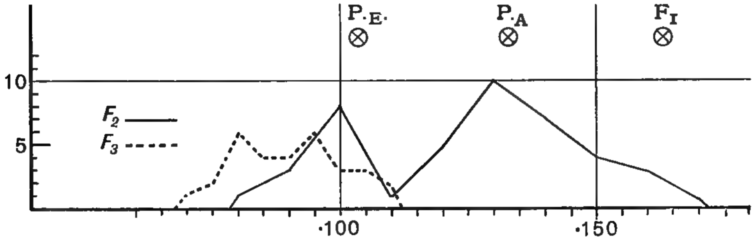


FIG. 66.—MEAN SEED-WEIGHT.

Afifi × Truitt, showing extraction of small seed in F_3.

Whether the segregation was simple or compound, it was clear that the size of the seed—expressed by us as weight—was an inherited characteristic.

In another cross, namely Charara × King (Fig. 68), the matter became more interesting, and the inheritance obviously complex. The seed weights of the two parents were substantially the same, being 0·085 for the American, and 0·095 for the Egyptian. The weight of the F_1 seed was 0·145. Thus a very marked "intensification" had taken place, and the problem of finding the cause was set to the author. The seed weight in F_2 gave an unexpected frequency polygon; instead of a 3 : 1 form we obtained a modal curve, otherwise fairly symmetrical, which ranged from 0·055 to 0·170; the principal modes were situated at 0·085, 0·105, 0·120, and 0·140.

Before discussing this graph any further we may note that the F_3 data were of the same nature as those described under the preceding character; the parental small seed was extracted and bred true, while larger seeds sometimes threw small ones in a way which suggested a 3 : 1 ratio, or less commonly bred true. In the latter case a new character, not found in either parent, had been "fixed." In the ordinary Mendelian characters such phenomena are usually due to the meeting of cryptomeres, but we shall see that our cryptomeres in this case are even less cryptic than Miss Wheldale's enzymes in *Antirrhinum.*

The attempt to dissect the F_2 graph into its components led to the plotting of numerous correlation tables, and to the preparation of "dissected graphs" (Fig. 69). In the latter method, which is more rapid than the former, we take plants possessing some character in common, such as a very large boll, and mark off their position on the graph of the whole family. The mean of the special group, as compared with the general mean, serves to indicate any displacement, while the form of the "dissection" is usually less complicated than that of the general graph. On dissecting in this way for the fifteen plants which had the greatest boll-width of the whole 181 F_2 individuals, the mean seed-weight was raised by 0·0105 g.; moreover, though these large-boll plants constituted the greater part of the 0·140 mode, yet four of them were found in the 0·085

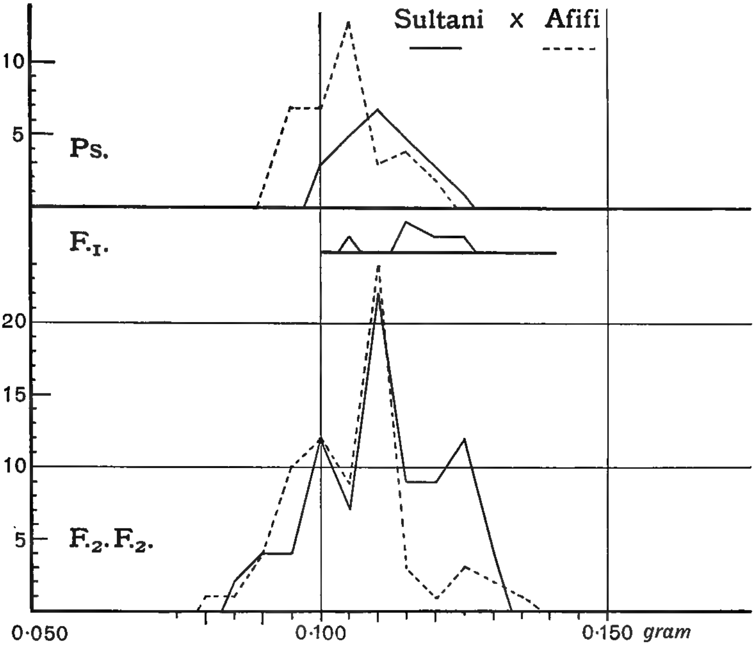


FIG. 67.—MEAN SEED WEIGHT IN INTER-EGYPTIAN CROSS.

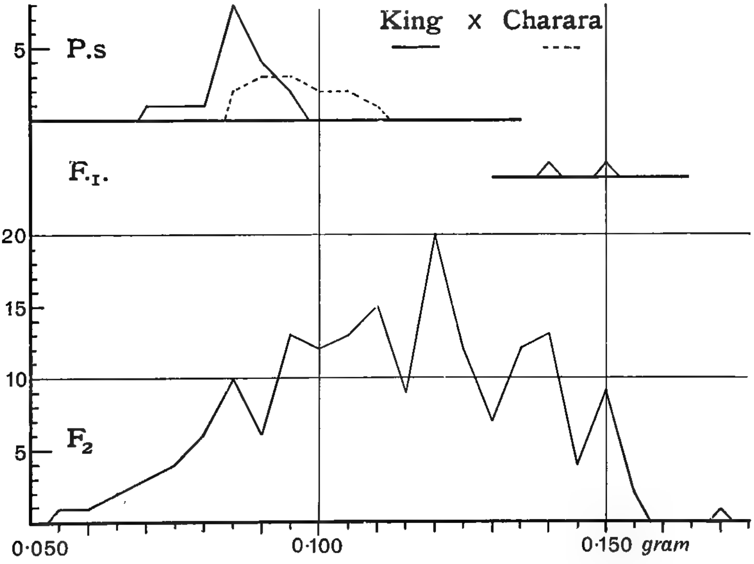


FIG. 68.—MEAN SEED-WEIGHT IN ÆGYPTO-UPLAND CROSS.

mode. This result indicated correlation of big-boll and big-seed, with segregation of big seed from small within the group. Similarly, on dissecting for the twenty-four smallest bolls, the modes were at 0·105 and 0·075. On plotting the correlation diagram it was found to give a value for "*r*" of about 0·3, but this diagram was distinctly modal, the points being grouped, so that the true value of "*r*" was probably very much higher.

Similar dissections were made in respect of almost every character available. In no case did the groups show uniform seed weight within the error of fluctuation. Either the new group was evenly distributed over the graph, there being no correlation, or else it moved to one side. In the latter case, the group always assumed the 3 : 1 form. The most interesting of these for comparison with the big-boll dissection was the dissection for "discontinuous habit of growth"; the twenty plants which most resemble the Upland parent in this respect did not exceed 0·130, and formed two modes, one on and behind 0·085, the other on 0·105. Again, though classification according to habit of branching showed no marked shifting of the group-centre, yet the "unbranched" plants filled up the 0·120 mode, while "freely branched" occupied the mode at 0·140 (Fig. 69).

Two general conclusions result from this analysis. Firstly, that the modes in the F_2 curve are genuine, and largely due to autogenous fluctuation.

Secondly, that the F_2 curve consists of superposed curves having the 3 : 1 form, but mutually obscurant until groups of comparable individuals are taken.

Thus we have shown that light seed is segregating from heavy seed in F_2, probably as a simple pair of allelomorphs, just as in the Afifi × Truitt series. The only serious weakness of this view lies in the fact that both the parents were light-seeded! The Upland parent, however, bore these light seeds inside a boll of 32 mm.

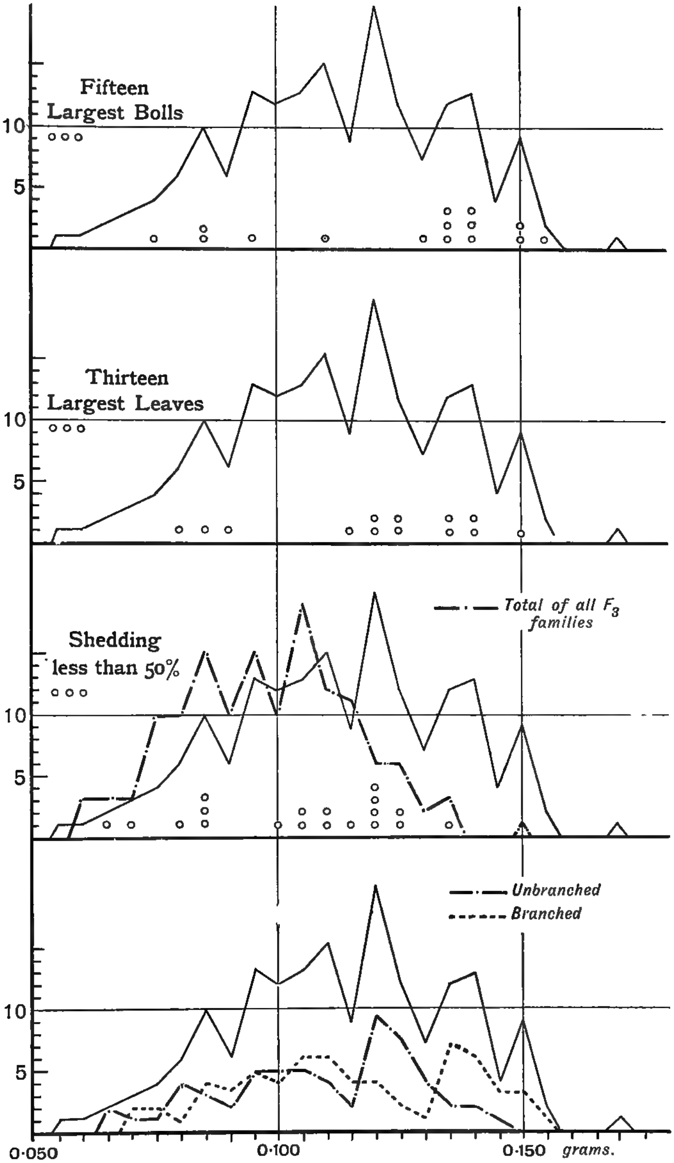


FIG. 69.—DISSECTION OF MEAN SEED-WEIGHT IN F_2.

The F_2 curve of Fig. 68, dissected in respect of four correlated characters.

diameter, while the Egyptian boll was only 27 mm. in diameter. On crossing the two strains we effectively placed the Egyptian seed inside a boll whose cubic capacity had been doubled, and an increase in seed-size followed. Thus we may regard the Egyptian seed as being constitutionally large, and dominant over the genuinely small Upland seed. At gametogenesis in F_1, the two seed-weight allelomorphs separate from one another, and the 3 : 1 ratio appears in F_2 if we clear away the lumber brought in by autogenous fluctuation.

We have discussed this masking of the difference in seed-weight, and the development of the difference under equal opportunities, in terms of boll-width alone for convenience, though other factors are also involved. The displacement of the means for such dissected graphs, when compared with the probable error of a pure strain, which is obviously too stringent a test for these heterogeneous groups, gave significant deviations in respect of "discontinuous growth"; a slight but significant deviation with respect to branching; a slight indication of connection between extensive shedding and heavy seed, which is probably indirect, since "discontinuous growth" sheds less than the other types; and a very marked relation between wide or narrow boll and heavy or light seed respectively. In the last case the figures were as follows:—

36 Widest bolls.	Mean seed-weight	+ 9·4%	(*P.E.* × 3·2 = 4·3%)
24 Narrowest bolls.	,, ,,	− 13·2%	(*P.E.* × 3·2 = 5·3%)

The simple cross of Sultani × Afifi showed dominance of heavy seed over light in F_1 (Fig. 67), and although the difference between the two parents was very small, yet some indication of segregation is shown. This takes the form of two modes in the F_2 curve, which appear in both the brother families; since the mean weights are computed, and hence do not suffer from any subjective error, this coincidence is probably significant, and due to the superposition of a small-seed mode on the flank of a large-seed mode.

Summarising the evidence, it would seem that beneath all the complexity involved by fluctuation, by autogenous fluctuation and by correlation, there existed in all these hybrids a straightforward segregation of seed-size, controlled by a single allelomorphic pair of factors in every case.

The mean maximum length of the lint.—The inheritance of this character has been curiously similar to that of seed-weight, but the evidence is not so clear. The Afifi × Truitt cross showed segregation which was ostensibly simple, long being dominant over short; the Charara × King cross gave dominance of length in F_1, with subsequent modal composition in F_2. Sultani × Afifi again gave dominance of length, and the F_2 curve was almost symmetrical between the parental extremes (Fig. 70).

Subsequent generations have shown that pure parental length can be extracted, while new intermediate lengths may also breed true.

Dissection of the F_2 revealed a similar series of phenomena to those shown by seed-weight. In this case, the most definite result was obtained by grouping to seed-weight; the 28 largest seed-weights had a mean lint-length which was 5·9 per cent. above the general mean, with modes at 26½ and 32 mm., the form of the dissection being that of the 3 : 1 type (Fig. 70). Conversely, the 27 smallest seed-weights were 5·9 per cent. below the mean general lint-length, with modes at 21 and 27 mm.

It thus seems highly probable that lint-length is also inherited simply, in spite of the seeming complication of the Charara × King second generation.

Miscellaneous.—All the characteristics mentioned in the chapter on Fluctuation have been made the subject of

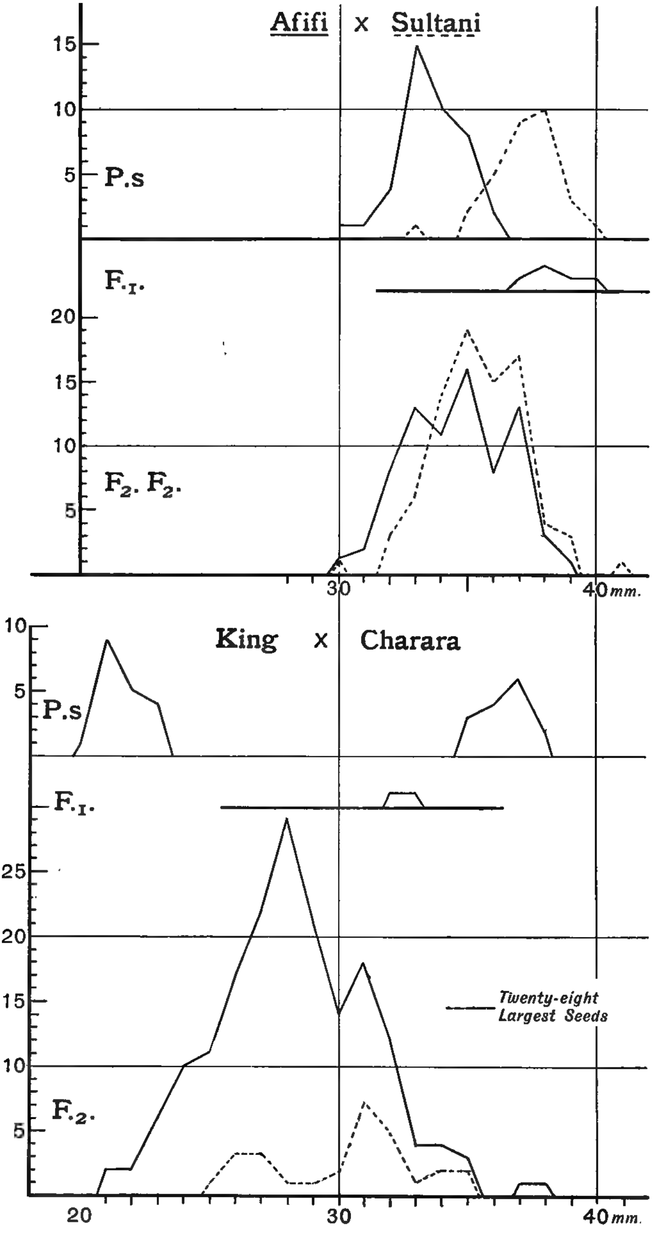


Fig. 70.—Mean Maximum Lint-Length.

statistical records in the ordinary course of routine observations. Thus we possess the curves for growth, flowering, bolling, and shedding for almost every individual studied. Data for weight of lint per seed, and for ginning out-turn are also to hand, but the majority of these records are of more value as supplementary sources of information in physiology than from the standpoint of Genetics. At the same time, they are frequently of interest as showing the commercial resultant of those conflicting gametic forces whose lines we have endeavoured to trace.

SECTION IV

CHAPTER X

ECONOMICS *

WITHIN the limits of this volume we can do no more than glance at the many matters of economic interest to which those researches are linked. Their most direct and immediate application has been found in the Sub-Soil Water controversy, from which many of the inquiries originated. No attempt has here been made to emphasise the economic importance of root asphyxiation and restriction, but the text and diagrams should show that a deep water-table is essential, and that a rise of the water table to the roots is deadly in July, prejudicial in September, and almost harmless in December. For several years the yield per acre in Egypt had been lessening (Fig 71), and many causes[24] had been invoked to account for it, but the matter was obscure until Mr. J. R. Gibson, assisted by M. Audebeau, showed that the level of the water-table had risen on the State Domains, and pointed out the probability that such a rise, produced by improvements in the system of irrigation, might suffice as a general cause.[13, 15] Mr. Gibson's death deprived the author of his collaboration

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* See Todd, J. A., for discussion of the purely economic problems of cotton in Egypt and Lancashire.

in developing the biological side of this hypothesis, which —after three years of animated discussion [16, 17, 18, 24, 27]— has now become a factor in the administration of Egypt.*

The original hypothesis is still unproven, and must so remain, in the absence of extensive records to show the water-levels of past years, but so strong a case has been made out for the presumption † that, when taken in conjunction with the physiological evidence summarised in the present volume, the proof may be regarded as exhaustive. The preliminary solution of one of the neatest problems ever set to agricultural science has thus been

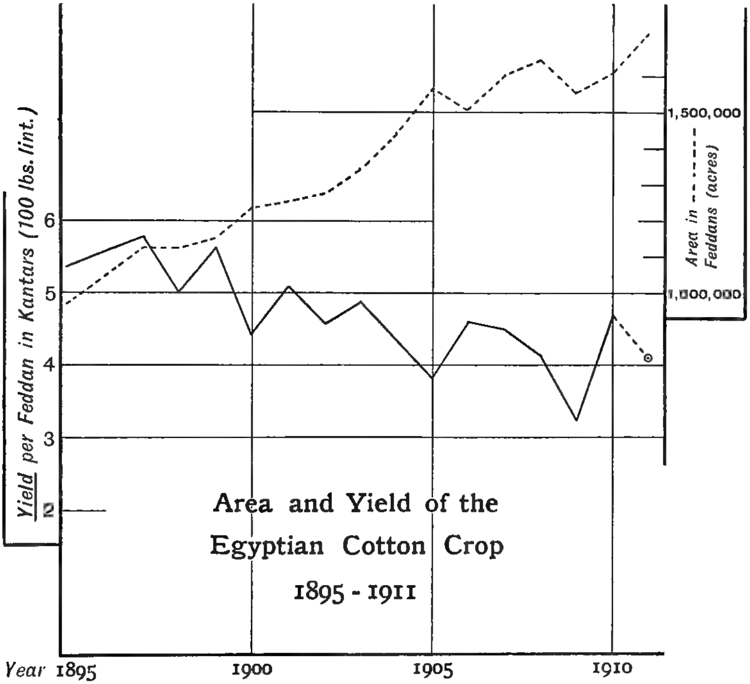

FIG. 71.—AREA AND YIELD OF THE EGYPTIAN COTTON CROP, 1895-1911.

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* Report of Cotton Commission, 1910; Reports of H.M. Agent and Consul-General on Egypt and the Sudan (Egypt No. 1) 1910, 1911, and 1912.

† Ferrar, H. T.; Lucas, A; Audebeau, C.

achieved, on a crop which is worth twenty to thirty millions of pounds per annum.

Concurrently with the depreciation of yield, there had also been a depreciation of quality in the chief variety grown.[7, 15, 32] This latter trouble was partly due to the same cause, but chiefly to varietal "deterioration."

The coincidence was extremely unfortunate, for the short crops led to inflated prices,* which were intolerable with a degrading quality; the consumers, driven to experiment with inferior cottons, succeeded beyond all expectation in the substitution of long-staple Upland, and even of ordinary Upland, for Egyptian cotton. The typical Egyptian cotton has thus lost the monopoly which it formerly enjoyed.

The remedies for these two troubles are now being applied,† to wit, drainage and restricted irrigation in the first case, together with the supply of better seed in the second. With regard to seed-supply we have seen that the problem is essentially the avoidance of natural crossing, since "deterioration" must ensue if a single foreign pollen-grain enters the pedigree. By cultivating pure lines in bee-proof cages, propagating from these in isolated sites, or in plots protected by related populations, and by *renewing continually* the seed-supply of any strain in this way from the laboratory through seed-farms, the varieties of the future will be proof against "deterioration," unless mutation takes place. It cannot be too strongly insisted upon, that any scheme for the introduction of new cottons is doomed to ultimate failure unless continual replacement of contaminated stocks is taking place every year from the original pure strain.[5, 32]

The demands of Egyptian cotton upon the cotton-breeder,[5, 7, 15] apart from this question of purifying and

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* Todd, J. A.

† Lord Kitchener's Report on Egypt and the Sudan, 1912.

distributing the existing varieties, have sunk of late years into insignificance, through contrast with the urgent call for physiological information. Still, they are by no means trivial, and once stability is restored to the supply of Egyptian cotton, there will be room for much improvement in detail. The chief interest of the data on genetics [5, 8, 15, 20, 30] relates to the extension of cotton cultivation into fresh countries and climates. The reader will probably concede, whatever may be the soundness of the interpretations given, that there is no doubt as to the formal nature of the inheritance of various characters in cotton crosses, even where such inheritance appears most dependent on simple chance. Such characteristics as yielding-capacity, earliness of maturity, climatic suitability, and others of agricultural importance, are the outcome of complex and interacting combinations of allelomorphs, and must in no way [19, 20, 25, 30] be considered as simple things; but sufficient time and research will ultimately deduce the laws of their transmission, now that the said research has been placed on a precise basis. The outcome of such deductions must be that the colonial agriculturist of the near future will no longer carry a bag of seed, searching for a district in which it will grow to the consumer's liking, but will choose his district first, and then manufacture a cotton plant to suit it. A further impetus towards the precise study of genetics will be given by the specialisation of manufacturing processes, demanding more various types of raw material, each suited to special purposes, and therefore worked up with greater economy. The aeroplane is already beginning to affect the Egyptian fellah.

An important advantage of seed-supply projects lies in their simplicity from the viewpoint of the native cultivator, who is usually prejudiced and frequently unskilled. A change in the variety of cotton supplied to him causes no change in his habits or methods, and interferes less with his personal freedom than any other manifestation of the "march of progress."

With regard to the general cultivation of cotton, these researches have thrown into prominence the immense importance of the root-system, whereof—in a limited sense—the aërial portions are only the visible expression.[7, 13, 15, 16, 26, 27, 29] It seems probable that a great deal of botanical research in the coming twenty years will be subterranean. Researches have also cleared up the causes of seed-failure, have obtained some general expressions for the effect of environment on development, and by means of a system of records, which can be kept with no more trouble than meteorologists' observations, they have thrown light on the causes of variation in crops from year to year, and from place to place, in the form of certain curves of flowering, bolling, and growth, which have a precise value.

The designation of lines upon which to drive our wedges still further into the mass of available material is almost impossible, since the most valuable results are usually obtained by following out a side line, which in its turn has been detected through the accidental direction of attention to a commonplace phenomenon. Knowledge of the changes in water-content of various layers of soil can be applied directly to irrigation practice, study of the growth processes in the fruit will demonstrate the causes of fluctuation in the grade of the commercial product, and any information about the infectivity of foreign pollen may reveal the way by which the contamination of varieties can be eliminated. Lastly, it should be borne in mind that most of these researches are based on evidence collected at the apex of the Egyptian Delta, so that there is a long field of operations in which our present results may be re-examined, stretching from the Mediterranean into the heart of the Sudan.

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