Proceedings Joint BCPC and BPGRG Symposium - 'Opportunities for Chemical Plant Growth Regulation' (1978)

ECONOMIC FACTORS AFFECTING THE FUTURE DEVELOPMENT OF PLANT GROWTH REGULATORS IN AGRICULTURE

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Summary The development and introduction of new technology has been a fundamental ingredient of economic growth in agriculture. Many of the advances which have contributed to the rapid productivity improvements since the 1940s are of recent origin, but have already become very widely adopted. Further output increasing and cost saving innovations are needed if the momentum of growth is to be sustained, and it is possible that plant growth regulators could provide an area for advance. If progress is to be made, however, greater resources will have to be devoted to growth regulator research. This will in turn rest upon the development of a greater understanding of the exact nature of research targets large enough to repay very large investments - essentially targets related to major arable crops - and advances in developing suitable screening techniques.

ECONOMIC FACTORS AFFECTING POTENTIAL DEMAND

Agriculture has played a vital role in the economic development of the developed world by providing abundant supplies of food at constant or declining real prices and releasing large numbers or workers to the expanding industries in the non-farm sectors of the economy. This process has been made possible by a steady rise in agricultural productivity; increases in the efficiency of use of land, capital and, most strikingly, labour. The increases in labour productivity have occurred both as a result of rising yields per hectare and increases in the area of land farmed per man (1, 2, 3, 4). Continued agricultural productivity increases are important to the future economic progress of the community. Failures of food produciton to keep pace with demand would result in large price rises and contribute to a reduction in available consumer expenditure to support growth of the non-farm economy. This would increase the risks of continued "slumpflation" problems akin to those of the last few years. Continued productivity growth is also important to individual farmers who have no control over the prices they receive for their products but who can, by using improved technology, reduce their unit cost of production and thereby increase their profits.

It is very important to remember, however, that the technological advances which have enabled the rate of improvement in efficiency which we have come to expect are relatively recent phenomena. Prior to the 1940s, many of the improvements which occurred came at infrequent intervals and remained unchanged for long periods. Since then technologies contributed by the world chemical industry (eg the development of inorganic fertilizers, herbicides and other pesticides) together with the scientific breeding of crop varieties and increased mechanisation have all made major contributions to a rapid increase in agricultural output and increases in labour productivity.

It is arguable that there are diminishing returns to the future productivity gains which can be expected from these technologies. Fertilizer use in the UK, for example, is at its economic optimum for available crop varieties (5.6) and areas treated with pesticides are nearing, or have reached, saturation. Some authors (7) question whether the rate of technical progress might be slowing down, with risks of technology stagnation creating long run economic problems. It could be of great importance whether or not there is the potential scope in the sciences of plant growth regulation or perhaps genetic engineering to produce new generations of technology which can maintain the momentum of growth.

With these thoughts in mind, the following sections examine the possible role of PGRs in terms of their potential contribution to (a) increasing agricultural ouput and (b) reducing production costs and, thereby, raising productivity.

HISTORICAL EXPERIENCE

The idea of using chemicals to improve the growth and development of crop plants is not new. The effects of ethylene and acetylene in inducing flowering of pineapples were known in the 1930s as were some of the properties of Gibberellins. Also, much of the early work conducted with auxins during the 1930s, which eventually led to the discovery of the hormone weedkillers, was originally aimed at stimulating plant growth, but ther herbicidal discoveries at that time were particularly exciting and stole the research interest.

A number of PGR uses have now become established and are exemplified below to illustrate the diversity of output promoting and cost saving roles which can be filled.

Output increasing uses:

(a) Yield increasing

- CCC to shorten and stiffen wheat straw, allowing increased use of nitrogen fertilizers.
- GA_3 to increase fruit set of mandarines, clemantines, tangerines and pears.
- GA_3 to overcome losses of apple yield due to frost damage.
- GA_3 to increase the berry size of seedless grapes.
- GA_3 to overcome low temperature constraints to sugar cane growth in Hawaii.
- Ethephon to stimulate latex flow in rubber.

(b) Quality Improvement

- GA_3 coupled with mechanical thinning to increase the berry size of seedless grapes in California to give a premium table product.
- GA_3 to reduce the incidence of skin creasing of Valencia organges (a physiological rind disorder which renders the fruit unacceptable for export).

(c) Value Increase

- GA_3 to advance or retard maturity of globe artichokes in order to capture higher prices outside the main production season.

Cost Saving Uses:

(a) Direct Labour Replacement

- Maleic hydrazide and fatty alcohol contact bud killers to control the growth of axial sucker in tobacco.
- NAA to thin overset fruit.

(b) Facilitating Mechanisation

- Fruit looseners (eg Ethephon) to aid synchronised ripening and loosening of fruit for mechanical harvesting.

(c) Simplifying Plant Breeding

- A Gibberellin A4/A7 mixture + NAA is being developed to encourage precocious flowering of conifers (1 year old as opposed to 12-15 years old) to enable breeding programmes to become possible.

Despite their diversity and importance within particular cultural systems, virtually all of the uses described above are commercially small and specialist. None of the growth regulators which have been developed during the last 20 years are of comparable market value to a major herbicide. The total value of the current market for growth regulatory chemicals is an order of magnitude smaller than that for the major groups of pesticides and is expected to remain so for the immediate future (Table 1).

Table 1

Estimated value of sales for the major agrochemical effects $m
(Source : Farm Chemicals)

	1974	1980 Forecast
Herbicides	2190	3819
Insecticides	1822	2575
Fungicides	961	1418
Soil Fumigants	69	134
Desiccants	19	49
Plant Growth Regulators	40	50

THE INVENTION AND DEVELOPMENT OF PGRs

The first part of this paper has argued that there is a real need for new output increasing and cost saving technologies in agriculture, and illustrated that PGRs have already begun to make a small contribution. If, however, they are to make a really significant impact on the economics of agriculture as a whole, products will have to be developed which have application to major crops in major areas of world agriculture. This, in turn, will require the commitment of sufficient biological and chemical R & D effort to the discovery and development process; a commitment which can only be made if those responsible for controlling resources believe that the potential rewards are large enough in relation to the costs and risks involved in new product R & D to merit the investment. A balance has to be struck between, on the one hand, pessimism drawn from the historically poor relative performance of this area of business and a lack of understanding of either the true nature of market needs or suitable biological testing procedures and, on the other hand, euphoric ideas about the possible returns from a totally new and wide open area of potential business. The second part of this paper considers some of the costs and risks which have to be weighed in the PGR R & D investment decision.

COSTS AND RISKS IN R & D

The R & D cost and risk issue has been considered first here because it helps to set the scale for the type of effect sought into perspective. Inevitably, our ability to make an accurate assessment of the scale of costs which would be borne in the course of discovering and developing a new PGR is limited by the lack of any meaningful experience within the agrochemicals industry. There is, however, every reason to suppose that it would be at least as great, and probably significantly greater, than would be expected for a new herbicide, insecticide or fungicide. Expectations of greater cost derive from the more complex experimental programmes likely to be required to identify more subtle effects and establish their reliability under varying environmental conditions. Particular problems are likely to be encountered with perennial crops where long run effects must also be studied.

To give a rough base line from which to discuss costs and risks, Tables 2 and 3 given an indication of the rapidly rising costs of discovering and developing pesticidal compounds and the numbers of compounds which are tested at each stage of screening per commercially successful product finally marketed. These costs, and the reasons for their increases are discussed in detail by Lever and Strong (8).

Table 2

Estimated total cost of R & D per product commercialised (8,9)

Year of Estimate	1956	1964	1967	1969	1970	1973	1974	1976
Total Cost in Current $ million	1.2	2.9	3.4	4.1	5.5	6.1	7.4	8
Total Cost 1976 const $m	2.5	5.3	5.8	6.3	8.1	7.8	8.5	8

Table 3

Number of compounds passing through each R & D stage per commercial product (8,9)

Activity	1956	1964	1967	1969	1970	1972	1975
Synthesis and initial bio-screen	1800	1600	5500	5040	8000	10000	8500
Advance screening	60	36	NA	126	80	NA	NA
Field evaluation	6	4	NA	9	4	NA	NA
Development	2	2	NA	2	2	NA	NA
Sales	1	1	1	1	1	1	1

In the early stages of screening for conventional pesticidal compounds one is looking directly for very gross effects (usually total kill of unwanted species) which are directly representative of the desired field response; also one is usually dealing with a phenomenon whose effects are directly proportional to the rate of application, ie increasing the dose rate of a herbicide will increase the degree of phytotoxicity. In searching for new PGRs, one has to define a new set of test criteria which may be more subtle in nature and may not be related to dose rate in a unidirectional way. To elaborate on these points, suppose one is searching for some way of increasing crop yield. On the scale of preliminary tests that one can run in a screening glasshouse, it is not possible to screen directly for yield increases. A number of proxy situations have to be devised, either attempting to look for effects on perceived major components of yield or accepting the induction of major unrelated morphological changes such as growth inhibition, changes in leaf posture or bud development as indicators of biological activity. The need to move further towards proxy "abstractions" in the test procedure and away from direct measurement of the end effect increases the risk of test error - either raising the chance of falsely rejecting potentially effective compounds or carrying on unsuitable compounds to subsequent tests, and, thereby, increasing costs*. Both sources of error raise the total expected costs of developing a new product.

Further problems arise from the fact that responses to a chemical may be very dependent on time of application in relation to the stage of physiological development and on the environment. The stresses on plants in pots in a glasshouse during an English winter will be very different from those on plants in the US Delta States in the middle of summer, and very different responses to chemicals could occur. Responses may also be very rate dependent, occurring within but not above or below a particular dose range.

Analoguous, though probably less severe, problems occur in the field. An illustration of this difficulty at a very late stage of development is given by TIBA on soyabeans in the USA. Treatment results were good enough to encourage commercial sales to be made, giving beneficial results through reduction in crop lodging and, under certain conditions, increases in yield. Success was, however, curtailed by unreliability of performance across the wide range of soyabean varieties and under varied weather conditions.

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* This problem is discussed in greater detail in the Author's unpublished D Phil Thesis - Planning Technological Change - a Case Study of the Agrochemical Industry. Univ. Sussex Science Policy Research Unit.

The greater complexity of testing required and the problems of reduced test accuracy which are likely to accompany increased abstraction from the desired end biological effects under practical growing conditions are likely to both reduce the total screen throughput which can be achieved with screening resources of comparable scale to conventional pesticides, and increase the number of potential failures still in the test system at relatively late stages.

Mitigation of the effects of these adverse tendencies requires the application of much greater skill and thought in the selection of candidate compounds for test, in understanding the end effects sought and the ways in which these can be proxied than has been necessary for previous agrochemical discoveries. This will probably require far closer co-operation between professionals of relevant disciplines outside the chemicals industry and those within.

They also emphasise the importance of selecting major crops as targets for focusing R & D effort rather than the more specialist historical markets with, in all probability, very major reliance on specialised research institutions to develop minor specialist uses for compounds; uses which could generate significant benefits to the user industry but require specialist skills which chemical companies cannot offer in relation to their expected returns, allowing for the risks that they may never come up with a compound for that market sector at all.

SELECTION OF TARGET EFFECTS

It has been stated very broadly that target effects for PGRs lie in increasing output or reducing production costs of major crops. Such statements, however, hide a multitude of further technical and commercial questions which must be answered before one has tangible objectives. Fairly detailed understanding is needed of the current agronomic practices in major crops coupled with conceptual insights into the ways in which chemically induced effects could beneficially modify those practices or alleviate constraints.

Consider, by way of example, the broad objectives of raising the yield of a major field crop, such as wheat or soyabean. It is necessary to develop some understanding of the physiological and environmental determinants of yield which are likely to constitute significant constraints over large areas of agriculture before one can define a target effect. Searches could be made, for example, for compounds which would directly influence plant metabolic processes (such as photosynthesis, photorespiration or transport mechanisms), for compounds which influenced different stages of the formation of yield organs (such as the differentiation of flower primordia, grain set or grain fall) or chemicals which alter gross morphological characteristics in some way (eg retardants).

In the latter example, one may expect that yield benefits could be derived from diversion of assimilates from vegetative growth to yield organs, or intend that the altered morphology would, in turn, allow beneficial changes in husbandry systems (eg higher planting densities or greater use of fertilizers). Each would require a totally distinct screening procedure. Judgement then has to be made about the feasibility of finding compounds to meet alternative biological objectives and the acreage of that crop for which the effect could (a) be technically applicable and (b) be practically adopted, has to be assessed. Inevitably, first estimates will be very inaccurate, but it is important to sift the possible from the impossible and the potentially large from the potentially small. Once a number of apparently worthwhile areas of activity have been selected there will be a long process of learning and revision of views on both the technical feasibility of the objectives and on the understanding of the real market needs. The importance of this learning process is such that it is necessary to choose a limited number of areas of activity to ensure that resources are not spread so thinly that the requisite depth of understanding of any one is never reached. Those areas need intuitively, therefore, to be both large and technically feasible on the currently available scientific knowledge.

The identification of areas of difficulty to be resolved is not grounds for pessimism. It is the first step towards developing the co-ordinated understanding of objectives which is going to be necessary if large new PGR uses are to be developed and it will be those organisations most able to take resolute action who will reap the greatest reward from opening up new areas of business.

CONCLUSION

This paper has illustrated that there is a continuing economic need for new technological developments in agriculture and that there is historical evidence that plant growth regulators can play an active part in the development of more efficient agricultural production systems. If they are to make the contribution to total productivity that pesticides have done in the past, however, there will have to be a major switch in emphasis from a focus on small specialist markets to an onslaught on the large area field crops - a switch which will require the intensive detailed application of a range of specialist biological and chemical skills with greater levels of total resource commitment than has been achieved in the past. There is now evidence that increased attention is being paid to this area of potential agrochemical development, and, once one major breakthrough has been made, the extent of R & D activity and consequent rate of development of major products is likely to expand rapidly.

Acknowledgements

I am indebted to a number of my colleagues from ICI Plant Protection Division for help in producing this paper; to Dr G C Mees for a number of the ideas on research problems and risks; Mr G W Elson for examples of GA usage and Mr C J Lewis for comments on drafts.

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PLANT BREEDING AND THE EXPLOITATION OF VARIATION IN PLANT HORMONE SYSTEMS

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Summary The aims of the plant breeding and growth regulator industries are similar. The economics of both technologies ensure that most effort will be put into the major arable crops. However new varieties and new PGRs do not represent alternatives to the farmer. He will use the one to optimise returns under average conditions and exploit the other according to the actual environment that pertains while his crop is in the field.

Genetic variation in most of the better understood aspects of endogenous and applied growth regulator systems either already exists or may be generated. Genes that operate on these fundamental control systems may provide the plant breeder with the means of making new kinds of adjustments to crop plant phenotype.

It is probable that selection directly for hormonal variation will be used in breeding programmes in only a few isolated cases where the hormonal differences are easier to assay than the yield related effects on plant phenotype. However a combined genetic-physiological approach in strategic research programmes could reveal genes of value to the breeder. Such genes may be those that mimic the effects of relatively expensive growth regulators, those that determine specific agronomic effects or those that interact advantageously with applied growth regulators.

INTRODUCTION

Today we are aware of several groups of natural endogenous plant hormones. We are becoming aware of many of their various roles in the control of plant growth and development. This branch of plant physiology has stimulated research into the various ways in which plant growth regulators (PGRs) may be used to modify the growth and form of crop plants. We are also aware of differences among the genes which control the biosynthesis and metabolism of the endogenous hormones. Thus the plant breeder may, by employing this variation, achieve the same objectives as the PGR chemist.

The main objectives of the two technologies are identical, that is to modify crop plant performance in an agronomically advantageous way. However the products of the two approaches, the new variety and the new chemical, represent to the farmer different ways to improve his crop - not alternatives. Thus conflict should be kept to a minimum.

Plant breeding is a slow process, for example about twelve years are required to produce a new wheat variety. In order to exploit new variation, the breeder must first integrate the expression of the new genes with all the many other facets of plant phenotype. He will aim for new cultivars which are generally adapted which will often involve a degree of compromise. The development of a new PGR, on the other hand, can be faster than the production of a new variety. More importantly the PGR may be developed to create a specific growth effect following its application at a specific time.

The farmer is thus presented with decision opportunities at different times. He must choose his variety to be compatible with the average environment in which it is to be grown. He can however choose his PGRs to optimise his returns in the actual environment that pertains while the crop is in the field. From this argument it follows that the scope for the PGR chemist will be greatest in non-annual crop species.

However, the expenses involved in new PGR development are high and the major arable crops provide the only viable market. By the same token, the relative costs of present-day plant breeding ensure that the major effort is concentrated on the same crops. In those cases where the desired modifications to plant growth are identical and possible by both approaches, the breeding solution must ultimately be the less expensive. The farmer may however still look to the PGR industry for a quick result.

It is with these crops that this presentation is concerned, with an emphasis on wheat. A summary of the available genetic variation in hormonal systems is followed by a speculatory overview of the ways in which these genes may be exploited to meet various crop improvement objectives.

CROP IMPROVEMENT OBJECTIVES

An analysis of the objectives of those concerned with crop improvement shows the increasing complexity of the task. The main objectives are always either to increase or stabilise the yield or the quality of the crop. However these improvements must relate to the total environment in which the crop is to be grown, processed and consumed. These environments may be,

Edaphic	soil type and fertility, weather and daylength.
Biological	weeds, pests and diseases, usually genetically dynamic.
Agricultural	new mechanisation, application of fertilisers, herbicides, pesticides and PGRs.
Processing	changing concepts of quality, the shape, colour and constitution of yield.
Economic	relative availability and value of crop products, requirements for plant breeders rights such as distinctness and uniformity.

Traditionally the breeder has concentrated on adaptation only to the edaphic and disease environments. In recent years he has had increasingly to consider the changing husbandry, processing and economic environments. Some factors have reduced in priority over the years, for example the development of selective herbicides and the application of fertilisers have obviated to some extent, the necessity to breed varieties that compete well with weeds and varieties that will perform at varying soil fertility levels. Relatively unpredictable factors such as the weather and the prevalence of some pests and diseases can only be accommodated by compromise solutions. Other factors change so quickly that the breeder may often be caught half way through a programme with obsolete objectives. The rapid breakdown of some race specific disease resistance mechanisms and major changes in the economic environment are examples of such factors. The wheat varieties being released today were undergoing their early stages of hybridisation and selection long before Britain's entry into the EEC. While the new Common Market arrangements demanded more emphasis on breadmaking quality, the wheat breeder was embarked on programmes which had only high yield and not good quality as their objectives.

The breeder has a further problem imposed by the system in which his varieties are nationally tested before their release to the farmer. The competition for the limited number of places on the Recommended Lists precludes, at present, objectives other than fairly general adaptation. Some local agricultural requirements, such as that for later ripening wheat varieties for the South of England, will not be met by the breeder under the present system.

Within these limitations, the breeder must first formulate his ideal plant. The concept of an ideal plant will depend on the environment for which the plant is designed and will be based on physiological knowledge and agricultural experience with the crop. He must then introduce the genetic variation necessary to attain his objective and provide himself with the means to recognise the ideal combination of genes among segregating populations.

Thus the breeder may exploit variation in hormonal systems at two levels. He may introduce such genes to achieve specific yield related effects or he may use such variation directly as a selection criterion.

GENETIC VARIATION IN PLANT HORMONE SYSTEMS

In no single species has a systematic search been carried out to identify a full range of hormonal variants. Therefore, to assess the extent of the available variation, we can only extrapolate from the isolated examples that have been documented in different higher plant species.

A recent review[1] shows that major genes are known that cause alterations in the rates of synthesis of auxin, gibberellins, ethylene and abscisic acid. While most of these genes cause reductions in synthesis, at least one mutant is known in barley in which synthesis is enhanced. Major genes exist which affect the rates of removal of IAA and GA. Similarly genes are known which reduce the sensitivity of plant tissues and organs to IAA, GA, ethylene and a range of synthetic hormone analogues.

The range of variation known is, of course, biased because the genes have generally been identified by physiologists investigating gross morphological differences, especially dwarfism. Differences in response to applied hormones have often initiated an investigation, thus those hormones which have spectacular effects on whole plants such as gibberellins and ethylene have been worked with in preference to auxin and cytokinins. However, since the auxins were the first group of hormones discovered, much of the early work concentrated on this group.

Most of the variation known is associated with major and usually single gene differences. Analysis of the quantitative effects of minor and multiple gene systems is, of course, more tedious and requires analytical techniques with finer precision. Two studies in which a range of genotypes have been investigated for ABA levels in wheat[2] and ethylene production rates in *Pteridium*[3] have revealed just such variation.

It is reasonable to assume that in any species both major and minor gene variation in any of the known hormonal systems may either exist or be generated by mutation techniques. It is also reasonable to expect that much of this variation will be associated with relatively subtle morphological alterations. Furthermore it is likely that a desired plant form may be attained in different ways, by manipulating genes which affect different hormone and response systems. For example dwarfism in cereals has been found to be associated with reduced IAA and GA synthesis, increased metabolism of IAA and differential sensitivity to GA.

The extent of our comprehension of plant hormone systems limits our ability to recognise some aspects of this kind of genetic variation. For example we know little of the mode of action of the hormones or of the way in which cells and tissues are preprogrammed to respond in specific ways at specific times of development. Thus manipulation of genes determining the synthesis, metabolism or effectiveness of endogenous hormones would seem to offer the means of effecting quantitative changes in plant forms, such as accelerating or retarding the rates of natural growth processes. At present, however, our knowledge of the ways in which plant development is mediated by changes in hormonal balance at specific times is too rudimentary to permit the exploitation of genetic variation except in an *ad hoc* way.

SELECTION FOR YIELD RELATED VARIATION

For any character to be used in selection there must be a strong relationship between its expression and the desired yield effect. Also it should be easier to assess than yield itself, thus reducing the time or expense of the selection procedure.

The basis for selection criteria is the current concept of an ideal plant model for a particular range of environments. Austin and Jones[4] outlined the attributes of such a wheat plant in four categories: (a) morphological and anatomical, (b) compositional, which may include yield constituents and hormone levels, (c) process rates, such as photosynthesis, respiration, winter hardiness and (d) process controls, which include enzyme levels and control of stomatal apertures.

In general, while recognising the importance of process rates and controls, breeders have tended to concentrate on morphological criteria and disease resistance. While much of this variation may be expected to arise from hormonal differences, it will usually be easier, and as effective, to score for morphology, rather than the causal hormonal differences.

A notable exception is the seedling GA response test currently being used to identify the widely used Norin 10 dwarfing genes in bread wheat, durum wheats and triticale.[5] The genes, *Gai/Rht1* and *Gai/Rht2*, operate by restricting the plant's responsiveness to endogenous GA and cause increases in number of fertile ears per plant and numbers of grains per ear[6] as well as causing a reduction in plant height. By using the GA response test, plants carrying the genes may be identified more quickly, less expensively and with greater accuracy than by measuring final plant height.

Another potentially useful hormonal selection criterion is afforded by the recognition that variation in ABA metabolism may be associated with drought tolerance in wheat.[2] Since ABA can be assayed rapidly[7], there now appears to exist the possibility of selection for drought tolerance by a method that is as effective, and certainly more practicable, than selecting for yield response to drought.

BREEDING FOR RESPONSES TO PGRs

Several examples of variation in response to applied hormones, their synthetic analogues and herbicides provide a good basis for a combined genetic and PGR approach. These include simazine resistance in oil seed rape[8] and metoxuron resistance in wheat[9] and potatoes.[10] Thus exploitation and development of this natural variation in response to existing herbicides could be used as an alternative to developing new chemicals. Whether such an approach is desirable will depend on the extent of the weed problem that may be solved, the extra constraint on the breeder who will already be selecting for numerous other characters and the possibility of creating a further weed problem of the new herbicide-resistant variety as a contaminant in a following crop. Among wheat breeders the present opinion is that, while it is useful to know of such resistance, it is not worthwhile actively breeding for the character.[9]

In ryegrass, however, this breeding objective promises to be most beneficial. Faulkner[11] has described the development of a paraquat-resistant variety of *Lolium perenne*. In a perennial the advantages extend beyond the ability to clear weeds and weed grasses in the field to obviating the costly process of reseeding badly contaminated pastures.

The uses of hormonal variation discussed above are those that may be employed by the practical plant breeder. Other applications may be developed by strategic research programmes for ultimate use in breeding programmes but not necessarily as selection criteria. Possible approaches are to mimic genetically the effect of a useful but costly PGR or to achieve specific phenotype variants by direct manipulation of a hormonal system.

DUPLICATION OF A PGR EFFECT

Although this idea has not as yet been successfully applied, there is one notable plant breeding success that might have come about this way. It concerns the Norin 10 dwarfing genes and the growth retardant chlormequat (CCC).

CCC was developed and promoted as a chemical which, when applied to wheat, reduced stem length and thus reduced lodging losses under conditions of high fertility and rainfall. However CCC was soon shown to have other advantageous effects on yield even in the absence of lodging, (see review by Humphries[12]). It is probable that CCC operates in the plant by reducing the availability of endogenous GA by blocking an early step in the biosynthetic pathway.[13]

The Norin 10 dwarfing genes, *Gai/Rht1* and *2*, appear to operate by similarly reducing the physiological availability of GA, although by affecting the response system rather than GA synthesis. Recently these genes have been shown to have remarkably similar effects on wheat yields to those obtained with CCC (see Table 1).

These genes were, of course, being used by breeders before the release of CCC. However, had there not been a requirement for shorter, stiffer straw, the Norin 10 genes might have been discovered and used because they had physiological effects similar to those produced by CCC. A search for similar genes may still be worthwhile in other cereals or in potatoes where CCC promotes tuber growth.

Clearly the responses to PGRs that would lend themselves best to this type of plant breeding application are those of the natural growth substances or those known to affect endogenous hormone systems, such as CCC. However responses to other chemicals, such as herbicides, may provide attractive systems. For example, simazine and terbacil may increase protein yields in beans and forage crops and grain yield in some cereals.[15] These effects might be duplicated by genes acting in similar ways to the herbicide. In the long term the genetic solution would be the cheaper.

Table 1

A comparison of the effects of CCC and the semi-dwarfing gene *Gai/Rht2* in winter wheat

	-CCC	+CCC%	*gai/rht2*	*Gai/Rht2* %
Ear no/m^{-2}	76.4	104%	215.6	109%
Grain no/ear	23.8	118%	45.4	127%
100 grain wt (gm)	3.57	95%	4.65	84%
Yield (kg/ha)	4785	116%	3975	107%

Note. The CCC data, after Humphries[14], was obtained with variety Kloka in an unirrigated, unlodged field trial sown at low density. The *Gai/Rht2* data, from Gale[6], are the means of homozygous F3 lines in a spaced plant field trial. The within ear yield components are those of the tallest tiller per plant. For both sets of data the effects of the chemical and the gene are shown as a percentage of the tall control.

HORMONAL VARIATION AS A SOURCE OF SPECIFIC PHENOTYPES

Our knowledge of the involvement of hormones in the control or initiation of physiological processes allows us to speculate upon many ways in which hormonal differences could bring about advantageous effects in crop plants.

One area of interest in this respect is plant pathology. The observations that many diseases have symptoms brought about by hormonal aberrations, see review by Brian[16], provide possible starting points both for the chemist and the breeder. In some diseases the symptoms are probably a direct response of a hormone, or hormone-like substance, released by the pathogen. Examples are witch's broom in various trees and the bakanae disease of rice. In these and similar instances there is a possibility of breeding for insensitivity to the active substance. Indeed, this may be the way in which the *Gai/Rht* genes evolved in Japan.

In other diseases the pathogen may cause a change in the host's hormonal biosynthetic system. Such diseases may include some rusts, bacterial wilt in tobacco, *Verticillium* wilt in tomatoes and anther smut in *Silene*.

Any genetic manipulation of the hormone system to preclude the effects of such a pathogen may, of course, have many unwanted side effects. Nevertheless experiments by Butcher *et al*[17] indicate that such an approach may be practicable. Having shown that auxin release by the host may be associated with its susceptibility to club root, *Plasmodiophora brassicae*, they were further able to demonstrate that resistance was inversely correlated with endogenous levels of indole glucosinolates, which are potential auxin precursors. They suggested that selection for low levels of these compounds in Brassica crops might be effective in producing varieties with general resistance to the disease. Investigations of other hormonal variants may reveal general resistance mechanisms that could be of particular value in breeding for resistance to diseases such as cereal smuts where resistance is, at present, often extremely race specific and is prone to collapse after only a few years as the pathogen evolves.

A quite different type of plant breeding problem suitable for a hormonal solution concerns the enzyme α-amylase which, when present in high levels in wheat flour, has deleterious effects on its suitability for breadmaking. The enzyme is synthesised and released in response to GA and may be present as a residue in mature grain or as a product of pre-harvest sprouting in the ear, especially in wet years.

A third *Gai/Rht* gene, known as the Tom Thumb dwarfing gene, which is more potent than those from Norin 10, confers GA-insensitivity upon the aleurone cells in which the enzyme is synthesised and thus may be exploited as a source of low α-amylase wheats with an apparent resistance to sprouting.[18] Work has been started to examine the possibility of incorporating *Gai/Rht3* in high yielding commercial varieties.

Other yield related characters include photosynthetic and respiration rates and possibly the activities of enzymes such as nitrate reductase and ribulose diphosphate carboxylase. These are involved respectively in nitrogen fixation and photosynthesis and may be under hormonal control. They may therefore be characters which could be improved by genes affecting specific hormonal systems.

Many of the ways in which hormonal variation could be exploited in plant breeding must remain in the realm of speculation, especially while impressive improvements in yield of many crops continue to be made using conventional breeding techniques. However, continued research into the mode of action of endogenous hormones, the mode of action and effects of a range of PGRs, not just the ones which are commercial successes, and improved techniques of genetic manipulation should be persued vigorously. Ultimately these areas of science should combine to provide a powerful tool for crop improvement.

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