

PREFACE

OPPORTUNITIES FOR CHEMICAL PLANT GROWTH REGULATION

This Symposium was organised jointly by the British Crop Protection Council and by the newly formed British Plant Growth Regulator Group and was held at the University of Reading on the 4th and 5th January 1978. The meeting followed the lines of previous BCPC Symposia in taking a multi-disciplinary look at the subject.

The search for novel plant growth regulators is taking an increasing part of the Research effort of Companies with an interest in agricultural chemicals. However, despite the large number of experimental compounds which are field tested each year, relatively few have been accepted so far as beneficial to horticulture or agriculture. The Symposium looked at technical opportunities for plant growth regulators and constraints on their development and discussed some of the ways in which such chemicals might be best employed to improve plant phenotype, whether by modifying environmental influences or by altering physiology and development patterns.

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OPPORTUNITIES FOR PLANT GROWTH REGULATION
PGRs IN PLANT IMPROVEMENT AND MANAGEMENT

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The scientific programme of this Symposium has been arranged by the British Plant Growth Regulator Group, which was formed about a year ago with the aim of encouraging interaction and co-operation in research on plant growth regulators, especially between scientists in the public sector and in industry. This is the first major meeting to be organised by the Group; in putting the meeting together the Group has benefited greatly from the active sponsorship of the British Crop Protection Council, to whom we are grateful.

In the past the major aim of the agrochemicals industry has been to provide chemicals that control the competition to the crop - the weeds, insect pests, fungi and nematodes that reduce yield or quality or interfere with harvesting. Product performance has been judged in relatively simple terms; thus for herbicides it has been the death of the weed and adequate margins of safety for the crop.

Meeting this aim has been a difficult enough task in itself, and the costs of discovering, developing and commercialising new products have risen steeply in recent years. The R and D bill is now counted in several millions of pounds sterling for each new product that is introduced.

Plant growth regulators have more subtle performance criteria. These are to modify the crop itself, by changing the pattern of response to the many internal and external factors that govern

germination
vegetative growth
reproduction
maturity
and senescence

of the plant. There are many processes of importance, notably the carbon balance involving photosynthesis, dark respiration and photorespiration, the translocation of assimilates and their partitioning especially in the later stages of the plant's life, the uptake and transport of water and minerals, and the hormonally controlled differentiation of the various stages of the life cycle. Of key importance, too, is the influence of external environmental factors - radiation, temperature, the availability of water, nutrients and minerals - upon these processes, and the need to provide a chemical that can produce a consistent, economically important response.

Scientifically and technically our task is an exciting one. Over the past 25 years or so there have been major advances in our broad understanding of plant growth. It is therefore a very seductive thesis to assert that a greater use of

this strategic understanding, and less reliance upon empiricism, could pay handsome dividends in providing new plant growth regulators of major economic importance. With one or two exceptions, however, the existing products are peripheral to the main tasks of crop production and the potential many of us believe in lies very much in the future. I hope that some of our speakers will comment on past constraints and point a way to the future that will reduce the cost of innovation and direct attention to the areas of greatest reward.

There are many problems. The discovery of regulatory properties is at least as difficult as the detection of herbicidal activity, and continuation of a mainly empirical approach will be very expensive. The introduction of innovative thought based upon understanding of plant processes seems to be the only rational approach to cost saving. Probably more important, however, is the subtle nature of the effects we are seeking. Evaluation of the utility of performance, and the optimisation of the research lead is more complicated and lengthy than the comparable search for a novel herbicide. Indeed, the analogy should perhaps more pertinently be drawn with the search for a new drug. Consistent performance, with different phenotypes growing under widely varying environmental conditions, is also difficult to achieve and the transition from glasshouse to the field difficult to bridge.

Farmers are used to herbicides and the like, and have had long practice in fitting them into agronomic systems and judging the rewards to be obtained from their use. The proper exploitation of plant growth regulators will make greater demands upon the farmer's skill, and upon his advisers. Using commercial jargon, there is a marketing job to be done.

The biologist seeking plant growth regulators has very comparable aims to those of the plant breeder. Ideally, therefore, the two approaches should be complementary and interactive rather than competitive. An excellent example of complementarity, at least in concept, will be illustrated by the paper that deals with chemical gametocides for use in wheat and barley. I hope the Symposium will deal with this prospect of closer collaboration between biologist and plant breeder at some length.

Finally, I should like to remind you again that one of the underlying themes of this Symposium is to examine how scientists in the public sector and in industry can collaborate in this scientifically fascinating but commercially risky field of research.

THE POTENTIAL AND LIMITATIONS OF GROWTH REGULATORS IN CROP PRODUCTION

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Summary Some growth regulators may mimic endogenous hormones or change their concentration in the plant through effects on biosynthesis, degradation or transport, or through competition for active sites on a substrate. Such growth regulators mainly affect specific processes such as cell elongation, abscission or senescence. Other types of growth regulator could act directly on rate-limiting enzymes concerned with carbon or nitrogen assimilation, giving the possibility of stimulating overall plant growth and yield. Like the traditional methods of crop improvement, the use of growth regulators has its biological limitations, the main ones being variability in their uptake and translocation leading to inconsistency in response, and multiple actions which can lead to undesirable side effects.

INTRODUCTION

Since the dawn of agriculture man has been striving to improve his crop plants. Until recently there were only three ways in which he could do this:- by altering the plant environment; by altering the genotype; or by manipulative techniques such as grafting or pruning. Although much has been accomplished over the centuries, all these techniques have their limitations.

The environment can be ameliorated by freeing the crop from weed competition and by controlling pests and diseases; the soil can be improved by drainage and manuring; irrigation can be provided; but the main environmental factor influencing crop yield is the weather which we are unlikely to be able to control, except over small areas, within the foreseeable future.

The genetical techniques of hybridization, induced mutation and selection are powerful tools for crop improvement, by the use of which almost anything is possible in theory: but in practice they too have their limitations, the main one being the long time required to assemble in one individual all the desirable genes - not to mention the elimination of the undesirable ones. Genetic improvement has thus been most successful in crops with a short reproductive cycle, particularly outbreeders such as maize, which has been so improved that its natural progenitors can no longer be recognised with certainty. By comparison, the difference between a wild crab apple and a Cox's Orange Pippin is relatively small and in forestry we are still using genotypes not far removed from the wild.

Manipulative techniques for the modification of crop growth are limited mainly to woody perennials, though operations such as grass mowing, or the rolling of wheat to increase tillering would also come into this category, as would also the de-suckering of tobacco or the dis-budding of chrysanthemums.

In addition to these three traditional methods of crop improvement we must now add a fourth - the use of growth regulating substances - which forms the subject of our present symposium. On the 7000 year time scale of agriculture, this is a very

recent development, dating only from the mid-1930's, when synthetic auxins were first used for promoting the rooting of cuttings and for the induction of synchronous flowering in the pineapple fields of Hawaii. Since then, many hundreds of active compounds have been discovered and tested on a wide range of crops throughout the world. A few of these have made major impacts on agricultural practice: many more have found limited uses on specific crops; but the largest number, whilst potentially useful, are not yet in general use for reasons connected with economics, inconsistency in performance, undesirable side effects or possible consumer hazards.

Many growth regulator effects mimic those produced by gene modification, but whereas genetic effects are persistent, those resulting from growth regulator treatment are transitory. Against this possible disadvantage must be set the advantage of immediate results: plant growth regulators enable us to do today what takes many decades or even centuries to accomplish by genetical means. Consequently the greatest biological potential for growth regulator use is in crops, such as the perennial tree fruits, where breeding is slow and difficult. On the other hand, we are often told that the greatest economic potential lies in crops such as cereals that are grown on a large scale throughout the world. However, following this argument to its logical conclusion, perhaps we should all be working on forest trees, where the greatest biological and economic benefits should result from the discovery of a chemical to increase the rate of timber production! The flaw in this argument, of course, is that in addition to crop acreage, the value of the crop must be high in relation to the cost of the growth regulator. Before getting more deeply involved in economics which I am sure will be more ably dealt with by Mr Lever later in this session, let us return to science and examine the biological potential and limitations of different types of growth regulators.

TYPES OF GROWTH REGULATORS

Most growth regulators, though by no means all, produce their effects by interfering in some way with the balance of the endogenous hormone systems which control plant physiological processes. We can distinguish the following types of active compounds:-

1. Naturally occurring hormones These may be either extracted from natural sources (gibberellins) or synthesised (IAA) and applied to plants to counteract deficiencies of endogenous hormones. They are effective only in situations where the native hormone is limiting and their main disadvantage is that they are often rapidly inactivated, either by degradation or by conjugation with other molecules, by the same mechanisms that control the levels of endogenous hormones.
2. Hormone transport inhibitors Substances which block the transport of endogenous hormones can produce profound effects on plant growth, particularly on apical dominance, and hence have some potential as growth regulators. The best known is 2,3,5-tri-iodobenzoic acid (TIBA), an inhibitor of auxin and gibberellin transport, which in recent years has found limited application in soybean where, by inducing a more bushy type of growth and improving light penetration, it can improve yields.
3. Synthetic analogues of natural hormones Where these can be produced they are often more active than the native hormone whose action they mimic, because they are less susceptible to enzymatic inactivation. IBA, 2,4-D and NAA are classical examples of auxin mimics. Some plants, however, possess decarboxylating enzymes that can rapidly degrade the side chains of these synthetic auxins leading to a loss of activity, so that their effects can vary widely, often between different cultivars of the same species. A clear example is seen in the reaction of apple cultivars to 2,4-D. Many show quite violent growth reactions when treated with even low concentrations; but Cox and many of the seedlings derived from it are highly tolerant because they can rapidly decarboxylate the molecule (13). Such

reactions can be usefully exploited if one is searching for a selective herbicide, but inter-cultivar differences in the reaction to a growth regulator can seriously limit its usefulness and potential in agricultural practice.

4. Competitive antagonists Competitive antagonism is a phenomenon of widespread importance in pharmacology which has so far found little application in the field of growth regulation. A competitive antagonist is defined as any biologically inactive compound which competes with an active compound for a specific reaction site in the cell. The trick is to find molecules sufficiently similar in structure to the active one to bind on to the receptor site, but sufficiently dissimilar to be devoid of activity. If this can be done then we have a means of lowering or blocking completely the action of the active compound by adjusting the amount of anti-hormone added.

There are many examples of this principle in auxin chemistry, the most striking perhaps being the antagonism between the stereo-isomers of synthetic auxins containing an asymmetric carbon atom. Normally, the D-forms show auxin activity: the L-forms are not only inactive but can act as anti-auxins, blocking the activity of the D-enantiomorphs (5). Competitive antagonism has been recorded also between cis- and trans-isomers and between auxins and a wide range of non-auxin-like compounds. Compounds that function as anti-auxins, such as PCIB (4-chlorophenoxy-iso-butyric acid) are often found to promote root growth (4), presumably by lowering supra-optimal auxin concentrations to levels more favourable to growth. One such anti-auxin, 3,4-di-iodo-4-hydroxybenzoic acid, can induce a 300% increase in root growth, but only in light (25), suggesting that it is counteracting the normal inhibition of root growth by light.

In contrast to the many examples of competitive antagonism amongst the auxins, comparatively few are recorded for other groups of plant hormones. However, pseudo-gibberellin A₁, which differs from GA₁ only in the orientation of a single hydroxyl group, has been shown to act as a competitive inhibitor of the GA₃-induced growth of rice seedlings (10), and some fluoro-substituted gibberellins appear to competitively antagonise the action of the unsubstituted molecules (9). Much further fundamental work is needed in this field, but the phenomenon is one which seems to hold potential for the future development of new growth regulators of value in agriculture once the nature of the active binding sites is understood.

5. Enzyme co-factors and antagonists There is considerable circumstantial evidence that levels of endogenous hormones in plants are maintained by homeostatic mechanisms operating through enzymes. These enzymes control, not only the biosynthesis and degradation of the active substances, but also their conjugation with other molecules to form inactive complexes from which the active hormones can again be released when required. If this view be accepted then it follows that one method of influencing growth would be by the application of substances which inhibit or promote, in a specific manner, the activities of the enzymes involved. This is a field where our present knowledge is very incomplete, though we are possibly exploiting the principle to a greater extent than we realise.

The best known examples again come from the auxins, where certain *o*-diphenols such as phloroglucinol, chlorogenic acid and hydroquinone are known to act as inhibitors of IAA-oxidase, the enzyme that inactivates native auxin. They can therefore increase auxin levels in the plant. It is also possible that many of the synergistic reactions recorded between auxins and gibberellins depend on a similar mechanism. There are many examples of where the application of gibberellins has induced large increases in the amount of auxin diffusing from plant tissues. Sastry and Muir (21), for instance, found that an unpollinated tomato ovary produced no diffusible auxin until it was treated with gibberellic acid, when it produced as much as a pollinated ovary.

The converse situation can also occur, leading to a reduction in the internal concentration of endogenous hormones. For instance, 2,4-dichlorophenol and some other monophenols, can function as co-factors of IAA-oxidase, thereby increasing its activity and lowering auxin levels in the plant. Growth retardants such as chlor-mequat and daminozide are believed to reduce the amounts of free gibberellins in the plant by blocking biosynthesis, rather than by increasing the rate of breakdown, and they presumably do this by their effects on specific enzymes involved in the biosynthetic pathway. Some of the recently discovered anti-ethylene compounds such as benzyl-iso-thiocyanate (17) and canaline (15) may also act in a similar way.

The potential for influencing the growth of crop plants through effects on enzymes involved in the biosynthesis, degradation or conjugation of natural hormones is immense; but our knowledge of the biochemistry involved is so fragmentary that, for many years to come, the discovery of effective agents must continue to be based on an empirical approach.

6. Other enzyme inhibitors and co-factors If we accept the principle that we can increase or decrease the activity of specific enzymes by the exogenous application of growth regulators, a whole field of new possibilities is opened up. Why stop at those enzymes controlling the synthesis and degradation of hormones? What about other vital enzyme-controlled processes such as photosynthesis? It is well known that the triazine and uracil herbicides exert their primary phytotoxic effects through the inhibition of photosynthesis: could we therefore not find a growth regulator that would promote photosynthesis? Wareing *et al* (26) produced evidence suggesting that, under conditions of light saturation, photosynthesis might be limited by the levels of carboxylating enzymes, and Treharne and Stoddart (22) found a close correlation between the photosynthetic rate of bean leaves, the activity of the enzyme ribulose-1,5-diphosphate carboxylase and the concentration of endogenous gibberellin. In a later paper Treharne *et al* (23) showed that, following the application of GA or kinetin to *Phaseolus* leaves, photosynthesis and ribulose-1,5-diphosphate carboxylase activity increased in parallel, strongly suggesting hormonal control of this rate-limiting enzyme.

The other possibility for increasing photosynthesis is by inhibiting light respiration which, in temperate crops - the so-called C₃ species - can result in the loss of half the carbon assimilated. Most of this loss is accounted for by the synthesis and subsequent oxidation of glycolate and, in laboratory experiments using leaf discs; both these processes have been successfully inhibited by specific chemicals, resulting in substantial increase in apparent photosynthesis (16). Clearly, the biochemical groundwork has been laid; the great challenge now is - can we find growth regulators that will increase photosynthesis under field conditions?

Nitrate reductase, which controls the rate at which nitrate is assimilated into simple organic forms and eventually into protein, is another enzyme that can limit the growth rate of plants (8) and which is susceptible to control by exogenously applied compounds. Sub-lethal doses of simazine and atrazine promote the growth and protein content of some crops through their stimulating effect on nitrate reductase (19), and it is likely that the increased growth, chlorophyll content and nitrogen content of winter cereals which follows spraying with 2,4-dinitro-o-cresol is attributable to the same basic mechanism (3).

2,4-D is another growth regulator which can enhance nitrate reductase activity in cell free extracts of maize and cucumber (1) and which, when applied at very low dose rates to crops in the field, can induce significant increases in the yield of sugar beet, potatoes and other crops (28).

More recently we have the discovery of the growth promoting properties of triacontanol, a straight-chain fatty alcohol with 30 carbon atoms, which occurs naturally as a component of the cuticular wax of lucerne (20). When applied

at rates equivalent to only 10 mg per hectare; this compound is claimed to increase significantly the growth and productivity of crops such as wheat, rice, maize, soybean and tomato. Its mode of action is unknown, but one can speculate that it might be acting on an enzyme controlling some rate-limiting process such as photosynthesis or nitrogen reduction. Alternatively, as suggested by Ries, it may be involved in some way with promoting transport through cell membranes.

These possibilities will be dealt with in more detail by other speakers: the main point I wish to make is:- although we have become conditioned to thinking of growth regulators as compounds acting through hormone mechanisms and influencing specific processes such as abscission, shoot growth, flower initiation or senescence, we must not close our minds to the idea of general growth promoting substances capable of enhancing dry matter production and yield of many crops through effects on key enzymes. When Bottomley (2) first coined the term 'auximones' for organic substances present in decayed animal and plant remains that would markedly stimulate the growth of wheat and other crop plants, his data was regarded with scepticism by most plant physiologists. Today, the indications are that such substances do exist and, in future, we can expect to see exploitation of their agricultural potential. One can envisage the possibility of such substances, formulated in slow-release capsules, being incorporated into soils low in organic matter to increase their fertility.

7. Selective necrosis Several growth regulators of horticultural importance are based on this principle, killing by contact action only certain plant parts whilst leaving others undamaged. The best known compounds of this type are fatty acid esters or alcohols with a chain length of six to twelve carbon atoms, and their selective action seems to be based on their differential penetration through young and old cuticles. Depending on the stage of growth when they are applied they can be used to kill terminal buds, thus releasing lateral buds from apical dominance and promoting side shoot development (e.g. young fruit trees and woody ornamentals), or, when applied following the loss of apical dominance they can be used to kill young lateral shoots (e.g. de-suckering of tobacco). The term 'chemical pruning agents' has been applied to growth regulators of this type.

SOME BIOLOGICAL LIMITATIONS OF GROWTH REGULATORS

In this broad survey of the various possibilities which exist for chemical growth regulation in crop plants I have mentioned the potential and also some of the limitations associated with each type of regulator. There are also two further problems associated with the use of these compounds which can limit their value as agricultural tools.

Penetration and transport All foliar applied growth regulators must enter the plant through the cuticle, which can be a formidable barrier. Once inside the plant they must then be translocated to the site of action, which may be far removed from the point of uptake. The early phenoxy-acid growth regulators were relatively efficient both in cuticle penetration and movement within the plant, but some more recent growth regulators are much less efficient in these respects, necessitating the external application of high concentrations in order to ensure that a very small proportion will reach the site of action. This blunderbuss approach may be good for sales, but it is biologically inefficient and can give rise to residue problems. It also means that a relatively small percentage change in penetration can result in a large difference in the absolute amount of chemical entering the plant.

Variability in uptake, and consequently in the effects produced, is a problem with all systemic compounds, but perhaps more serious for growth regulators where the internal concentration can be more critical, than for a herbicide, fungicide or insecticide. Lloyd-Jones (12), using ^{14}C -labelled daminozide showed that pene-

tration into leaves of fruit plants after 96 hours could vary from 10 to 80 per cent, depending on temperature, humidity, cultivar and the presence or absence of surfactants. Foliar penetration, however, also depends to a very large extent on cuticle structure, which can vary widely, depending on the environmental conditions under which the leaf has grown. In practice, therefore, foliar uptake of a systemic chemical will be influenced by many uncontrollable factors such as the temperature, humidity and light conditions in the weeks before spraying, at the time of spraying, and also after spraying when, for example, re-wetting of the leaves by dew can sometimes lead to renewed uptake of a chemical deposited on the leaf surface. It therefore seems inevitable that growth regulators will show variable and inconsistent results under field conditions and that this will mitigate against their use in situations where a high degree of precision is necessary (e.g. in fruit thinning).

Unwanted side effects Five clearly defined groups of endogenous plant hormones have been recognised (gibberellins, auxins, cytokinins, abscisins and ethylene). More may yet be discovered but it seems certain that their number will remain small relative to the large number of plant functions that are hormone controlled. Since each type of hormone, acting in conjunction with the others, controls many aspects of plant growth, growth regulators which act through the natural hormone system can also be expected to show multiple effects. To take but one example: the growth retardant daminozide is believed to exert its main influence by blocking gibberellin biosynthesis at the trans-geranylgeraniol to kaurene stage (29), but it also inhibits the oxidation of tryptamine to indoleacetaldehyde (18), stimulates peroxidase and IAA-oxidase activity (6), increases membrane permeability (24), inhibits respiration and senescence (7), stimulates apparent photosynthesis (14) and inhibits protein turnover (11). It is perhaps not surprising that such a compound should produce many different effects on crop growth and development. Some of these are highly desirable, but others must be classed as unwanted and often undesirable side-effects. Such unwanted side effects are a frequent consequence of chemical growth regulation and may often limit the value of an otherwise useful compound. They can sometimes be avoided by careful attention to time of application and concentration, by altering the formulation or by the use of mixtures of different types of growth regulators. For example, when ethephon is used to promote fruit ripening of apples it will also stimulate fruit abscission, which is not what the fruit grower wants: but the fruit drop can be readily prevented by the incorporation of an auxin into the spray. By contrast, to aid mechanical harvesting of small fruits we need to promote abscission without also speeding up ripening, and this has not so far been possible to achieve.

In conclusion, whilst we must recognise and try to overcome the limitations inherent in chemical growth control, let them not discourage us from exploiting the very great potential which growth regulators offer, for, in the words of Wittwer (27) they "bring new possibilities in circumventing environmental limitations, relaxing genetic restraints, improving the quality, and aiding the production, harvesting and preservation of food and other crops".

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NOTES

RESEARCH ON PLANT GROWTH REGULATORS IN THE
AGRICULTURAL RESEARCH SERVICE

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The Agricultural Research Council supports a broad spectrum of growth regulator research within Institutes, in ARC Units and through research grants to individual scientists in Universities. Table I indicates the spread of endeavour both geographically and by commodity. Plant growth regulator research is carried out in a number of research institutes and, in addition, the Unit of Developmental Botany in Cambridge and the Unit of Plant Growth Substances and Systemic Fungicides at Wye College have been very substantially committed to the subject; the Unit of Developmental Botany was disbanded in 1977 with the retirement of Professor P. W. Brian and the Unit of Systemic Fungicides will be disbanded in 1978 when Professor R. L. Wain retires, but much of the work will be continued by the staff after dispersal to Institutes.

The research may be somewhat arbitrarily divided into three categories:-

- a) application
- b) process
- c) biochemical

and the approximate effort in each of these, broken down by commodity, is given in Table 2. Application research is self-explanatory and, within this category, investigations are largely concerned with the use of growth regulators in the manipulation of processes of agricultural importance. The spread of investigations is quite considerable and extends from experiments with new chemicals and new methods of application to semi-commercial or even commercial trials; normally, however, the latter and other aspects of development work are undertaken by ADAS scientists, often working in association with ARS scientists. A very substantial part of the application research is concerned with horticultural commodities, particularly fruit: these are often labour-intensive crops where even relatively high cost chemicals may be of economic benefit. Examples include the chemical control of habit and shape in fruit trees (EMRS) and pot-grown ornamentals (GCRI), and the control of variability of yield in tree fruits by using fruit setting and thinning agents (EMRS, LARS). Predictably, there is relatively little application research in forage and arable crops.

Process research covers investigations into the physiology of processes that are under hormonal control. This type of investigation gives the necessary back-up for applied research and results can ultimately lead to improvements in practice. For example, the use of growth regulators for fruit setting and thinning in top fruits often gives variable results from season to season and from place to place, and a deeper and better understanding of the basic causes that underlie this variation in response should improve the reliability of commercial applications. A second objective of this type of research is to

identify the physiological processes that limit yield and to investigate the hormonal involvement in the regulation of these processes, ultimately using the information as an input into breeding programmes. For example, there is currently work in progress at the PBI to investigate the ABA concentrations of various cereal genotypes in relation to their ability to withstand water stress. Similarly, because harvestable product is a function of the partitioning of assimilates as well as of the overall photosynthetic capacity of the plant, an understanding of the role of hormones in the regulation of partitioning could contribute substantially to breeding programmes for maximum yield. A third objective is the possible control of processes that might have an economic input. Examples can be drawn from research into weed physiology at WRO. For some years now, rhizome regeneration in Agropyron has been studied in the hope that a better understanding of this hormonally controlled process will lead to improved methods of control; similarly, research into the physiology of the abscission process is being started with the ultimate objective of better control of black grass, in which seed shedding prior to cereal harvest is a major factor in its success as a weed; dormancy in wild oat seeds is also under study. A fourth objective is the possibility of direct application of results to production techniques. For example, work on the hormonal control of differentiation and regeneration is being carried out in relation to micropropagation techniques for a range of horticultural crop plants. The benefits of micropropagation are many, including freedom from disease, rapid regeneration of limited clonal material, and the maintenance of good clones. Flowering is another process of great importance in agriculture and any better understanding of the hormonal basis of the switch from vegetative to reproductive growth, and the control of subsequent reproductive development, might have far reaching implications. The physiology of flowering is being studied in a range of crops including grasses (WPBS), glasshouse flowers and fruits (GCRI), cereals (PBI) and fruit (EMRS, LARS).

These process oriented investigations range from biochemical and metabolic approaches to those which are almost applied in nature. Studies of the effects of environmental, ontogenetic, or genotypic variables on the content and turnover of endogenous hormones comprise a significant part of this research.

Underlying both the physiological and applied investigations are the fundamental biochemical studies in category (c). About half of the ARC funded research into the biochemical aspects of plant growth regulators is carried out in Universities. A major limitation to the exploitation of plant growth regulators in agriculture is the paucity of precise information concerning hormone function and the details of hormonal control in the processes that are regulated. This is true of all the major classes of hormones, and research effort is needed to elucidate the pathways of synthesis and breakdown, transport and movement, modes of action and interaction at the molecular level, and interaction with the environment. ARC supports such fundamental research and this may best be illustrated by reference to work on gibberellins; there are studies on metabolism and turnover (Bristol), on mode of action and receptor molecules (WPBS), on environmental effects (Aberystwyth) and on genetic aspects (PBI, USF). These studies in themselves are not aimed at a particular process of agronomic relevance but the information is necessary before we can develop a real understanding of the functions of hormones and achieve their effective exploitation.

Table 1

| COMMODITY | T Y P E O F R E S E A R C H | | |
|-------------|-----------------------------|---|---|
| | (a) Application | (b) Process | (c) Biochemical |
| General | LARS HRD | LARS LL RES UDB USF WPBS Aberystwyth Wye | UDB USF Aberystwyth Bedford Bristol Stirling |
| Forage | | WPBS | WPBS |
| Cereals | RES | PBI RES | RES |
| Vegetables | | NVRS JII | |
| Glasshouse | GCRI | GCRI | |
| Fruit | EMRS LARS Wye | EMRS | |
| Weeds | WRO | WRO Aberystwyth | |
| Ornamentals | EMRS GCRI | GCRI | |

Table 2

| COMMODITY | TYPE OF RESEARCH (1977) | | |
|-------------|-------------------------|-----------|---------------|
| | Application % | Process % | Biochemical % |
| General | 2 | 27 2 | 3 3 |
| Forage | | <1 | <1 |
| Cereals | 2 | 8 | <1 |
| Vegetables | | 3 | |
| Glasshouse | 3 | 3 | |
| Fruit | 22 <1 | 9 | |
| Ornamentals | 6 | 3 | |
| Weeds | <1 | <1 <1 | |
| Total | 36 | 57 | 7 |

Abbreviations

| | |
|------|---|
| EMRS | East Malling Research Station |
| GCRI | Glasshouse Crops Research Institute |
| HRD | Hops Research Department |
| JII | John Innes Institute |
| LARS | Long Ashton Research Station |
| LL | Letcombe Laboratory |
| NVRS | National Vegetable Research Station |
| PBI | Plant Breeding Institute |
| RES | Rothamsted Experimental Station |
| UDB | Unit of Developmental Botany |
| USF | Unit of Plant Growth Substances and Systemic Fungicides |
| WPBS | Welsh Plant Breeding Station |
| WRO | Weed Research Organisation |