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HORMONAL REGULATION OF ASSIMILATE MOVEMENT

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Summary The mode of action of plant growth substances in promoting the transport and accumulation of ^{14}C-photosynthates is discussed. IAA and cytokinins can promote both acropetal and basipetal transport by effects produced at the site of application. Application of IAA to decapitated, non-growing internodes of Phaseolus vulgaris causes no detectable increase in metabolic demand or in the rate of uptake of ^{14}C-sucrose by the stem tissues over a 12 h experimental period. The effect of IAA can only be demonstrated when phloem transport is involved. It is suggested that IAA acts by facilitating the transfer of sugars from the phloem, probably by stimulating the 'unloading' process. The results are discussed in relation to recent evidence that phloem loading involves proton co-transport of sugars, and since IAA is known to stimulate proton excretion it is suggested that it may act on the unloading process by stimulating a proton pump.

INTRODUCTION

It is generally agreed that the increased productivity of crop plants over that of their wild ancestors is due primarily to improved distribution of dry matter to the harvested part of the plant, rather than to increased production of total dry matter. Hence a better understanding of the processes controlling the partition of assimilates within the plant is of paramount importance for the further improvement of crop yields.

Many observations on the distribution of assimilates are consistent with the hypothesis that assimilates are partitioned within the plant in response to demand by the various 'sinks', arising either from the utilization of assimilates in growth or their accumulation in the form of immobile food reserves, such as starch, lipids and proteins. The 'strength' of any given sink is measured by its absolute rate of increase in dry weight and is the product of its size and its 'activity', which is the potential rate of metabolite uptake per unit weight of sink tissue per unit time

i.e. sink strength = sink size x sink activity.

Now the supply of assimilates to a sink involves their transfer from the phloem to the sink tissue, and this appears to occur via the apoplast (Glasziou & Gayler, 1972) so that it will involve transfer across two membrane systems viz. (1) transfer across the plasmalemma of the sieve tube into the apoplast ('unloading') and (2) uptake from the apoplast into the symplast of the sink tissue, the rate of which will be measured by its sink activity. It is probable that both unloading from the phloem and uptake by the sink tissues are active processes. The rate at which assimilates are accumulated by a sink can presumably be limited either by the rate of unloading or the rate of uptake from the apoplast.

HORMONES AND SINK ACTIVITY

It is now well-established that plant growth substances, especially auxins and cytokinins, are essential for the growth of many types of callus culture, while gibberellins and/or auxins appear to be required for various aspects of normal growth, including internode extension, cambial activity and fruit growth. Thus, hormones must be required for sink activity wherever this involves the utilization of assimilates in growth, and it would seem significant that sites of active growth, such as shoot apices and young leaves and fruits, are regularly found to contain high levels of endogenous growth substances. Thus, adequate levels of endogenous growth substances appear to be essential for all aspects of normal growth and their importance for sink activity would be unquestioned even if they played no other role.

However, there is now a well established body of evidence that application of exogenous growth substances to non-growing tissues can lead to increased movement of assimilates to the point of application. Thus, Mothes and his co-workers (1959) showed that application of a cytokinin to a small area of lamina of detached tobacco leaves resulted in the movement of amino acids towards the site of application; this effect did not appear to be dependent upon increased metabolic demand e.g. in protein synthesis. Similarly, application of IAA to a decapitated, mature (non-growing) internode of dwarf bean or pea stimulates the movement of ^{14}C-sucrose from a site several cm. remote from the point of hormone application (Booth et al., 1962; Davies & Wareing, 1965).

In these latter experiments the growth substances were applied in lanolin and in the initial experiments it was found that although IAA and other synthetic auxins were active in promoting such 'hormone-directed transport', cytokinins and gibberellic acid had little effect when applied alone, although they acted synergistically with IAA when applied in combination (Seth & Wareing, 1967). More recently we have found that both kinetin and gibberellic acid applied in solution will promote the movement of ^{14}C-sucrose (Johnston & Wareing, unpubl.), so that the phenomenon is not specific for auxin-type substances.

In the earlier experiments, the hormones were applied only to the cut upper surface of the decapitated internode of a rooted plant and only the acropetal movement of ^{14}C-sucrose was studied, but it was later shown that both IAA and kinetin are even more effective in stimulating the basipetal movement of ^{14}C-sucrose when applied to isolated 10 cm stem segments of dwarf bean (Patrick & Wareing, 1973; Altman & Wareing, 1975; Johnston & Wareing, unpubl.).

The normal duration of our experiments is 12 h and over this period there is no detectable increase in internode length or of dry weight of the terminal 1 cm of internode. Hence, there is no detectable stimulation of growth over the period of the experiment, although after 2-3 days visible callus growth can be observed. However it is possible that during the 12 h of hormone treatment an increase in the rate of metabolism may occur as a prelude to subsequent renewed growth. However, no increase in respiratory activity in a 1 cm stem section below the site of hormone application can be detected (Patrick & Wareing, 1972). Moreover, there is no evidence of an increased rate of protein synthesis as indicated by the rate of incorporation of ^{14}C-leucine into protein (Patrick & Wareing, 1976).

Several other lines of evidence also seem to indicate that increased ^{14}C-sucrose mobilization in response to applied IAA is not the result of increased metabolic demand at the site of hormone application. Thus, it seemed possible that IAA might increase the utilization of the sucrose pools in the stem tissues, but the rate of metabolism of ^{14}C-sucrose in decapitated internodes was found to be unaffected by treatment with IAA (Patrick & Wareing, 1976). Moreover, the levels of sucrose appeared to be higher in the stems treated with IAA than in those treated with plain

lanolin. Again, when 1 cm stem segments from decapitated internodes pretreated with or without IAA were then immersed in ^{14}C-sucrose, the uptake of ^{14}C-sucrose was not increased but reduced by pretreatment with IAA (Patrick & Wareing, loc.cit.).

Thus, in various types of experiment no evidence could be obtained that application of IAA to decapitated internodes results in a detectable increase in the general rate of metabolism or in the demand for sucrose in the stem tissues immediately below the site of hormone application. Hence, it would seem that the transport of ^{14}C-sucrose during the 12 h following hormone application is not due to increased metabolic demand in the ground tissues at the site of application. It would seem more likely, therefore, that the hormone is stimulating the active transfer of sucrose from the phloem to the ground tissue in the region of hormone application and that this process is not regulated directly by metabolic demand. That is to say, it is postulated that IAA stimulates the unloading of sucrose from the phloem and/or its active uptake by the cells of the adjacent ground tissue. Striking evidence in support of this conclusion was provided by an experiment in which ^{14}C-sucrose was supplied at various distances from the site of IAA application; when ^{14}C-sucrose was supplied at the site of IAA application its uptake was unaffected by the presence of IAA, but when the distance between the sites of hormone and sucrose application were increased to 2 cm or more, then IAA greatly increased the movement of ^{14}C-sucrose (Johnston & Wareing, unpubl.). Thus, IAA only increases the accumulation of ^{14}C-sucrose at the site of application when phloem transport is involved.

This conclusion must imply that the hormone affects either the phloem transport process itself or the transfer of sucrose from the phloem to the ground tissue at the 'sink', or both processes. The question as to whether IAA may affect the transport process directly will be discussed below, but there seems no doubt that growth substances have an effect at the site of application as indicated by the fact that IAA is even more effective in promoting mobilization of ^{14}C-sucrose when supplied to the base of a stem segment (Patrick & Wareing, 1973; Altman & Wareing, 1975; Johnston & Wareing, unpubl.), although there is little acropetal movement of IAA under these conditions. Hence IAA can act at the site of application, but only when phloem transport of ^{14}C-sucrose from a distant point is involved, and its effect is apparently not mediated through increased metabolic demand or general increased uptake by the ground tissues; the only possible conclusion from this evidence seems to be that the hormones act by stimulating the active transfer of sugars from the phloem to the surrounding ground tissue, i.e. by stimulating the unloading process from the sieve tubes into the apoplast and/or active uptake by the ground tissue from the apoplast.

Preliminary experiments to test the effects of IAA on unloading by studying the efflux of ^{14}C from the free space of stem segments of Phaseolus did not give conclusive results (Patrick, 1976), but if there is active sugar uptake from the apoplast by the ground tissue this type of experiment may not provide a valid test.

EFFECTS REMOTE FROM THE SITE OF HORMONE APPLICATION

When basipetally-applied IAA promotes the basipetal movement of ^{14}C-sucrose in a stem segment there are good grounds for assuming that its effect is exerted primarily at the point of application, since there is little acropetal movement of IAA in bean stems. Similarly, the effect of kinetin, whether applied apically or basally, is likely to be restricted primarily to the site of application since kinetin is highly immobile in plant tissues. By contrast, when IAA is applied to the apical end of a decapitated internode or stem segment, some will be transported from the site of application in a basipetal direction, so that its effect is not likely to be restricted to the point of application. That apically-applied IAA appears to have an effect throughout the path of ^{14}C-sucrose transport is shown by the fact that application of tri-iodo benzoic acid (TIBA) and other inhibitors of polar (basipetal) transport of auxin markedly reduce the accumulation of ^{14}C at the site of IAA

application (Davies & Wareing, 1965; Patrick & Wareing, 1978).

If there is exchange between the phloem and the surrounding ground tissues during normal phloem transport it seems likely that this exchange will be promoted by the presence of IAA along the path of transport. This conclusion is supported by the finding that if IAA is applied laterally, as well as apically, to a bean internode there is a local accumulation of ^{14}C in the region of lateral application (Patrick & Wareing, 1976; Johnston & Wareing, unpubl.). It may be possible, therefore, to interpret the effects of IAA throughout the path of sucrose transport, as well as the effects at the site of application, in terms of its effects on the unloading process. However, whether this hypothesis fully accounts for the blocking effect of TIBA requires further investigation.

HORMONES AND PHLOEM LOADING

There is, as yet, little information on the possible effects of growth substances on the loading of assimilates into the phloem. Bidwell et al (1968) reported that IAA stimulates the export of carbon from mature leaves to buds, shoot apices and young leaves. Application of gibberellic acid or benzyladenine to leaves of Vitis vinifera stimulated ^{14}C-photosynthate transport to the shoot tips (Shindy & Weaver, 1967). Some evidence that IAA and kinetin may affect phloem loading was found for bark strips of Salix, in which transport of ^{14}C-sucrose away from the point of hormone application was observed (Lepp & Peel, 1970, 1971).

THE POSSIBLE MECHANISM OF HORMONE-PROMOTED TRANSPORT

Hitherto, it has been difficult to envisage how growth substances might promote the active transport of sucrose across membranes. However, it has recently been proposed that loading into the phloem involves the proton co-transport of sugars. Following the earlier demonstration that the uptake of sugars by bacteria, fungi and algae involves proton co-transport (Tanner et al, 1977), it has been suggested (Giaquinta, 1977a, b) that the loading of sugars into phloem involves the establis - ment of a pH gradient between the apoplast (pH 5-6) and the sieve tube sap (pH 8-8.5), across the plasmalemma of the sieve tube. It is postulated that the proton gradient across the plasmalemma provides the driving force for sucrose uptake, and is maintained by an ATP-driven proton-extrusion system. A charged complex (sucrose - H^+ carrier) is held to be driven across the membrane by the electrical potential difference generated by the proton extrusion mechanism

A very similar model for phloem loading has also been suggested by Malek and Baker (1977), who showed that loading of ^{14}C sugars into the phloem of Ricinus communis is stimulated by low pH and by K^+. A model was proposed for a proton co-transport of sugars from the apoplast driven by a linked proton efflux/potassium influx pump which is ATP energised.

Now these ideas seem to provide a clue as to the mechanism of IAA-promoted transport. Firstly, it is very probable that the mechanism of phloem unloading is the reverse of that for loading. Secondly, there is now considerable evidence that the mode of action of IAA in stimulating cell extension involves the stimulation of an electrogenic proton pump coupled with passive K^+ uptake (Cleland & Lomax, 1977). The nature of this proton pump remains to be elucidated, but there are good reasons for thinking that it may involve an ATP-ase.

Thus, current views regarding the mode of action of IAA derived from studies of its action in promoting cell extension correspond almost exactly with the hypotheses put forward to explain phloem loading, based upon an entirely independent approach. Thus, it is entirely logical to envisage that auxin may stimulate phloem loading and unloading by its effect upon a proton pump involving the co-transport of sugars.

Moreover, if this conclusion is valid, it follows that IAA is probably involved in the normal processes of phloem loading and unloading and that the phenomenon of hormone-directed transport is not simply an artefact. Some years ago Zimmerman (1960) argued that the exchange of sugars between phloem and surrounding tissues may be analogous to the active secretion of sugars by nectaries, which is known to be stimulated by IAA.

The effects of cytokinins on the electrogenic transport of protons has been less intensively studied, although such an effect has been reported (Marrè et al, 1974).

IMPLICATIONS OF HORMONE-DIRECTED TRANSPORT

Although the simple hypothesis that the partitioning of assimilates is determined by the metabolic demands (sink strengths) of the various sinks within the plant is consistent with many observations and is no doubt applicable under certain conditions, the pattern of assimilate distribution is frequently modified by other factors. Thus, the translocation of assimilates frequently appears to be directional, so that transport from each leaf is towards specific parts of the plant. For example, it is well-known that translocation from younger leaves is frequently acropetal, towards the shoot apices, whereas export from older leaves is downwards, towards the roots. Similarly, the assimilate supply to the developing ear of wheat is mainly derived from the uppermost, ('flag') leaf. Such directional translocation can sometimes be shown to be attributable to the vascular connections between the 'source' leaf and the sink.

However, a further complicating factor arises where there is competition for assimilates between the various sinks within the plant and the effectiveness of a given sink to accumulate assimilate will depend upon its competitive ability. It is well-known that the various types of sink within the plant differ in their competitive abilities; thus flowers and fruits frequently show high competitive ability as against vegetative shoot apices and roots. Little is known as to the physiological basis of competitive ability, although clearly factors such as vascular connections and proximity to sources of assimilates are likely to be important. However, if the unloading of assimilates and their uptake by sink tissues is under hormonal control it would seem likely that the hormonal status of a given sink may be an important factor in determining its competitive ability.

The practical implications of hormone-promoted transport are difficult to assess. If hormones are involved both in the transfer of assimilates from the phloem to the sink and in the growth of the sink itself, then either or both of these processes might be limited by low levels of endogenous hormones. It is possible to envisage that the growth processes might be limited directly by hormone deficiencies in various situations, e.g. in dwarf mutants deficient in endogenous gibberellins, and in seedless grapes and other fruits, so that expernal application of gibberellins leads to increased growth. Similarly, it is possible that where intensive breeding has led to greatly increased growth of certain parts of the plant (e.g. cereal grains or sugar beet roots) the growth rate may be limited by inadequate endogenous hormone levels.

There is no information as to whether transfer of assimilates from the phloem is ever limited by low endogenous hormone levels, but it would seem possible that the stimulation of fruit set and the production of seedless fruits by external application of growth regulators may result partly from the increased ability to mobilize assimilates which the exogenous growth substances confer. Moreover, increased movement of assimilates into fruits by application to them of exogenous growth substances has been demonstrated (Weaver et al, 1969).

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NOTES

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ASSIMILATE PARTITIONING AND HIGH YIELD IN CEREALS

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INTRODUCTION

Early studies of cereal yield emphasised the importance of the partitioning of dry matter (d.m.) between the grain and the rest of the plant (Beaven 1920). The ratio of grain d.m. to total plant d.m. at harvest - the harvest index (H) - has still to be accepted as a useful variable in crop yield studies (Donald & Hamblin 1976). Indeed, only shortly after Beaven's early work the emphasis of yield studies shifted to the morphological "factors" into which yield can be resolved: the number of plants per unit field area (N_p), the number of ears per plant (N_e), the number of grains per ear (N_g) and the mean weight per grain ($\overline{W}_g$). Whereas Engledow and Wadham (1923) explored the dynamics of these factors many later workers measured them only at harvest. Analyses based entirely on these incomplete measurements failed to reveal how yield was related to environmental history.

For the last three decades, many aspects of cereal growth, development and yield have been studied and the results frequently reviewed (e.g. Evans, Wardlaw & Fischer 1975; Thorne 1974; Bingham 1972). This paper uses the results of such studies to give a general outline of the processes involved in determining H and yield, thereby providing a physiological background within which the possibilities for growth regulation can be viewed. Attention is centred on winter wheat and spring barley which together constitute about 80% of the U.K. cereal acreage.

ASSIMILATE PARTITIONING AT HARVEST

Because of different, and often unreported, methods of harvesting cereal crops there are few consistent measurements of both grain and straw+chaff yields which can be validly compared. However, grain and straw yields are recorded each year as part of the Broadbalk and Hoosefield classical experiments at Rothamsted Experimental Station. These measurements have been used to illustrate typical variations of H in cereal crops grown with different fertilizer treatments, cropping rotations and weather (Rothamsted 1971-76). From 1970 to 1975, treatments were picked randomly from each section of the Broadbalk and Hoosefield experiments and grain d.m. plotted against grain+straw d.m. (Fig. 1). Straw weights were increased by one third to allow for the stubble left after combine harvesting (Holliday & Willey 1969). While this procedure neglects chaff weight and introduces other slight inaccuracies, for instance in a dry season when straw tends to be shorter, it provides a good general picture which would otherwise be difficult to obtain.

Figure 1b shows that the grain yield of Julia spring barley is closely correlated with total d.m. production and that the range of H is only about $\pm$ 10% of its mean value. For Cappelle-Desprez winter wheat the correlation between grain

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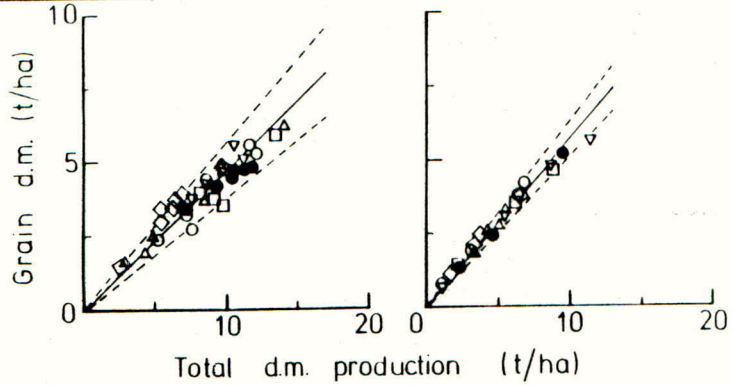
and total d.m. is weaker and the range of H is about ± 20% of its mean value. Analysis of fewer, but more precise measurements made at Sutton Bonington on Proctor barley and Huntsman winter wheat confirmed the relations of Figure 1 and showed that taking account of root weight altered the relations only slightly. The implications for yield are clear. First, because the range of H is small compared to the total range of d.m. produced, a high production of total d.m. is a pre-requisite for high yield - especially in the case of spring barley. Second, the variation in H is independent of total d.m. production so that at high levels of d.m. production small changes of H are associated with quite large yield differences.

Fig. 1. The relation between grain yield and total d.m. production for (a) Cappelle-Desprez winter wheat and (b) Julia spring barley. The solid lines represent the average harvest index (H) of the crops; for (a) y=0.48x, and (b) y=0.59x. Pecked lines define for (a) ± 20% of H and for (b) ± 10% of H; symbols are for 1970 (o), 71 (Δ), 72 (□), 73 (▽), 74 (◇) and 75(●). See text for further details.



The d.m. production of cereal crops depends on how much sunlight they intercept and the efficiency with which photosynthesis converts this radiant energy into the chemical energy of plant d.m. The amount of radiation that crops intercept is the more important factor in determining dry matter production and this depends on the rate of leaf expansion early in the growing season and the persistence of leaves and other green organs during crop development (Gallagher & Biscoe 1978). It is hard to envisage how growth regulators could be used to increase leaf area expansion rate early in crop development when temperatures are usually low and nearly all assimilate not required for root growth is used for leaf growth. Previous attempts to use GA for this purpose were not successful (Morgan 1968). Flattening of the cereal crop after ear emergence by wind and rain (lodging) slows photosynthesis markedly, encourages the spread of fungal diseases and decreases grain yield substantially. The use of CCC (2-chlorethyl trimethyl ammonium chloride) in preventing wheat crops from lodging is well known and is one of the outstandingly successful examples of plant growth regulation. Unfortunately CCC does not affect barley straw to the same extent (Humphries 1968). Prolonging the persistence of crop green area towards the end of crop development per se is unlikely to increase grain yield which, as will emerge later, is largely determined by about two weeks after anthesis. More likely to be important at this time is chemical control of pathogenic fungi which slow photosynthesis and decrease grain yields Ellen & Spiertz 1975; Alberda et al. 1977). Drought also slows photosynthesis and attempts to ameliorate its effects are discussed by Mansfield and Davies (p. 45), while possibilities for increasing photosynthetic rates of unstressed tissues are considered by Treharne (p.153). The rest of this paper is therefore devoted to processes determining how plant d.m. is partitioned between grain and other organs and concentrates on winter wheat because of its more variable H (Fig. 1).

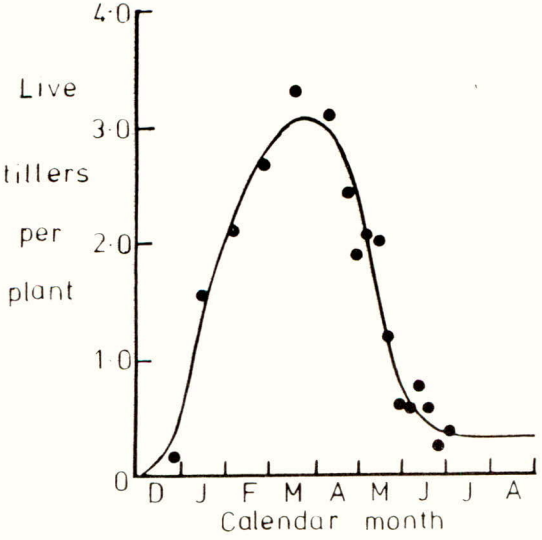
PARTITIONING PROCESSES

While harvest measurements of the grain, straw and chaff d.m. of a cereal crop allow a precise value of H to be calculated, they contribute little to understanding how, why and during what developmental phases that particular value of H was determined. Clearly, there are many combinations of the four yield factors which can result in variations of H for a given total crop d.m. production. The problem in understanding variations of H is therefore to understand how the processes determining the number of grains that a crop produces and the average weight of those grains are influenced by internal plant physiological conditions and the external physical environment. With such knowledge the task of manipulating both the physical environment and the physiology of the plant to maximise H should be simpler. With this aim in mind, and assuming typical commercial plant establishment (N_p, plants/m^2), the processes concerned with determining the value of the remaining yield factors are now examined.

Ears per plant

Determination of N_e depends on the process of tillering, tillers being the side 'shoots' of grasses formed in the axils of the lower leaves. Winter wheat plants usually form about six tiller buds but typically only 3-4 of these extend beyond their subtending leaf sheaths and become externally visible. However, under typical growing conditions, very few of these visible tillers actually produce grain-bearing ears at harvest because of severe tiller death in the 6 weeks preceeding anthesis. Figure 2 shows a typical time course of the appearance and death (defined by yellowing of the youngest visible leaf) of tillers in an early sown winter wheat crop. Although about three live tillers per plant were present

Fig. 2. The change with time of tiller numbers per plant for a Huntsman wheat crop sown 30 October 1974 at Sutton Bonington and receiving 100 kg N/ha on 1 May 1975.



at peak tillering (mid-March), on average only one in every three plants had an ear-bearing tiller at harvest (Fig. 2). Expressing the number of ear-bearing tillers at harvest as a percentage of the maximum number of tillers per plant gives a tillering efficiency for this crop of only about 10%. The precise time and the reasons for tiller death, which occurs at a time of increasing insolation and crop photosynthesis, remain unknown (Gallagher, Biscoe & Scott 1976). In general, fast production of dry matter by plants between tiller appearance and anthesis is associated with the production of many tillers and a high tillering efficiency (Kirby 1969; Langer, Prasad & Laude 1973). This appears to be associated with a complex interplay of growth promoting and inhibiting hormones (Langer et al. 1973; Johnston & Jeffcoat 1977).

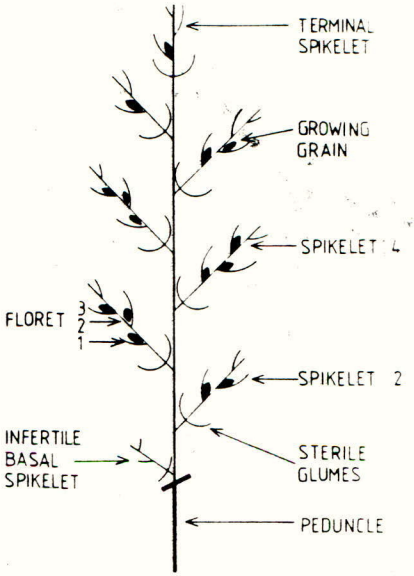
The ability of cereal plants to tiller is frequently advantageous for yield under normal growth conditions. For instance, the effects of insect pests which destroy mainstems can be greatly lessened because more tillers will bear ears; similarly, cereal crops can compensate for low plant populations following severe winters. However, from the start of tiller bud growth until the time that the tiller is autotrophic, assimilates for tiller growth must be supplied from the parent plant and it has been suggested that this assimilate might be better directed elsewhere, e.g. to the developing main stem ear (Donald 1968). This argument is particularly relevant for later-formed tillers which do not usually bear ears. Recent experiments with pot-grown barley plants showed that the main stems of plants whose tillering was limited by careful surgery, produced ears with more and heavier grains although their H was not increased (Kirby & Jones 1977). With better control of plant establishment and pests the possibility that later-formed tillers may decrease yield warrants closer attention. At present however, it is hard to see how growth regulators could be used either to limit the number of tillers formed or to increase tillering efficiency. In this respect it is probably significant that many recently bred winter wheat cultivars have a much lower tillering propensity and this attribute is associated with higher H (Bingham 1978).

Tillering efficiency is usually greater in spring than winter cereals (Gallagher, Biscoe, Scott & Dennis-Jones 1978). However as ear numbers per unit field area are very strongly associated with the yield of spring cereals, raising the tillering efficiency of these crops is still probably a worthwhile objective. (R.H.M. 1975; Gallagher et al. 1978).

Grains per ear

The determination of N_g depends essentially on the process of ear development. Figure 3 represents diagrammatically the parts of a mature wheat ear which are relevant to this paper. The first spikelet is usually initiated on the plant growing point when only four out of a total of twelve leaves have unfolded. The terminal spikelet is initiated when about eight leaves have unfolded at the beginning of May and is clearly distinguishable because it is rotated through 90°. Floret initiation starts in the larger central spikelets of the ear at the beginning of May. Although 5-6 florets are initiated per spikelet, on average only about two of these usually bear grain at harvest (Fig. 4a). The grains are not distributed evenly on the ear; a group of spikelets at the base of the ear does not bear grain, whereas spikelets in the centre of the ear bear more grain than those at the tip or towards the base. Figure 4a shows that most floret death occurs before anthesis when the number of fertile florets - those possessing viable ovaries and pollen - is determined.

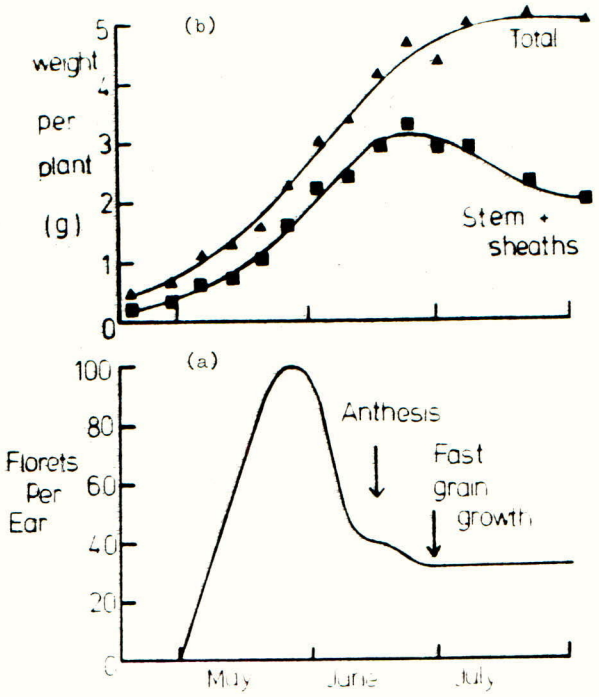
Fig. 3. Diagram showing the main floral parts of a mature wheat ear.



Considering first floret death between the attainment of maximum floret number and anthesis, much circumstantial evidence shows that this is due primarily to assimilate shortage. Shading crops, to decrease assimilate production between the start of floret initiation and anthesis, decreases grains per spikelet markedly at harvest (Willey & Holliday 1971; Fischer 1975). One reason why the developing ear may be short of assimilate at this time is the large demand for assimilate caused by fast stem and sheath growth (Fig. 4b). Supporting this idea, Bingham (1972) suggested that one of the advantages of semi-dwarf wheat cultivars whose stem growth stops early was that more assimilate was available for ear growth. This explanation is consistent with the high values of N_g typical of these cultivars. In many instances the application of CCC to cereals, which decreases stem length and reduces the risk of lodging, has increased yield even in the absence of lodging by increasing the number of grains per ear (Humphries 1968). It is tempting to speculate that this effect is caused by decreased competition between stem and ear growth but the detailed measurements required to substantiate this claim have not been made.

When cultivars are compared, very small differences in ear size at early stages of development persist throughout growth and result in heavier ears at harvest (Lupton, Oliver & Ruckenbauer 1974; Bingham 1978). It follows that if the

Fig. 4. Change with time of (a) florets per ear and (b) total and stem+sheath d.m. per plant for the Huntsman wheat crop shown in Figure 2.



ear size of winter wheat could be increased by making more assimilate available for ear growth in the spring the effect would last until harvest and result in increased grain yield. This may be one of the effects of restricted tillering (p.116). Application of cytokinin-like chemicals has also been reported to increase ear size of some cultivars but the mechanism of the effect is unknown and because of plant damage associated with applications of this chemical it is unlikely to be used for field crops (Stamp & Geisler 1976a & b).

In typical winter wheat crops about 20% of fertile florets at anthesis do not bear grain (Fig. 4a; Evans, Bingham & Roskams 1972). Neither crop shading after anthesis by DCMU (3-(3,4-dichlorophenyl)-1,1 dimethylurea) alter the fraction of florets which set grain (Willey & Holliday 1971; Langer & Dougherty 1976); so shortage of assimilate is unlikely to be implicated. However, sterilization of basal florets on spikelets results in compensatory behaviour when the more distal florets - which are usually infertile - set grain (Evans et al. 1972). Together with other evidence from similar experiments this suggests that the failure of distal florets to set grain may be caused by hormonal inhibition (Langer & Dougherty 1976). Evidently, if the failure of potentially fertile florets to set

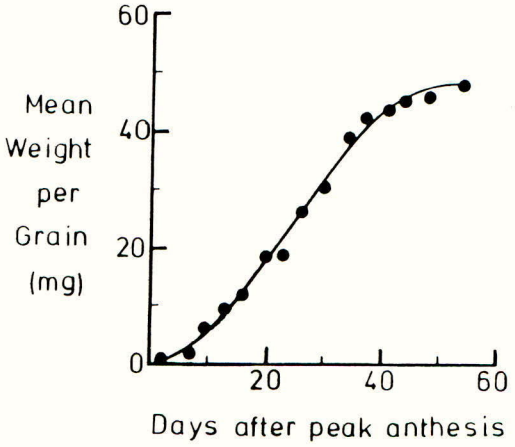
grain could be prevented chemically, and if the grains achieved typical values of $\bar{W}_g$, yield could be substantially increased; this possibility is considered later (p. 120).

In barley crops about 35-40 spikelets per ear are initiated of which only about 20 are fertile at anthesis because of spikelet death at the tip of the ear (Kirby 1973; Gallagher, Biscoe & Scott 1976). In two-rowed spring barleys each of these spikelets has only one fertile floret and can therefore bear only one grain. As with wheat, it has been suggested that floret death is due to poor assimilate supply to the distal florets (Kirby & Faris 1973). Unlike wheat however, most of the barley florets which are fertile at anthesis bear grain at harvest and opportunities for increasing N_g at this stage therefore appear negligible (Gallagher et al. 1976).

Mean weight per grain

The determination of $\bar{W}_g$ depends on the processes of ovary and grain growth. Figure 5 shows the typical pattern of grain d.m. growth of a winter wheat crop in a cool season. For a short period after pollination, grain weight increases exponentially, a long period of steady growth then follows after which growth gradually stops (Fig. 4). In warm seasons grain growth starts and stops more abruptly.

Fig. 5. Change of mean weight per grain with time after peak anthesis (29 June 1977) for a Huntsman wheat crop.



Cereal physiologists have devoted much time to answering two key questions about grain growth. First, is it the supply of assimilate or the ability of grains to grow which controls grain weight? Second, which organs supply the assimilate necessary for grain growth? Many results of experiments investigating these two questions are apparently contradictory and resolution of these differences is hindered by the fact that results from experiments done with pot-grown plants in glasshouses and growth chambers are not easily reconciled with field results. However, survey of relevant work reveals four features of grain growth and associated processes which are salient to the present discussion.

1. Potential grain size seems to be controlled largely by the amount of cell division occuring in the two weeks after anthesis when cell numbers per grain are determined; a plentiful supply of assimilates during this time increases cell division rate and $\bar{W}_g$ (Brocklehurst 1977).

2. $\bar{W}_g$ varies according to spikelet position up the ear and floret position up the spikelet. Spikelets towards the centre of the ear bear the heaviest grains in both barley and wheat; distal florets bear lighter grains in wheat with the exception of floret 2 where grains are often heavier than floret 1 (Evans et al. 1975). These grain size gradients are established early in the course of ear development and the period of ovary formation may be important in determining potential grain size (Kirby 1974; 1977).

3. It has been shown that when grain growth stops, leaves may still be green and photosynthetically active and sucrose concentration in both free space and endosperm cells high; growth may therefore stop because of a decline in the capacity of grain to synthesise starch (Jenner & Rathjen 1975; Evans & Wardlaw 1976).

4. The contribution made by different plant organs to the carbohydrate accumulated in grains varies widely depending on organ size and environmental conditions during grain growth. In addition, when supplies of assimilate after anthesis are insufficient to sustain grain growth, at least some cereal cultivars appear to use carbohydrates produced before anthesis and stored in the stem for grain growth (Begg & Turner 1976). When combined with the point above, this information helps to explain why the correlation of yield with leaf area duration after anthesis is often poor (Thorne 1974; Evans et al. 1975).

With respect to grain growth, it is clear that more work needs to be done to determine more precisely what processes govern final grain size. From existing evidence attempts to increase assimilate production during the later phases of grain growth are not as likely to increase yield as are attempts to increase ovary size and cell number during earlier phases. Both nutritional and hormonal factors have been implicated in controlling the number and size of endosperm cells and grain weight (Holmes 1974). If, as suggested above, assimilate supplies in well managed cereal crops exceed requirements for grain growth, it may be possible to increase grain yields with growth regulators. First, it might be possible to increase grain numbers per ear by improving grain setting in distal florets (p.118) but these grains would be lighter and yield would not increase proportionately. Second, it might be possible to increase $\bar{W}_g$. Herzog and Geisler (1977) showed in a pot experiment that an application of benzyladenine at ear emergence significantly increased $\bar{W}_g$ of spring wheat (cv. Solo). The main effect of this hormone, which is known to increase cell division rates, was to increase grain d.m. growth during the first 10 days following anthesis, after which treated grains grew at a similar rate to the control. This result emphasises the importance of the early stages of grain growth but Herzog and Geisler (1977) warned that grain size might not be increased should assimilates be in short supply.

As well as quantitative aspects of grain yield, three main qualitative aspects can be distinguished. First, both barley and wheat grains should be above a certain minimum diameter (2.2 mm for barley and 2.0 mm for wheat). Failure to reach these sizes is usually caused by extensive foliar disease, severe drought or trace element deficiencies (Swain & Melville 1973). With the exception of alleviating drought stress, opportunities for growth regulators in improving this aspect of grain quality appear limited.

The second aspect of grain quality concerns grain nitrogen and protein contents; for milling wheat, high protein content is desirable, whereas for malting barley low nitrogen is required. The question of wheat grain protein content and and quality is very complex (Hinton 1966; Pushman & Bingham 1976) but as some growth substances are known to increase grain nitrogen (Stamp & Geisler 1976b), they may yet prove useful for this purpose. In the case of malting barley, production would be much simplified if, by the application of growth regulators, generous nitrogen fertilization to achieve high yield did not nearly always carry the penalty of high nitrogen content. However, it appears that careful plant breeding and malting procedures will be used to achieve progress with this aspect of grain quality (Morgan 1968).

The third aspect of grain quality is that of premature germination of cereal grains in the ears of parent plants, a problem in some wheat cultivars when the weather is wet during grain growth and harvest. Although plant breeders are trying to remove this trait, an effective chemical germination inhibitor would, at present, be a useful aid to maintaining grain quality in rainy regions or seasons.

DISCUSSION

Despite several decades of intensive research into cereal yields it is clear that there are still serious gaps in our knowledge of the processes controlling cereal yield factors and dry matter partitioning. Undoubtedly, part of the reason for this is that because ears and tillers are inaccessible for much of their life without destructive dissections, cereals and grasses have not proved popular for physiological studies. In addition, investigations into the determination of yield factors of field grown cereal crops are long and tedious. In this respect it is unfortunate that cereal plants grown in controlled environments frequently fail to resemble their counterparts in the field and caution must be exercised in extrapolating results from one environment to the other (Summerfield, this volume p. 125). Nevertheless, existing physiological knowledge is enough to identify several aspects of crop growth and development where growth regulators may provide ways of increasing H and yield.

Compared with some crops, however, cereals have a breeding system well suited to selection for yield. As a result of intensive selection, values of H for winter wheat have increased from about 0.35 for cultirars common at the beginning of the century, to about 0.5 for recently bred cultivars (Ellen & Spiertz 1974; Austin 1978). In addition, the growth characteristics of wheat and barley enable these species to adapt well to variations of soil type, fertility and weather. This adaptability derives from the ability of cereals to vary widely the yield factors determining grain numbers per unit field area in accordance with growing conditions (Biscoe & Gallagher 1977). Adaptability is manifest both in the conservative nature of H for cereals of a given cultivar and, in the fact that the cereal yield for any year in this country seldom differs by more than $\pm$ 10% from that estimated by the long term regression of yield on time, as shown for wheat by Elston and Dennett (1977).

Nevertheless, with farm crops steadily approaching theoretically determined limits of total d.m. production of about 20 t/ha, small increases in H are associated with a relatively large yield increase and are important (Gallagher & Biscoe 1978). Equally relevant is the fact that economic planning would be much easier, and cereal grain processing more efficient, if national cereal yields were more consistent both in quality and quantity. If growth regulators can be developed to improve cereal performance in these ways, they will come to play an important role incereal crop production.

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