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Physiological Aspects of Crop Choice [and Discussion]

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Phil. Trans. R. Soc. Lond. B 1977 **281**, 107-119
doi: 10.1098/rstb.1977.0127

Phil. Trans. R. Soc. Lond. B. **281**, 107–119 (1977)
Printed in Great Britain

Physiological aspects of crop choice

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As a result of the lag in the spring rise in temperature behind the improvement in light conditions, crop growth in the spring is frequently limited by the rate at which assimilates can be used in growth rather than by the rate of production of assimilates in photosynthesis. Hence there is a loss of potential dry matter production in the spring, both in perennial crops such as grasses, and in spring sown arable crops. There is considerable genetic variation within and between crop species in ability to grow in cool conditions, and there are good prospects for achieving earlier growth of grasses and arable crops in the spring by breeding. Spring sown arable crops, such as sugar beet and potatoes, are slow to build up an adequate leaf cover and greater yields can be achieved in mild southwestern areas than in the traditional areas for these crops. Climatic conditions in lowland areas in the west are quite favourable for crop growth, and much land in these areas at present under permanent grass is potentially capable of producing high yields of arable crops. Some alternatives to the present extensive use of home grown barley and wheat for animal feed are discussed and it is shown that certain root crops produce higher yields of metabolizable energy (m.e.) and protein than cereals. Since silage is relatively rich in protein in relation to its content of m.e., luxury levels of protein have to be consumed and a re-examination of the cost of using silage for winter feed is required in the light of increased costs of nitrogenous fertilizers. On poor marginal land yields of animal protein from sheep are very low and such land would seem to be better suited for forestry, which can produce high yields of wood for relatively low inputs of soil nutrients.

Introduction

A rational approach to the problem of increasing crop production depends upon the identification of the factors or processes limiting the growth rate throughout the plant life cycle, from germination to harvest. Some of the main rate limiting steps for the major British crop plants have now been identified, and continuing research is providing information which allows an increasing understanding of the effects of light, temperature, water and mineral nutrients on the growth of field crops (Monteith, this volume).

A complementary approach to this problem involves studies to identify the rate limiting biochemical and physiological processes within the plant itself, in relation to both 'source' and 'sink' limitations. A good example of this type of approach is provided by the very detailed studies which have been carried out on wheat to identify the internal and external factors affecting the grain-filling process, and hence yield (Bingham 1969). This improved knowledge of the physiological and biochemical components of yield in wheat is being put to good effect by the breeders. Similar studies are being made for grasses and the results applied in grass breeding (Cooper & Breese 1971), but progress with our other major crop plants such as sugar beet and potatoes lags far behind.

The better understanding of crop growth may be used to improve yields in several ways. First, in individual crops improved utilization of available resources may be achieved through the adoption of better agronomic practices. Secondly, the identification of morphological, physiological and biochemical limitations to yield in individual crop species may allow their correction through breeding and introduction of improved varieties. Thirdly, the geographical distribution of crops within the U.K. may be assessed in terms of the known effects of environmental variables on growth so as to determine whether the current distribution is likely to result in maximum yields. This paper is principally concerned with the two latter aspects of yield improvement. We shall approach these problems primarily from a physiological standpoint but we appreciate that many other considerations including problems of animal management and economic, social and political factors must ultimately influence policy in these matters. Clearly, however, any policy decision involving crop production must be consistent with sound plant physiological principles.

Variation in temperature/growth relations

In temperate climates the rise in temperature in the spring lags behind the improvement in light conditions, and since growth processes such as leaf growth appear to show higher temperature minima and higher temperature coefficients than photosynthesis (Monteith & Elston 1971), the crop growth rate in the spring is frequently limited by the rate at which assimilates can be utilized in growth rather than by the rate of production of assimilates in photosynthesis. Hence there is a loss of potential production of dry matter during the spring. The loss of potential production arising from this lag is endemic for the whole country but is accentuated in the hill areas, where the length of the growing season declines rapidly with increasing altitude and active leaf growth of grasses may not commence until mid-April or even later, although light intensities may have improved sufficiently to support growth several weeks earlier. Hence, there is a need to consider what other measures are available to ameliorate this difficulty by securing earlier growth in the spring.

Although it is generally assumed that the threshold (minimum) temperature for growth of most crop plants is about 5 °C, it is a commonplace that there are wide differences between plant species in the dates at which they begin growth in the spring, and this variation almost certainly reflects differences in their temperature minima for growth. Moreover, there is good evidence for considerable genetic variation within a single species, affecting the ability to grow in cool conditions. Thus, Mediterranean races of perennial ryegrass (*Lolium perenne*), cocksfoot (*Dactylis glomerata*) and tall fescue (*Festuca arundinacea*) show higher leaf growth rates during the winter months than do Scandinavian races of these species, and studies in controlled environments have shown that there are marked differences between populations in their ability to grow at low temperatures (Cooper 1964; Eagles 1967). Unfortunately, the Mediterranean races capable of earlier growth in the spring show low frost hardiness and the problem is to combine these two qualities if possible. Similar genetical variation in growth responses to temperature have recently been shown for *Festuca rubra* (Ollerenshaw, Stewart, Gallimore & Baker 1976). Thus, both field observations and studies in controlled environments indicate that there is genetical variation in the temperature/growth relations of these plants, and it would therefore appear feasible to breed for earlier and more rapid growth in the spring.

However, we need more precise information not only on the temperature minima for growth but on growth rates over the whole of the temperature range to which the species is normally exposed. Until recently such detailed information was very costly and time consuming to

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obtain, but we have recently been able to carry out studies on this problem for several species using a controlled environment cabinet providing a linear temperature gradient over the range 5–25 °C (Mason 1976). These studies confirmed that seedlings from different seed lots of cocksfoot and perennial rye grass collected from a wide geographical area ranging from North Africa to Northern Norway show marked differences in their growth responses to variation in temperature (T. R. Elias & P. F. Wareing, unpublished). There are significant differences not only in the temperature minima, but in the shapes of the temperature/growth curves over the whole range, between the different populations. Thus, some populations (such as those of Mediterranean origin) show a relatively low temperature minimum, but the growth rates increase relatively slowly with increasing temperatures above the minimum (low temperature coefficient), whereas others show a steeper increase in growth rate with rising temperature (high temperature coefficient). Thus, these controlled environment studies provide a high degree of precision regarding temperature/growth relations and the extensive genetical variations in this characteristic.

The relative growth rates of the seedlings of the various populations were found to be highly correlated with those obtained from observations on mature plants of these populations growing in the open, although the controlled environment data were obtained with very young seedlings maintained in a temperature gradient for only 7–10 days. Thus, it is possible to obtain accurate temperature data for different genotypes rapidly and at a very young stage, and it should be possible to use the method for screening large numbers of seedlings thereby speeding up the breeding of grass varieties for ability to grow at low temperatures. There are, of course, many other problems to be considered, including the winter hardiness of genotypes selected for ability to start growth early in the spring.

There are good reasons to expect that genetic variability with respect to growth at low temperatures occurs in other crop plants, such as sugar beet and potatoes, where slow growth in the spring limits yield. Similar genetic variability apparently occurs in tender crop plants such as dwarf beans (Innes & Hardwick 1974) and maize (Mock & Vakri 1976); indeed, the progress which has been achieved in the breeding of maize varieties adapted to British conditions offers further evidence of the potentialities in this field.

The effects of temperature on plant growth have been very neglected by physiologists in the past, partly due to the technical difficulties already referred to. There are now signs of increased interest in this field, but there is a need for much more intensive work to gain a better understanding of the biochemistry and physiology of plant growth responses to temperature and of the basis of genetic differences in ability to grow at cool temperatures. Studies of this type, carried out in collaboration with plant breeders, offer potential returns which could be of great benefit to agriculture.

Physiological aspects of crop distribution

The time lag between the improvement in light conditions and the rise in temperature in the spring not only affects the growth of perennial crops such as grass, but it has important further implications for spring sown arable crops. Owing to the sensitivity of leaf growth to temperature, spring sown seedlings are slow to develop an adequate leaf area index (i.e. leaf area per unit area of soil), so that during the period of high solar radiation in May and June, a substantial proportion of the incident light is not intercepted by the leaves of the crop but falls directly on the soil and is not used in photosynthesis: a crop of sugar beet frequently does not develop an adequate leaf area index until July, by which time light conditions are already beginning to decline (Watson 1947). Hence, conditions which allow an earlier attainment of a high leaf area index can lead to a higher annual production of dry matter with an arable crop such as sugar beet. Thus, small improvements in the rate of growth of leaves may produce large increases in dry matter production as more of the available light is intercepted.

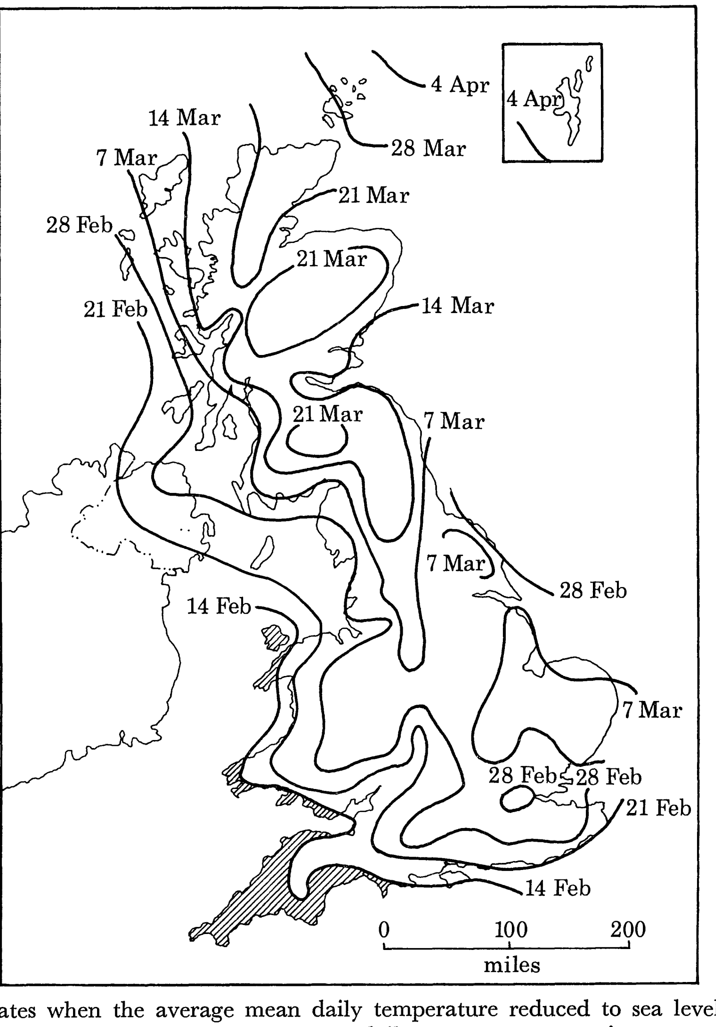

FIGURE 1. Average dates when the average mean daily temperature reduced to sea level rises above 5.5 °C (1901–30). Hatched are areas where the average mean daily temperature remains at or above 5.5 °C. (From Taylor 1967.)

Now, apart from seasonal and altitudinal variations in temperature, there are also temperature differences between the eastern and western regions of the country, with milder winters and cooler summers occurring in the west due to maritime influences. These conditions not only lead to a longer growing season for grasses in the west, but they also offer advantages for arable crops, since the temperatures reach the threshold for seedling emergence and leaf growth considerably earlier in the west, this difference amounting to as much as 3 weeks as between South West England and East Anglia (Taylor 1967) (figure 1). Consequently, spring sown arable crops can attain an adequate leaf area index much earlier in the west than the

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east, and substantial improvements in yield may be expected where the earlier sowing which is possible in the west leads to earlier emergence and an earlier onset of rapid growth. This conclusion is borne out by recent studies on the growth and yields of maincrop potatoes at the experimental farm of the University College of Wales, at Tenby, Dyfed.

Table 1. Total and graded tuber yields for two maincrop potato varieties at Trefloyne, Tenby, Dyfed 1973–1976

	1973	1974	1975	1976
	total yields/(t/ha)			
Desiree	58.0	61.0	53.6	44.5
Maris Piper	62.0	68.1	—	46.0
	yields for tubers exceeding 38 mm diameter (t/ha)			
Desiree	55.4	58.9	48.1	39.5
Maris Piper	57.9	60.1	—	40.1

Fertilizer: 160 kg/ha N and P_2O_5, 228 kg/ha K_2O. Row width: 66 cm 1972–5, 71 cm 1976. Within-row spacing: 31–41 cm.
Data from Ifenkwe (1975); Bean & Allen (unpublished).

The growth of maincrop potatoes at Tenby is characterized by early emergence and rapid growth of leaves so that a leaf surface capable of intercepting much of the incident radiation can be regularly established by late May (Allen 1977). As there is no premature senescence a high leaf area index can be maintained for a longer period than in other more easterly environments and a very high yield results (table 1). These yields are achieved by the end of August so that harvesting may begin in good soil conditions. A major advantage of these far western sites is that planting can begin much earlier than further east but in a joint experiment carried out in 1976 at Tenby and the School of Agriculture, Nottingham University, at Sutton Bonington the variety Maris Piper was planted at the same date and subjected to the same agronomic treatments at the two sites, and it was found that a more rapid increase and longer maintenance of leaf surface was achieved at Tenby than at Sutton Bonington. As a consequence, tuber yields were approximately twice as high in Tenby (40 t/ha) compared with those at Sutton Bonington at the end of July.

The growth pattern of potatoes in this western environment, i.e. the early attainment of a high leaf area index and its maintenance for a prolonged period of the growing season, is close to that suggested by Watson (1952) for achieving high yields. This growth pattern is more difficult to achieve in the traditional areas for the potato crop in the east, since early soil temperatures are lower than in the west, and frequently do not rise sufficiently to permit emergence until April or May. As a consequence it is often possible to plant on successive dates over the period mid-March to late April and yet obtain almost simultaneous emergence in the middle 2 weeks of May irrespective of planting dates. Moreover, there is a greater risk of frost damage with earlier plantings in the east. There would appear, therefore, to be a case for considering more extensive cultivation of maincrop potatoes in more westerly areas where it would seem possible to obtain higher and more consistent yields. It is of interest to note that in 1875 the main areas of potato production were West Scotland, Lancashire, Cheshire and North Wales, and there were relatively low acreages in East Anglia (Ministry of Agriculture, Fisheries and Food 1968).

A similar case can be made with respect to sugar beet. It has been shown (Scott, English,

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Wood & Unsworth 1973) that sugar yield is determined by the amount of radiation intercepted. As the crop is biennial and maintains an adequate leaf surface into the late autumn, the principal limitation to yield is in the early attainment of a high leaf area index. Many approaches have been suggested and are being studied to overcome this problem, including the use of larger embryos, fluid drilling, sowing either very early in the spring or in winter and the screening of genotypes for improved growth at low temperatures. All of these possible improvements may be expected to show greatest benefit in regions with mild winters and an early rise in spring temperatures. In the east the rise in temperature in the spring is normally later than in the west, and the date on which it commences may vary by as much as 2 months from year to year. It would seem, therefore, that the production of sugar beet would benefit from greater acreages in western environments.

There would seem to be a good case, on physiological grounds, for considering some redistribution of sugar beet and potatoes. Moreover, there is considerable interest in the possibilities of introducing 'new' crops to the U.K. to increase our home production of oil, protein and animal nutrients, and the establishment of any of these crops would result in some amendment of the present distribution of crops. The greatest potentiality for increasing production by securing early establishment of high leaf area indices occurs in western coastal localities, and there would seem to be extensive favourable areas of this category in the southern and western regions of England and Wales. We are not suggesting that there should be immediate changes in crop distribution, but rather that there is a *prima facie* case for further studies to provide a basis for long term planning. Particular attention should be given to those areas on the fringe of maritime influences to determine whether their climates offer useful advantages over areas further east.

Apart from the special advantages which the mild conditions of the southwest offer for crops such as potatoes and sugar beet, a critical reassessment of the present distribution of farming systems in England and Wales would seem to be called for. The very marked distinction between the predominantly arable farming systems in the south and east and the mainly grassland systems in the north and west dates back to the late nineteenth century, with the coming of cheap imported cereals as a consequence of the bringing into cultivation of virgin lands in North America and other parts of the world. Prior to this the acreages of arable land had been significantly higher in the western region than at present; the acreage of arable land in Wales has declined by about one third since 1875 (Ashby & Evans 1944), and this is no doubt true also of other western areas. Formerly, cereals, pulses and fodder crops were extensively cultivated throughout Wales, in areas which at present are regarded as suitable only for permanent grass (Thomas 1963). In competition with cheap imported wheat and other grains, the acreages of home grown cereals declined markedly and only in eastern regions did their production remain economic. Thus, the present distribution of farming systems in Britain must be seen in the context of the availability of cheap imported cereals during the past 100 years.

However, the dramatic increases in the world prices of cereal grains and of fertilizers which has occurred since 1973 has radically changed the economic scene and the conditions which led to the establishment of our present farming pattern no longer apply. While our entry into the E.E.C. may indicate that British agriculture should concentrate on grassland farming as Dexter (this volume) suggests, on the other hand our balance of payments deficit requires that we should reduce our imports of bread wheat and feed grain, and become more

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self-sufficient in this respect. It is therefore pertinent to consider to what extent it would be possible to increase the acreage of arable crops in the present grassland areas.

There are a number of obvious reasons why arable farming has been less favoured in the west, particularly the difficulties in tillage and harvesting operations and the greater liability to mildew and other diseases consequent upon the higher rainfall. However, if we examine the yields of some of the major crops on a county basis it is remarkable how similar they are in the eastern, Midland and western regions (table 2). Thus, so far as the climatic conditions are concerned, the northern and western regions would appear to be far from unfavourable.

Table 2. Comparative average yields of crops for the period 1968–1972 for counties in eastern, Midland and western regions of England and Wales

(From *Agricultural Statistics England & Wales 1973*, 1975. London: H.M.S.O.)

county	wheat t/ha	barley t/ha	maincrop potatoes t/ha	mangolds t/ha
Bedfordshire	4.5	3.7	26.2	67.0
Cambridgeshire	4.1	3.7	27.2	63.5
Norfolk	3.8	3.2	31.5	59.5
Lincolnshire (Lindsey)	4.1	3.5	28.0	50.2
Yorkshire (E. Riding)	4.8	3.8	28.5	56.8
Northumberland	4.9	4.1	30.8	58.5
Berkshire	4.0	3.5	28.2	47.3
Cheshire	3.3	3.6	29.0	59.8
Staffordshire	3.5	3.6	30.8	69.2
Shropshire	3.5	3.6	29.0	59.5
Cumberland	4.8	4.0	26.8	59.5
Lancashire	4.0	3.6	29.0	55.8
Somerset	4.0	3.6	29.5	63.3
Anglesey	4.0	4.1	28.0	49.5
Pembrokeshire	3.3	3.5	30.0	58.3
Radnorshire	4.2	4.0	26.3	73.0

Moreover, the introduction of new systems of tillage such as direct drilling, and the availability of modern harvesting equipment, reduce many of the traditional handicaps to arable farming in the west. Again, the introduction of improved varieties of cereals such as short-stemmed forms of barley and wheat offers new opportunities for the cultivation of these crops in more westerly areas. Thus, the reports of very high yields (more than 10 t/ha) of wheat from localities such as Cumbria suggest that the potential of modern varieties may be exploited well away from traditional wheat areas. Moreover, no doubt fodder crops could be grown in many areas which are unsuitable for cereals.

There seems no doubt that there are extensive areas of good grade land, at present under permanent grass, where the rainfall is not excessive (less than 150 cm) and which could be used for arable crops if required. The new techniques available for processing data for surveys of soil and land use capability should be of considerable value in such studies (Rudeforth 1975). It would seem important to carry out critical agronomic and economic studies to assess the potentiality for increasing the area of arable crops in traditional grassland areas, should the need arise.

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Alternative crops for winter feed

The need to reduce the use of imported and home grown cereals for animal feed and to use more of our home grown cereals for direct human consumption raises the question as to possible alternative sources of home grown winter feed. While high quality hay and good silage can go a long way to provide substitutes for cereal grain and other concentrates, hay of average or poor quality requires supplementation and there is a limit to the voluntary intake of silage. At present a high proportion of home grown barley and wheat are used as energy supplements, but the productivity of cereals in terms of the yield of metabolizable energy (m.e.) for animals is lower than for some other crops (table 3), for the following reasons.

Table 3. Comparative yields of metabolizable energy and crude protein for some major crops

crop	yield t/ha	dry matter t/ha	metabolizable energy $10^3 \times$ MJ/ha	crude protein kg/ha
wheat	4.0	3.5	50.0	350
barley	3.5	3.0	42.5	250
sugar beet	36.0	8.3	102.5	275
turnips	45.0	4.0	45.0	292
swedes	45.0	5.5	70.0	500
mangolds	62.5	7.5	92.5	415
potatoes	18.5	3.5	37.5	165
kale	37.5	6.0	62.5	660
hay	4.0	3.5	30.0	138
grass silage	27.5	5.5	47.5	550
maize silage	—	10.3	120.3	812

The yields shown in column 2 are the average yields for England and Wales for the years 1968–72, as given in *Agricultural Statistics England & Wales, 1973*, 1975. London: H.M.S.O.

The figures for dry matter, metabolizable energy and crude protein are based upon the data given in *Energy Allowances & Feeding Systems for Ruminants 1975*. M.A.F.F. Technical Bulletin, no. **33**, H.M.S.O.

First, the grain constitutes only half of the total dry matter of the crop, i.e. the 'harvest index' is relatively low. Secondly, the carbohydrate which is accumulated in the grain is mainly the product of photosynthesis in the 'flag leaf' and in the grain itself over the relatively short period (4–6 weeks) of grain filling, and the photosynthesis in the other parts of the plant contributes little directly to reserves in the grain. Hence only a small proportion of the potential photosynthesis is used in the production of the crop (Watson 1971), although the utilization of dry matter is increased where the straw is also used for animal feed. Of course, the relatively low productivity of cereals is offset by other advantages, such as the low water content, which not only renders cereal grains easy to transport and store, but also avoids the problems of bulky feed which may arise with succulent feeds such as kale and root crops.

From a biological standpoint, the most efficient and productive crop plants are, in general, ones which accumulate dry matter throughout the entire growing season and in which the whole plant can be consumed. The productivity of grassland is high because it has a long growing season and the whole of the shoot is cropped, but our commonly grown grass species do not have storage organs in which reserves of carbohydrates or fats can be accumulated, nor do they accumulate large masses of standing green crop which can be consumed in the winter, as do crops such as kale.

Root crops such as turnips, swedes, mangolds and fodder beet provide excellent means of accumulating fodder throughout the growing season which retains its quality in the field until required during the winter months. Their pattern of growth is 'open ended' in the sense that the roots are potentially capable of indefinite increase in size so long as climatic conditions remain favourable, and hence they have a long potential growth period (Watson 1971). They are also efficient in that both roots and tops can be consumed and they can be lifted mechanically if necessary. However, turnips do not accumulate reserves of sugar or starch to any great extent and their total organic content is low. As a result, the average yields of m.e. and protein from turnips are not appreciably higher than those of barley or wheat, although much higher yields are obtained in Scotland and the north of England. Their very rapid growth rate renders them very useful as a catch-crop. By contrast, the other major root crops, swedes, mangolds and beet, have a much higher organic matter content than turnips and are capable of producing a very high yield of dry matter, often 2–3 times greater than those obtainable from barley (table 3). Moreover, they have relatively high contents of soluble carbohydrate, namely sugar, and hence provide high yields of m.e. Thus, mangolds and swedes provide partial substitutes for home grown barley or imported feed grain as supplements for conserved grass for winter eed.

In the past, root crops formed an essential part of the traditional rotation in arable farming and large areas were under roots, but these have now declined to only about 5% of their former maximum areas. This decline, which has been most dramatic in the south east, has been due largely to the increasing cost of hand labour, but four modern developments have helped to offset the cost of manual labour: namely direct drilling, precision drilling, chemical herbicides and mechanical harvesting. Indeed, substantial acreages of root crops are still grown in Scotland, northern England and in certain parts of Wales, especially in Brecon and Radnor (approximately equivalent to Powys). In fact, the decline in areas put to root crops in many of these areas in recent years appears to have been arrested and the steep rise in world prices for cereal grain seems likely to give added incentive to the production of root crops.

The extent to which root crops can substitute for cereal grain will depend on the type of livestock and the system under which they are kept, but it is already well established that for many purposes they are entirely suitable as supplements to conserved grass. Moreover, there seems to be considerable scope for further improved yields from such root crops. Varieties of swedes and mangolds with improved dry matter content are available, and no doubt still further improvements could be made.

As with sugar beet, early sowing of mangolds and swedes tends to lead to bolting which is promoted by cool temperatures. Hence sowing cannot normally take place before late April so that, as already noted, a high leaf area index is not achieved until long after light conditions have become favourable. If varieties of swedes and mangolds can be produced which are suitable for early sowing, it should be possible to achieve increased yields in the northern regions, where they are already extensively cultivated.

Although to the crop physiologist and agronomist consideration of the total yields of metabolizable energy and protein point strongly to the advantages of root crops over cereal grains as supplements to conserved grass for ruminants, there are clearly many problems in animal production, such as digestibility, toxic constituents, and the maximum intake possible with bulky foods such as roots (apart from economic probems connected with harvesting and transport), which must be taken into account in deciding policy in these matters. Hitherto, problems of crop production and animal production have tended to be studied independently and often in different institutions, but there seems to be a real need for workers in these two fields to come together to assess not only the possible alternative sources of feed, but also the possible levels of production and utilization of animal nutrients from different cropping systems. Comparison of average yields of crops are too imprecise to allow meaningful conclusions to be derived.

There are also a number of possible replacements for grass as conserved fodder. Maize has been shown to produce high dry matter yields and the commercial acreage of the crop is increasing. As the crop produces yields comparable with those produced by grass, from a lower nitrogen application and only one harvest, it has considerable attraction for farmers. Bunting (1975) has shown that the grain is less important in our conditions than in North America in determining the quality of the conserved product. Cutting may therefore become earlier than at present advised. Breeding may be directed specifically towards forage quality rather than grain yield, in the belief that varieties for grain will be most suitable for forage. The suitability of this crop to many of our environments is likely to increase and intensify the competition with grass as the forage species.

Table 4. Nutritive ratios of crops†

wheat (grain)	7	mangolds (tops and roots)	23
barley (grain)	9	potatoes	22
sugar beet (roots)	33	kale	7
sugar beet (tops)	7	hay	9
turnips	13	grass silage	8
swedes	12	maize silage	14

† Nutritive ratio = digestible carbohydrate and oil/digestible protein (calculated on an energy basis). From Halnan & Garner (1953).

Dry matter production and mineral nutrition

In the vegetative phase, widely different plants show close similarities in the proportions of the major plant nutrients they contain when grown under optimum conditions, although there are significant differences in calcium. This is not surprising when one remembers that the composition of the protoplasm is very similar in all plants. On the other hand, different plant species and different parts of the same plant show large differences in the ratio of mineral nutrients to total dry matter. There are a number of reasons for this. For example, the ratio of cell wall material to cell contents varies very widely between different species and between different tissues of the same species, depending upon the thickness of the cell walls. Similarly, tissues which store sugar in solution, or starch as an insoluble reserve, will have a higher ratio of organic matter to mineral nutrients. In most of our crop plants these variations in organic content involve primarily carbohydrates, such as sugars, starch and cellulose, but certain seeds, such as soybeans or oil seed rape store significant amounts of protein and oil.

The content of digestible carbohydrate and oil will determine the m.e. value of the crop, while the protein content will reflect the nitrogen taken up into the tissues. Hence the 'nutritive ratio' (digestible carbohydrates and oil divided by digestible protein) will give a measure of the return of m.e. for a given unit of nitrogen (and probably also other major nutrients) taken up. From table 4 we see that the ratio for whole sugar beet plants is much greater than that for grass, this difference reflecting the fact that in grass the crop is leaf tissue with a high protein

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content and the m.e. is derived primarily from the cell wall material, there being relatively little sugar or starch in the leaf.

There is no doubt that properly managed grass is a highly productive crop in terms of total annual dry matter production (Cooper & Breese 1971) due to its high leaf area index, perennial nature and high harvest index. As a food for ruminants it consists of two major fractions: the cell constituents, with their high contents of protein and nucleic acids, and the cell wall material. The latter constitutes the chief energy source for ruminants. The microorganisms in the rumen are able to synthesize protein from inorganic nitrogen and a proportion of this protein becomes available to the animal. Hence ruminants can exist on a diet with a high ratio of m.e. to protein, provided other sources of nitrogen are supplied. However, grass is relatively rich in protein in relation to total dry matter and contains luxury levels of nitrogen for cattle and sheep, so that the excess is lost in the excreta. Hence, when fresh grass or grass silage is used for animal feed a relatively large amount of protein has to be taken in to obtain a given amount of m.e., whereas in crops such as swedes, mangolds or potatoes, and even in maize silage (table 4) we appear to get a better return of m.e. for a given input of nitrogen. While this relative inefficiency of grass as a producer of m.e. in relation to nitrogen input was still economic when fertilizers were cheap, a re-examination of the economic aspects of using grass silage as compared with root crops, or fractionation of leafy crops (Pirie, this volume), would now seem to be called for. Such a study would need to take into consideration the fact that nitrogen applied to grassland is largely absorbed by the sward, whereas a significant part of nitrogenous fertilizer applied to arable land is lost in the drainage.

The question of biological efficiency with respect to the input of mineral nutrients is particularly pertinent in relation to infertile soils of marginal land in the hills, where the low production arising from climatic conditions and losses of nutrients due to leaching by high rainfall reduces still further the profit margins. Much of this land is, of course, suitable only for grazing by sheep or cattle, but the annual production of animal protein per hectare is very low (3–30 kg ha^{-1} live weight of lamb on poorer land (Eadie & Cunningham 1971), particularly in comparison with the 350 kg ha^{-1} of wheat protein for direct human consumption which can be obtained in the lowlands. The conversion of plant protein to animal protein is, even under the most favourable conditions, an inefficient process, and to use marginal land for protein production would seem not only to compound this inefficiency but to be working against the natural ecological processes.

In common with most of our other land, the original natural vegetation of the hills was forest. In a natural forest ecosystem there is a regular nutrient cycle in which the mineral nutrients taken up by the trees are ultimately returned to the soil in dead leaves, branches and trunks. In production forestry the boles of the trees are harvested and removed, but the mineral content of the wood of conifers such as Sitka spruce is very low (table 5) and a high proportion of the mineral nutrients is returned to the soil as needles, branches and other residues. Some fertilizer input, in the form of phosphate and sometimes nitrogen, is required by the young trees at the time of planting and sometimes during the early years of growth, but thereafter there is normally little further application of fertilizers during the normal rotation cycle of 50–60 years. Hence the average annual fertilizer input for forestry over the whole rotation is very low, and the loss of mineral nutrients will be partly balanced by the release of nutrients from rock weathering and biological nitrogen fixation, although precise information regarding the supply of nutrients by these processes is still lacking (Ovington & Madgwick 1958; Stone 1975).

Thus forestry produces a large crop of harvestable cellulose for a relative low input of mineral nutrients.

The question of whether our poorest hill land, much of it heathland and moorland, is best used for forestry or for sheep grazing, is a highly complex one which has been discussed elsewhere (Gimingham 1972). Timber, as well as food, constitutes a large item in our import costs, and to assess on economic grounds the best use of our poorer hill land in these terms involves estimates of world prices of timber and food 50 years hence. A study of this problem was carried out by the Land Use Study Group in 1966 (Anon. 1966), but world prices have changed drastically during the last 10 years, and a fresh approach to this problem seems to be called for. However, on biological grounds much of our marginal land seems to be better suited to the production of cellulose rather than animal protein.

Table 5. The average chemical composition of *Quercus robur* and *Picea abies* (from Ovington 1958)

	ash	C	N	Na	K	Ca	Mg	P
Quercus robur								
leaves	5.63	56.15	2.91	20	1200	1030	220	250
canopy	1.12	55.08	1.01	6	485	336	82	95
bole	0.64	59.25	0.14	2	111	162	22	11
Picea abies								
leaves	4.38	60.58	1.53	60	500	660	90	120
canopy	2.31	59.18	0.71	11	207	385	62	80
bole	0.41	63.41	0.07	2	33	109	19	10

The first three columns are expressed as percentages of oven dry mass, the last five as mg/100 g oven dry mass.

The authors are indebted to Professor J. P. Cooper, F.R.S., and Professor W. Ellison for reading the manuscript of this paper and for their helpful and constructive criticism; however, responsibility for the views expressed here rests solely with the authors.

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Discussion

H. C. Pereira, F.R.S. (*Ministry of Agriculture, Fisheries and Food, 10 Whitehall Place, London SW1*). Professor Wareing has made a good case for the greater dry matter yields of roots as compared with grass or cereals, but he dismissed the problems of a wet harvest rather light-heartedly. Lifting and shifting a heavy root crop in wet conditions can damage soil structure in a way that will take 2 or 3 years under a grass ley to restore. In heavy soils with high rainfall such root crops could be taken only rarely between leys.

P. F. Wareing. I agree that there may be problems on heavy soils in very wet years, but I do not think that general policy should be dictated by these extreme conditions. I am reliably informed that the improved weight distribution in modern harvesting equipment results in only minimal damage on the majority of soils in most years. Moreover, the harvesting of swedes is a surface operation, as compared with the lifting of potatoes and sugar beet, for example. Even if root crops have to be lifted early to avoid wet conditions, the dry matter yields will still be higher than for cereals. Finally, a certain proportion of root crops will be taken by stock *in situ* in the field, of course.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES