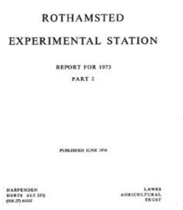
Rothamsted Experimental Station Report for 1973 Part 2



ROTHAMSTED
EXPERIMENTAL STATION
REPORT FOR 1973
PART 2

Full Table of Content

Physiology of Grain Yield of Wheat and Barley

Gillian N. Thorne

Gillian N. Thorne (1974) *Physiology of Grain Yield of Wheat and Barley ;* Rothamsted Experimental Station Report For 1973 Part 2, pp 5 - 25 **- DOI: https://doi.org/10.23637/ERADOC-1-34631**

Physiology of Grain Yield of Wheat and Barley

GILLIAN N. THORNE

Introduction

It has long been recognised that to understand the causes of variation in final grain yield previous growth must be studied. Early attempts to do this (e.g. Engledow & Wadham, 1923) involved recording changes in height, plant and shoot number throughout the season and, at maturity, the components of grain yield—number of ears, number of grains per ear and grain size. Such studies provided much information about the structure of cereal crops but little about the fundamental causes of variation in yield. One reason is that the components of yield tend to be inversely correlated with each other so when grain yield is positively correlated with one component it is often negatively correlated with others. Census studies of this kind were done at Rothamsted and elsewhere until about 1940 (Russell & Watson, 1940) and attempts are still made to correlate grain yield with particular components (e.g. Fonesca & Patterson, 1968; Hsu & Walton, 1971).

Another approach is to regard crop yield as a quantity of dry matter per unit area of land and to enquire into the growth processes that produce it. Such studies have been greatly helped by the concepts of growth analysis originated by Gregory (1917) and Blackman (1919) and developed at Rothamsted for field crops by D. J. Watson (1952; 1968).

The total dry weight of a crop at the end of the season depends on the length of the growth period and the crop growth rate, C (increase in dry weight per unit land area per unit time). As the dry matter in cereal crops is predominantly carbohydrate produced by photosynthesis, C at any one time will depend on the size of the photosynthetic system, usually estimated as the leaf area index, L (area of green leaf per unit land area), and the rate of dry matter increase per unit leaf area, the net assimilation rate (E). The latter is a measure of the excess of photosynthesis over respiration and represents the efficiency of the leaf area in dry matter production. Such growth analysis techniques, applied to cereal crops at Rothamsted from 1937 onwards, led to the conclusion that variation in dry matter yield depended more on differences in L than in E (Watson, 1947a). Net assimilation rate varied with the seasonal trend in climatic factors, and slightly between species of cereals (Watson, 1952), but the effects of fertiliser, season, species and variety on C were closely correlated with differences in L and only rarely related to the much smaller differences in E (Watson, 1947a and b). Net assimilation rate and leaf area index are not independent growth attributes: E decreases with increase in L, mainly because increased mutual shading by the leaves decreases the average light intensity at the photosynthetic surfaces (Watson, 1958). Optimal leaf area index, i.e. the value of L at which C is maximal, occurs when about 95% of the incident photosynthetic radiation is intercepted and the lowest leaves are at the compensation point. It is probably about nine for wheat and barley, which is considerably greater than for some other crops such as potatoes and sugar beet (Bremner & Taha, 1966; Scott & Bremner, 1966; Goodman, 1968). An optimal L of nine was found by direct measurement of C and L in crops of barley (Watson & French, 1958) and wheat (Watson, Thorne & French, 1963). Measurements of the penetration of visible radiation into crops of spring and winter wheat indicate values for optimum L ranging from seven to eleven, depending on the growth stage (Szeicz, 1970; Osman, 1971).

Growth analysis showed that the economically useful part of cereal crops, the grain, grows during only a relatively short part of the growth period in contrast to the roots and tubers of sugar beet and potatoes which grow during most of the life of these species (Watson, 1971). So it seemed possible that leaf area and dry matter production at different stages of growth might not contribute equally to yield, and hence the analysis of total dry matter production into C and its components L and E might not be as meaningful in cereals as in some other crops. Moreover, by 1950 Porter (Archbold, 1942; Porter, Pal & Martin, 1950) had shown that most of the dry matter that enters the grain of barley, and probably also wheat, is derived from photosynthesis after the ears emerge. So growth studies on cereals at Rothamsted from 1954 onwards have concentrated on the factors that cause variation in *grain* yield.

Many physiological aspects of grain yield in cereals were summarised in 1965 (Thorne, 1966a); this paper reviews developments since then. One aspect of cereal growth which received little attention before 1965 is root growth and its connection with top growth. These topics are the subject of another paper in this volume (p. 26).

Sources of carbohydrate in the grain

In 1965 I concluded that most of the carbohydrate in the grains comes from photosynthesis after the ears emerge, mainly in the green tissues above the flag-leaf node. Most of what is not lost by respiration during this period moves to the grain and only little remains in other parts of the plant. The relative contributions of different organs can be understood from the equation $W = P_E - R_d - R_n + S$, where W = grain yield, P_E = contribution from CO_2 uptake by the ear, R_d and R_n = loss by respiration of the ear during the day and night respectively, S = contribution from the shoot (Thorne, 1965). S can be further subdivided into contributions of various parts of the shoot. P_E and R_d can be estimated only approximately but $(P_E - R_d)$, the net uptake of CO_2 by the ear in the light, can be measured easily with an infra-red gas analyser or by long-term feeding with radio-active carbon dioxide ($^{14}CO_2$). Average values for the percentage contribution of the different plant parts to final grain yield of wheat and barley, derived from data quoted by Thorne (1965), are shown in Table 1.

TABLE 1

Percentage contribution to grain yield (W) of carbon derived from different sources of carbon dioxide

P_E = uptake by ear, R_d = ear respiration in the light, R_n = ear respiration at night, S = contribution from shoot

See text for full explanation. (From Thorne, 1965)

	Barley	Wheat
P_E	79	24
R_d	−24	−28
R_n	−10	−11
$R_d + R_n$	−34	−39
$P_E - R_d$	55	−4
$P_E - R_d - R_n$	45	−15
S	55	115
W	100	100

Relation between shoots. It has generally been assumed that little carbohydrate moves between shoots of cereal plants. Autoradiography of spring and winter wheat showed this to be true after the stems start extending (Quinlan & Sagar, 1962; Lupton, 1966), although a more sensitive technique showed that main shoots of wheat may import small amounts of carbohydrate from tillers supplied with $^{14}CO_2$, provided the tillers had not differentiated ear initials (Lupton & Pinthus, 1969). Rawson and Hofstra (1969) reported from Australia an experiment in which tillers of Sunset wheat imported ^{14}C from all leaves of the main stem throughout growth, including the grain filling period. When the leaf below the flag leaf was given $^{14}CO_2$ several weeks after anthesis, 20% of the labelled assimilate was recovered from the tiller ears. This unusually large movement into the tillers probably occurred because many tillers were produced late, the maximum number of seven being reached shortly after ear emergence. This is unlikely to occur in the field. Natr (1967) also found that unusual circumstances could induce movement of assimilate between mature shoots. With several Czech varieties of spring barley and winter wheat, the decrease in grain per ear caused by defoliation was greater when all the shoots of a plant were treated than when only one was, suggesting that intact shoots supplied carbohydrate to the ears of defoliated shoots, so partly compensating for the photosynthesis of the missing leaves.

Contribution of reserves. Recent evidence supports the conclusion reached in 1965 that most of the carbohydrate in the grain is derived from photosynthesis after ear emergence, i.e. relatively little of the photosynthate produced before the ears emerge contributes to the final grain yield. When whole plants or single leaves were allowed to absorb $^{14}CO_2$ more than five days before ear emergence, less than 10% of the activity remaining in the plant at maturity was in the grain (Birecka & Dakic-Wlodkowska, 1966; Birecka, Skupinska & Bernstein, 1967; Rawson & Hofstra, 1969). This percentage increased rapidly with successively later feeding of the $^{14}CO_2$. Different results are reported with a Japanese six-rowed barley that had seven green leaves per shoot at ear emergence: when the flag leaf was supplied with $^{14}CO_2$ shortly before ear emergence, 20% of the radioactivity in the plant at maturity was in the ear (Hozyo & Kobayashi, 1969). The percentage of the final grain weight attributed to photosynthesis before anthesis cannot be calculated from the results of these experiments, though it is clearly small. It can be calculated from experiments in which the rates of photosynthesis and the fraction of the photosynthate translocated to the mature ear are both measured (e.g. Lupton, 1968). From such direct measurements, and from estimates derived from a model, Lupton (1968, 1969, 1972) concluded that photosynthesis between ear emergence and anthesis by tissues above the third leaf (flag leaf = first) contributed less than 12% of the dry matter in the grain at maturity.

Photosynthesis after ear emergence. The relative contribution of the various green organs to final grain weight depends on their rates of photosynthesis and on the fraction of the photosynthate produced in each organ that is found in the grain at maturity. Both rates of production and pattern of translocation change during the grain-filling period and vary with variety and environment. The percentage contribution of the ear depends only on its photosynthesis relative to the contribution to the grain from the other organs, because more than 80% of ear photosynthate is recovered from the grain (Carr & Wardlaw, 1965; Birecka, Wojcieska & Glazewski, 1968). Ears of awned wheat varieties photosynthesise about twice as fast as awnless ears (Carr & Wardlaw, 1965; Evans, *et al.*, 1972a). Barley ears have larger awns than wheat and these contributed over 80% of the net photosynthesis of the whole ears (Biscoe, Littleton & Scott, 1973). The proportion of total plant photosynthesis contributed by the ear also depends on the angle of illumination; it varied from 33% when the elevation of the sun was 17° to 13% at 67° (Puckridge, 1972). Hence it will also vary with latitude. Birecka estimated ear photosynthesis by supplying $^{14}CO_2$ to whole plants (a) with only the ear exposed to light and (b) with all the green tissues exposed. The radioactivity in the mature grain for treatment (a) as per cent of (b) estimates the contribution of ear photosynthesis. Averages for exposures made at several stages of grain filling were: awnless winter wheat 11%, awned winter wheat 18%, awnless spring wheat 9%, awned spring wheat 29%, spring barley 40% (Birecka, Skupinska & Bernstein, 1964; Birecka & Dakic-Wlodkowska, 1964; Birecka, Wojcieska & Glazewski, 1968).

The percentage contribution of leaves and stems depends on their total photosynthetic production and on the fraction of this that moves to the grain. The latter is usually very small for leaves below the second (flag leaf = 1) and much greater for the flag leaf than for the second; when each of four leaves on a wheat shoot were supplied with $^{14}CO_2$ at ear emergence, the percentage of the radioactivity in the plant at maturity recovered in the grain was 55% when the flag leaf was treated, 5% when the leaf below was treated and only 2% when the next two lower leaves were treated (Rawson & Hofstra, 1969). The second leaf may contribute much more than this: up to half of its photosynthate may be recovered in the grain (Lupton, 1968) and its contribution to the grain may be more than a third of that of the flag leaf (Evans *et al.*, 1972a). The results of Hozyo and Kobayashi (1969) with barley were again unusual: about half the activity in the plant 21 days after feeding the flag, third or fifth leaf at ear emergence was in the ear.

A large fraction of the CO_2 absorbed after ear emergence is lost before maturity by respiration, and especially by respiration of the grains. Birecka and her co-workers report that about 40% of the radioactivity present in the plant immediately after supplying $^{14}CO_2$ at various times after ear emergence had disappeared by maturity. Most of the loss occurred in the first few days after treatment. When wheat was given $^{14}CO_2$ 15 days after anthesis, 20% of the radioactivity absorbed by the ear had disappeared 15 days later and 20% of that absorbed by the flag leaf was lost in 48 hours (Rawson & Evans, 1970; Carr & Wardlaw, 1965). Photosynthesis by green grains, as well as by the rest of the ear, helps to conserve CO_2, even when the ear contributes little to the net CO_2 uptake of the whole plant. All wheat grains seem to be able to re-fix their own respiratory CO_2 (Kriedeman, 1966) and those of some, but not all, varieties can also absorb exogenous CO_2 (Carr & Wardlaw, 1965; Evans & Rawson, 1970).

Few estimates of all sources of grain carbohydrate have been made in the same experiment. Lupton has attempted to estimate the contributions to the wheat grain of photosynthesis in (a) the ear, (b) flag leaf and sheath and (c) second leaf and sheath of field crops by measuring photosynthesis of these three parts at several times during the grain filling period and measuring the fraction of fed $^{14}CO_2$ reaching the grain. When plants were temporarily moved from the field to the laboratory for measurements of photosynthesis, the calculated contributions for the whole period of grain growth were: (a) ear 10%, (b) flag leaf and sheath 58%; (c) second leaf and sheath 32%, with no difference between the varieties Cappelle-Desprez and Professeur Marchal (Lupton, 1968). Later, estimates were obtained from photosynthesis measurements done *in situ* in the field and other data fed into mathematical models. The first model gave estimates very similar to those quoted above: (a) 12%, (b) 62%, (c) 26%, with no difference between Cappelle-Desprez and Professeur Marchal (Lupton, 1969). The second model gave estimates of (a) 23%, (b) 74%, (c) 3% with no difference between Cappelle-Desprez and a semi-dwarf winter wheat selection (Lupton, 1972). The accuracy of these estimates partly depends on the validity of the assumptions incorporated in the models. The lack of agreement between observed and calculated yields shows that some of the assumptions may be invalid: yields predicted by the first model ranged from 119 to 136% of the observed values and those predicted by the second were 53–54% of the observed values. Similar measurements of photosynthesis and translocation were made by Evans *et al.* (1972a) at one stage of development, 15–17 days after anthesis, on two closely-related lines, one awned and one awnless. The relative contributions of different organs in the awnless and awned line, respectively were: ear 13 and 34, flag leaf lamina 66 and 47, second leaf lamina 21 and 19% of the combined contribution of these three parts.

Absence of irrigation increased the contribution of the ear relative to that of the leaves. Lupton (1972) suggests that the contribution of the second leaves may have been over-estimated by himself in 1969 and Evans, *et al.* in 1972 because upper leaves were displaced so that the second leaves received more light when their photosynthesis was measured. The second leaf contribution was almost certainly over-estimated in 1968 too, because photosynthesis of all parts was measured in the same light intensity—a condition that does not occur in the field.

Summary. Recently developed methods of estimating the contribution of different plant parts to the carbon in the grain, involving the use of $^{14}CO_2$ to measure movement to the grain from the various photosynthesising organs, suggest that the general picture presented in 1965 (see p. 6 and Table 1) was broadly correct. However, the ear and shoot contributions estimated using $^{14}CO_2$ are not identical with $P_E - R_d - R_n$ and S in Table 1; they are physiologically more meaningful. The ear contribution is P_E less respiratory loss in the ear of CO_2 absorbed by the ear, and the shoot contribution is the carbohydrate from the shoot not lost by respiration in the grain. Methods used in the papers summarised in 1965 did not permit the separation of the two sources of respiratory substrate and all ear respiration had to be debited against CO_2 absorbed by the ear. Hence the contribution of the ear in awnless wheat varieties is probably larger than shown in Table 1—the data quoted above suggest a value of about 10–15%. Similarly, the contribution of photosynthesis by barley ears may be larger than the 45% in Table 1 and larger than the 35% estimated with an infra-red gas analyser by Biscoe, Littleton and Scott (1973). However, the only estimate based on $^{14}CO_2$ absorption is Birecka's 40%. The relative contributions to the grain of different organs evidently depend on whether awns are present and their size, and on the environment, but too few comprehensive studies have been done to show how differences in the various sources of grain carbohydrate affect variations in grain yield between varieties or variations in yield caused by differences in cultural practice, weather, incidence of disease, etc. This is particularly true for barley which has been studied much less than wheat in recent experiments.

Grain yield and leaf area duration

Measurement of leaf area. As most of the carbohydrate in the grain is produced by photosynthesis after ear emergence it is not surprising that grain yield is often closely correlated with the photosynthetic area present after ear emergence, or after anthesis, while the grains are growing. The area of leaf laminae alone is not an appropriate estimate of leaf area index because of the contribution to the grain of photosynthesis in other green organs. So, green sheaths and stems as well as laminae have been measured in recent experiments at Rothamsted. The photosynthetic area of the green sheath and stem is taken as that of the exposed outer surface and this is added to the conventional estimate of leaf area of one side of the leaf lamina to give total leaf area. This basis for summing leaf and sheath area is justified because leaves are orientated nearer to horizontal than vertical and so receive light mainly on one side, but the vertical stems receive diffuse radiation on all sides, and in England 50–60% of the incident radiation is diffuse (Szeicz, 1970). Also, when measured on this basis the rate of CO_2 uptake ('true' photosynthesis) per unit area of a naturally illuminated leaf was similar to that of a sheath and enclosed stem of equal age (Thorne, 1959). The *net* CO_2 exchange of the sheaths was less than that of leaf laminae because of the greater respiration of the larger amount of underlying tissue. Other estimates of stem area, such as the projected area, may be appropriate when considering phenomena other than photosynthesis, for example light interception by leaf canopies (Angus, Jones & Wilson, 1972). The proportion of the total area contributed by stems and sheaths is considerable—about 50% at ear emergence and increasing progressively until leaf area becomes zero at maturity. The surface of the ear has not usually been included by us in estimates of leaf area index although it has by some other investigators (Fischer & Kohn, 1966; Spiertz, ten Hag & Kupers, 1971; Yap & Harvey, 1972). The tedious measurements involved were considered unjustified until a method of estimating the light and CO_2 absorbing surface of the ears comparable to that used for leaves and sheaths was established. Moreover, during most of the grain filling period the surface of the ear, estimated as projected area, is only a tenth of that of the stem and leaf above the flag leaf node in wheat, although about a third in barley (Thorne, 1965).

Correlation of yield with leaf area duration. Most of the differences in grain yield in experiments done at Rothamsted before 1965, for example those between spring and winter wheat varieties or those caused by different amounts of nitrogen fertiliser, could be accounted for by differences in leaf area integrated over the period following ear emergence, the leaf area duration (*D*). Workers from Holland, Australia and Canada have also reported good correlations between grain yield and *D* during the grain filling period (Fischer & Kohn, 1966; Simpson, 1968; Spiertz, ten Hag & Kupers, 1971; Puckridge, 1971; Yap & Harvey, 1972). Welbank, French and Witts (1966) found that grain yield of several varieties of wheat sown in autumn or spring with two amounts of nitrogen were correlated more closely with *D* when it was based on leaf area above the flag-leaf node from anthesis onwards than when based on leaf area of the whole plant or when leaf area integration started at ear emergence instead of anthesis, presumably because most of the carbohydrate in the grain came from the area above the flag-leaf node after anthesis. The basis used for calculating *D* may not always affect the correlation between yield and *D* because the factors causing variation in yield may have similar relative effects on area of all parts of the shoot and at all times near anthesis. For example, area above the flag-leaf node contributed about 50% of *D* for Kloka, two Mexican short spring wheat varieties and Cappelle-Desprez, but 62% for Gaines winter wheat (Thorne & Blacklock, 1971). Consequently, the basis on which *D* was calculated affected the closeness of the correlation between grain yield and *D* for winter varieties but not for the spring ones.

Effects of large leaf area indices. In recent experiments the correlation of grain yield with *D* after anthesis has not been as good as observed formerly. Increases in *D*, for example those caused by additional nitrogen fertiliser, no longer cause proportional increases in yield (Thorne & Blacklock, 1971; Thorne, 1974). Such effects of nitrogen can be detected in some of the earlier experiments but were not as great as in the recent ones. Thorne and Blacklock (1971) suggested that grain yield ceased to be well correlated with *D* after anthesis when grain yields exceeded about 500 g/m^2 and leaf area index at anthesis exceeded a value of about seven, which did not occur in the earlier experiments. Data from crops with such leaf area indices are provided by the joint experiments of P. J. Welbank (Botany Department) and F. V. Widdowson (Chemistry Department) which examined the growth of winter wheat and spring wheat on different sites (Welbank & Widdowson, 1972; 1973). Leaf area index at anthesis ranged from 4 to 13 depending on the amount of nitrogen applied (six levels from 31 to 186 kg N/ha) and whether the crop was irrigated. The graphs of grain yield *v*. leaf area index (*L*) at anthesis (Fig. 1) show that grain yield increased with increase in *L* at anthesis up to a maximum value which was between 6 and 11. The curves on the figure were derived from nitrogen response curves for grain yield *v*. *L* calculated by P. E. Sparrow of the Statistics Department. Since each curve is based on only six points, the values of optimum *L* were not

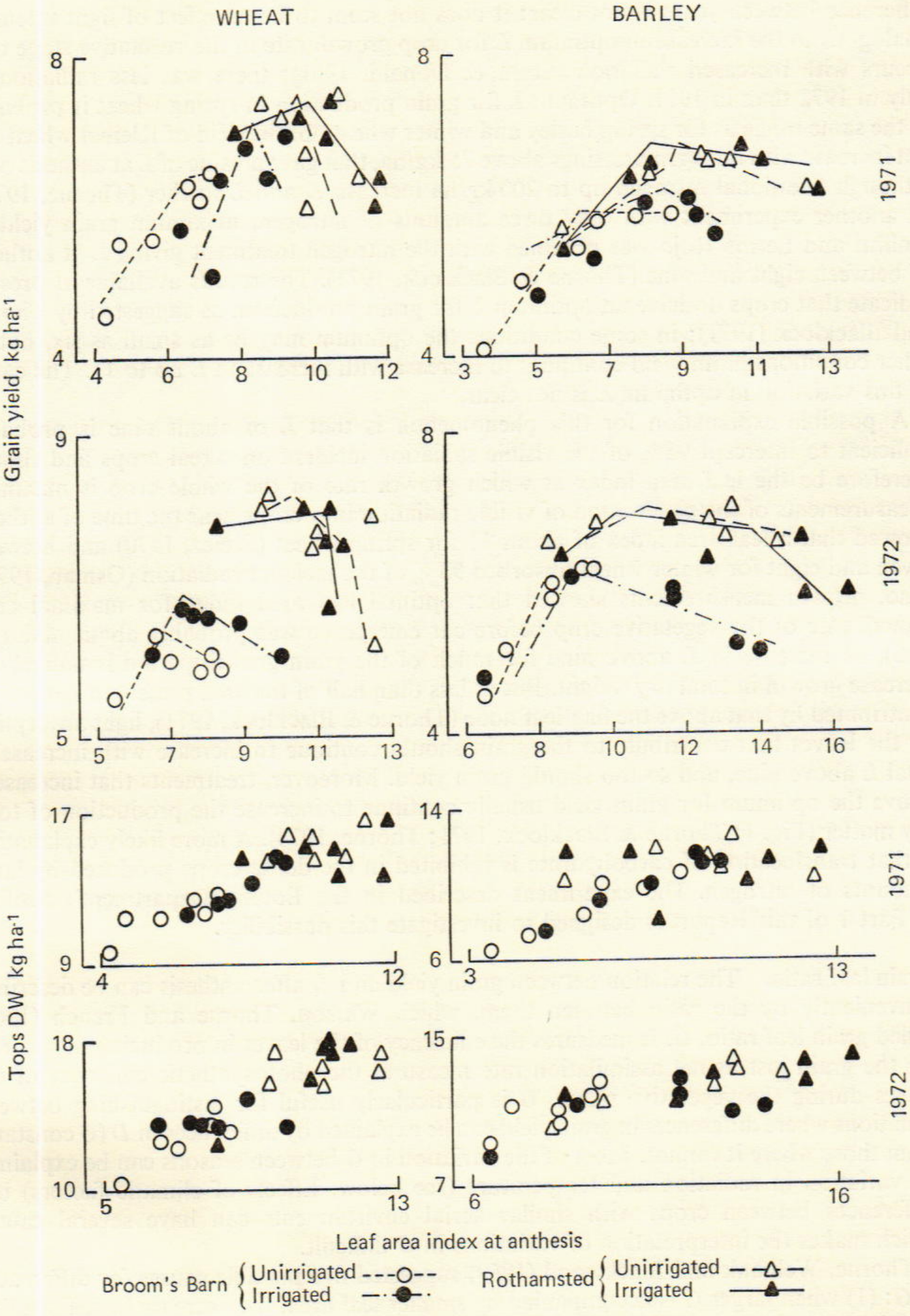


FIG. 1. Relation of leaf area index at anthesis with grain yield (85% DM) and with dry weight of tops at maturity for winter wheat and barley. See text for full explanation (p. 10). Data of P. J. Welbank and F. V Widdowson.

https://doi.org/10.23637/ERADOC-1-8

determined precisely; they seemed to be less at Broom's Barn than at Rothamsted especially without irrigation, and greater in 1972 than in 1971. The reason for the difference between years is not clear: it does not seem to be an effect of light intensity analogous to the increase in optimum *L* for crop growth rate in the vegetative stage that occurs with increased radiation (Stern & Donald, 1961); there was less radiation in July in 1972 than in 1971. Optimum *L* for grain production in spring wheat is probably in the same range as for spring barley and winter wheat. Grain yield of Kleiber wheat did not increase with nitrogen dressings above 75 kg/ha, that gave a value of *L* at anthesis of 7, although additional nitrogen up to 200 kg/ha increase *D* and *L* further (Thorne, 1974). In another experiment with only three amounts of nitrogen, maximum grain yield of Kolibri and Lerma Rojo was obtained with the nitrogen treatment giving *L* at anthesis of between eight and nine (Thorne & Blacklock, 1971). The results available at present indicate that crops do have an optimum *L* for grain production, as suggested by Thorne and Blacklock (1971); in some conditions the optimum may be as small as six, but in other conditions grain yield continues to increase with increase in *L* up to 11. The cause of this variation in optimum *L* is not clear.

A possible explanation for this phenomenon is that *L* of about nine is probably sufficient to intercept 95% of the visible radiation incident on cereal crops and should therefore be the leaf area index at which growth rate of the whole crop is maximal. Measurements of the penetration of visible radiation into crops near the time of anthesis showed that a leaf area index of about 11 for spring wheat (Szeicz, 1970) and between seven and eight for winter wheat absorbed 95% of the incident radiation (Osman, 1971). Also, growth measurements showed that optimal leaf area index for maximal crop growth rate of the vegetative crop before ear emergence was probably about nine (see p. 5), so increase in *L* above nine for much of the grain growth period is unlikely to increase growth in total dry weight. But as less than half of the area present at anthesis is contributed by that above the flag-leaf node (Thorne & Blacklock, 1971), light absorption by the leaves that contribute to the grain should continue to increase with increase in total *L* above nine, and so too should grain yield. Moreover, treatments that increase *L* above the optimum for grain yield usually continue to increase the production of total dry matter (Fig. 1; Thorne & Blacklock, 1971; Thorne, 1974). A more likely explanation is that translocation of carbohydrate is inhibited in the dense crops produced by large amounts of nitrogen. The experiment described in the Botany Department's Section of Part 1 of this Report is designed to investigate this possibility.

Grain leaf ratio. The relation between grain yield and *D* after anthesis can be described conveniently by the ratio between them, which Watson, Thorne and French (1961) called grain leaf ratio, *G*. It measures the efficiency of the leaves in producing dry matter for the grain just as net assimilation rate measures the photosynthetic efficiency of the leaves during the vegetative phase. *G* is particularly useful for distinguishing between situations where differences in grain yield can be explained by differences in *D* (*G* constant) from those where it cannot. Most of the variation in *G* between seasons can be explained by variation in radiation and temperature (see below, Effects of climatic factors) but differences between crops with similar aerial environments can have several causes which makes the interpretation of variations in *G* difficult.

Thorne, Welbank and Blackwood (1969) suggested five possible causes for differences in *G*: (1) when larger *G* is accompanied by smaller leaf area, the decrease in self shading may increase the average intensity of light incident on the leaves and hence increase the rate of photosynthesis per unit leaf area; (2) change in leaf orientation may increase light intensity and hence photosynthetic rate and *G*; (3) greater *G* may be caused by inherently faster photosynthesis of the leaves without any change in illumination; (4) ears may photosynthesise more, thus seeming to increase *G* which is based on area of leaves and stems only; (5) total photosynthetic production may not change but a greater proportion of it may move to the grain and hence increase *G* (see below, p. 18). The smaller *G* of Kloka and Jufy I than of short-strawed wheat varieties derived from Norin 10, observed by Thorne, Welbank and Blackwood (1969), was almost certainly caused in part by (1) which occurs whenever there are large differences in leaf area, for example those caused by nitrogen fertiliser; it is analogous to the decrease in net assimilation rate that accompanies increase in leaf area during the vegetative phase (Watson, 1958). Greater photosynthesis by the awned ears of the short varieties (4) also undoubtedly contributed (see p. 7, above). There was no obvious difference in leaf orientation (2) and there were no differences between tall and short varieties in extinction coefficient in another experiment (Thorne & Blacklock, 1971). Difference in photosynthetic rate (3) is also unlikely to be involved as faster photosynthesis has not yet been proved to cause greater yield in any comparison between cereal varieties, although estimates derived from a model suggest that the large yield of a semi-dwarf selection was caused by faster photosynthesis (Lupton, 1972). The final dry weight of straw and grain indicates that (5) may be concerned, although this cannot be proved without frequent measurements of dry matter distribution or, preferably, estimates of the distribution of photosynthesis using $^{14}CO_2$. Watson, Thorne and French (1958) concluded that the greater *G* of new than of old barley varieties was a consequence of more ear photosynthesis; leaf areas were similar and dry weight changes of the stem indicated no difference in (5). Later measurements of CO_2 exchange of ears using an infra-red gas analyser supported the possibility (Thorne, 1965). Growth data suggested that neither (1), (3) nor (5) caused the large *G* of modern wheat varieties as compared with older ones and Watson, Thorne and French (1963) concluded that more ear photosynthesis was the most likely cause but direct measurements of CO_2 exchange did not confirm this (Thorne, 1965). Another explanation is suggested below (p. 20).

Since ears of barley photosynthesise more than those of wheat (see p. 7) and *G* is based on area of leaves and stems only, *G* should be larger for barley than for wheat, but was not in the data examined by Welbank, Witts and Thorne (1968), possibly because the rest of the shoot photosynthesised slower in barley than in wheat. The rate of photosynthesis of the combined flag leaf, flag-leaf sheath and peduncle of barley was less than of wheat, when measured in the field with an infra-red gas analyser (Thorne, 1965), but no difference was found between flag-leaf laminae measured in a growth room having a light intensity of only 65 W/m^2 of visible radiation (Thorne, 1966b). In the comparison of winter wheat and barley done by P. J. Welbank and F. V. Widdowson at Rothamsted in 1971 (see p. 10), *G* of barley was more than 20% greater than of wheat when crops with similar leaf areas at anthesis, and hence presumably similar degrees of self shading, were compared. But more favourable weather during the grain filling period of barley could account for its *G* being about 10% greater than that of wheat. The rest of the difference might reflect the greater ear photosynthesis in barley but it could have other causes, such as a difference between the crops in the pattern of change of *L* with time, resulting in a difference in productivity per unit of *D*. Further investigations are obviously needed to reconcile the small differences in *G* between wheat and barley with other knowledge about the sources of grain carbohydrate in the two crops.

Summary. Recent experimental evidence clearly shows that variation in leaf area after anthesis does not explain variation in grain yield as well as was thought in 1965. However, it is essential to estimate leaf area duration after anthesis when investigating causes of variation in grain yield, in order to distinguish between situations in which grain yield can and cannot be explained by differences in leaf area duration. In the first, factors

https://doi.org/10.23637/ERADOC-1-8

affecting leaf expansion and senescence are likely to be involved, whereas in the second factors affecting photosynthetic efficiency and the distribution of dry matter are more probably concerned. Some of these are discussed in the following sections.

Effects of climatic factors

Since Rothamsted acquired controlled environment equipment in 1962 the effects of temperature and radiation on growth of wheat and barley have been studied in some detail (Thorne, Ford & Watson, 1967, 1968; Thorne, 1971). Some experiments have also been done outdoors to investigate the effects of radiation by shading, and the effects of natural variation in radiation and temperature by multiple regression analysis (Welbank, Witts & Thorne, 1968). This latter technique often does not give useful results, especially when used for analysing effects on final yield or on growth over long periods, because it fails to discriminate between effects of different factors at different stages of growth and between the effects of temperature and radiation, which are closely correlated in England. Even with yields and weather data for many years from crops otherwise uniform, such as wheat on Broadbalk field, little information has been obtained with multiple regression techniques (Buck, 1961).

The effects of water supply on growth of cereals have also been studied at Rothamsted (Welbank & Widdowson, 1972, 1973; Lawlor, 1971, 1972, 1973a, 1973b) but will not be discussed here.

Temperature and radiation after anthesis. Experiments in growth rooms where temperature and amount of daily radiation during the grain filling period were varied independently showed that increase in temperature, within the range found outdoors in England at this time, decreased grain yield by hastening senescence of the leaves (Thorne, 1970). Increasing the radiation by increasing either the intensity or the daylength increased grain yield (Thorne, Ford & Watson, 1968; Thorne & Ford, 1971). These results suggest that cereals yield well in fine summers because of the extra radiation rather than the warmer temperatures. Fig. 2 shows the effects of halving the amount of daily radiation received by wheat plants during a 16-day period starting either 5 or 21 days after anthesis. The larger amount, 740 J cm^{-2} day^{-1}, is similar to the average value outdoors in July. Halving the daily radiation during either period decreased final ear dry weight and final grain yield by about 12%. The earlier treatment decreased the number of grains per spikelet and grain size; the later treatment affected only grain size. Halving the radiation during both periods decreased grain yield by 22%. In experiments on field crops of wheat in two years, halving the daily radiation received by the crop by shading continuously between 50% ear emergence and maturity decreased grain yield by about 60%, affecting both grain size and number of grains per ear (Welbank, Witts & Thorne, 1968). However, Willey and Holliday (1971a and b) found that halving the radiation during grain growth had no effect on grain yield of barley and decreased the grain yield of wheat by only 30%. In Illinois a 30% decrease in radiation after anthesis decreased grain yield by 25% (Pendleton & Weibel, 1965). It seems that decreased radiation during the grain filling period affects grain growth directly by decreasing photosynthesis and the supply of assimilate and hence decreases grain size. Also, when radiation is severely restricted close to the time of anthesis grain set may also be decreased. So decreased radiation after anthesis will normally lessen grain yield unless this is already limited by some internal factor and not by carbohydrate supply.

The effects of variation in temperature during grain filling are more complicated. Although increase in temperature from 15 to 20°C throughout the grain filling period decreased final ear dry weight, it increased the rate of ear growth during the first 20 days

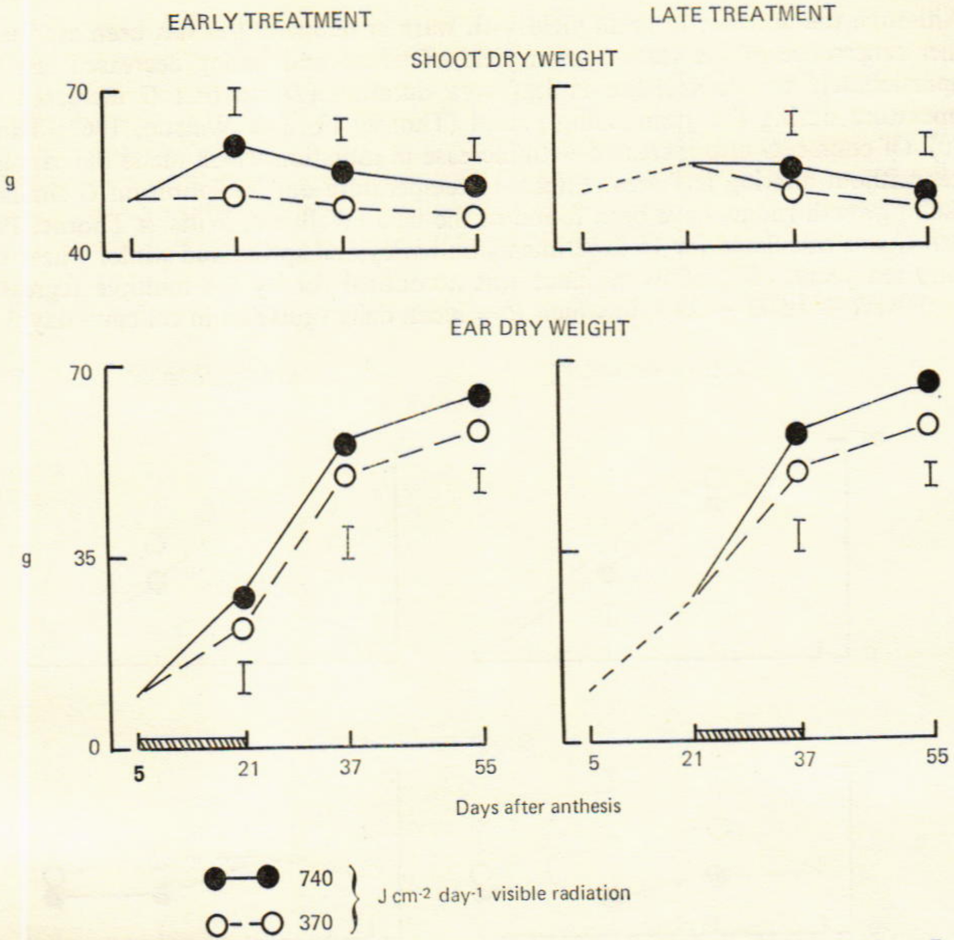


FIG. 2. Effect of a difference in radiation after anthesis on ear and shoot dry weight of wheat. Per pot of ten plants. Vertical lines are least significant differences ($P = 0{\cdot}05$).

after anthesis and decreased stem growth (Thorne, 1970). Apparently, warm temperatures altered the distribution in the plant of carbohydrate rather than altering the supply. This was probably less at 20°C than at 15°C because leaf area was less, the rate of photosynthesis of the flag leaf was unaltered and that of the sheath and stem was decreased. Faster initial growth of ears was also observed at 25°C than at 22°C by Asana and Joseph (1964), and with day/night temperatures of 27/22°C compared with 21/16°C by Wardlaw (1970), who showed that cell division in the endosperm was faster at the warmer temperature but ceased sooner so that the final number of cells was unaffected. Increased temperature had similar effects early or late during grain growth: a 5°C increase in temperature imposed for 16 days starting either 5 or 21 days after anthesis increased ear dry weight but decreased dry weight of the rest of the shoot and leaf area immediately after treatment, and decreased final ear dry weight by 5–10% (Fig. 3). When the difference in temperature was imposed continuously for 32 days, ear and grain weight was 14% less at 20°C than at 15°C (Thorne & Ford, 1971). These effects suggested that temperature may act directly on the growth of the grains, i.e. on their capacity to accumulate carbohydrate. This conclusion is supported by the results of experiments in which temperature of the ears but not the rest of the shoots was altered: warming ears only enhanced their early growth but caused them to mature sooner, with a smaller final dry weight, than cool ears (Thorne, 1972; 1973).

Although the decrease in grain yield with warmer temperatures has been ascribed to earlier senescence of the leaves, grain yield of wheat and barley decreased less than proportionately to the decrease in leaf area duration (*D*) so that *G* increased with temperature during the grain filling period (Thorne, Ford & Watson, 1967; Thorne, 1970). Of course, *G* also increased with increase in radiation which made the ears grow faster without altering leaf area. Effects of temperature and radiation on *G* similar to those in growth rooms have been found in the field (Welbank, Witts & Thorne, 1968). When *G* was calculated for 15 experiments on barley and spring and winter wheat done during ten years, 88% of its variance was accounted for by the multiple regression: $G = 0{\cdot}048R + 1{\cdot}80T - 29{\cdot}8$, in which R = mean daily radiation in cal $\mathrm{cm^{-2}\,day^{-1}}$ and

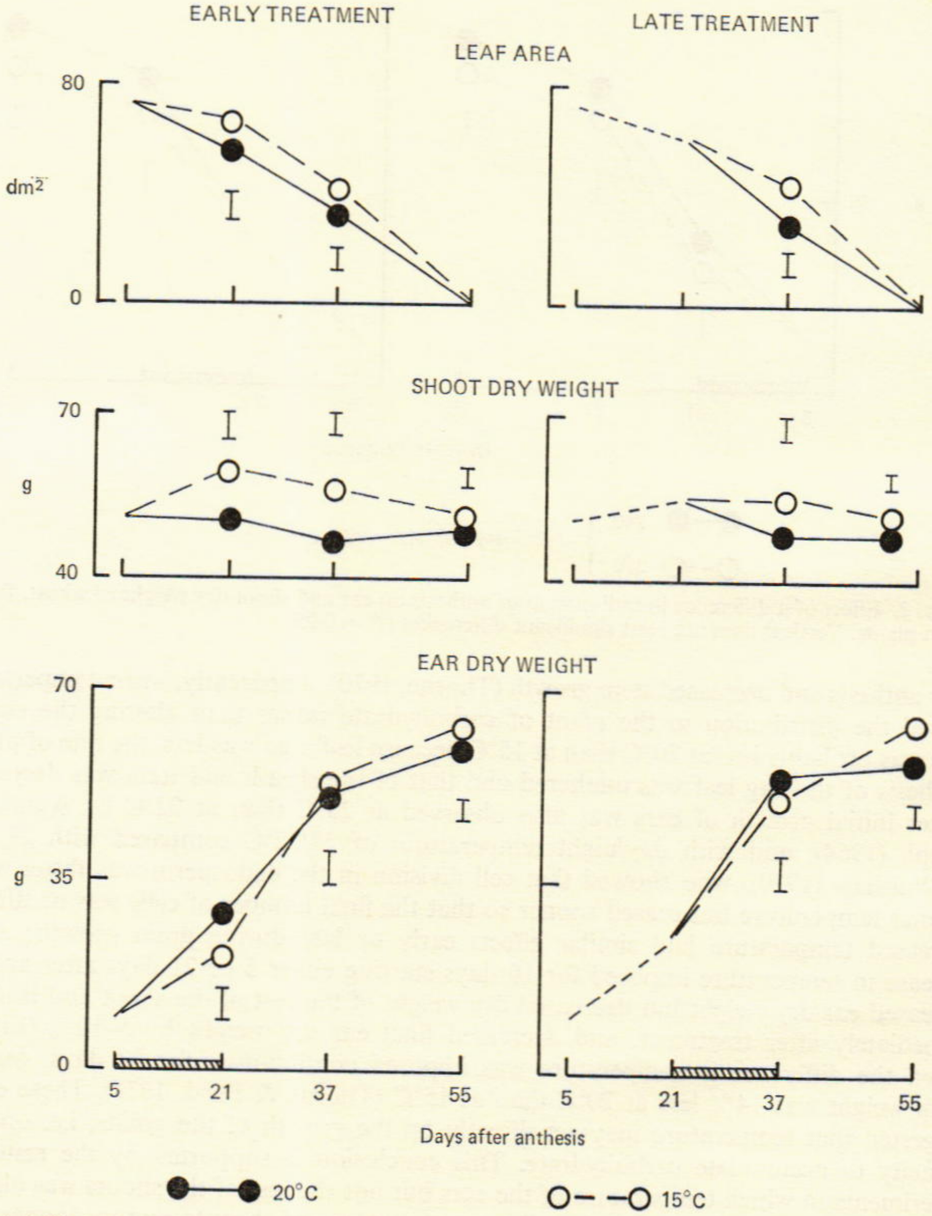


FIG. 3. Effect of a difference in temperature after anthesis on dry weight and leaf area of wheat. Per pot of ten plants. Vertical lines are least significant differences ($P = 0{\cdot}05$).

T = mean daily temperature during the grain filling period in °C. The units of G are g cm^{-2} week^{-1}. The effect on G of change in temperature predicted by this equation are similar to those observed in growth rooms having constant radiation. This agreement between field and growth room increases our confidence that extrapolation from the growth rooms was justified and that the independent effects of temperature and radiation shown by the multiple regression analysis were real.

Temperature and radiation before anthesis. Increased radiation before anthesis usually increases growth immediately but does not necessarily also increase grain yield. Doubling the amount of visible radiation given to wheat plants from 370 to 740 J cm^{-2} day^{-1}, during two weeks in May, either immediately after initiation of the ear or two weeks later, increased plant dry weight immediately after treatment by 25–29% (Thorne & Ford, 1971). But neither dry weight two weeks after treatment nor leaf area at any time was affected. Neither tillering nor the number of grains per ear at maturity were affected by the light intensity treatments in this experiment. Shading before anthesis has been tested in the field, but usually for four weeks or more. Often it decreases grain yield apparently through effects on both number of ears and number of grains per ear (Pendleton & Weibel, 1965; Willey & Holliday, 1971a and b).

The effects of variation in temperature before anthesis can usually be explained by its effects on tillering, leaf expansion and senescence. Over the relevant temperature range, 10–20°C, photosynthesis is affected negligibly. Warmth (i.e. warmer temperatures compared with cooler ones) early increased growth by hastening germination, increasing tillering and leaf expansion; increasing day/night temperatures during the four weeks immediately after sowing from 9·0/4·5°C to 15·0/10·5°C more than tripled the dry weight and leaf area of barley and doubled the shoot number (Thorne, Ford & Watson, 1967). Later, warmth no longer increased shoot number and sometimes decreased it. The maximum shoot number of wheat plants that spent the period between initiation of ears and anthesis at 20°C was only 78% of that of plants which spent the same period at 15°C (Thorne, Ford & Watson, 1968). A 5°C increase in temperature imposed for two weeks immediately after ear initiation increased leaf area and dry weight, but not shoot number (Thorne & Ford, 1971). Two weeks later, four weeks before anthesis and nearer the time when leaf area was maximal, a similar increase in temperature had no effect on dry weight or leaf area. Few of these effects of temperature persisted for long after the treatments ceased, and did not change leaf area after anthesis or grain yield. This is true even for the very large relative effect of a temperature difference applied from sowing because the effect was absolutely very small compared with subsequent growth.

These variable effects of climatic factors before anthesis can be understood better by realising that change in temperature or radiation before anthesis will affect grain yield in two circumstances: (1) when they cause differences in growth that produce differences in leaf area at anthesis and hence in leaf area duration during the grain filling period and in the supply of photosynthate for the grain; and (2) when they cause differences in growth that affect the number of grains per acre, and, particularly, the number of grains per unit of leaf area index, which can affect grain yield when the capacity of the crop to accumulate carbohydrate is restricting yield (see below, p. 20).

Effects on development. Studies at Rothamsted on the effects of climatic factors have been concerned mainly with weather, that is with the effects of short term deviations from the normal seasonal trend, rather than with a comparison of our climate with that elsewhere. Variations in weather affect growth in dry weight more than morphological development because the latter is determined mainly by the seasonal change in daylength and the gross seasonal change in temperature. Thus the increasing daylength in the spring and the cold vernalising temperature of winter cause winter wheat to flower at about the same date every year. The main cause of differences in the pattern of development between years is variation in temperature: differences in light intensity have negligible effects (Friend, Fisher & Helson, 1963). Warmer temperatures hasten development of many species of Gramineae, except when they have a de-vernalising effect (Evans, 1964; Ryle & Langer, 1963; Friend, 1965). A temperature of 15°C compared with 20°C imposed from sowing delayed ear initiation of wheat by two days and increased grain number and final grain weight by 6% (Thorne, Ford & Watson, 1968). A similar temperature difference between ear initiation and anthesis lengthened this period by 20 days and increased tillering and grain yield. The extra tiller development could be a consequence of decreased apical dominance associated with delayed flowering, or because less carbohydrate was respired at the cooler temperature leaving more for tiller growth.

Larger effects of climatic factors than the ones described in this Section are reported in the literature, but most of them come from experiments on plants grown continuously in the different conditions, whereas in our experiments the environmental differences were imposed for only two or four weeks. Even so, the differences in temperature and radiation we used were large compared with those that occur naturally. During the ten years between 1961 and 1970 the mean monthly temperature between April and August never differed from the long term means by more than 2·5°C and the biggest deviation in mean monthly daily radiation was 25%. This compares with experimental differences of 5 or 6°C in temperature and 50% in radiation imposed for two or four weeks.

The movement of assimilate

Source versus sink. There is controversy about the extent to which grain yield of cereals is controlled by the supply of photosynthate or by the capacity of the ear to accumulate available carbohydrate. Factors controlling supply (the source) are the area of photosynthetic tissue and the rate of photosynthesis. Factors controlling the capacity to accumulate carbohydrate (sink capacity) are the number of grains, and their maximum growth rate and ultimate size when these are determined by factors other than carbohydrate supply. Sink capacity can affect grain yield by affecting the distribution of photosynthate only, or both its distribution and the rate of photosynthesis per unit leaf area. Australian research workers, especially those at Canberra using plants in pots, are the main exponents of the view that wheat plants produce ample photosynthate to fill the ears and that grain yield is controlled by the sink capacity of the ear. They cite four types of supporting evidence: (1) treatments that decreased total photosynthesis per shoot, such as shading ears or removing leaves, decreased grain yield less than expected from the decrease in photosynthesis because compensatory movement of photosynthate from other organs to the grains occurred (Wardlaw, Carr & Anderson, 1965; Rawson & Evans, 1971; Bremner, 1972; Bremner & Rawson, 1972); (2) treatments that increased grain number, e.g. vernalisation and change in daylength, increased grain yield even when leaf area was decreased (Rawson, 1970); (3) the rate of photosynthesis of the flag leaf changed as the demand for assimilates by the ear changed; flag leaf photosynthesis increased when photosynthesis of the ear was stopped by spraying it with DCMU (King, Wardlaw & Evans, 1967) and was greater 15–16 days after anthesis when grains were growing fastest, than earlier or later during the grain filling period (Evans & Rawson, 1970; Rawson & Evans, 1971); (4) photosynthetic production of only part of the green tissues, estimated from measurements of gas exchange was adequate to support observed rates of grain growth; e.g. photosynthesis of the ear and flag-leaf lamina alone was sufficient to meet the requirements of the ear during the period of most rapid grain growth (Rawson & Evans, 1971).

The contrasting view that grain yield is determined by the supply of photosynthate is supported by the positive correlations of grain yield with leaf area duration after anthesis discussed already (see p. 10) or with total crop photosynthesis measured in an enclosure by gas exchange: the variation between three years in yields of three varieties in South Australia were almost entirely accounted for by variation in total crop photosynthesis after anthesis (Puckridge, 1971). The importance of the supply of photosynthate is also supported by the numerous experiments in which decreasing the supply, for example by shading or removing leaves, decreased grain yield considerably (e.g. Welbank, Witts & Thorne, 1968; Stoy, 1965).

The true situation seems to be, as suggested by Bingham (1967, 1971), that grain yield of wheat usually depends on both the supply of photosynthate and on the sink capacity of the ears. Bingham showed that, in the very different climates of England and Mexico, removing some grains from an ear increased the size of the grains remaining. This implies that in the intact plants grain size was less than maximal because of insufficient photosynthate. But increase in grain size did not entirely compensate for the grains removed; the sink capacity of the smaller number of grains was insufficient to absorb as much carbohydrate as did the grains in the intact ears. Removing grains had similar relative effects in full light or when carbohydrate supply was restricted by severe shading or removing half of each flag-leaf lamina. The simultaneous control of grain yield by source and sink was also evident in the experiment of Thorne, Ford and Watson (1968): grain yield was greater when daylength after anthesis was 18 hours than when it was 14 hours, because individual grains were larger, but in both light regimes grain yield increased with increase in number of grains per ear.

The relative importance of source and sink will vary with stage of grain filling and with the environment (Watson, 1971). Soon after anthesis, before grains start growing at their maximum rate and while leaf area index is large carbohydrate supply is likely to be adequate for current grain growth in most climates, but later, when leaf area decreases photosynthate supply may restrict grain growth. Hence it is not surprising that warm temperatures, which seem to increase the sink capacity of ears and also decrease leaf area (see p. 15), initially increased ear growth but later decreased it. Sink capacity is likely to be relatively more important as a factor controlling yield in environments that favour photosynthesis. So it is probably not coincidence that the importance of the sink is supported by evidence from Australia, where daily photosynthesis of well-watered plants in pots used in most of the experiments may be greater than in Western European countries with a maritime climate. In the experiments of Rawson and Evans (1971), average daily radiation during the grain filling period was 697 cal cm^{-2} day^{-1}, whereas radiation for this period at Rothamsted between 1955 and 1965 ranged from 294 to 463 cal cm^{-2} day^{-1} (Welbank, Witts & Thorne, 1968). There is also recent evidence from Australia that when radiation during the grain filling period averaged only 470 cal cm^{-2} day^{-1} grain yield of barley in the field was controlled about equally by source and sink (Gifford, Bremner & Jones, 1973). Measurements of CO_2 exchange also indicate that photosynthesis is more likely to restrict yield in England than in Australia. In contrast to the Australian results in which photosynthesis of the ear and flag-leaf lamina alone was adequate to supply the grain, photosynthesis of all green tissues above the flag-leaf node was required at Rothamsted (Thorne, 1965), and in unpublished experiments at Sutton Bonington by E. J. Littleton, P. V. Biscoe, R. K. Scott and J. N. Gallagher total photosynthesis of a barley crop after ear emergence was insufficient to account for the observed grain yield.

Effect of sink on rate of photosynthesis. There is ample evidence that in temperate climates sink capacity affects the distribution of photosynthate, but little evidence that it affects the rate of photosynthesis in cereals, though it does in other crops such as sugar beet and potatoes (Thorne & Evans, 1964; Nösberger & Humphries, 1965). When parts of plants are removed or shaded carbohydrate that would not normally move to the ear often does so (Puckridge, 1968), thus partially compensating for the carbohydrate deficit in the same way as observed in Australia. However, in Swedish experiments photosynthate was apparently so limiting that no compensation occurred and removing leaf laminae decreased grain yield only (Stoy, 1965). In British, unlike Australian, conditions wheat plants seem to have ample capacity to accumulate surplus carbohydrate elsewhere than in the grain if the main sink provided by the ear is missing or becomes full, and the rate of photosynthesis is not affected. Thus, removing ears or decreasing their sink capacity by cooling them caused carbohydrate to accumulate in the stem or tillers but did not affect the rate of photosynthesis of the flag leaf (Lupton, 1968; Thorne, 1966, 1972; Austin & Sutherland, 1973). The compensatory movement of carbohydrate that occurs when photosynthetic production is decreased suggests that the *potential* photosynthesis of cereal crops could support grain yields greater than at present. However, this does not mean that grain yield is never limited by actual photosynthesis; this would only be true if grain yield was unaffected by a change in photosynthesis.

Control of sink size—grain number and size. Grain yield might be increased by an increase in ear sink capacity that would allow the grains to absorb more of the photosynthate that remains in the stem when the supply of photosynthate is abundant. One way of increasing sink capacity might be to increase grain number per unit leaf area, i.e. to increase grain number per unit area of land without changing leaf area. In wheat, if not in barley, there seem to be an excess of potential grains, and what determines final grain number is not clear (Beveridge, Jarvis & Ridgman, 1965). Many of the florets that fail to form grains are capable of doing so until about five days after anthesis; they are apparently prevented by the presence of other fully developed florets by some means probably not related to competition for photosynthate (Evans, Bingham & Roskams, 1972). Another factor that may limit sink capacity of ears is the maximum size to which the grains can grow which depends on the genotype. There is little evidence that this factor limits barley yield. In NIAB trials between 1956 and 1963, 1000-grain weight of 12 barley varieties increased nearly linearly with yield and there was no curvature towards the yield axis when yield was large, such as would be expected if grains have a limited maximum size that is approached when growing conditions favour large yields (Thorne, 1966a). Equivalent data for the varieties Proctor, Zephyr and Julia from trials between 1970 and 1972 lead to the same conclusion, perhaps not surprisingly as maximum yields were no greater than in 1956–63. There was no similar linear relationship between 1000-grain weight and grain yield of wheat. It is very difficult to establish whether yields would be greater if size or number of grains were increased because the ways of doing this—by breeding or by daylength and vernalisation treatments—alter many factors besides sink capacity of the ear. At present most of the evidence is based on correlations and so is inconclusive. Fischer and Kohn (1966) found that grain yield was correlated with number of grains per unit area of land, suggesting control by the sink, but it was also correlated with leaf area duration after anthesis, suggesting control by the supply of photosynthate. A re-examination of the data of Watson, Thorne and French (1963) suggests that varietal difference in grain number might have been a factor that caused grain yield and efficiency of leaves in grain production (*G*, see p. 12) of new wheat varieties to be greater than old ones. Old and new varieties have similar leaf areas but the number of grains per dm^2 of land for the new varieties Cappelle-Desprez and Jufy I were 96 and 87 compared with 67 and 66 for the older varieties Squarehead's Master and Atle. The new varieties also had larger grains. A similar explanation for the greater yield and efficiency of modern than old barley varieties is less likely for although the new varieties had more grains than Plumage Archer (Proctor 156, Herta 138, Plumage Archer 111/dm^2), the grains were smaller (Watson, Thorne & French, 1958). We do not know whether many potentially small grains provide a better sink than few potentially large grains.

Control of sink size—growth substances. The number and potential size of grains may limit the eventual capacity of the ear to store carbohydrate; number and possibly potential size may also restrict the rate of ear growth, as temperature seems to do. We know very little about other factors that may control the rate of grain growth when carbohydrate supply is ample, or about the mechanisms involved, but they probably act within the grain itself. Measurements of phloem cross-sectional area suggest that this is unlikely to restrict carbohydrate supply to the grain (Evans, Dunstone, Rawson & Williams, 1970) and measurements of the concentrations of carbohydrates in stems, ear structures and grains indicate that, when supplies are ample, sugar accumulates in the ear structures because the rate of transport into the grain has an upper limit (Jenner & Rathjen, 1972). The rate at which grains accumulate carbohydrate may depend on their content of growth substances. Some growth substances are known to affect the distribution of carbohydrates; cytokinin, gibberellin and auxin have been extracted from developing wheat grains, and their concentrations and amounts per grain change during development (Wheeler, 1972). Detached wheat ears supplied with sucrose solutions synthesise gibberellin and their synthetic capacity increases for some time after anthesis and then decreases (Radley & Wheeler, 1972). Starch and gibberellin accumulate simultaneously in wheat ears. Some evidence that the synthesis of gibberellins may affect the accumulation of starch has been shown with detached wheat ears supplied with sucrose solutions. When the gibberellin precursor (-)-kaurene was also supplied, ears synthesised more gibberellin and accumulated more starch than when given only sucrose. The addition of gibberellic acid had no positive effect at the concentration tested, between 0·01 and 1·0 μg/ml (Radley & Wheeler, 1973). The small amount of information now available about the occurrence and effects of growth substances in cereals suggests that growth substances may be involved in controlling the distribution of dry matter but the mechanisms are probably complicated and involve interactions between different growth substances.

Summary. The idea that grain yield is controlled by the source *or* the sink may have delayed progress in the understanding of factors that control grain yield because it has sometimes restricted the design of experiments and the interpretation of results. But the source-sink concept has been helpful when used to guide thought about how physiological processes in the whole plant control grain yield. A better understanding of source–sink relations is essential if a physiological basis for further improvements in grain yield of healthy cereal crops is to be established. Without this knowledge efforts to improve yield through increasing total photosynthetic production may be frustrated. In any case historical evidence indicates that the most likely way to increase grain yield is through better distribution of dry matter (Thorne, 1971). The rate of photosynthesis per unit leaf area of modern wheat varieties is no greater than that of ancestral types (Evans & Dunstone, 1970; Khan & Tsunoda, 1970; Dunstone, Gifford & Evans, 1973), and total dry matter production of modern stiff strawed cereals is only greater than that of older varieties because they can be given more nitrogen without lodging. But there has been a continual increase in the proportion of the total dry matter contributed by the grain, with the latest increase shown by varieties of wheat derived from the Japanese variety Norin 10. The mechanisms controlling both the distribution and the production of photosynthate must be further studied by crop physiologists aiming to provide knowledge that will help increase crop yield.

References

Angus, J. F., Jones, R. & Wilson, J. H. (1972) A comparison of barley cultivars with different leaf inclinations. *Australian Journal of Agricultural Research* **23**, 945–957.

Archbold, H. K. (1942) Physiological studies in plant nutrition. XIII. Experiments with barley on defoliation and shading of the ear in relation to sugar metabolism. *Annals of Botany* **6**, 487–531.

Asana, R. D. & Joseph, C. M. (1964) Studies in physiological analysis of yield. VII. Effect of temperature and light on the development of the grain of two varieties of wheat. *Indian Journal of Plant Physiology* **8**, 86–101.

Austin, R. B. & Sutherland, J. A. (1973) Photosynthesis, translocation and grain filling in wheat. *Plant Breeding Institute. Annual Report for 1972*, 156–158.

Beveridge, J. L., Jarvis, R. H. & Ridgman, W. J. (1965) Studies on the nitrogenous manuring of winter wheat. *Journal of Agricultural Science, Cambridge* **65**, 379–387.

Bingham, J. (1967) Investigations on the physiology of yield in winter wheat, by comparisons of varieties and by artificial variation in grain number per ear. *Journal of Agricultural Science, Cambridge* **68**, 411–422.

Bingham, J. (1971) Physiological objectives in breeding for grain yield in wheat. In: *The way ahead in plant breeding: (Proceedings of the sixth congress of Eucarpia, Cambridge, 29 June–2 July 1971).* Ed. Lupton, F. G. H., Jenkins, G. & Johnson, R., 15–29.

Birecka, H. & Dakic-Wlodkowska, L. (1964) Photosynthesis, translocation and accumulation of assimilates in cereals during grain development. IV. Contribution of products of current photosynthesis after heading to the accumulation of organic compounds in the grain of spring wheat. *Acta Societatis Botanicorum Poloniae* **33**, 407–426.

Birecka, H. & Dakic-Wlodkowska, L. (1966) Photosynthetic activity and productivity before and after ear emergence in spring wheat. *Acta Societatis Botanicorum Poloniae* **35**, 637–662.

Birecka, H., Skupinska, J. & Bernstein, I. (1964) Photosynthesis, translocation and accumulation of assimilates in cereals during grain development. V. Contribution of products of current photosynthesis after heading to the accumulation of organic compounds in the grain of barley. *Acta Societatis Botanicorum Poloniae* **33**, 601–618.

Birecka, H., Skupinska, J. & Bernstein, I. (1967) Photosynthetic activity and productivity before and after ear emergence in spring barley. *Acta Societatis Botanicorum Poloniae* **36**, 387–409.

Birecka, H., Wojcieska, U. & Glazewski, S. (1968) Ear contribution to photosynthetic activity in winter cereals. I. Winter wheat. *Bulletin de l'Academie Polonaise des Sciences Cl. V* **16**, 191–196.

Biscoe, P. V., Littleton, E. J. & Scott, R. K. (1973) Stomatal control of gas exchange in barley awns. *Annals of Applied Biology* **75**, 285–297.

Blackman, V. H. (1919) The compound interest law and plant growth. *Annals of Botany* **33**, 353–360.

Bremner, P. M. (1972) Accumulation of dry matter and nitrogen by grains in different positions of the wheat ear as influenced by shading and defoliation. *Australian Journal of Biological Sciences* **25**, 657–668.

Bremner, P. M. & Rawson, H. M. (1972) Fixation of $^{14}CO_2$ by flowering and non-flowering glumes of the wheat ear, and the pattern of transport of label to individual grains. *Australian Journal of Biological Science* **25**, 921–930.

Bremner, P. M. & Taha, M. A. (1966) Studies in potato agronomy. I. The effect of variety, seed size and spacing on growth, development and yield. *Journal of Agricultural Science, Cambridge* **66**, 241–252.

Buck, S. F. (1961) The use of rainfall, temperature and actual transpiration in some crop weather investigations. *Journal of Agricultural Science, Cambridge* **57**, 355–365.

Carr, D. J. & Wardlaw, I. F. (1965) The supply of photosynthetic assimilates to the grain from the flag leaf and ear of wheat. *Australian Journal of Biological Sciences* **18**, 711–719.

Dunstone, R. L., Gifford, R. M. & Evans, L. T. (1973) Photosynthetic characteristics of modern and primitive wheat species in relation to ontogeny and adaptation to light. *Australian Journal of Biological Sciences* **26**, 295–307.

Engledow, F. L. & Wadham, S. M. (1923) Investigations on yield in cereals I. *Journal of Agricultural Science, Cambridge* **13**, 390–439.

Evans, L. T. (1964) Reproduction. In: *Grasses and grasslands.* Ed. C. Barnard, London: Macmillan, 126–153.

Evans, L. T., Bingham, J., Jackson, P. & Sutherland, J. (1972a) Effect of awns and drought on the supply of photosynthate and its distribution within wheat ears. *Annals of Applied Biology* **70**, 67–76.

Evans, L. T., Bingham, J. & Roskams, M. A. (1972) The pattern of grain set within ears of wheat. *Australian Journal of Biological Sciences* **25**, 1–8.

Evans, L. T. & Dunstone, R. L. (1970) Some physiological aspects of evolution in wheat. *Australian Journal of Biological Sciences* **23**, 725–741.

Evans, L. T., Dunstone, R. L., Rawson, H. M. & Williams, R. F. (1970) The phloem of the wheat stem in relation to requirements for assimilate by the ear. *Australian Journal of Biological Sciences* **23**, 743–752.

Evans, L. T. & Rawson, H. M. (1970) Photosynthesis and respiration by the flag leaf and components of the ear during grain development in wheat. *Australian Journal of Biological Sciences* **23**, 245–254.

Fischer, R. A. & Kohn, G. D. (1966) The relationship of grain yield to vegetative growth and post-flowering leaf area in the wheat crop under conditions of limited soil moisture. *Australian Journal of Agricultural Research* **17**, 281–295.

Fonesca, S. & Patterson, F. L. (1968) Yield component heritabilities and interrelationships in winter wheat (*Triticum aestivum* L.). *Crop Science* **8**, 614–617.

Friend, D. J. C. (1965) Ear length and spikelet number of wheat grown at different temperatures and light intensities. *Canadian Journal of Botany* **43**, 345–353.

Friend, D. J. C., Fisher, J. E. & Helson, V. A. (1963) The effect of light intensity and temperature on floral initiation and inflorescence development of Marquis wheat. *Canadian Journal of Botany* **41**, 1663–1674.

Gifford, R. M., Bremner, P. M. & Jones, D. B. (1973) Assessing photosynthetic limitations to grain yield in a field crop. *Australian Journal of Agricultural Research* **24**, 297–307.

Goodman, P. J. (1968) Physiological analysis of the effects of different soils on sugar-beet crops in different years. *Journal of Applied Ecology* **5**, 339–357.

Gregory, F. G. (1917) Physiological conditions in cucumber houses. *Third Annual Report. Experimental and Research Station, Cheshunt* 19–28.

Hozyo, Y. & Kobayashi, H. (1969) Tracer studies on the behaviour of photosynthetic products during the grain ripening stage in six-rowed barley plant (*Hordeum sativum*, Jessen). *Bulletin of the National Institute of Agricultural Sciences* (*Japan*) Series D, No. 20, 35–77.

Hsu, P. & Walton, P. D. (1971) Relationship between yield and its components and structures above the flag-leaf node in spring wheat. *Crop Science* **11**, 190–193.

Jenner, C. F. & Rathjen, A. J. (1972) Factors limiting the supply of sucrose to the developing wheat grain. *Annals of Botany* **36**, 729–741.

Khan, M. A. & Tsunoda, S. (1970) Evolutionary trends in leaf photosynthesis and related leaf characters among cultivated wheat species and its wild relatives. *Japanese Journal of Breeding* **20**, 133–140.

King, R. W., Wardlaw, I. F. & Evans, L. T. (1967) Effect of assimilate utilisation on photosynthetic rate in wheat. *Planta* **77**, 261–276.

Kriedemann, P. (1966) The photosynthetic activity of the wheat ear. *Annals of Botany* **30**, 349–363.

Lawlor, D. W. (1971) Effects of water stress on growth. *Rothamsted Experimental Station. Report for 1970*, Part 1, 100.

Lawlor, D. W. (1972) Influence of water content on plant metabolism. *Rothamsted Experimental Station. Report for 1971*, Part 1, 109–110.

Lawlor, D. W. (1973a) Growth and water absorption of wheat with parts of the roots at different water potentials. *New Phytologist* **72**, 297–305.

Lawlor, D. W. (1973b) Cereals—plant water relations. *Rothamsted Experimental Station. Report for 1972*, Part 1, 92 and 99–100.

Lupton, F. G. H. (1966) Translocation of photosynthetic assimilates in wheat. *Annals of Applied Biology* **57**, 355–364.

Lupton, F. G. H. (1968) The analysis of grain yield of wheat in terms of photosynthetic ability and efficiency of translocation. *Annals of Applied Biology* **61**, 109–119.

Lupton, F. G. H. (1969) Estimation of yield in wheat from measurements of photosynthesis and translocation in the field. *Annals of Applied Biology* **64**, 363–374.

Lupton, F. G. H. (1972) Further experiments on photosynthesis and translocation in wheat. *Annals of Applied Biology* **71**, 69–79.

Lupton, F. G. H. & Pinthus, M. J. (1969) Carbohydrate translocation from small tillers to spike-producing shoots in wheat. *Nature, London* **221**, 483–484.

Natr, L. (1967) Study of the formation of the grain yield of cereals. III. The influence of the cutting-off of leaves and awns on the reduction of the yield elements in spring barley and winter wheat. *Rostlinna Vyroba* **13**, (XL), 797–818.

Nösberger, J. & Humphries, E. C. (1965) The influence of removing tubers on dry matter production and net assimilation rate of potato plants. *Annals of Botany* **29**, 579–588.

Osman, A. M. (1971) Dry-matter production of a wheat crop in relation to light interception and photosynthetic capacity of leaves. *Annals of Botany* **35**, 1017–1035.

Pendleton, J. W. & Weibel, R. O. (1965) Shading studies on winter wheat. *Agronomy Journal* **57**, 292–293.

Porter, H. K., Pal, N. & Martin, R. V. (1950) Physiological studies in plant nutrition. XV. Assimilation of carbon by the ear of barley and its relation to the accumulation of dry matter in the grain. *Annals of Botany* **14**, 55–68.

Puckridge, D. W. (1968) Photosynthesis of wheat under field conditions. I. The interaction of photosynthetic organs. *Australian Journal of Agricultural Research* **19**, 711–719.

Puckridge, D. W. (1971) Photosynthesis of wheat under field conditions. III. Seasonal trends in carbon dioxide uptake of crop communities. *Australian Journal of Agricultural Research* **22**, 1–9.

Puckridge, D. W. (1972) Photosynthesis of wheat under field conditions. V. The effect of solar elevation on the distribution of photosynthetic activity within the crop canopy. *Australian Journal of Agricultural Research* **23**, 397–404.

https://doi.org/10.23637/ERADOC-1-8

QUINLAN, J. D. & SAGAR, G. R. (1962) An autoradiographic study of the movement of ^{14}C-labelled assimilates in the developing wheat plant. *Weed Research* **2**, 264–273.
RADLEY, M. E. & WHEELER, A. W. (1972) Growth substances in the wheat plant. *Rothamsted Experimental Station. Report for 1971*, Part 1, 110–111.
RADLEY, M. E. & WHEELER, A. W. (1973) Growth substances: cereals. *Rothamsted Experimental Station. Report for 1972*, Part 1, 97–98.
RAWSON, H. M. (1970) Spikelet number, its control and relation to yield per ear in wheat. *Australian Journal of Biological Sciences* **23**, 1–15.
RAWSON, H. M. & EVANS, L. T. (1970) The pattern of grain growth within the ear of wheat. *Australian Journal of Biological Sciences* **23**, 753–764.
RAWSON, H. M. & EVANS, L. T. (1971) The contribution of stem reserves to grain development in a range of wheat cultivars of different height. *Australian Journal of Agricultural Research* **22**, 851–863.
RAWSON, H. M. & HOFSTRA, G. (1969) Translocation and remobilisation of ^{14}C assimilated at different stages by each leaf of the wheat plant. *Australian Journal of Biological Sciences* **22**, 321–331.
RUSSELL, E. J. & WATSON, D. J. (1940) The Rothamsted Field Experiments on the growth of wheat. *Commonwealth Bureau of Soil Science. Technical Communication* No. 40.
RYLE, G. J. A. & LANGER, R. H. M. (1963) Studies on the physiology of flowering of Timothy (*Phleum pratense* L.). *Annals of Botany* **27**, 213–231.
SCOTT, R. K. & BREMNER, P. M. (1966) The effects on growth, development and yield of sugar beet of extension of the growth period by transplantation. *Journal of Agricultural Science* **66**, 379–388.
SIMPSON, G. M. (1968) Association between grain yield per plant and photosynthetic area above the flag-leaf node in wheat. *Canadian Journal of Plant Science* **48**, 253–260.
SPIERTZ, J. H. J., TEN HAG, B. A. & KUPERS, L. J. P. (1971) Relation between green area duration and grain yield in some varieties of spring wheat. *Netherland Journal of Agricultural Science* **19**, 211–222.
STERN, W. R. & DONALD, C. M. (1961) Relationship of radiation, leaf area index and crop growth rate. *Nature, London* **189**, 597–598.
STOY, V. (1965) Photosynthesis, respiration and carbohydrate accumulation in spring wheat in relation to yield. *Physiologia Plantarum Supplementum* **4**, 1–125.
SZEICZ, G. (1970) Spectral composition of solar radiation and its penetration into crop canopies. *Ph.D. Thesis, University of London.*
THORNE, G. N. (1959) Photosynthesis of lamina and sheath of barley leaves. *Annals of Botany* **23**, 365–370.
THORNE, G. N. (1965) Photosynthesis of ears and flag leaves of wheat and barley. *Annals of Botany* **27**, 155–174.
THORNE, G. N. (1966a) Physiological aspects of grain yield in cereals. In: *The Growth of Cereals and Grasses*. Ed. F. L. Milthorpe and J. D. Ivins. London: Butterworth, 88–105.
THORNE, G. N. (1966b) Photosynthesis of flag-leaf laminae of cereals. *Rothamsted Experimental Station. Report for 1965*, 100–101.
THORNE, G. N. (1970) Use of controlled environments for studying the effect of climatic factors on growth and yield. In: *Prediction and Measurement of Photosynthetic Productivity*. Wageningen: PUDOC, 399–404.
THORNE, G. N. (1971) Physiological factors limiting yield of arable crops. In: *Potential crop production.* Ed. J. P. Cooper and P. F. Wareing. London: Heinemann, 143–158.
THORNE, G. N. (1972) Effect of temperature on grain growth in wheat. *Rothamsted Experimental Station. Report for 1971*, Part 1, 104.
THORNE, G. N. (1973) Effect of temperature on grain growth. *Rothamsted Experimental Station. Report for 1972*, Part 1, 93–94.
THORNE, G. N. (1974) Response of spring wheat to large amounts of nitrogen. *Rothamsted Experimental Station. Report for 1973*, Part 1, Botany Department Section.
THORNE, G. N. & BLACKLOCK, J. C. (1971) Effects of plant density and nitrogen fertiliser on growth and yield of short varieties of wheat derived from Norin 10. *Annals of Applied Biology* **68**, 93–111.
THORNE, G. N. & EVANS, A. F. (1964) Influence of tops and roots on net assimilation rate of sugar beet and spinach beet and grafts between them. *Annals of Botany* **28**, 499–508.
THORNE, G. N. & FORD, M. A. (1971) Sink capacity of wheat ears. *Rothamsted Experimental Station. Report for 1970*, Part 1, 94–95.
THORNE, G. N., FORD, M. A. & WATSON, D. J. (1967) Effects of temperature variation at different times on growth and yield of sugar beet and barley. *Annals of Botany* **31**, 71–101.
THORNE, G. N., FORD, M. A. & WATSON, D. J. (1968) Growth, development and yield of spring wheat in artificial climates. *Annals of Botany* **32**, 425–445.
THORNE, G. N., WELBANK, P. J. & BLACKWOOD, G. C. (1969) Growth and yield of six short varieties of spring wheat derived from Norin 10 and of two European varieties. *Annals of Applied Biology* **63**, 241–251.
WARDLAW, I. F. (1970) The early stages of grain development in wheat: response to light and temperature in a single variety. *Australian Journal of Biological Sciences* **23**, 765–774.
WARDLAW, I. F., CARR, D. J. & ANDERSON, M. J. (1965) The relative supply of carbohydrate and nitrogen to wheat grains, and an assessment of the shading and defoliation techniques used for these determinations. *Australian Journal of Agricultural Research* **16**, 893–901.
WATSON, D. J. (1947a) Comparative physiological studies on the growth of field crops. I. Variation in net assimilation rate and leaf area between species and varieties, and within and between years. *Annals of Botany* **11**, 41–47.

WATSON, D. J. (1947b) Comparative physiological studies on the growth of field crops. II. The effect of varying nutrient supply on net assimilation rate and leaf area. *Annals of Botany* **11**, 375–407.

WATSON, D. J. (1952) The physiological basis of variation in yield. *Advances in Agronomy* **4**, 101–145.

WATSON, D. J. (1958) The dependence of net assimilation rate on leaf-area index. *Annals of Botany* **22**, 37–54.

WATSON, D. J. (1968) A prospect of crop physiology. *Annals of Applied Biology* **62**, 1–9.

WATSON, D. J. (1971) Size, structure, and activity of the productive system of crops. In: *Potential crop production.* Ed. J. P. Cooper and P. F. Wareing. London: Heinemann, 76–88.

WATSON, D. J. & FRENCH, S. A. W. (1958) Dependence of net assimilation rate of barley on leaf-area index. *Rothamsted Experimental Station. Report for 1957*, 90–91.

WATSON, D. J., THORNE, G. N. & FRENCH, S. A. W. (1958) Physiological causes of differences in grain yield between varieties of barley. *Annals of Botany* **22**, 321–352.

WATSON, D. J., THORNE, G. N. & FRENCH, S. A. W. (1963) Analysis of growth and yield of winter and spring wheats. *Annals of Botany* **27**, 1–22.

WELBANK, P. J., FRENCH, S. A. W. & WITTS, K. J. (1966) Dependence of yields of wheat varieties on their leaf-area durations. *Annals of Botany* **30**, 291–299.

WELBANK, P. J. & WIDDOWSON, F. V. (1972) Growth and yield of cereals on different sites. *Rothamsted Experimental Station. Report for 1971*, Part 1, 60–61 and 106–107.

WELBANK, P. J. & WIDDOWSON, F. V. (1973) Growth and yield of cereals on different sites. *Rothamsted Experimental Station. Report for 1972*, Part 1, 48 and 90–91.

WELBANK, P. J., WITTS, K. J. & THORNE, G. N. (1968) Effect of radiation and temperature on efficiency of cereal leaves during grain growth. *Annals of Botany* **32**, 79–95.

WHEELER, A. W. (1972) Changes in growth-substance contents during growth of wheat grains. *Annals of Applied Biology* **72**, 327–334.

WILLEY, R. W. & HOLLIDAY, R. (1971a) Plant population and shading studies in barley. *Journal of Agricultural Science, Cambridge* **77**, 445–452.

WILLEY, R. W. & HOLLIDAY, R. (1971b) Plant population, shading and thinning studies in wheat. *Journal of Agricultural Science, Cambridge* **77**, 453–461.

YAP, T. C. & HARVEY, B. L. (1972) Relation between grain yield and photosynthetic parts above the flag-leaf node in barley. *Canadian Journal of Plant Science* **52**, 241–246.