SOME ASPECTS OF THE GROWTH OF TWO WHEAT VARIETIES UNDER FIELD CONDITIONS

A thesis presented in partial fulfilment of
the requirements for the degree of
Master of Agricultural Science in Plant Science
at
Massey University

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1970

SUMMARY

Two spring wheats, Raven, a standard commercial variety, and Pitic 62, a Mexican semidwarf variety, were grown in the field at densities of 11.1, 44.4 and 177.7 plants . m^{-2}. Plants were sampled from each plot at 5 to 9 day intervals from shortly after emergence until maturity and the dry weights of plant parts together with relevant morphological information were recorded. The appearance of leaves and tillers on marked plants was also recorded in parallel with these samplings.

Pitic 62 outyielded Raven at all densities because of higher grain numbers and despite lower grain weights. Tiller numbers, which were similar for both varieties, were responsible for most of the yield variation with density. Infection by barley yellow dwarf virus was a factor complicating the interpretation of these results since it appeared that Pitic 62 was more susceptible to this disease than Raven.

Total dry matter production per plant or per area was similar in each variety and growth analysis, in which the polynomial regression technique was employed, indicated that this was also true of growth rates. Varietal differences in unit photosynthetic rates (net assimilation rates) appeared from ear emergence onwards because leaf senescence was more rapid in Pitic 62 and because ear area made a larger contribution to total photosynthetic area in this variety. Approximately 55% of the ear area in Pitic 62 was due to awns. The grain to straw ratio of Pitic 62 was greater than that of Raven because of heavier ears and lighter stems. These differences were thought to arise from varietal differences in the activity of apical and intercalary meristems. It was concluded that further study of the physiological regulation of growth processes would be required before the differences in plant form and growth patterns observed in the experiment could be more closely correlated with grain yield.

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INTRODUCTION

This study provides some basic information on the growth and development of two wheat varieties under field conditions. The varieties chosen, Raven, a standard commercial variety of Australian origin, and Pitic 62, a high-yielding Mexican semidwarf wheat, provided a contrast in grain to straw ratio which reflected the trend in wheat breeding towards varieties with an increased proportion of grain to total dry weight. In field trials in the Manawatu Pitic 62 had outyielded Raven and the difference had been attributed to increased tillering in the semidwarf variety (J. M. McEwan, pers. comm.). However critical information on the physiological processes underlying the superior yields of semidwarf wheats such as Pitic 62 under New Zealand conditions was lacking and there was little published work elsewhere. A preliminary attempt to rectify this deficiency by examining the growth of one semidwarf and one standard variety was made in this experiment.

1.1 THE ANALYSIS OF GROWTH

Growth may be defined in many ways (Bloch, 1961; Steward, 1968) but no definition can be satisfactory under all circumstances. A pragmatic approach to this problem is to express growth in terms of its most accessible attribute, that of mass measured as dry weight. In this thesis the term growth will, unless otherwise specified, refer to the increase in the mass of an organism in time. In following sections the study of growth will be discussed first in terms of the method of "growth analysis", an approach traditionally associated with the plant sciences, and second in terms of the quantitative analysis of growth, an approach which has arisen diffusely from a wider background.

1.1.1 Growth Analysis

In the method of growth analysis plant growth is seen primarily as a balance between carbon assimilation and respiration. By measuring the amount of plant material and the size of the supporting photosynthetic system it is therefore possible to derive quantities which indicate the amount, rate and efficiency of photosynthesis and thus of growth processes (Watson, 1968; Steward, 1969). The development of this concept has been reviewed by Williams (1946), Watson (1952, 1968), Blackman (1961) and Richards (1969).

The relationships used in growth analysis are conveniently divided into two groups, those typifying the morphogenetic condition of the plant and those describing its growth processes (Evans and Hughes, 1961). The following notation will be used in definitions of the more important of these quantities:

W = total plant dry weight or dry weight per unit area of ground;
W_1 = leaf dry weight;
A = total leaf area per plant;
L = leaf area per unit area of ground.

Morphogenetic relationships

i) The leaf weight ratio (LWR) is the ratio of leaf dry weight to total dry weight.

$$\mathrm{LWR} = \frac{W_1}{W}$$

ii) The leaf area ratio (LAR) is the ratio of leaf to total weight.

$$\mathrm{LAR} = \frac{A}{W}$$

Other morphogenetic relationships are defined by Evans and Hughes (1961).

<u>Growth process relationships</u>

i) The <u>growth rate</u> (GR) of a plant at any instant of time is the increase in dry weight per unit time.

$$\mathrm{GR} = \frac{dW}{dt}$$

A similar definition is used for the <u>crop growth rate</u> (C) introduced by Watson (1958).

ii) The <u>relative growth rate</u> (R) of a plant at any instant of time is the increase in dry weight per unit weight present per unit time.

$$R = \frac{1}{W} \cdot \frac{dW}{dt} = \frac{d(\log_e W)}{dt}$$

Similar quantities may be calculated for other plant parts, including the relative rate of leaf area increase.

iii) The <u>unit leaf rate</u> (E) of a plant at any instant of time is the increase in weight per unit leaf (or assimilatory) area per unit time.

$$E = \frac{1}{A} \cdot \frac{dW}{dt}$$

This quantity is also called the net assimilation rate following Gregory (1926) but the older term, unit leaf rate (West, Briggs and Kidd, 1920), is preferable since confusion with "net assimilation" is avoided. Similar quantities have also been calculated on bases such as leaf weight, leaf protein nitrogen (Williams, 1946) or total chlorophyll (Hunt and Cooper, 1967).

There are interrelationships between and within the morphogenetic and growth process relationships. Some of these are given by Blackman, Black and Kemp (1955), Evans and Hughes (1961, 1962), Whitehead and Myerscough (1962) and Jackson (1963), while Emecz (1962) has proposed an alternative system of relationships. The two most important relations

$$R = E \cdot \mathrm{LAR}$$

$$\mathrm{GR} = E \cdot A$$

were first given by West et al. (1920) although the second generally appears in the form

$$C = E . L$$

The separation of the biologically important but complex parameter, R, into components E and LAR has been long used as a means of partial discrimination between the internal and external groups of factors affecting growth. The early expectation that E would be substantially independent of internal factors and reflect changes in the external environment (Briggs, Kidd and West, 1920; Gregory, 1926; Heath and Gregory, 1938) was shown by Williams (1946) and Watson (1947) to be unfounded. Continued research on the variation in E has shown its dependence on the degree of self-shading in the plant or canopy (Watson, 1958; Williams, Loomis and Lepley, 1965; Buttery, 1970), on age (Thorne, 1960, 1961) and upon sink size (Milthorpe, 1963; Thorne and Evans, 1964; Moorby, 1970). Further analyses such as those of Watson and Hayashi (1965) and Watson et al. (1966) on the magnitude of the photosynthetic and respiratory components of E indicate that this is not a quantity lending itself to simple interpretation. Similarly the leaf area ratio, once thought to depend mainly on internal factors, has been shown to be affected in a complex manner by both internal and external factors (Evans and Hughes, 1961). The leaf area index, L, which appears in place of LAR in the alternative form of growth analysis based on crop growth rate is likewise a complicated parameter (Watson, 1956). In spite of such difficulties these relationships remain the key equations of growth analysis since they permit the study of growth in terms of components reflecting the capacity (LAR, L) and efficiency (E) of the process, a virtue first stressed by Gregory (1926) and since exploited by many others.

The formulae and relationships given above state the instantaneous values of the quantities in question. In practise it is impossible or difficult to record changes in W and A continuously so that mean values for the growth analysis parameters must be calculated from samples taken from the populations under study at intervals through the period of the experiment. To derive formulae giving these means, the instantaneous values must be integrated over the period between samplings, a process which in all cases requires assumptions about relationships between W, A and time. Radford (1967) gives derivations of and discusses the assumptions which underlie the traditional equations for the means of quantities used in growth analysis. Once appropriate formulae for means have been obtained the remaining problem of traditional growth analysis is the calculation of the values from experimental data. Methods used to calculate means and variances are considered by Cornish (1936), Goodall (1945), McIntyre and Williams (1949) and Evans and Hughes (1961).

These classical methods of growth analysis contrast with a more recent approach in which use is made of regression techniques to obtain the growth analysis quantities. This approach has been used in related studies for a number of years (Hammond and Kirkham, 1949; Glenday, 1955; Kheiralla and Whittington, 1962; Rees and Chapas, 1963) but only more recently has it been used directly for growth analysis (Vernon and Allison, 1963; Milthorpe, 1963; Williams, 1964; Muramoto, Hesketh, El-Sharkawy, 1965; Buttery, 1969; Laing, 1969; Moorby, 1970; Goldsworthy, 1970). The method consists of fitting polynomials or other curves to dry weight and leaf area data and using derived curves for growth analysis. For example if

$$W = f(t)$$

$$A = p(t)$$

then

$$GR = \frac{dW}{dt} = f'(t),$$

$$E = \frac{1}{A} \cdot \frac{dW}{dt} = \frac{f'(t)}{p(t)},$$

and

$$R = \frac{1}{W} \cdot \frac{dW}{dt} = \frac{f'(t)}{f(t)}$$

This technique is described by Vernon and Allison (1963), Hughes and Freeman (1967) and Radford (1967). The method is relatively free from the assumptions associated with the traditional approach (Radford, 1967) and is more accurate and less laborious. Disadvantages have not been stressed in the literature although the analysis of Williams (1964) demonstrates some of the difficulties.

1.1.2 The Quantitative Analysis of Growth

When an attribute of growth is plotted against time the growth curve formed is characteristically sigmoid. Such curves lend themselves to mathematical description, and, by their very ubiquity, are suggestive of some deeper significance. For this reason there have been attempts over the years to develop a quantitative analysis of growth with the hope that the mathematical description of the process will provide clues to its nature (e.g. Reed, 1920; Laird, Tyler and Barton, 1965). The fact that the complex processes of growth can be adequately described with a comparatively simple equation cannot, however, constitute proof that the function in question represents a physiologically meaningful generalization about growth, for, as Gray (1929) and others (Kavanagh and Richards, 1934; Thompson, 1942; Bertalanffy, 1960) have pointed out, the fit of an equation to observed points is determined mainly by the number of constants and the flexibility of the function used.

An alternative approach to the quantitative analysis of growth which has been more widely followed is based on the derivation of a law of growth from axioms. The growth functions in Table 1 have all, at one time or another, been deduced, using physiological arguments, and advanced as more or less comprehensive laws of growth (Blackman, 1919; Glaser, 1938; Robertson, 1923; Bertalanffy, 1960; Medawar, 1940, respectively); these and others are reviewed by Prodan (1968), Steward (1968) and Richards (1969). There have also been independent but conceptually similar attempts to derive models of growth from different starting points (Weiss and Kavanau, 1957; Collot, 1968; Monsi, 1968; Richards, 1969). The difficulties of the axiomatic-deductive approach to the quantitative analysis of growth are considered by Medawar (1945) and Steward (1968), while less pessimistic views are put forward by Bertalanffy (1960) and Richards (1969).

Table 1 Common Growth Functions.

Function	Synonyms or related (*) functions	Equation
Exponential	Compound interest law	$W = be^{kt}$
Time-power	Parabola	$W = bt^{k}$
Logistic	Autocatalytic, Verhulst-Pearl law, generalized logistic *, hyperbolic tangent *	$W = \frac{a}{1 + be^{-kt}}$
Negative exponential	Decaying exponential, monomolecular, diminishing returns, (Putter-) Bertalanffy *, Mitscherlich *	$W = a(1 - be^{-kt})$
Gompertz	Spillman *	$W = ae^{-be^{-kt}}$

A further approach to the analysis of growth is one in which an accurate empirical description of the growth of an organism is sought without the form of the function used for this purpose being regarded as of any particular physiological importance. For this purpose the most commonly used functions are those of Table 1 or polynomial regressions. Richards (1969) has reviewed the application of these equations to plant growth. The same author (Richards, 1959, 1969) has shown that the three asymptotic equations, the logistic, the negative exponential, and the Gompertz can be derived as special or limiting cases of a generalized four parameter logistic and Nelder (1961) presents an iterative least-squares method for fitting this function. Since these and other equations have two or more empirical constants they give a flexible description of most observed data, granted the restricted application of the exponential and time-power functions to non-asymptotic cases. Where extended asymptotes occur an ordinary polynomial is inadequate but inverse polynomials (Nelder, 1966) may be used. The empirical description of growth has also been attempted using a combination of several functions, usually exponentials (Hammond and Kirkham, 1949; Hansen and McGregor, 1954; Williams, 1964).

The empirical approach has value in that it summarizes explicitly information which may be otherwise hidden in raw data. Such curves also provide accurate estimates for growth rates in place of geometric and numerical approximations, a use which has been mentioned already in relation to growth analysis. Descriptive curves are in addition useful in directing attention to the reasons underlying the form of a growth curve (Williams, 1964) and in the comparison of treatment effects (Sprent, 1967; Mead, 1970). However in all these cases, as a number of authors have stressed (Thompson, 1942; Weiss and Kavanau, 1957; Bertalanffy, 1960; Putter, Yaron and Bielorai, 1966; Steward, 1968), the use and interpretation of empirical curves must be tempered by a consideration of the underlying biological realities.

1.2 THE GROWTH OF WHEAT

In this part of the review physiological aspects of grain yield in wheat, the growth of the wheat plant in relation to yield, and current knowledge on the agronomy and physiology of the short stature dwarf and semidwarf wheats are discussed.

1.2.1 Physiological Aspects of Grain Filling in Wheat

There is an extensive literature on the physiology of grain filling in cereals and, particularly, in wheat and barley. Early in the present century the accepted view on this subject was that reserves accumulated during vegetative growth constituted the principal source of carbon in the grain (Brenchley and Hall, 1909; Brenchley, 1912). This idea found expression in the "migration index", the ratio of grain to total shoot weight, which supposedly indicated the efficiency of grain filling (Engledow and Wadham, 1923-24). The same index, stripped of physiological significance, currently appears as the "harvest index" (Donald, 1962). The two lines of research which led to a reconsideration of this concept have been reviewed by Archbold (1945). First, shading and defoliation experiments in wheat (Boonstra, 1929, 1931; Smith, 1933) and barley (Watson and Norman, 1939) demonstrated that a proportion of the grain weight was derived from photosynthesis in the ear and other plant parts, thus confirming much older experiments by Deherain and Dupont (1901 : see Archbold and Mukerjee, 1942). Second, detailed examination of changes in dry weight and chemical composition in barley (Archbold and Mukerjee, 1942; Archbold, 1942) showed that any reserves from vegetative growth were in the nature of surpluses and too small to be of major importance in grain filling.

Current views on grain formation (Thorne, 1966, 1969; Langer, 1967) have developed directly from this point. There is much experimental evidence to show that most of the carbohydrate in the wheat grain is formed from CO_2 assimilated after ear emergence (Asana and Mani, 1950; Thorne, 1965; Stoy, 1965; Birecka and Dakic-Wlodkowska, 1966; Rawson and Evans, 1970) while the contribution of reserves is minor (Wardlaw and Porter, 1967; Rawson and Hofstra, 1969). All parts of the plant which are photosynthetically active after anthesis, lower leaves, the flag leaf, leaf sheaths, peduncle and the spike itself, contribute to grain formation. In the ear the outer sterile glumes, the flowering glumes, the awns, the grain and the rachis are capable of photosynthesis (Carr and Wardlaw, 1965). Ear photosynthesis involves the assimilation of atmospheric CO_2 and re-fixation of CO_2 respired by the ear (Kriedemann, 1966). Grain respiration accounts for some two-thirds of the total ear respiration (Carr and Wardlaw, 1965) and the grains themselves reassimilate most of their respired CO_2 (Evans and Rawson, 1970). In the intact ear photosynthesis by the rachis and rachillae must presumably serve a similar function. The contribution of ear photosynthesis to grain yield is substantial, particularly in awned wheats (Evans and Rawson, 1970) and may reach as high as 50% of the total requirements for grain filling (Carr and Wardlaw, 1965).

The other major sources of assimilates for grain formation are the photosynthetic parts above the flag leaf node which include the flag leaf lamina, the flag leaf sheath and the exposed part of the peduncle (Asana and Mani, 1950; Quinlan and Sagar, 1965; Voldeng and Simpson, 1967). Among these organs the flag leaf is the most important contributor to grain filling having a net photosynthetic rate approximately twice that of the stem and leaf sheaths in both barley (Thorne, 1959) and wheat (Evans and Rawson, 1970). In wheat the role of assimilates from leaves below the flag leaf node in grain filling is small although photosynthesis in these parts may be of indirect importance to the process (Quinlan and Sagar, 1962; Lupton, 1966). By way of summary the approximate contributions of the ear and other parts to grain formation presented by Thorne (1969) are given in Table 2 (FLN = flag leaf node). These figures can be taken as no more than a rough guide since the actual contributions vary with variety, experimental method and environment (Thorne, 1966; Langer, 1967; Puckridge, 1969), and, in the light of work by Carr and Wardlaw (1965) and Evans and Rawson (1970) they appear to underrate the importance of ear photosynthesis.

Table 2 Estimates of % of Final Grain Weight from Various Sources (Thorne, 1969).

	%
Ear gross photosynthesis	24
Ear respiration by day	- 28
Ear respiration by night	- 11
Ear net photosynthesis	- 15
Assimilates from above FLN	100
Assimilates from below FLN	15

The economic importance of grain filling has also stimulated much research on the translocation and distribution of assimilates within the plant (Wardlaw, 1968; Milthorpe and Moorby, 1969). This work has shown that translocation from the glumes (Lupton, 1966) and the flag leaf (Buttrose and May, 1959; Lupton, 1968) is largely towards the grain, although the peduncle may act as a temporary sink at anthesis and for some days after (Carr and Wardlaw, 1965; Birecka, 1968; Wardlaw, 1970). Some of the assimilate stored in the peduncle may subsequently be retranslocated to the ear (Wardlaw and Porter, 1967; Rawson and Hofstra, 1969). In the same period there may be downwards translocation from lower leaves to roots (Wardlaw, 1965) and tillers (Rawson and Hofstra, 1969). The complexity of assimilate distribution within the plant during the grain filling period is further shown by the work of Rawson and Evans (1970) and Walpole and Morgan (1970) on the pattern of grain growth within the ear, and that of Buttrose and May (1959) demonstrating changes in assimilate uptake which reflect the synthetic activity of different regions within the caryopsis itself.

The major question yet to be answered is that concerning the nature of limitations to grain yield. Here there are three main possibilities:

i) inadequacy of assimilate supply;

ii) inability of the developing grains, the "sink", to utilize available assimilates;

iii) inefficiencies in translocation between source and sink.

Limitations in grain yield due to inadequate photosynthesis have been suggested by Stoy (1966) and, in the later stages of grain filling, by Walpole and Morgan (1970). On the other hand Evans and Rawson (1970) have shown photosynthesis is adequate for grain filling in a range of varieties, while the work of Evans and Dunstone (1970), which shows that photosynthetic rates per unit leaf area are inversely related to grain yield in lines representing the evolutionary development of modern wheats, does not support the idea that assimilates limit yield, especially since increases in leaf size are accompanied by a proportionate increase in grain size in these lines.

The experimental evidence for and against a sink limitation is also conflicting. In wheat (King, Wardlaw and Evans, 1967) and other species (Neales and Incoll, 1968) the rate of photosynthesis in leaves can be reduced by lowered sink capacity; increases in the rate of photosynthesis in the flag leaf during grain filling have also been shown in some cases

(Birecka and Dakic-Włodkowska, 1966; Rawson and Hofstra, 1969; Evans and Rawson, 1970). However Lupton (1968) and Birecka, Szczypa and Kozlowska (1969) working on plants with ears removed were not able to show limitations to photosynthetic rates of the flag leaf. Nevertheless there is much evidence that sink size does affect the translocation of assimilates in a regulatory role (Thorne, 1966; Langer, 1967; Wardlaw 1968) and may in this way constitute a limitation to grain yield.

Translocation may also limit grain yield. Doodson, Manners and Myers (1964) and Milthorpe and Moorby (1969) consider that there is little restriction on the movement of assimilates, this being controlled by sinks and sources, while Wardlaw (1965) gives some evidence that the movement of assimilates between the flag leaf and ear is controlled by the vascular anatomy at the flag leaf node. Evans et al. (1970) raise the further possibility that the cross-sectional area of phloem available for translocation may be limiting in modern wheat varieties. There is also evidence of a xylem discontinuity which restricts flow of material from the xylem in the rachilla to that in the pericarp (Zee and O'Brien, 1970) although the physiological significance of this is unknown.

The central problem in deciding which physiological factors may limit yield is one of complexity. In a number of investigations mentioned above apparent limitations were not closely related to yield while in others the limiting factors, if any, were obscure. Evans (1970) has suggested that one source of this difficulty is a buffering effect due to mobilization of reserves or to compensatory changes in the rate of photosynthesis in various parts. In a general discussion of the problem Good (1969) criticizes over-simplification of the "source-sink" concept, pointing out that the sink for assimilates is a complex system representing the whole catabolism of the plant so that simple experimental manipulations are unlikely to yield conclusive answers. This fact appears sometimes to have been overlooked in experiments in which limitations to yield are investigated.

1.2.2 The Growth of the Wheat Plant in Relation to Yield.

The growth of the cereal plant is determined by the activity of the apical meristems of the shoot and roots, the lateral meristems of leaves, tillers, nodal roots, and the spike, and the intercalary meristems of leaf sheaths and stem internodes (Bunting and Drennan, 1966). The growth of grain, while affected by many modifying factors, remains primarily an expression of the activity of these meristems. In the following section aspects of the relation of yield to the growth and development of the wheat plant will be considered.

As a consequence of the processes of grain filling described in the preceding section there has arisen the view that grain yield depends primarily on the growth and development of the plant in the period after ear emergence with prior growth of importance only in so far as it affects the size of photosynthetic surfaces available during grain filling and the number and potential size of the kernels themselves (Thorne, 1966, 1969). Support for this view comes largely from growth analysis experiments involving varietal comparisons. In wheat Watson, Thorne and French (1963) showed that varietal differences in the unit leaf rate, prior to ear emergence, were associated with compensatory changes in leaf area index, so that differences in dry matter production were small. In other experiments no association between grain yield and unit leaf rate in the vegetative phase within a range of varieties has been found (Quinlan and Sagar, 1965; Cannell, 1967; Lupton, Ali and Subramaniam, 1967) On the other hand the duration of photosynthetic area after ear emergence, and particularly of area above the flag leaf node (Welbank, French and Witts, 1965), has been shown to be closely related to yield (Watson et al., 1963; Thorne, Ford and Watson, 1967) while leaf area duration prior to heading is not (Thorne, 1966). The apparent efficiency of the photosynthetic area after ear emergence can be measured by the grain leaf ratio, G, which is the ratio of grain yield to leaf area duration (Watson et al., 1963). Examination of this ratio in varietal comparisons has shown some differences (Watson et al., 1963) but in general the close dependence of grain yield upon duration of photosynthetic structures has been confirmed.

A closer examination of the relationship between plant growth and grain yield reveals however that the importance of the later stages of growth may be overemphasized. Davidson (1965) has shown that leaf removal at ear emergence has no significant effect on grain yield (cf. Stoy, 1965) but leaf area control prior to this decreased grain yield substantially by reducing spikelet number and grain weight. Similar effects have been noted by Lucas and Asana (1968) and Puckridge (1968), while Thorne, Ford and Watson (1968) have shown that differences in grain yield can be related to the effect of early environmental conditions upon grain number.

Further evidence for the importance of the early stages of growth in determining yield comes from work in which the relation of grain yield to plant density has been studied. In wheat and most cereals grain yield exhibits a broad maximum over a range of plant densities with a tendency for a decrease in the ratio of grain dry matter to total dry matter as density increases (Holliday, 1960; Donald, 1963; Kirby, 1967). The stability of yields over this range of densities may be analysed further in terms of the yield components, the numbers of plants per unit area, of tillers per plant, of spikelets per ear, of grains per spikelet and the weight per grain. These, and particularly the latter four, since plant mortality after establishment is generally low (Puckridge and Donald, 1967), are major yield controlling factors reflecting the determination of grain yield during the growth and development of the plant.

The number of tillers per plant and tiller fertility vary markedly with plant density (e.g. Kirby, 1967) and are related to light interception, crop growth, and thus yield (Puckridge and Donald, 1967). In wheat, and also in barley, tiller number increases early in growth, peaks, and then declines to a relatively stable plateau prior to ear emergence (Thorne, 1962; Watson et al., 1963; Quinlan and Sagar, 1965; Laude, Ridley and Suneson, 1967; Bremner, 1969, Cannell, 1969). This trend is related to the death of late tillers (Thorne, 1962; Cannell, 1969) which depends on internal competition (Aspinall, 1961) and apical effects (Friend, 1966). The effect of late unproductive tillers on ear-bearing shoots appears to be minor and they may in fact contribute to the growth of fertile shoots (Bremner, 1969; Lupton and Pinthus, 1969; Rawson and Donald, 1969). Since the upper limit of tillers on a shoot is determined at spikelet initiation and tiller survival largely prior to ear emergence it is apparent that tiller number per plant depends mainly on the early stages of growth.

Two other yield components, the number of spikelets per ear and number of grains per spikelet, are also determined in the period up to and including anthesis. Spikelet number depends largely on the duration of primordium production (Rawson, 1970; Kirby and Faris, 1970) and this can be affected by a number of environmental factors (Friend, 1966; Langer, 1967) and also by correlations within the apex which may be partly related to internal competition for nutrients (Williams, 1966b; Kirby and Faris, 1970; Rawson, 1970). Floret number, which later sets an upper limit to grain number per spikelet, is determined after spikelet number and the control of this will presumably depend upon similar factors to those affecting spikelet number. Floret fertility is a further determinant of grain yield and there is evidence that this may be fixed early in the growth of the ear by the effects of internal competition on stamen and carpel growth (Williams, 1966a, 1966b). While failure to set seed at anthesis due to lack of pollination is said to be rarely important in cereals such as wheat (Heslop-Harrison, 1969) it is apparent that a number of florets, particularly those in distal positions, do not set seed even though fertile (Walpole and Morgan, 1970). This may reflect the earlier regulation observed by Williams (loc. cit.) or a competitive disadvantage of later flowering florets (Rawson and Evans, 1970).

Thus, of the yield components, all but one, the weight of the grains (Section 1.2.1), are determined in the period of growth up to anthesis. Growth in this period is therefore of direct consequence to grain yield since it sets the potential which can be realized in the period after flowering.

Grain yield also depends upon root growth. Aspects of the growth of roots in cereals have been reviewed by Brouwer (1966) and Hackett (1969). In wheat and barley, as in most grasses, the proportion of root weight to shoot weight is initially high (Bray, 1963) but declines in time (Williams, 1960; Welbank and Williams, 1968). Nevertheless roots are still active until late in the growth of the plant as evidenced by their apparent sink activity well after anthesis (Wardlaw, 1965). The size, distribution and activity of the root system affects grain yield (Boatwright and Fergusson, 1967; Hurd, 1968) and these factors in turn depend on aspects of shoot growth such as tillering (Pinthus, 1969). Correlations between root and shoot growth (Pope, 1932, Williams, 1960; Brouwer, 1966) serve as a further reminder that above-ground growth leading to grain yield is inseparably linked to that below ground.

1.2.3 Short Stature Wheats

The most important agricultural advance for many decades, the so-called "green revolution" of the sixties,has hinged on the exploitation of the superior yielding ability of the new short stature varieties of all the major grain crops. In wheat the new varieties were developed in the United States and at the Rockefeller Foundation in Mexico, using the dwarfing genes found in Japanese strains (Vogel et al., 1956; Borlaug, 1965; Reitz and Salmon, 1968). These have proved phenomenonally successful in many countries (Borlaug, 1965, 1968; Swaminathan, 1968; Reitz, 1970).

The agronomic advantages of the dwarf and semidwarf wheats over standard height varieties are attributed to a number of factors.

1. Resistance to lodging, permitting heavier application of water and fertilizer (Woodward, 1966; Syme, 1967; Porter et al., 1964) and contributing to the greater responsiveness to fertilizers (Beech and Norman, 1968).
2. Day length insensitivity (Reitz and Salmon, 1968) leading to earlier flowering and a longer duration of grain growth (Syme, 1967); absence of a vernalization requirement NO (Pugsley, 1964) contributing to earliness. ?
3. Large ear and high ear : straw ratio allowing more photosynthesis and grain set (Syme, 1967). Awnedness is an important character here (Vogel et al., 1963).
4. Resistance to disease, particularly rusts (Borlaug, 1965).

The major disadvantage of the short stature wheats appears to be poor seedling emergence (Pugsley, 1964; Sharma, 1968), which is related to their shorter coleoptiles and less rapid coleoptile elongation (Burleigh, Allan and Vogel, 1965). Differences in physiology such as this, and also in phenology, have, in India at least, demanded altered farming practices for these varieties (Sharma, 1968; Swaminathan, 1968).

The physiological features characteristic of short stature wheats do not appear to have been extensively investigated. Dwarf and semidwarf varieties do not respond to giberellic acid (Allan, Vogel and Craddock, 1959; Radley, 1970) and their response to CCC is negative (Appleby, Kronstad and Rohde, 1966). The reduced stem length which is the characteristic feature of dwarf and semidwarf varieties is due mainly to shorter peduncles and upper internodes (Johnson, 1954; McNeal,Berg and Kages, 1960) and not to fewer internodes (Thorne, Welbank and Blackwood, 1969). Work on the genetics of the short stature character has been reviewed by Powell and Schlehuber (1967).

Work at Rothamsted (Thorne et al., 1969) shows semidwarf varieties have a greater apparent grain production efficiency, as measured by the grain leaf ratio for area above flag leaf node, than standard varieties. This was attributed in part at least to greater ear photosynthesis. Evans and Rawson (1970) have demonstrated that ear photosynthesis in awned short stature varieties can be higher than in non-awned standard varieties. There is also evidence (Sharma, 1968; Subbiah et al., 1968) that the shorter stature wheats have a more extensive and better distributed root system than some normal varieties. High tillering capacity has been cited as another yield advantage of the semidwarf wheats (Vogel et al., 1963; Woodward, 1966; Sharma, 1968) but there is evidence that it may be unimportant (Syme, 1967; Thorne et al., 1969). It is apparent that for this, and other characteristics, environment and variety must play a large part in determining which factors contribute to the yield advantage of the dwarf wheats. Beech and Norman (1968) note, for example, that within the semidwarf wheats they studied, different patterns of development gave equally high yields, whereas Vogel et al., (1963), in another environment, found that any selections differing distinctly from a certain pattern gave much lower yields.