

## INTRODUCTION

1. 0. 0.

In 1961, a new wheat cultivar "Gaines" was released for commercial cultivation in the Pacific Northwest of the United States. At the time of its release this new cultivar was unusual amongst its contemporaries in that it was of very short stature. In 1962, two related short stature cultivars, Pitic 62 and Penjamo 62, were released in Mexico by the Rockefeller Programme. The impact made by these and subsequent wheats of similar parentage and stature, on both wheat breeding and general wheat production throughout most areas of the World, has been unprecedented. The grain yield potential of this new, short stature wheat class has proved such that the new germplasm has been widely described as "the catalyst of agricultural revolution" and "the basis of the green revolution" respectively.

Within a decade short stature wheats, or dwarfs and semi-dwarfs as they have become generally known, have spread from the Americas to India, Pakistan, the Middle East, Europe, the U.S.S.R. and Australia. They have provided the means by which traditional wheat importing nations have suddenly achieved self-sufficiency of grain. Further, they have been partly responsible for the massive over-production which has suddenly confronted traditional exporting nations. The short stature wheats have provided in many countries the key to a new level of technical efficiency in agriculture. In other countries, realisation of the high potential yield has been elusive.

Despite the widespread success of dwarf and semi-dwarf wheats

and their current domination of many plant breeding programmes throughout the world, to date there is little published information available on the physiological mechanism of this enhanced yield potential. In view of the importance of these wheats, a study of some aspects of whole plant physiology of representative short stature types, as compared to Australian standard height cultivars, was initiated in June 1967.

Van Dobben (1962) defines yield of grain as "the sum of dry matter production and its distribution in subsequent phases of development." This definition embraces two parallel systems, namely, growth and development. The former implies increase in volume, dimension, number and dry matter accumulation of plant parts. The latter implies progression in time by the plant through successive, characteristic stages. The possibility that within this relationship of growth and development there existed either a developmental sequence, or specific growth characteristics, which enhanced the grain yield potential of short stature wheats, seemed a suitable foundation from which to initiate the following study. However, from this foundation, two additional factors could not be divorced; namely, nitrogen response by dwarf and semi-dwarf wheats, and the relative contribution towards grain yield made by various plant organs.

Imported to Australia with the original short stature germplasm was a legend of an extra-ordinary ability to respond to applied nitrogen with increased grain yield. Australian wheat cultivars have always been considered as marginally responsive only to nitrogen applied in the early stages of the life cycle, and unresponsive in

grain yield to late application. Such was the reputed response to nitrogen fertilizers by dwarf and semi-dwarf wheats that, as soon as the new germplasm had been introduced to breeding programmes in Australia, dual planes of nitrogen, normal and luxury levels, were employed by plant breeders as a selection technique. Response of such magnitude could be expected to be manifest in plant parameters other than grain yield, such as leaf area, leaf area duration, tiller number and grain sink size.

The reduction in overall height of the semi-dwarf and dwarf plants, as compared to standard height cultivars is a result of reduction in the length of internodes. In the shortest dwarfs one such internode may be completely absent. As the last formed internode is shortened to a greater degree than others, the contribution towards grain filling by this organ may well be reduced in semi-dwarf wheats, in relation to other organs. This suggests that other plant parameters, e.g., heads, awns, flag leaves, etc., may be correspondingly more important in contribution of photosynthates in short stature cultivars.

The dwarf character which has made such impact on wheat production originates from a selection of Japanese origin and is referred to as the Norin type short stature, (Vogel, Craddock, Muir, Everson and Rohde 1956). Other forms of short stature are now recognised, but their contribution, to date, to world wheat improvement has been insignificant relative to that of the Norin derivatives.

## REVIEW OF LITERATURE

2. 0. 0.

### SOME CHARACTERISTICS OF SHORT STATURE WHEATS

2. 1. 0.

Short stature wheats are by no means a modern phenomenon. They have been cultivated in India since ancient times (Swaminathan 1968) where they were favoured for their heat tolerance and consistency of yield under adverse environmental conditions (Hutchinson pers. comm.) In Japan short stature wheats have been grown for at least several hundred years and were selected for resistance to lodging under culture in irrigated, high fertility soils (Frankel and Bennett 1970).

Modern recognition of the potential of short stature wheats was made by C.A. Vogel and F.C. Elliot at Washington State University in a collection of Japanese wheats imported to the United States of America in 1946 by S.C. Salmon (Reitz 1970). Initially believed to be mutants, these short stature types are now accepted as Japanese cultivars bred at Tohoku National Breeding Institute by Inazuka and Asanuma who were awarded the "Association of Agricultural Scientists Award for Outstanding Achievement in Agricultural Science" in 1969 (Gotoh 1969).

The history of these wheats is of interest for appreciation of their agronomic characteristics. Records indicate that two American wheats, Fultz and Turkey Red were included in the lineage of Norin 10, the cultivar which has contributed the modern dwarf germplasm source. The cultivar Fultz arrived in Japan in 1892, and

Turkey Red probably about the same time (Reitz and Salmon 1968). A selection of Fultz named "Glassy Fultz" was subsequently isolated and crossed with a Japanese cultivar, Daruma, in 1917. Seven years later a Fultz-Daruma selection was crossed with Turkey Red. A selection, "Tohoku No. 34" was named Norin 19 (Norin being an acronym of the first letter of each word in the Romanised title of the Japanese Agricultural Experiment Station) and both registered and released in 1935.

Following quarantine in the United States Norin 10 together with 23 other Japanese introductions was sown at seven locations in 1948 and was classified as a winter wheat which was very susceptible to the diseases, powdery mildew (Erysiphe graminis f. sp. tritici E. Marchal) and leaf rust (Puccinia recondata Rob. ex Desm.). It was crossed by Vogel and Elliot with the cultivars Brevor and Baart in 1948-49 (Vogel, Craddock, Muir, Everson and Rohde 1956). The intention of the crosses was to produce a plant intermediate in height between the "short" commercial cultivars and genetic "grass clumps". The cross of Norin 10 x Brevor 14 produced a small number of semi-dwarf plants in the F2 generation with good kernel types which were more productive than either parent. In the F4 generation three lines outyielded the parent Brevor, despite a large measure of male sterility. Re-selection produced several lines in which the flowering habit was more normal and two of these lines (Nos. 14 and 17) were considered to be most efficient in grain production (Vogel et al. 1956). The height of these was approximately 65% that of Brevor which is classified as a very short cultivar (Bayles and Clark 1954).

"Selection 14" of the Norin 10 x Brevor 14 cross was considered the best of the material (Vogel pers. comm.) and was used as a parent extensively in the Washington State Programme, subsequently producing the now famous cultivar, "Gaines". Selection 14 was also widely distributed to plant breeders in the United States and abroad. It is the progeny of crosses with the Norin derivative, Selection 14 both in the Pacific Northwest of the United States and in Mexico which has been used almost exclusively for the synthesis of current semi-dwarf wheat cultivars throughout the world.

Other forms of the short stature character are now widely recognised. These include the cultivar Seu Seun brought from Korea to Nebraska in 1949 by H. Florell (Briggle and Vogel 1968), Suwon 92 which was introduced to the U.S. as a source of mildew resistance, Tom Thumb and derivatives from Britain and Holland, Ghurka from Australia and a number of Italian short stature wheats, e.g., Funello. Several sources of evidence (Reitz and Salmon 1968) indicate that ancestry of these Italian cultivars may be traced to Japanese wheats used from 1911 onwards for early maturing, short culm, non-lodging characteristics (Maino 1954). Further, there is evidence (Fletcher 1971) to indicate that the Korean semi-dwarfs have the same genes ("in whole or part") as those in Norin 10. However, little is yet known of either the physiological characteristics or genetic constitution of these forms - nor has their parental contribution been significant in commercial wheat cultivars to the present. It is the Norin 10 derivatives, principally from The Rockefeller Foundation's Programme and more recently the International Centre for Wheat and Maize Improvement (Cimmyt) in

Mexico, which have become synonymous with short stature or semi-dwarf wheats in current cereal terminology.

The contribution of the Norin derivative short stature wheats and the improved agronomic practices associated with them towards the alleviation of world carbohydrate shortages is now widely documented (Stakman, Bradfield and Mangelsdorf 1967). The rate and extent of distribution of this germplasm to all continents has been unique in man's history. Seed shipments of previously unknown magnitude (e.g., 42,000 metric tons of seed from Mexico to Pakistan in 1967-68) have made possible the rapid "agricultural revolutions" in some countries. Nations such as Mexico, India, Pakistan, and Turkey have already revitalised their wheat industries. "Other nations, among them Afghanistan, Guatemala, Kenya, Nepal, Rhodesia, South Africa and the United States are now making use of the improved dwarf varieties". (Anonymous 1967). Quinones, Maya, Klatt and Borlaug (1969) estimate that the Mexican dwarf wheats and their derivatives were grown on 7,457,000 hectares in Asia and North Africa in 1968-69, and in addition a considerable but unknown area was sown with these wheats in East and South Africa and in North and South America.

As a class the short stature wheats are from 20-50% shorter at maturity than standard, medium height cultivars. The degree of difference in straw height between dwarf, semi-dwarf and standard height types depends to some extent on the availability of moisture to the plants during growth, particularly over the period of stem elongation. Reduction in plant height as a result of moisture stress however decreases

with decreasing stature. The approximate height relationships are illustrated in Table 1 (Matheson 1971).

TABLE 1

HEIGHT OF STANDARD, SEMI AND DWARF WHEAT CULTIVARS AT TWO MOISTURE LEVELS				
CULTIVAR	CLASSIFICATION	HEIGHT (cm)		
		Dryland (D)	Irrigated (i)	Difference (i - D)
Gamut	Medium Standard	102	132	30
Chile 1B	Semi-dwarf	64	76	12
Mexico 120	Dwarf	46	51	5

The reduction in overall height of the short stature, Norin type plants as compared to standard height cultivars is the result of a reduction in the length of the internodes (Vogel, Allan and Peterson 1963). In the shortest dwarfs one such internode may be completely absent (Krause 1966). It is the same shortened internode pattern, with other plant organs of normal size, which was described by Waldron (1924) and is referred to by maize breeders as "brachytic dwarfism."

The short stature wheats are commonly classified on the basis of stem height into three categories, semi or single dwarf (sd), dwarf or double dwarf (dd), and triple dwarf (ddd). Within each category further sub-classes are recognised, e.g., tall semi-dwarf (tsd) and medium semi-dwarf (msd). Allan and Vogel (1963) report that in the

Norin derivative material used in the Pacific Northwest, two major recessive genes as well as a number of modifier genes control the dwarf character in breeding. The semi-dwarfs are believed to possess one of these genes whereas the dwarfs possess both genes. The presence of modifier genes gives rise to intermediate height levels. The third recessive gene for dwarfing which was in the original Norin parental material, was purposely discarded during early selection in the Washington State material (Vogel pers. comm.). In recent years there has been renewed interest in the three gene material for further plant height reduction, particularly in India (Gill and Anand 1969) where the height classification on the basis of gene number is now commonly used, e.g., single gene (semi-dwarf), two gene (dwarf), and three gene (triple dwarf).

Konzak et al. (1968 and 1969) have reported the identification of several new height reducing genes produced by artificial mutagenesis of the cultivars Burt and Marfed, one of which behaves as a completely dominant semi-dwarf gene.

The semi-dwarf height level is the one which has been most utilised by plant breeders, for it is in this class that the greatest yield potential has been demonstrated. The full dwarfs are considered to be more specific in environmental requirements, and to have less adaptability (Pugsley 1964).

Not all semi-dwarfs are capable of producing very high yields but amongst the highest yielding cultivars there appears to be a striking similarity in head type, leaf, culm and growth characteristics

(Vogel et al. 1963). For the Pacific Northwest, Pugsley (1964) states that "the general pattern is one of high tillering capacity, coarse awns, medium semi-dwarf plant height, medium culm diameter and head size, and medium to small length and breadth of leaf". In the Mexican Wheat Breeding Programme a broader leaf is generally favoured.

Both spring and winter type short stature wheats, with either red or white grain, are currently available in Australia, amongst introduced semi-dwarf material. It is however, popularly believed that all semi-dwarf wheats, both winter and spring, have at least a moderate cold or vernalization requirement. This was certainly the case with the earlier introductions which became available in Australia, e.g., Mexico 120 and Gaines. However, in local breeding programmes there is now available semi-dwarf material devoid of any vernalization requirement.

The majority of dwarf and semi-dwarf wheats are heavily awned. Vogel et al. (1963) consider that awn is more important in semi-dwarf than in standard height cultivars. - "awnedness in a semi-dwarf contributes at least 10% to yield and test weight". Krause (1966) states that "as culm length decreases the yield advantage for awned selections as opposed to awnless increases. This may be at least 10% at the semi-dwarf level."

The Norin type semi-dwarf character has been transferred by Lebsack (1963) from the hexaploid to the tetraploid wheat species, Triticum durum where it has been developed by Borlaug and colleagues in Mexico. Parental material of semi-dwarf durum type was introduced from

Mexico by Pugsley in 1962 and was used in the breeding of the Australian semi-dwarf durum, Duramba (Matheson and Wark 197<sup>2</sup>~~3~~).

Early commercial experience in the Pacific Northwest of the United States indicated that short stature wheats were responsive to substantially higher levels of soil nitrogen than was the case with standard height cultivars. This was subsequently substantiated by research findings in India (Swaminathan 1968), in Mexico (Anon 1966), and in the United States (Woodward 1966). Although the main ability of the short wheats in this regard appears to be associated with lodging resistance, the belief has become common amongst research workers that wheats of Norin origin have the additional ability to absorb and utilise advantageously greater quantities of nitrogen (Beech and Norman 1968). In India time and method of application of nitrogen fertilizer is regarded as of major importance.

"Foliar fertilization of the dwarf wheats Sonora 64 and Lerma-Rojo with urea (half at first irrigation in the soil and the other half through foliage at heading stage) resulted in an increase in grain production by 70.4 kg/ha as compared with the same dose of urea applied through the soil" (Swaminathan 1968). It has been further suggested (Krause 1966) that the semi-dwarfs have an ability to utilise nitrogen added at anthesis to increase grain yield.

The most important characteristic of the short stature, Norin derivative wheats is without doubt, their ability under some conditions to produce very high grain yields. The cultivar Gaines is

attributed with producing yields in the Columbia Basin, in excess of 13440 kg/ha (Guettinger 1966). In Mexico yields of up to 5400 kg/ha were recorded from commercial crops in 1965 (Anon 1965). In Arizona plot yields of 5400-6720 kg/ha have been recorded from semi-dwarf cultivars. These represent yield increases of 25-50% over recommended standard height cultivars (Thompson pers. comm.). In India yields in excess of 7380 kg/ha have been reported, and in Pakistan semi-dwarfs have exhibited a yield potential of "almost double that of local standard height varieties" (Anon 1964).

In Australia to date yield increases from imported semi-dwarf material in general have neither been spectacular nor consistent. In 37 trials conducted over three years (1966-68) in north western New South Wales by the author, the imported dwarf cultivar Mexico 120 showed marked yield superiority in 5 trials only - it was within the yield range of standard height cultivars in 26 trials and was inferior to these cultivars on 6 occasions. Similar results have been recorded over a more limited range of sites and seasons with the Mexican cultivars Pitic 62 and Sonora 64A.

That the imported short stature wheats do have a yield potential well in excess of local standard height cultivars, under certain environmental conditions, is generally appreciated by plant breeders in Australia most of whom have, on occasions, recorded particularly high yields from semi-dwarf material. At Temora in southern New South Wales a Norin 10 Brevor 14 back cross derivative of the cultivar Javelin 48 produced a mean plot yield of 5429 kg/ha in 1963,

the highest yield recorded to that time in trials in the area (Pugsley 1967).

In irrigated wheat trials, conducted by the Agricultural Research Institute, Wagga, at Coleambally N.S.W. in 1967, a selection from Mexico, WW15 out-yielded the recommended standard height cultivar Falcon by 2507 kg/ha and recorded a mean yield of 7090 kg/ha (Pugsley 1967).

The reasons for failure of regular expression of this yield potential under Australian wheat-belt conditions, have however, proved elusive. Such reasons as insufficient moisture, inadequate soil fertility and extreme frost susceptibility have been variously suggested. It is significant that expression of yield potential by the semi-dwarfs has generally been associated in Australia with above average rainfall during the final (Seed) phase of development of the crop. However, trials with supplementary irrigation in this vital phase of development have not regularly expressed the yield potential of semi-dwarfs. Similarly the raising of soil fertility particularly by addition of nitrogen and phosphate fertilizers in trials, has resulted in yield decreases at some sites and yield increases at others (Tuohey 1967).

In other arid areas of the world, where moisture stress can be expected, yield responses from semi-dwarfs have also been disappointing, (Heyne pers. comm.) and until more is known of the physiology of these short stature wheats, it is unlikely that they will have wide application in such areas.

Although currently the object of widespread research at many institutions, the physiological basis of the high potential yield of short stature wheats is not known. Lupton and Bingham (1969) have reported that the rate of photosynthesis of the semi-dwarf wheats was greater than that of the standard height cultivars used in their experiments. Both Syme (1967) and Beech and Norman (1968) have remarked on the length of the Seed phase of development of the dwarf cultivar Mexico 120. Briggie and Vogel (1968) have referred to the long period from anthesis to maturity for the cultivar Gaines. Paquet (1968), following on a study of productivity, regularity of yield and grain quality of Norin derivative semi-dwarfs, stated that there was "no evidence thus forthcoming to suggest unfavourable physiology to be linked with semi-dwarfism with respect to productivity, regularity and quality of yields". Thorne, Welbank and Blackwood (1969) found leaf area duration after anthesis to be of lower values in semi-dwarfs examined than in tall European cultivars, and concluded that the apparent mean efficiency of the green area above the flag node in grain production may be substantially higher in those short stature cultivars.

The dwarf and semi-dwarf wheats are not without disadvantages. The milling and baking qualities of all introduced short straw wheats, grown in Australia to date have been grossly inferior to local standards of quality (Jacob 1971). Many have presented a serious threat to the overall quality of Australian wheat, if grown commercially.

Seedling emergence problems associated with the short coleoptile produced by the seed have been encountered in Australia as well as

abroad, (Allan, Vogel, Russell and Peterson 1965). Partial floral sterility, low thousand grain weight, and increased susceptibility to Septoria leaf spot (Septoria tritici ROB.) appear to be characteristics of the earlier, Norin 10 derivative germplasm.

Despite such disadvantages the short stature wheats of Norin origin have, by virtue of their yield potential alone, made unprecedented impact on world food production. The mechanisms responsible for the superior yield potential of these short stature wheats remain obscure. Engledow and Wadham (1923) stated that "to plant physiologists we must look for the final solution to the yield problem". For the Norin derivative no less than other wheats this solution may lie in the pattern of physiological development; in superior efficiency of photosynthetic tissue; in response to nutrients, or in some other characteristics. It is in these areas that a solution may be forthcoming.

## PHASIC DEVELOPMENT OF WHEAT

2. 2. 0.

The definition of final grain yield by Van Dobben (1962) quoted in the Introduction embraces two parallel systems, namely growth and development :- the former implies increases of dry matter, whereas the latter implies the passage of the plant through successive characteristic physiological periods or stages. These two parallel systems of growth and development, which collectively constitute the life cycle of the plant, are both independent and related. They are independent in the sense that either can proceed whilst the other is stationary, but related in the sense that they are joint integers in the biological summation of crop growth where the duration of one system will affect the extent of the other system.

Wardlaw (1965) stated that "in trying to understand the physiological mechanism that underlies and determines the orderly formation of floral organs, i.e., development, it is essential to consider the organization and functional activities of the apex of the antecedent leafy shoot". It is the result of such study which has provided the foundations for the current knowledge of physiological development of the temperate cereals.

Credit for the initiation of modern developmental physiology is generally given to Klebs who worked during the period 1911-1919 (Murneek 1948) although the effects of very low temperature or "chilling" on subsequent plant development were appreciated well beforehand, (Von Seelhorst 1900, and Gassner 1918). Amongst the earliest workers

in this field were Jensen (1918) who attempted to look at physiological development outside the framework of growth, and Percival (1921) who studied the progressive development of the wheat spike. Hudson (1934) described the development of wheat within the context of phenotype and time, by progressive sampling of a population at regular intervals from germination to maturity. The discovery of photoperiodic induction by Garner and Allard (1920) pointed the way to developmental behaviour, and the control of flowering in many plant species (Marcellos 1970). In the field of thermo-induction of flowering however, despite the earlier discoveries of Gassner (1918) the work of Lysenko (1931 and 1932) which gave rise to the Lysenko Theories of Development is most widely known. The postulates of Lysenko - that growth and development are not identical, rather they are independent, - that the entire process of development consists of individual phases or stages, - that phases occur in strict sequence and a subsequent stage or phase cannot commence until the preceding phase has been completed, - and that different phases require different environmental conditions for their completion, have provided a lasting foundation for the appreciation of developmental physiology and remain pertinent to this day. Whereas Klebs (1918) had recognised three stages, Lysenko working entirely with winter wheats recognised two developmental phases only, which he referred to as the Thermo-phase (from germination to floral initiation) and the Photo-phase (from initiation to maturity). Subsequent workers (Hudson 1934, Bonnett 1936 and 1961, Van Dobben 1962, Gaastra 1962 and Blake 1967) have originated both individual terminology for, and definition of phases of development. In the following text the terminology of Bonnett (1961) consisting of

the Vegetative phase (from germination to floral initiation), the Reproductive phase (from initiation to anthesis), the Seed phase (from anthesis to maturity), and the Resting Seed phase will be adhered to, unless otherwise specified. Cooper and Calder (1964) have proposed a sequential developmental terminology which has received considerable support. They refer to a Juvenile stage during which no inductive response may occur, and an Inductive phase, during which the plant is responsive to cold, short day or darkness exposure which may bring that plant to a state of competence or "ripeness to flower". The sequence of Cooper and Calder fails to consider the post flowering stage which, although not under inductive control by day length (Forster and Vasey 1930 and 1935) is influenced by temperature and perhaps by cultivar (Marcellos and Single 1971).

The differentiation of floral primordia by the growing apex is the first visible sign that a plant has passed from a purely vegetative to a reproductive condition (Whyte 1960). The developmental morphology of the cereal inflorescence has been reported on by Purvis (1934) and illustrated by Bonnett (1935, 1936, 1937) and Barnard (1955, 1964, 1966, 1971). Its histogenesis and ontogeny has been described by Sharman (1945) who worked with Agropyron repens but compared this with a wide range of cereals and grasses. The overall development of the inflorescence in the Gramineae has been reviewed by Williams (1966).

The ready recognition of phase end-points has caused considerable difficulty depending upon the phasic terminology that has been chosen. The end-points of Cooper and Calder's Juvenile and Inductive phases

have, to date, defied definition on a morphological or correlation index. Wellensiek (1962) defines the Juvenile stage as the period of vegetative growth when flowering formation is impossible due to lack of the necessary substrate.

Zeevaart (1963) considers it as the phase from germination to "ripeness to flower and the plant cannot respond to vernalization until it is ripe to flower". Cooper (1956) takes competence or ripeness to flower to "represent the state of the plant after vernalization". Cooper and Calder (1962) have found evidence of a Juvenile phase in certain temperate, perennial grasses. Some annuals may also have a significant Juvenile phase. Evans (1960) reported that the first leaves of Lolium temulentum do not respond to inductive long day. The rather subjective nature of the morphological point of initiation was responsible for the introduction by some research workers prior to this phase of a Transitional stage.

Bonnett (1961) states that each of these stages or phases of development can be distinguished from the others by its morphological characteristics and by the developmental events that occur in it. The change from the Vegetative to the Reproductive stage is marked by the appearance of double ridges on the elongating growing point or apex. The upper of these ridges produce the spikelet and its parts. During the Reproductive stage the spike and its parts differentiate and develop. When the spikelets differentiate the number is fixed but adjustment to environment may be made subsequently in the number of fertile flowers within a spikelet. During the Reproductive phase the

internodes of the stem elongate and carry up the developing spike until it finally emerges through the flag or youngest leaf and is exposed. Flowering, normally, occurs 10-14 days thereafter.

The Seed stage begins with flowering and ends with maturation of the seed. During the early stages of the Seed phase, the stem continues to elongate for a short time and although there is little other visible growth, a considerable proportion of the final dry weight of the plant is added during the period.

The end of the Vegetative phase or the beginning of the Reproductive phase is obviously the most difficult to identify, and various workers have looked for techniques to establish the end-point more definitely. These techniques can be broadly classified into two categories, scoring techniques and correlation techniques.

Bonnett (1936) utilised a series of nine photomicrographs of the consecutive stages of development of the apex of winter wheat. Barnard (1955) in his study of the histogenesis of the wheat ear used a series of fourteen photomicrographs, as did Nicholls and May (1963). Nicholls also used a technique of scoring, utilising apex length as a measure of initiation. Similar methods have been used by Gregory and Purvis (1936, 1938a, 1938b), Gott, Gregory and Purvis (1955), Gott (1957, 1961), Pinthus (1959), Single (1961), Ahrens and Loomis (1963), as well as others. Scoring techniques necessitate mass dissection which is satisfactory when populations are large and treatments are few. They are however subjective, tedious and time consuming.

To overcome such disadvantages a number of workers have looked at correlation methods to establish phase end-points. The most common methods have involved either leaf number appearance (Andersen 1952), or time scales of apex length after germination (Nicholls and May 1963), or the plastochron index system (Erickson and Michelini 1957). To date however, all correlation techniques have suffered serious limitation when applied to cereals. Other than Nicholls and May (1963) few people appear to have attempted to combine time series of apex length with scoring techniques.

A major part of the current knowledge of plant development is the result of the study of either low temperature (vernalization) or photo-period response. Following the early lead given by Gassner (1918), reviews of the theoretical basis of the method of vernalization, and the hypothesis of phasic development, were published by White and Hudson (1933), Maximov (1934), Whyte (1939) and McKinney (1940). The work of Purvis (1934, 1948, 1960), McMillan (1934), Forster and Vasey (1935), Macindoe (1937), Purvis and Gregory (1937, 1952), Gott (1957, 1961), Aitken (1961, 1962), Friend (1962, 1965a, 1965b), and Pugsley (1963) has done much to elucidate the mechanics of vernalization, its significance and relationship to plant development, and its role in the maturity of Australian wheat cultivars. The concept of vernalization has been reviewed by Thompson (1946), Murneek and Whyte (1947), Gregory (1948), Lang (1952) and Chouard (1960).

Chouard (1960) in his review draws attention to the original meaning as opposed to derived meanings of the term and defines the

process of vernalization as "the substitution of chilling for natural exposure to winter to make possible later initiation of flowering primordia". He further points out that vernalization is only effective when applied over a period of time in the presence of oxygen in moist enough tissue containing enough carbohydrates to support adequate respiration. Concomitant growth may be either moderate or slow; if it stops completely vernalization does not occur. It is sensed at a certain age which may be very early (the embryo) or much later (the leafed plant). It consists in the attainment of a new functional ability (the flowering ability) that is later revealed by flowering under special conditions (long or short day, various temperatures, etc.), which are characteristic for each species or variety.

The phenomenon of de-vernalization which is pertinent to Australian conditions has been reported on by Efeikin (1939), Purvis and Gregory (1945), Stout (1946) and Derera (pers. comm.). The role of light as a flowering induction quantity has been reported on by Garner and Allard (1929), McKinney and Sando (1933, 1935), Guitard (1960), Friend (1965a), Langer and Khatri (1965) and Garg and Chinoy (1964).

Once the vernalization requirement has been saturated by low temperature a further temperature reaction is imposed on development. This is, in effect, an acceleration through developmental phases by increased temperature. There is available data to support such response through the Vegetative, Reproductive and Seed phases (Marcellos 1970). Guitard (1960) found that increasing temperature from 12°C to 24°C

accelerated the rate of internode elongation of the barley cultivar Olli, but delayed the same stage in the cultivar Vantage. Friend, Helson and Fisher (1962) found that in Marquis wheat an increase in temperature from 10°C to 30°C caused earlier floral initiation and higher rates of leaf initiation. The Reproductive phase was also shortened by increased temperature due to the increased rate of apex growth. Riddell and Gries (1958) have shown that increasing temperature from 15°C to 27°C delayed ear initiation in the wheat cultivar White Federation; however, post-initiation development was accelerated by increasing temperature so that developmental response to temperature may well be largely a varietal characteristic. Marcellos (1970) reported that for Australian spring wheats raising the mean daily temperature of the post-flowering period from 17.5 to 22.5°C may reduce the number of days available for photosynthesis by about 30%. The significance of the effect of high temperature on development in the Seed phase is considerable in the environment of the northern wheat-belt of Australia where super optimal temperatures for grasses of temperate origin are common during the period of grain development.

Effects due to different combinations of day and night temperature on development have been reported (Murneek 1948). In reviewing literature of this effect on grasses Evans (1966) concluded that in many long day grasses night temperature above 12°C to 18°C inhibited flowering. The evidence suggests that the inhibitory effect of high temperature is largely confined to the dark periods. Short day grasses on the other hand may not flower in short days unless night temperature exceed 12°C to 16°C. As the size of the plant at flowering

has considerable bearing on the potential yield of the plant, the effect of temperature on development is of prime importance, and provides the explanation as to why very high agricultural yields are associated generally with cool climates, i.e., climates in which temperatures are sub-optimal to development.

Surprisingly little is known of the effects of nutrients on development, and Murneek (1948) in reviewing the role of nutrients as related to development, stated "in general the information secured to this time is conflicting". Blondon (1964) in reviewing the influence of mineral nutrients concluded that concentration of mineral nutrients in the nutrient solution influence flowering but its exact role is unknown. It seemed that mineral nutrition has an influence mainly on plants indifferent to photo-period while its effect is secondary in photo-sensitive plants. In general, long day plants flower earlier when nutrients are deficient for nitrogen while flowering in short day plants is favoured by high nitrogen levels. Purvis (1934) found that nitrogen deficiency had no effect on the flowering of Petkus rye under any day length. Cooper (1956) and Aitken (1961) each indicated that mineral nutrition had no effect on time of floral initiation. Single (1964) was able to demonstrate increases in both spikelet and leaf number resulting from increased nitrogen levels over the range 0 - 8 p.p.m.N. during the Vegetative phase, but time of floral initiation was little affected. Halse et al. (1969) however reported that high extreme deficiency delayed both initiation and ear emergence. Smith and Jewiss (1966) in a study of Timothy (Phleum pratense) considered there was

a temperature relation with nitrogen response. At high temperatures and high nitrogen levels anthesis was accelerated but at lower temperatures, nitrogen level had no effect.

The effect of moisture stress on development is most pronounced in the duration of the Seed phase, which can be substantially curtailed by water shortage. Aspinall (1965) found that under conditions of prolonged moisture stress the Seed phase was reduced from 35 to 25 days. Fischer and Kohn (1966) also recorded reduction of the Seed phase by moisture stress. Further, Nicholls and May (1963) reported that in barley moisture stress delayed initiation. The transition from one developmental stage to another occurs most readily when growth rate is slow and dry matter accumulation is high, conditions most commonly caused by moisture stress.

The effects of increased levels of plant competition on accelerating time of flowering are widely known by plant breeders but could not be documented from the literature.

## THE GROWTH OF THE VEGETATIVE STRUCTURE

### 2. 3. 0.

#### THE GROWTH OF LEAVES

### 2. 3. 1.

The growth of leaves, in cereals, has been reviewed in detail by Milthorpe (1956), Jewiss (1966) and Wardlaw (1971). It is from these sources that much of the following has been derived.

Bunting and Drennan (1966) described the "phytometer" or unit of structure of a cereal in the Vegetative phase, as consisting of "a node, a lateral bud, an internode and the leaf which is attached under the circumference of the next higher node". In the embryo there exist 2-5 leaf initials, depending on species. After germination the initiation of further leaves begins immediately and the growth of the plant takes place by "the initiation, in a regular sequence, of lateral structures on the apex of the shoot and their expansion into organs on whose characteristics the taxonomic characters are based", (Bunting and Drennan 1966). The final number of leaves which will be grown on the primary tiller is basically a varietal character but will vary with relative rates of vegetative and reproductive growth (Holdsworth 1956). Implicit in this statement is the effect of temperature and vernalization on leaf numbers.

In wheat (under optimum temperatures) the plastochron is 2 to 3 days so that the flag leaf may be initiated no more than 15 to 20 days after germination (Bunting and Drennan 1966). The time interval between initiation and emergence of each successive leaf

increases to a maximum with the flag leaf (Puckridge 1963). Similarly, the time taken for each successive leaf to reach its maximum size is decreased, progressively, from leaf to leaf. However, Williams (1960) found that the period during which maximum relative growth rate of the leaf was maintained (i.e., just prior to emergence) was extended by each successive leaf up to the fourth leaf. Puckridge (1963) reported that, at low nitrogen levels, the fourth leaf was the largest, whereas at higher nitrogen levels, the fifth leaf was largest. Thus the sequence of leaf size is determined, to a large extent, by the nitrogen supply available to the plant. Borrill (1959) found the largest leaf to be that which was elongating at the time of initiation of the apex. Thereafter, successive leaves are shorter and wider (Bakhuyzen 1937). Bunting and Drennan (1966) suggest that in the distribution of nitrogen within the plant, the needs of the ear and stem are met preferentially to those of the rest of the plant, so that if nitrogen is in short supply, the growth of later leaves is relatively restricted.

Other factors of the environment may also exert sizeable effect on leaf size. In a study with Marquis wheat, Friend, Helson and Fisher (1962) found that at 20°C leaf area was largest, whereas at 25°C leaves grew longest and at 15°C broadest. The effect of increased light values in the same study was to increase the breadth of the leaves. They concluded that cell number was the main determinant of leaf size and further that this was directly influenced by available nitrogen.

Fernando (1949) reported that high levels of phosphorus increased leaf area only up to 6 weeks after germination, whereas high

levels of nitrogen had the effect of increasing leaf area throughout the life of the plant. In the same study, high levels of potassium were found to delay the onset, and rate of, senescence of the leaves.

Each leaf matures from the tip downwards and the exposed part of the leaf is finished elongating prior to its emergence from the enclosing sheath of the next lower leaf (Wardlaw 1971). "The newly exposed tissue is photosynthetically active but while growth of the leaf continues most of the assimilates formed in the tip are utilised in the growing regions. As the photosynthetic area increases and extension growth of the leaf slows down, the export of assimilates to other parts of the plant increases. With the emergence of the sheath tissue this also becomes photosynthetically active" (Thorne 1959). Once the leaf is fully expanded it is no longer capable of importing assimilates. Doodson et al. (1963) showed that  $^{14}\text{C}$  fed to the 3rd leaf is exported to the 4th, 5th and 6th leaves and emphasises the importance of the Vegetative phase in establishing a vegetative structure capable of subsequently supporting a higher potential grain yield. Both the rate of photosynthesis and the export of assimilates are maximal immediately after leaf expansion is complete and both, subsequently, decline slowly at first as the leaf ages and then more rapidly as the leaf shows obvious signs of senescence. The rate of decline of activity is very dependent upon factors such as nutrition and water supply. Assimilates from the young fully expanded leaf are utilised largely by the shoot apex and growing leaves. As leaves higher up the shoot complete their growth, in turn, photosynthate is directed with time more and more to the root system (Doodson, Manners and Myers 1964, and Rawson and

Hofstra 1969).

When production of carbohydrates due to photosynthesis is greater than the translocation out of the leaf, storage of the excess occurs in the lamina and in the sheath (Archbold and Mukerjee 1942). Leaves also play a role in the uptake and distribution of mineral nutrients (Greenway and Pitman 1965), and many of the nutrients accumulated during the growth of leaves, particularly nitrogen and phosphorus, may be mobilised and redistributed to other parts of the plant during senescence (Williams 1955).

## THE GROWTH OF TILLERS

### 2. 3. 2.

In the embryo prior to germination there exists a lateral bud in the axis of the coleoptile (Percival 1921 and Bonnett 1936). Following germination, lateral bud primordia are initiated on the shoot apex 2-3 plastochrons after the primordia of the subtending leaves (Wardlaw 1971). Each bud is associated with the leaf above although situated in the axis of the leaf below (Sharman 1945). The initiation of tiller buds has been described in detail by Sharman (1942) - and the effects of environment on the actual initiation have been considered insignificant by Soper and Mitchell (1956). The subsequent development of tillers after initiation is, however, highly dependent on external conditions which determine whether the tiller will or will not survive after its initiation and early growth (Jewiss 1966).

Once a tiller has become "reproductive" (i.e., achieved competence) it commonly survives to the point of emergence. However when a reproductive tiller does die, its decline has generally started before the apex elongated and initiated floral primordia, but the morphological development of the apex continues for a time even though the fate of the tiller has already been determined (Krishnamurthy 1963).

Details of tiller growth between initiation and emergence of the tiller from the leaf sheath are scant (Jewiss 1966 and Evans, Wardlaw and Williams 1966). In view of the overall importance of tiller survival as a final grain yield factor, particularly under Australian conditions, this "paucity of information" is surprising.

When the primary shoot has reached a stage of development of 3-5 leaves, the first tiller emerges. Axillary buds on this tiller in turn produce further tillers and so the process is repeated. The proximity to the primary tiller, and earliness in the life cycle of the plant, will to a large extent determine the chance of the tiller's survival (Krishnamurthy 1963) and subsequently the size of heads formed as well as the weight of grain in the heads. The degree of tillering which takes place is a varietal characteristic, but within a cultivar this is strongly influenced by external conditions through their control on development, and by nutrition and moisture availability (Friend 1964).

While the tiller is enclosed in the sheath of its subtending leaf it is entirely dependent on the shoot for its supplies of carbohydrate and nutrient (Wardlaw 1971). Its dependence for photosynthates will continue until such time as the supply of assimilates has enabled development of the new tiller to achieve photosynthetic autonomy. The duration of dependence will be determined by the position in time in relation to the primary tillers, the photosynthetic capacity of the older tillers, and if initiation of the main shoot has occurred, the relative competitive stress for nutrients occurring in the plant.

Quinlan and Sagar (1962) have shown that in young plants  $^{14}\text{C}$  can move from the parent shoot to the tillers; as the shoots become older movement of  $^{14}\text{C}$  from shoot to shoot is restricted. When surplus tillers are removed, the grain yield of the remainder is increased, signifying that a competitive relation exists within the plant, and that materials can move from living tillers into the main shoot (Palfi and

Dezsi 1960). The death of tillers like leaves is associated with transfer from them of minerals and certain nitrogen and carbon compounds (Rawson and Donald 1969). Thorne (1962b) noted that when tillers died there was no check in the growth of the whole plant and concluded there was transfer of dry matter, or that remaining shoots grew faster because of less intra plant competition.

The dependence of the tiller for nutrients and water continues after emergence until such time as it has developed an independent root system. The time taken for this to occur will depend to a large degree on the position of the new tiller in relation to the primary shoot, the magnitude of the photosynthate translocation to the existing roots, and the availability of moisture to the plant. There is some evidence (Langer 1956) to suggest that main tillers must be self-supporting before they themselves can produce secondary tillers. Although tillers may eventually become independent, they are "still capable of acting as an integrated unit" with the plant, and both nutrients and carbohydrate may be induced to move between adjacent shoots (Wardlaw 1968). The tillers remain in vascular connection with one another, and if "a single root of one tiller is allowed to take up labelled sulphur, distribution of this nutrient to the rest of the plant is demonstrable" (Jewiss 1966). However in the case of sulphur distinction needs be made between movement of labelled sulphur within the plant and net transfer of nutrients. Similarly competence to flower in cereals once achieved by the primary shoot is transferred successfully to the following tillers. This is not necessarily the case, however, in all grasses (Bunting and Drennan 1966).

In the Vegetative phase, Bunting and Drennan (1966) point out that the axis of a plant is potentially able to initiate new tillers indefinitely. Once competence is achieved, however, this capacity becomes limited. This phenomenon, referred to as domination by the apex or apical dominance, is poorly understood by physiologists.

Factors other than the distribution of, and competition for, nutrients appear to affect the duration of the tillering process at or near its maximal rate. Langer (1966) considers that neither rapid stem elongation nor the effect of shading of the lower parts of the plant are entirely satisfactory explanations for the onset of decline in tiller production, which invariably follows stem elongation. Friend (1965) states that "a suppression of tillering by substances produced in the maturing ear of wheat would appear a likely explanation as Aspinall has shown with barley". Application of auxins does in fact increase apical dominance in wheat and barley (Leopold 1949, Salisbury and Ross 1969).

Langer (1966) further states that "until the problem of apical dominance has been solved, it is unlikely that a complete explanation for the decline in the rate of tiller appearance will be forthcoming." The degree of apical dominance is also a varietal characteristic. Friend (1965) suggests the use of the ratio of total number of leaves to total number of shoots as a measure of the degree of apical dominance.

A feature of apical dominance is its transient effect over the life cycle of the plant and its delicacy of control. In relation to the

former there appears in spring type cultivars a sudden onset of apical dominance after initiation of the reproductive apex and the associated beginning of stem growth. By the stage of inflorescence emergence repression of tillering has faded. In winter type cultivars there is a different pattern of control, suppression commencing before the "double ridge" stage of development of the apex and the effective inhibition fading shortly after the achievement of apex competence (Jewiss 1972).

The causes of sudden cessation and subsequent recommencement of tillering are unknown, but it is appreciated that the control is a delicate one and redirection of control can be associated with nutritional, environmental and artificially imposed hormone type chemicals of the auxin antagonist type. Most research however, has been associated with the effects of the environment on the tillering process.

#### The Effects of Light and Temperature on Tillering.

Both the pattern and rate of tiller production are responsive to the environment. Friend (1965) found that increases in light intensity over the range  $0.65-8.2 \text{ cal cm}^{-2}\text{h}^{-1}$  increased the rate of production of tillers relative to that of leaves, so that apical dominance was reduced. Increased photoperiod had similar results. Conversley, however, an increase in temperature from  $10^{\circ}$  to  $25^{\circ}\text{C}$  increased the rate of leaf production to a greater extent than that of tillering so that apical dominance was greatest at high temperature. Friend (1965) concludes that increased tillering at low temperatures

and high light intensities is brought about by the increased supply of photosynthates.

Through the effects of light and competition for nutrients, plant density has been observed by many research workers to have an effect on both the number of tillers initiated and their survival. Puckridge (1962<sup>3</sup>, 1968) recorded in detail the effects of density on tiller production at constant nitrogen levels and found that at high densities initial tiller production was lower and decline of tillers occurred at an earlier stage.

#### The Effects of Mineral Nutrition on Tillering.

The effects of nutrients on the quantity, rate and duration of tillering have been appreciated generally and for a long period. Gregory (1937) considered nitrogen and phosphorus to be the most important nutrients associated with tiller production, an opinion subsequently substantiated by Watson (1947) and Langer (1959).

Working with barley, to which nutrients were applied at different stages of growth, Aspinall (1961) found that when all nutrients were applied with the seed classical apical dominance was maintained. Split application of nutrients reduced apical dominance and regular doses gave continuous tillering. In this case the appearance of tillers was to a major degree controlled by supply of nutrients. Similar results have been observed with Gabo wheat (Evans per. comm.) and reported by Sekiya (1958) for rice. Such findings, together with those of Watson et al. (1958, 1963), De Silva (1961) and

Thorne (1962a) appear in contradiction to the suggestion by Gregory (1937) that uptake of nitrogen ceases in cereals when the plant enters the Reproductive stage.

#### Tiller Survival or Tiller Wastage.

Many research workers (De Silva 1961, Thorne 1962a, Krishnamurthy 1963 and Davidson 1965) have drawn attention to the wide difference between tiller appearance and tiller survival at maturity and refer to this difference as tiller wastage. De Silva (1961) found that modern European wheat cultivars were characterised by a lower degree of tiller wastage than older cultivars and considered the higher yield of the former to this character. The magnitude of tiller death was demonstrated by Davidson (1965) who reported that 1.8 tillers/plant resulted from an early total of 18 tillers, 5 of which survived as visible tillers at ear emergence. European workers have reported wastage of smaller magnitude, e.g., Thorne (1962b) reported survival of 5 tillers from an initial total of 7 tillers and Krishnamurthy (1963) reported 2.2 ears from an initial 4.3 tillers. Rawson (1971) concluded that highly tillering cultivars had low tiller survival rates and that high temperatures accentuated this wastage. The loss of tillers is affected to some extent by availability of nitrogen to the plant (Thorne 1962a) and differences between cultivars in tiller survival may be associated with varietal differences in nitrogen utilization.

Although sterile tillers may act as temporary reservoirs for nitrogen which is subsequently remobilised (Rawson and Donald 1969),

both water and assimilate used in their production is largely lost to overall grain production. The significance of such wastage in final grain yield cannot be accurately estimated.

## THE GROWTH OF ROOTS

### 2. 3. 3.

The role of plant roots is one of mechanical anchorage and physiological uptake of nutrients and water. Despite their importance to the plant, roots "have received comparatively little attention by physiologists" - (Brouwer 1966). During the past decade however, reviews by Troughton (1962), Brouwer (1966) and Whittington (1969) from which much of the following information has been derived, have provided a greater appreciation of the role, distribution and function of roots.

#### Growth and Function of Roots.

In common with the rest of the Gramineae, temperate cereals possess two root systems; the seminal, which develops from primordia within the seed and the nodal or crown, which develops adventitiously from the lower nodes of the stem (Troughton 1962). The number of potentially viable root primordia in the embryo varies with species (May 1964) and possibly with cultivar (Morozov 1950). In wheat there are 5 to 6 such primordia but the number which may be actually produced is highly variable and depends to a large degree upon environment (Taylor and McCall 1936). However, the variance in number of seminal roots produced by grains of the same cultivar is less than that encountered when grains of different cultivars are compared (Pope 1945).

On germination of the seed, the coleorhiza, enclosing the primordia and two lowest pairs of seminal roots, first emerges from the grain (Percival 1921). Following germination, May (1964) considers that

the seminal roots have two distinct phases of development. During the initial phase, root growth is rapid (1 to 2 cm. per root per day) and cessation of this phase coincides with the depletion of grain reserves. In the second phase, root growth is slower (0.5 to 1 cm. per root per day) but is "constant until 35 days at least after germination". Relationships between the number of seminal roots developed and grain yield have been suggested by Sallans (1942) and with drought resistance by Pavlychenko and Harrington (1935). Both Pervival (1921) and Todaro (1931) found that the extent of the seminal roots was determined largely by depth and texture of material in which the grains are grown. Of the seminal roots the primary root penetrates deepest (Troughton 1962); while the deeper roots generally follow a downward course, it is usual for the more shallow roots to grow obliquely outwards before later turning downwards. Differences in the direction of growth of seminal roots of hardy and non-hardy cultivars of winter wheat have been reported by Worzella (1932).

The growth of roots is restricted to a zone several millimetres behind the root tip (Eliasson 1955). Initially, the seminal roots make up the bulk of the total root system. Although it is generally considered that the nodal roots, arising endogeneously from the nodes of the stem, first appear within 20 to 24 days of germination, their subsequent elongation is highly variable and, under the environment of the Australian wheat-belt, occurs only under luxury, even if short duration, moisture conditions. Similar findings have been reported by Kravtson (1928). In most wheat growing areas of the world rapid

development of the nodal roots begins "automatically" in the early jointing phases (Pinthus and Eshel 1962).

Functionally, there appears to be little difference between seminal and nodal roots, both of which remain active over the major part of the life of the plant. Krassovsky (1962), considered that seminal roots supplied principally the main stem whilst nodal roots supplied the tillers. Root amputation studies of Simmonds and Sallans (1933) and Sallans (1942) on spring wheat in Canada indicate, that up to the jointing stage seminal roots make a greater contribution to the plant. Thereafter follows a period when both systems make equal contribution. Towards anthesis nodal roots achieve greatest functional importance. The proportion of the seminal root system in the total root weight is very small and frequently amounts to no more than 1% (Williams 1962). The relative area, however, "covered by 1 gram of the minute branches of seminal root systems" is very large compared to a similar amount of the nodal system (Brouwer 1966).

The growth rate of the overall root system is most rapid during the Vegetative phase (Troughton 1962) and the absorptive capacity of the root system is largely determined by the morphological extension which occurs during this phase (Schuurman and Geodewaagen 1965). Nielsen and Humphries (1966) point out however, that the gross size of the root system measured by dry weight, area or length is not an estimate of its absorbing capacity, because a large and changing proportion of the system ceases to absorb. Went (1945) concluded that 10% of the root system supports more than 50% of the growth rate of the overall plant. The

development rate slows down around the period of transition from Vegetative to Reproductive growth (Brouwer 1966), but a maximum root weight is attained either shortly before (Jonker 1959), during (Stucker and Frey 1960), or after anthesis. Thereafter the rate of decay of older roots progressively outstrips the rate of formation of new roots, and a decrease in the overall weight of the root system may occur during the later Seed phase (Aspinall 1961, 1963, and Brouwer 1966). As both root growth and decay are subject to influence by soil condition considerable variation in the point at which maximum root development takes place must occur. The vertical distribution of roots expressed as a percentage of total weight is indicated by the following Table 2 from <sup>HENDRIX</sup> Martin and Lloyd (1968).

TABLE 2

THE VERTICAL DISTRIBUTION OF ROOTS EXPRESSED AS A PERCENTAGE OF TOTAL WEIGHTS				
<u>Depth</u>		<u>Winter Wheats</u>		<u>Spring Wheats</u>
cms	%	Accumulated %	%	Accumulated %
0- 20	26.73		19.67	
20- 40	18.53		15.55	
40- 60	14.56		14.90	
60- 80	11.65		13.07	
80-100	9.07	80.54	10.37	73.56
100-120	6.95		8.40	
120-140	5.36		6.83	
140-160	3.61		5.19	
160-180	2.03		3.36	
180-200	0.92	99.41	1.88	99.22
200-220	0.39		0.66	
220-240	0.16		0.12	100.00
240-260	0.04	100.00	Trace	

Although this work was conducted in root mist chambers, it appears to be in general agreement with earlier findings of West (1934), and Stucker and Frey (1960) in soil, and signifies that the major bulk of the root system is to be found at relatively shallow depth.

Hackett (1969) demonstrated that cereal root systems develop in such a manner that relations between total number, length, surface area and volume of their members remain roughly constant during the Vegetative period. Subsequent work (Hackett 1971) has further indicated that although physical mutilation of the roots was responsible for the development of markedly different distribution patterns to intact systems relations between root dimensions was almost identical in the two groups, implying that extension and branching of roots is highly co-ordinated.

#### Genetic Influence on Root Systems.

Genetic differences in the size and also the distribution of root systems in temperate cereals are known to occur (Wardlaw 1971). Dittmer (1938) noted that winter rye had 50% more roots than oats grown under similar conditions. Troughton (1962) indicates that winter sown cereals generally produce a larger weight of roots than spring sown ones. This however, may well be environmental rather than a genetic difference. Derera (pers. comm.) has established varietal differences in a number of Australian wheat cultivars. Root systems of oat cultivars in relation to lodging have been studied by Hamilton (1951) who concludes, that the type of root system is a varietal

characteristic; and that cultivars which are resistant to lodging have a larger number of coarse thick strong roots which extend horizontally into the soil. Caffrey and Carrol (1938) found that non-resistant cultivars had smaller more fragile roots or had roots penetrating almost vertically downwards.

Koedzikov (1959) found that vernalization increased the rate of development of the root systems as well as altering its composition. The vernalized plants produced fewer nodal and more seminal and coleoptile nodal roots.

#### Environmental Influences on Root Systems.

In addition to genetic differences, environmental differences appear to have major effects on root distribution. Because the root depends on the shoot for carbohydrates and the shoot depends on the root for water and mineral nutrients, the growth of both is generally closely integrated. The effect of many environmental characteristics on the root system is the indirect result of the effect of these parameters on the shoot portion of the plant. When the light intensity is limited, the ratio of top growth to root growth increases (Shirley 1929, Blackman and Templeman 1940). Reid (1929a) found that the ratio changed with the season and was smaller in long days than in short days. Mitchell (1953) showed that the proportion of shoot to root is affected quickly by changes in light intensity and the readjustment is completed within a week. Increase of photosynthesis by increasing atmospheric CO<sub>2</sub> concentration increases the growth of roots more than

of shoots (Reid 1929b). White (1937) concluded that increased net assimilation rate, from any cause, produced longer root systems. Many other authors report similar effects on root growth. This was summarised by Mitchell (1954) "as the supply of energy metabolite available is decreased the proportion of that metabolite used, by the active meristematic centres closest to the point of origin on the plant, increase. Hence the large increase in relative growth of leaves compared with roots. Thus, the root system is a sink for carbohydrates and its growth is regulated, to a large degree, by the activity of the assimilatory system. Other instances of the competition between development of root and shoot are given in a review by Leonard 1962". Single (1971) has reported reduction in root weight resulting from severe frosting of internodes.

The effects of mineral nutrition on root growth have been reviewed by Troughton (1962). Generally by raising the level of nutrition within a certain range increased growth of the whole plant results, the growth of the shoot, however, being increased to a greater extent than that of the roots (Troughton 1962). High levels of nitrogen result in retardation of root growth (Bosemark 1954, and Troughton 1957) or a reduction in the root weight (Goedewaagen 1955). It is pointed out by Troughton (1962) that lower root weights may be the result of increased rate of decomposition of root, as indicated by Mulder (1954) rather than a decrease in root growth, resulting from high levels of nitrogen.

High moisture levels have been shown by many research workers

to substantially increase both root mass and branching. Kmoch, Ramig, Fox and Koehler (1957) reported that when the sub-soil was dry, root depth of wheat was reduced and lateral spread and the degree of branching were greatly increased. They further found that the greater the depth of water in the soil the greater was the root mass and depth of penetration. Troughton (1962) refers to the work of Robertson, Kezer, Sjogren and Koonce (1934) which showed that roots of wheat could not penetrate into soil which had been depleted of moisture to wilting coefficient or below.

Maximov and Kruzilin (1936) found that frequent irrigation over a dry sub-soil resulted in an increased proportion of the roots in the surface layers of soil and a decreased depth of penetration. From the literature available, it would generally appear that the distribution of moisture in a profile largely overrides genetic differences and determines, to a considerable degree, the distribution of roots and their pattern. Genetic differences appear important, however, in relation to drought resistance, in that rate of, and depth of penetration by the seminal roots will to a large extent determine the ability of the plant to withstand subsequent moisture stress as it will determine the depth at which the "absorbing roots" will be located in a profile (Kokkonen 1931).

#### Investigation of Root Systems.

The relative paucity of data available on root systems can be attributed to the problems associated with their critical examination

and quantitative evaluation. In assessment of the significance of the root systems two factors are of major consequence. The first is, obviously, the extent of the root system, including its form and structure and secondly, the efficiency of the root system as an absorption mechanism. The technical problems in the evaluation of the former are formidable but insignificant in relation to an assessment of the latter and apart from root pruning experiments, and attempts at separation of components of root systems, in both cases techniques of dubious significance, research has to date been largely directed towards morphological parameters of the root system. In this field the following properties of roots have been considered important by Schuurman and Goedewaagen (1965). The total amount of roots, which gives an approximate indication of the absorptive capacity of the root system and is commonly expressed in terms of oven dried weight. Andrew (1966) has suggested a technique for the expression of the root system in terms of root volume. Others have attempted the quantification of the root system in terms of total surface area; the formation of branch roots and their diameter which are indicative of the absorptive capacity of the root system and both have been used as a criteria for comparative studies. Other properties are the vertical and lateral distribution in the profile and the maximum depth, width and rate of development.

The techniques used for the measurement of such parameters can be divided into the following categories :-

a. Investigation of monoliths

These include the pinboard and excavation methods (Schuurman

- and Geodewaagen 1965).
- b. Soil coring systems (Kelly, Hardman and Jennings 1947, Gist and Smith 1948, Bloodworth, Burleson and Cowley 1958, and Welbank 1969).
  - c. Profile walls (Weaver 1926).
  - d. Container experiments which include cylinders, cases, glass panel boxes, and water culture (Obermayer 1939, Dean 1929 and Derera et al. 196~~6~~<sup>7</sup>).
  - e. Root mist chambers (Hendrix and Lloyd 1968).
  - f. Root observation chambers (Troughton and Whittington 1969).
  - g. Soil injection of  $^{32}\text{P}$  and its translocation to the shoot (Lieshout 1957).

Each technique has serious limitations which explain the overall paucity of information available in the literature on the detailed form and function of the cereal root system.

THE EFFECT OF LEAF AREA AND ITS DURATION ON YIELD

OF GRAIN

2. 4. 0.

Physiological studies have attempted, with some success, to relate grain yield to leaf area after flowering (Thorne and Watson 1955, Watson, Thorne and French 1958, 1963, Denmead and Shaw 1969, and Welbank, French and Witts 1966). Watson (1956) describes leaf area as an index of the size of the photosynthetic system in a plant and net assimilation rate as an index of its efficiency. Thus, the production of total organic matter by a plant "is mainly a function of the size of the total green area (= LAI in its widest sense), of the efficiency of this area (= NAR) and of the time during which it is functioning (= LAD)" (Stoy 1965). Watson (1956) considers that it is unlikely that agricultural yield can be improved by increasing the photosynthetic efficiency of the species at present cultivated. For practical reasons there is little scope for increasing duration of leaf area because of limits on available moisture so that "the main opportunity for increasing yield lies in increase of leaf area" (Watson 1956). In support of this Watson states, that agricultural practices which increase yield do so wholly or mainly by influencing leaf growth and this is supported, at least in part, when moisture is non-limiting by the work of Fischer and Kohn (1966).

In any annual crop, sown from seed, there exists an initial early vegetative period when leaf area is low, and much of the solar energy is lost to the plant due to low interceptive surface area:

and the system is referred to as an "open one" (Alberda 1962). As leaf growth increases, the interceptive surface of the plant enlarges to the point when the total area beneath the plant is covered and the system becomes a "closed one". Leaf area reaches a maximum value at ear emergence (Friend et al. 1962), and then declines during the Seed phase (Welbank, French and Witts 1966 and Stoy 1965), so that the interceptive surface of the plant again decreases to the point of returning to an "open system" shortly prior to maturity. During the total growing period only 1 to 2% of the solar energy falling on the plant is converted to chemical energy (Wassink 1948). This very low efficiency is largely the result of loss by the plant in the open system early, and later in its life cycle. Higher net efficiencies are commonly recorded during the period of the closed system, e.g., 4 to 9% (Gaastra 1962).

The magnitude of LAI reported for wheat in the literature appears highly variable and is influenced by cultivar, nutrition and environment. Watson, Thorne and French (1963) in a comparison of European cultivars, reported a range of maximum LAI from 5 to 8 which was maintained at a ceiling for a relatively long period (4 weeks). Davidson (1965), working with the Australian cultivar Olympic, reported that LAI rose to a value of 12 in the spring prior to head emergence and almost immediately started to fall to a LAI value of 6 by the time of emergence of the head. At this stage, the decline had not slowed and within a period of 3 weeks after emergence was down to an LAI of 3.

Watson, Thorne and French (1963) pointed out that in the European cultivars which they studied, the duration of maximum leaf

area was "largely the same before and after ear emergence." Davidson (1965) however, reported that immediately after ear emergence leaf area had fallen to 20% of the maximal value. However, in this period of declining LAI, NAR was greatest, which he attributed to the increasing photo period and to photo-synthesis occurring in the ear. A reduction of LAI before the emergence of the head, achieved by clipping of leaves, was found in this experiment to reduce the growth of the developing ear resulting in lower grain number per spike, lower grain weight and, subsequently, lower grain yield. The number of spikelets in the ear varies with plant spacing (Puckridge 1968) with nitrogen nutrition (Single 1964) with daylength (Wislocka 1959) with light intensity (Friend 1965a) and with the effect of temperature or photoperiod on the duration of the Vegetative phase and of the sub-phase from floral initiation to terminal spikelet appearance (Rawson 1970). Grain number however, may be regulated by the environment in the immediate pre and post anthesis stages (Rawson and Evans 1970). Davidson (1965) concluded that "leaf activity and distribution of assimilates, prior to ear emergence, largely determines the potential yield of a crop. Events after ear emergence determine the degree to which the potential is reduced."

This finding appears in conflict with the views expressed by Watson (1956) for the Northern hemisphere, that conditions influencing high yield of grain appear to be high leaf area duration after ear emergence. Obviously, LAD is not the sole determinant of grain yield, because the ears themselves, the peduncle and the leaf sheaths of a

plant make a sizeable contribution to grain yield. It is, however, a point of fundamental importance in regard to grain yield, and it is possible that a larger major difference exists in this character between European and Australian wheats, the latter having been selected under conditions of rising temperature and increasing moisture stress at the time of ear emergence. Wardlaw (1971) concludes that LAD, after anthesis, will affect grain growth in some cultivars but not others.

The relationship between vegetative growth (leaf area) and grain yield is obviously moisture dependant. Fischer and Kohn (1966) found that heavy fertilizer rates increased the vegetative structure of the plant and in so doing increased evapo-transpiration and moisture stress as measured by leaf turgidity. They concluded that "as the amount of growth at flowering increased, the amount of water available to the crop after flowering decreased. Thus, under dryland conditions, there is an optimal level of vegetative growth dependant upon water supply for maximal grain yield". The relationship between grain yield and leaf area duration after flowering has been studied in pot trials by Asana, Saini and Ray (1958), whose findings appear to support those of Fischer and Kohn reported above.

There is growing evidence (Wardlaw 1971), that the temperate cereals, under some conditions, at least have a photosynthate production when at maximal leaf area in excess of their ability for translocation, and that when this situation is arrived at, the rate of photosynthesis temporarily decreases. Asana (1965) has suggested that more use might be made of carbohydrate stored in vegetative tissues for grain

production. The possibility for the use of larger diameter stems resulting from chemical mutagenesis in future cultivars, to provide increased storage of carbohydrates for this purpose, is an intriguing one.

## SOURCES OF CARBOHYDRATES FOR GRAIN DEVELOPMENT

2. 5. 0.

There appears in the literature general agreement that in some cereals and these include wheat, barley, rye and corn, most of the carbohydrate in the developing grain is the result of carbon dioxide assimilated after ear emergence. However, the role of carbohydrate stored in the stem at anthesis, although making but minor contribution to the grain under normal circumstances (Wardlaw 1971) may, under adverse conditions, make a significant contribution to grain weight (Asana and Basu 1963).

There is also considerable evidence that the flag leaf, top internode and head or spike tissue generally provide the main source of assimilates for the developing grain (Vervelde 1953, Stoy 1965 and Evans and Rawson 1970). Leaves, sheaths and stems below the flag leaf contribute little towards grain filling (Thorne 1966). The relative contribution towards the grain of various organs above and including the flag leaf has been the subject of wide investigation with variable results (Puckridge 1969). The contribution made by ear photosynthesis to grain yield was found by Kriedemann (1966) to vary from 10-44%. Thorne (1963) reported that ear photosynthesis differs between species and also between cultivars.

Wheat cultivars with the highest photosynthetic rate in the head are often awned (Asana and Mani 1950, 1955), and the relative contribution to grain filling made by awns has been a matter of contention among research workers for forty years. The somewhat

contradictory reports in the early literature on the effects of awns on the productivity of spring wheats in Northern America were reviewed by Aamodt and Torrie (1934). Publication of this review appears to have influenced Rosenquist (1936) to adopt a novel technique of comparison of treated and untreated florets of the same spike to elucidate the contribution of awns. He concluded from this technique that kernels from awned florets were heavier than from florets on which the awn had been clipped. Miller, Gauch and Gries (1944) reported that removal of the awn reduced both bushel weight and 1000 grain weight in the majority of winter wheat cultivars studied in Kansas, but that there were disturbing anomalies in the results which they could not explain. More recently the results of studies using "near isogenic" lines have been reported by Suneson, Bayles and Fifield (1948), Atkins and Norris (1955) and Patterson, Compton and Caldwell (1962). In the majority of cases studied, awned lines appeared to have slight advantages, particularly under conditions of moisture stress (a finding supported by the results of Grundbacher 1963), although sufficient anomalies again occur to militate against any generalisation being made. Patterson et al. (1962), however, found "the greatest advantage of awns for yield and test weight was in the year most favourable for wheat production in contrast to the advantage proposed under conditions of drought". Leonard and Martin (1963) after reviewing American literature on the contribution of awns to grain development concluded that "the presence of awns on the florets of wheat has tended towards heavier kernels. High temperatures or limited rainfall generally favour awned cultivars, although certain awnless cultivars also may yield well under such

conditions".

Vervelde (1953) reviewed the principal European literature on the "agricultural value of awns in cereals" for the period 1892-1953 and summarised his results as follows. "Many investigators mention the positive influence of awns on the yield of cereal varieties. Only a few negative results are recorded. The better adaptation of bearded wheats to dry and warm climates can be ascribed to the fact that the awns have xeromorphous characteristics, their most productive stage coinciding with the period of the most rapid seed development." No published data could be located by the author on the effects of awns either on grain weight or productivity in the Australian environment where for reasons of harvesting equipment and grower preference awnless or awnleted cultivars have traditionally predominated over awned cultivars. However, Derera (pers. comm.) after studying awned and awnless segregates in a breeding programme over a number of seasons considers that the contribution by awns to grain filling is strongly varietal and on the basis of their contribution recognises three categories, "positive", "negative" and "neutral".

Patterson et al. (1962) reported that "differences in parental source of awns appeared unimportant. However it appears that awns are more advantageous to certain genotypes than others".

It seems evident from reviewing the limited literature available on the role of awns that advantages of awned over awnless wheat cultivars are somewhat variable but are more common when expressed in terms of 1000 grain weight and bushel weight than when expressed in

terms of absolute yield. As the awns are equipped with stomates and chloroplasts and have proven ability to photosynthesise (McDonough and Gaugh 1959) it is reasonable to assume that under some conditions at least, awns may make a contribution towards grain filling. If however the total photosynthetic area of the head tissue is in excess of the plant's requirement, under conditions of moisture stress awns then become superfluous to the process of grain maturation.

As ear photosynthesis falls from a high level in the early stages of grain development to a lower level throughout the remainder of the period (Wardlaw 1971), and as the growth rate of the grain changes with time, there is to be expected a change in the relative supply of photosynthate from different organs to the grains throughout their development (Buttrose 1962).

Thorne (1966) points out that there is evidence from other plants that "the size of the sink affects the production and movement of carbohydrate" and that the demand for carbohydrate can affect how much moves to supply that demand. In consequence, the size of the sink may be an important factor in determining the pattern of assimilate distribution and ultimate grain yield.

Similarly, environmental conditions can play a major role in determining the pattern of photosynthate supply (Wardlaw 1971). Reduction in the total supply of assimilates by moisture stress or low light intensity results in an above average utilisation by the grain of assimilates produced in the lower parts of the plant (Wardlaw 1967). Temperature through its effect on rate of grain growth, also affects

the pattern of distribution of assimilates (Wardlaw 1971).

In contrast to the supply of photosynthate the lower leaves of cereals do appear to have a role in supplying the grain with nutrients (Wardlaw 1971). In the field, uptake of nutrients by cereals is usually low during the latter stages of growth and grain development is dependent on a supply of nutrients from senescing leaves and stems.

Techniques used in the study of relative contribution of various organs may be grouped into the following categories - Labelled carbon tracing, shading, excision and gas exchange. The merits and failings of techniques in each of these categories has been discussed by Thorne (1966), Stoy (1966) and Lupton (1968). Variability in results obtained has been demonstrated by Puckridge (1969).

THE DISTRIBUTION OF DRY MATTER WITHIN THE PLANT AND  
FACTORS OF THE ENVIRONMENT WHICH AFFECT DISTRIBUTION

2. 6. 0.

The possibility of altering the distribution of dry matter in favour of the harvested portion or economic yield has long fascinated plant breeders. Selection, both conscious and unconscious, for more economically favourable distribution has in effect been practiced by man since the dawn of agriculture. Ancient examples of selection of this nature are to be found in the dwarf maize cultivars of Mexico and Peru, or the dwarf wheats of Asia (Frankel pers. comm.). Van Dobben (1962) quotes a modern example in the alteration in  $\frac{\text{grain}}{\text{straw}}$  ratios of wheat cultivars in Holland over the past half century, which have increased from approximately 0.51 to 0.66, whereas total production of dry matter has increased only to a very slight degree. Similar results have been reported in Britain by Thorne (1962) in a comparison of new and old barley cultivars and by Watson, Thorne and French (1963) for new spring wheat cultivars. Sims (1968) reports a change in harvest index between current cultivars in Victoria and Federation (1901) from 0.34 to 0.28.

The advent of the Norin type semi-dwarf wheats (Vogel et al. 1956) has refocussed attention on the theoretical potential of such altered distribution. Manipulation of this nature for further improvement is limited however by the close inter-relationship of growth rate, or attunement (Brouwer 1962) between various organs within the plant.

Interdependence of organs as well as inter-relations are

indicated by the findings of Single (1964) where size of the floral apex at initiation is determined to a large extent by the size of the vegetative structure at that time. Consequently, major changes in distribution of dry matter towards the harvested portion of the plant prior to ear emergence may well result in lower rather than higher total yield and may explain the inferior grain yields of mutagenically produced "mini-dwarf" wheat cultivars (Konzac, pers. comm.).

Temperature has been shown by Van Dobben (1962) to have a marked influence on the distribution of dry matter within the plant. At very low temperatures (0-3°C) cereals show low  $\frac{\text{Stem}}{\text{Root}}$  ratios. In the range 10-16°C much higher values are reached with great specific differences becoming apparent. Between 16-25°C several species seem to show a maximum value or at least no further increase, (Van Dobben 1962).

Van Dobben draws attention to the fact that at temperatures in a medium range  $\frac{\text{Stem}}{\text{Root}}$  ratios and dry matter production are very strongly varietal and may be used to explain differences in growth between cultivars and between related species.

Both light intensity and spectral composition (Downs, Hendricks and Borthwick 1957) influence the distribution pattern of photosynthates in the plant. Under conditions of very low light intensity growth is concentrated in the stem tissue at the expense of leaf and root growth (Van Dobben 1962) and results in the significant increase in  $\frac{\text{Stem}}{\text{Root}}$  ratios. At high light intensities the carbohydrate supply is increased which relieves competition for supplies; the result is

increased root development with consequent reduction in  $\frac{\text{Stem}}{\text{Root}}$  ratios. The effects of light colour are most obvious when the basic illumination is weak (Van Dobben 1962, and Downs et al. 1957). At threshold levels of illumination light of "far red" was shown by Downs et al. (1957) to produce longer leaves and stems.

As a generalisation, increasing the available moisture supply within the range of low to high increases the growth of the shoot relative to the roots (Brouwer 1962). However, the role played by water is an extremely complex one. It provides one of the raw materials for photosynthesis; it provides a medium for transport of supplies within the plant; it helps regulate plant temperature; it has a direct influence on stomatal behaviour and, in consequence, an indirect effect on the capacity of the diffusion processes; and it controls suction tension of cells. In view of such complexity of function it is obviously difficult to fit to a generalisation. However, when moisture is scarce the roots, by virtue of proximity to supply, are better endowed than are the aerial portions of the plant. As the supply improves, the level of competition between shoots and roots is reduced, so that both organs have an adequate supply. At very high levels of soil moisture root development is reduced. This is often referred to as the effect of oxygen deficiency at the root system, but in many cases may be the result of a carbohydrate starvation to the roots due to the greater use by the shoots of carbohydrate under conditions of lavish water supply (Brouwer 1962).

The influence of mineral nutrition on  $\frac{\text{Stem}}{\text{Root}}$  was demonstrated by

Turner (1922) working with nitrogen responses in barley which gave significant increase on  $\frac{\text{Stem}}{\text{Root}}$  ratio from low to high nitrogen treatments. Brouwer (1962) considers that at low levels of nitrogen root growth relative to shoot growth is enhanced; firstly by proximity to the source of supply, and secondly by increased availability of carbohydrate resulting from decreased rate of shoot growth when nitrogen is limiting. As supply of nitrogen increases and competition between shoot and root decreases, shoot growth is stimulated relative to root growth. At high levels of supply of nitrogen root growth may become further retarded due to shortage of carbohydrate supply which is being utilised by the shoot portions.

Shortage of carbohydrate supply which may also be the direct result of deficiency of some minerals required for synthesis, is commonly a limiting factor to root growth (Brouwer and De Wit 1969). A sudden cessation of shoot growth, due to deficiency of a mineral, creates a sudden increase in dry matter and carbohydrates become available for root growth. After an interval the increased root growth renders more of the deficient mineral available to the shoot so that again aerial growth is stimulated, carbohydrate becomes limiting to the root, and growth of root tissue slows down. It appears probable that under field conditions this rhythm of growth between shoots and roots is a common feature of the overall growth process, and is now incorporated in "the elementary crop growth simulator, Elcros" (Brouwer and De Wit 1969).

The essentials for growth are water, carbon dioxide, oxygen,

minerals, light within a particular range and a suitable temperature level. Variation in supply of any of these essentials causes change in growth rate of various organs. For any set of internal or external conditions an equilibrium is established between competing organs. While conditions remain unchanged the equilibrium is remarkably constant and a high level of regulation is implied.

Under field conditions shortage of either water or minerals is most likely to restrict growth and subsequently yield. When these are in adequate supply, however, carbon dioxide concentration and light are most likely to limit the partial processes of photosynthesis. As the efficiency of light utilisation cannot be materially increased, the prolonging of the photosynthesising state of the plant would appear to offer best prospects for increasing yield. In practice, however, limitations in water availability make prolongment of developmental phases unattractive, especially in the Australian environment.

## FIELD RESPONSE BY WHEAT TO NITROGEN FERTILIZER

2. 7. 0.

The effects of nitrogenous fertilizers on wheat yield, the components of yield, and flour quality have been extensively studied over a long period of time in most countries where the crop is grown. In Germany available data in this field were reviewed by Roemer (1953), who reported an average increase of 15.5kg. of grain for each kilogram of nitrogen added in the range of 39-50kg. N/ha. In Britain, Bullen and Lessels<sup>L</sup> (1957) after reviewing many years of nitrogen research on cereals concluded there was a response of generally similar magnitude to that reported by Roemer. In the United States response data have been more variable. Smith et al. (1946), Long and Ewing (1949), Patterson (1952) and McNeil and Davis (1954) have reported yield increases resulting from nitrogen fertilizer in Washington, Tennessee, Utah and Montana respectively. In the more arid wheat growing areas of the United States however, there has not been general yield response to applied nitrogen and Laude et al. (1954) concluded that in these areas response was highly variable and that moisture was of significantly greater effect on crop yield than mineral nutrition.

Under Australian climatic conditions, which are not unlike those of the more arid wheat areas of the United States numerous experiments were conducted over the period 1900-1940 to measure the effect of nitrogen on crop yield. Positive responses were recorded in this period by Scott and Bristow (1929) on long farmed land, by Birke<sup>S</sup> and Cole (1939) on continuous fallow-wheat rotations and by Richardson and Gurney (1935) in excessively wet growing seasons. For the same

period there were also numerous reports of nil response or yield depression, and after reviewing the published data in this field Callaghan and Breakwell (1937) concluded "there was little scope for the use of nitrogen fertilizer under normal farming systems". In all the early Australian literature there is no suggestion of the possibility of varietal differences in response to nitrogen.

More recently Colwell (1963b) working in southern New South Wales reported results from a series of trials which indicated a failure to respond to nitrogen fertilizer in terms of grain yields on all but the most deficient soils. He postulated that when nitrogen and phosphate deficiency was alleviated, then moisture stress became the limiting factor to yield increase. Barley and Naidu (1964) in South Australia after reporting on a series of nitrogen fertilizer trials on wheat came to a similar conclusion and noted that although there was vegetative response particularly in tiller number this hastened depletion of available soil moisture and resulted in either significant yield depression or absolute failure of positive grain yield response. These authors did record a significant varietal difference in response which was associated with varietal differences in tiller survival, grain number and grain weight.

Storrier (1965) working in southern New South Wales reported yield depression resulting from high levels of soil nitrogen and associated this with increased tiller formation resulting in induced competition for available soil moisture. In the same geographical area, Kohn (1965) reported varietal differences in response to nitrogen

but only at "moderately high" (45 kg/ha) levels of nitrogen.

Russel (1967) reviewed the results of 59 response type experiments with the cultivar Gabo in a semi-arid environment in South Australia and stated that the two important facts to emerge were the low level of response to nitrogen and the marked seasonal and site effects of this response. He concluded that the data indicated nitrogen fertilizer could depress grain yield and depression appeared to be associated with rainfall distribution and hot dry spring conditions. Subsequent work by Russel (1968<sup>a</sup>, 1968<sup>b</sup>) indicated there was a positive yield response from nitrogen during seasons with heavy rainfall and a negative response to high temperature experienced in the latter part of the growing season.

In northern New South Wales Freebairn (1968) reviewing the results of nitrogen trials over a number of sites and seasons with a range of cultivars considered there was a cultivar x fertilizer interaction only evident on sites of low soil fertility.

In the past decade the association of short stature wheats and nitrogen fertilizer has been responsible for renewed interest in nitrogen as a wheat fertilizer. Tuohey (1967) compared the semi-dwarf Mexico 120 with the standard height cultivar Olympic at both high and low fertility sites in Victoria over a two year period. Yield depression resulting from nitrogen application on the high fertility sites was consistent for both cultivars. At the low fertility sites results were variable between sites, seasons and cultivars, ranging from depression to minor grain yield increases.

Heard (1967) compared response to nitrogen fertilizer by the same semi-dwarf and the standard height cultivar Heron. On sites of low to medium fertility there was moderate grain yield response to light applications of applied nitrogen. Heavy applications on these sites resulted in yield depression, as did light application of nitrogen on high fertility sites. There was no indication of differential response between the two cultivars.

Syme (1967) used the same cultivars as Heard together with additional cultivars under irrigated conditions in southern New South Wales. Yield responses within the range of 12.9-17.4 kg/ha were recorded and attributed to increased ear density, but the author was not able to demonstrate a cultivar x fertilizer interaction.

Storrier (1971) in assessing the contribution of fertilizers to the Australian wheat crop considered moisture was a more serious deficiency than nitrogen but suggested that the limited genetic background of local cultivars may prevent a more efficient exploitation of high fertility under more favourable conditions. Apart from the cultivar Mexico 120 used by Tuohey (1967), Heard (1967) and Syme (1967) there is no indication in Australian literature relative to nitrogen response, that under local environmental conditions imported germplasm is more responsive to high fertility levels than imported cultivars.

Rather in this literature the importance of moisture availability, or climate in relationship to nitrogen response is a recurring theme and appears to be the principal explanation for the different patterns recorded between European and Australian research with nitrogen fertilizers.