# Understanding Shoot and Root Development

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# UNDERSTANDING SHOOT AND ROOT DEVELOPMENT

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## Abstract

Shoot and root development of the grass tiller is presented as a series of events on the tiller axis. Leaf, tiller bud, true stem, and root development are successive events in the life cycle of a single phytomer and the tiller is a co-ordinated series of phytomers, successive phytomers being progressively more advanced than the previous phytomer. In reviewing the individual growth processes of leaf, tiller, true stem, and root formation, fundamental determinants of light and nutrient capture are examined and examples presented to illustrate the link between component processes, plant morphogenesis, and plant performance. An example of the application of this understanding in plant improvement is given.

## Introduction

It is necessary at the outset to define the scope of this paper. The allocated title 'Understanding shoot and root development' includes a very broad range of topics, and each topic is capable of discussion at a spectrum of different levels from the detailed plant physiological level to plant-plant and plant-environment interactions (ecophysiology), as well as for different species. Therein lies a need for selectivity. More than that, there have been some excellent recent reviews around this theme. These include discussions of plant form and function (Robson *et al.*, 1988), of morphogenetic aspects of plant growth (Chapman and Lemaire, 1993), of reciprocal interactions between leaf growth and tillering (Nelson, 2000), of C and N use in growth zones (Schnyder *et al.*, 2000; Thornton *et al.*, 2000) and of root form and function (Dawson *et al.*, 2000).

While we do briefly review existing knowledge about the four primary growth processes in a grass plant: leaf appearance, tiller appearance, true stem[1] formation, and root appearance, we seek to move the focus to understanding of the inter-relationships between these processes. This approach raises a number of questions. How is the tiller as a whole organised? Does knowledge of the organisation within the tiller contribute to understanding of the constraints on the individual processes? What is the present state of knowledge about each of these processes individually? Our paper also raises some more integrative questions. How do these processes interact with each other to determine the overall performance of a forage grass? What opportunities does this knowledge present for plant improvement? Also relevant, but not considered here, are the perspectives of plant-plant and plant-environment

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[1] The term *true stem* is used here to mean vascular tissue associated with leaf formation below the apical meristem (Matthew *et al.*, 1999). These authors recognised four categories of stem: pseudostem, true stem, rhizome, and reproductive stem. The latter is not discussed in this paper.

interactions. These wider dimensions form the subject of the next paper (Lemaire, 2001).

## Segmental structure of the grass tiller

*Significance for sward dynamics*

For many years, there has been wide awareness of the segmental structure of the grass tiller. Each tiller comprises a chain of growth units, often called phytomers. These phytomers are laid down from an apical meristem (also called the growing point) in a linear succession (e.g. Sharman, 1945; Jewiss, 1993; Nelson, 2000). However, despite wide awareness of the segmental structure, the logical implication that the processes of leaf, tiller, true stem, root formation, and eventual root death, actually represent successive stages in the development of a phytomer is seldom explicitly stated. That an individual phytomer is responsible for formation of different organs at different stages in its own internal life cycle, and a single tiller is a co-ordinated chain of phytomers in different stages of their development cycle (Figure 1), are the fundamental reasons why a grass tiller maintains a more or less consistent appearance over a period of time.

*(Please insert Figure 1 near here)*

Moreover, because of the cycling process as new phytomers are introduced at the meristem and older phytomers eliminated by decay at the distal end, the morphology of a tiller is dynamic. This provides a mechanism for plasticity (within certain limits) and allowing for seasonal changes in sward structure (Chapman and Lemaire, 1993) and in root system distribution (Matthew, 1992; Dawson *et al.*, 2000). By contrast, in herbaceous or woody dicotyledonous plants, phytomer development involves primarily vascular tissue formation, and plant form and plant size change irreversibly over time. Such plants are generally not vegetatively self-replacing, and are only tolerant of defoliation where new stems can be formed from buds on older stem or crown tissue after defoliation.

The segmental structure of the grass tiller therefore, confers fundamental behavioural properties. This concept is expanded as individual growth processes are discussed in following sections.

*Quantitative information on tiller axis structure*

Despite awareness of the segmental structure in grass tillers, we have few quantitative descriptions of phytomer status for entire grass tiller axes. This is probably largely because collection of data describing tiller axis structure is very labour-intensive, with the data themselves being difficult to analyse and interpret. By contrast, data on rates of leaf and root elongation and rates of leaf, tiller, and root appearance are much easier to collect and interpret, even though they give only a part of the overall picture. Hence, historically, it has been more usual to study the individual processes of leaf growth, tillering and root growth in detail, and usually in isolation of each other.

One early example of a phytomer-map of a grass plant is that of Etter (1951) for *Poa pratensis*. He found that for a mapped plant, the net results of less than two years growth were 15 rhizomes, 30 shoots and 1 inflorescence. Details such as the

number of live leaves on each shoot and timing of root development do not appear to have been recorded. The analysis of the data was deductive rather than statistical, but focussed on the number of buds laid down, the proportion of those subsequently developing into shoots and rhizomes, and concluded with speculation on possible control mechanisms for bud development.

A more recent study, conducted to provide data for a simple computer model of the tiller axis, is that of Yang *et al.* (1998). These authors examined nine-month-old tillers of *Lolium perenne* and *Festuca arundinacea.* The *L. perenne* tillers typically had six leaf primordia, one leaf elongating within the pseudostem, one visible elongating leaf, three mature leaves and eight phytomers with roots in various stages of development from early root formation to root death, making a total of approximately 20 phytomers on the tiller axis. Figure 1 is drawn to approximately agree with these data. A typical *F. arundinacea* tiller in the same study had fewer phytomers at the leaf primordium stage (this difference also noted by Pearse and Wilman, 1984), but had an extra mature leaf compared with *L. perenne*. Phytomers with roots attached in *F. arundinacea* numbered only six, but it was noted that at nine months of age the tiller axis of *F. arundinacea* plants had not yet attained its final length. There seems to be little similar data to assess how the phytomer arrangement in tiller axis might vary within and between species and in response to environmental stimuli. However, it is known that the number of undeveloped leaf primordia at the apex may increase during periods when leaf elongation is reduced due to stress. More rapid release of these undeveloped primordia has been implicated in stress recovery.

Visual observations, yet to be followed up by more detailed research, suggest some grass species can show specialisation in development of particular phytomers. *Cynodon dactylon,* for example, produces leaves in triplets, and the appearance is that one leaf in a triplet is associated with root formation activity, a second with tiller formation at the associated axillary bud, and the third with internode elongation to form stoloniferous true stem (Sbrissia, 2000). Also, *Panicum maximum* seedlings have an unusually small and transitory primary root system, with the mesocotyl region of stem (Robson *et al.*, 1988) seemingly a mere transition phase in the development of a permanent crown structure derived from true stem formation associated with phytomer development (C. Matthew, unpublished data). Questions of possible links between tiller axis structure and growth strategy and the documentation of apparent specialisation of phytomers in some grass species should provide an interesting basis for further study.

## Leaf and tiller development

Leaf and tiller development will be together here, as both processes interact as determinants of light capture. Nelson (2000) has comprehensively reviewed the topics of leaf and tiller formation on the tiller axis. Whereas leaf growth at successive phytomers is overlapping and continuous, tiller bud release is regulated independently in an on/off manner at each site (Nelson, 2000). To the best of the authors' knowledge, in all studies to date every grass phytomer forms a leaf primordium and a tiller bud, and every leaf primordium develops into a leaf. The leaf appearance interval, or phyllochron, approximates the rate of phytomer appearance on the tiller axis (Nelson, 2000).

By contrast with leaf appearance, the probability of tiller buds at successive phytomers developing into new tillers is highly variable, ranging from near zero to near 1, depending on the circumstances. Therefore, control of tiller bud release, rather

than control of leaf formation parameters, is the principle means of regulation of sward leaf area index (LAI) (Simon and Lemaire, 1987; Matthew *et al.*, 2000). One physiological mechanism involved in the control of tiller bud release is response to increase in red:far red ratio (Casal *et al., 1985*). The proportion of tiller buds developing was first measured as the ratio of tiller appearance (Davies, 1974), with a maximum of 0.69 when prophyll buds develop into tillers (Neuteboom and Lantinga, 1989). The maximum value is less than one because of the delay between leaf and tiller appearance on the tiller axis. More recently measures of tiller appearance have been proposed that focus on the proportion of buds on the axis developing (site usage, Skinner and Nelson, 1992), or on the probability of a bud at a particular bud site developing (specific site filling, Bos and Neuteboom, 1998; nodal probability, Matthew *et al.,* 1998).

In generally accepted that tiller bud initiation normally occurs within a comparatively narrow time window in the phytomer development cycle (Nelson, 200), and this seems to be also true for range grasses (Hendrickson and Briske, 1997). The mechanism of bud release is not well understood (Murphy and Briske, 1992). It is clear that younger tillers in a tiller hierarchy have lower site filling ratios that the oldest tiller (Bahmani *et al.*, 2000; Bos and Neuteboom, 1998), and this is also suggested by the fact that recorded values for site filling in field swards tend to be higher than needed for tiller replacement (Matthew *et al.*, 2000).

Tillering is especially important during establishment of a sward or when the tiller density has been reduced considerably by e.g. winter damage or decapitation of a reproductive sward after a heavy silage cut. Tiller density reduction after a heavy silage cut can be considerable and it can take a long time for the tiller density to recover. The concomitant yield reduction can fully be explained by the reduced leaf area increase after defoliation with a lower tiller density (Van Loo, 1993). The generally lower tiller density of tetraploid cultivars compared with diploid cultivars of *L. perenne* in a fully established sward is linked to the larger leaf area per tiller in tetraploid cultivars. With their higher leaf area per tiller, tiller death through shading (Hernándex Garay *et al.*, 1999) occurs at a much lower tiller density than for the diploid cultivars.

*Co-ordination of leaf development on successive phytomers*

For *F. arundinacea,* Skinner and Nelson (1995) observed that commencement of lamina elongation at node N, ligule initiation at node N-1, and cessation of sheath division at node N-2 are approximately simultaneous. Recent development of computer modelling as a discipline provides a powerful tool for examining how various co-ordination rules might affect shoot morphogenesis (and population dynamics). In one study (Durand *et al.*, 2000) a leaf was conceptualised as having a meristematicmersitematic zone (m), elongation zones for lamina and sheath (operating at different times, g) and mature tissue (l). In this model the co-ordination rule is that when leaf length (m+g+l) of a particular leaf (leaf N) equals the longest sheath of the preceding leaves, the meristem stops producing new meristematic tissues, the addition of new cells to the lamina ceases (but developing cells continue elongating), and sheath elongation starts. The model gave realistic simulations of leaf elongation rate, leaf elongation duration, and predicted the progressive increase of successive final leaf lengths after defoliation. Cessation of meristematic activity at leaf N-1 at the same time as the start of activity at leaf N+2 was predicted by the model and did not need to be introduced as a co-ordination rule. Also predicted was

that leaf N+1 would at this time be about 1mm long, as observed by Skinner and Nelson (1994).

*The leaf growth-zone*

In grasses, the leaf meristem and the associated leaf elongation zone are located at the base of the leaf and are concealed by the sheaths of older leaves (Volenec and Nelson, 1983; Schnyder *et al.*, 1990). As a result of continued cell production and expansion at the basal location in the leaf, cells produced by the meristem are displaced upwards. These processes result in the formation of increasing epidermal cell length with increasing distance from the leaf base. Under ideal non-limiting growth conditions, during the period of active leaf elongation in grasses this gradient is constant and unidirectional (Schnyder *et al.*, 1990). The spatial gradient from the base to the tip of the growing leaf corresponds to a developmental gradient with cells at the base actively dividing, cells further up undergoing expansion and closer to the leaf tip the cells reach their final size. As a consequence of this, the cell length distribution along the basal part of a leaf can be used to ascertain the distribution of growth rates (Silk, 1984) and to quantify the length of the zone where cell division and expansion occurs (Figure 2).

*(Please insert Figure 2 near here)*

It is well recognised that the spatial distribution of growth rates in grass leaves can change. A range of both internal and external factors can influence this. These include genotype (Volenec and Nelson, 1981), nitrogen nutrition (Volenec and Nelson, 1983; Gastal and Nelson, 1994), drought (Spollen and Nelson, 1994; Durand *et al.*, 1995), temperature (Tonkinson *et al.*, 1997), time of day (Schnyder and Nelson, 1988), irradiance (Schnyder and Nelson, 1989) and defoliation (Schäufele and Schnyder, 2000). Responses within the tiller base to drought are outside the scope of this review but a number of characters correlated with drought tolerance were listed by Volaire et al. (1998).

*Defoliation effects on leaf growth and canopy leaf area*

Defoliation can cause a fast and dramatic decrease in leaf elongation rate (Davidson and Milthorpe, 1966) and the relationship between herbage mass and leaf tissue appearance rate (Bircham and Hodgson, 1983; Parsons *et al.,* 1983) is now well known, and underpins current grazing management theory and practice. Subsequent studies have sought to understand responses to defoliation in more detail. It has long been recognised that reserve carbohydrate is mobilised mainly from the leaf sheath in *L. perenne*, and is sufficient for no more than two days of regrowth, after which time, current photosynthesis must supply the energy for regrowth (Alberda, 1960, Parsons and Chapman, 2000). Also following defoliation, as a result of an increased sink strength of growing leaves, roots may become a source of carbon or nitrogen. Greater detail has been provided with the use of modern analytical techniques. For example, Morvan-Bertrand *et al.* (1999) observed that following defoliation the percentage of carbon incorporated into the youngest leaf but fixed before defoliation was 89% after two days, 59% after 6 days, and 9% after 14 days. Recognition of the rapid fall following defoliation and gradual recovery during the regrowth cycle, of plant soluble carbohydrate is the rationale for a "three" leaf grazing management criterion

(Donaghy and Fulkerson, 1996). However, it should not be assumed that other grasses do not store reserves in stems or roots. Data of Thom *et al.* (1989) indicate that in the C4 grass *Paspalum dilatatum*, the true stem has a reserve storage function in winter, for example.

At a morphogenetic level Van Loo (1993), in glass house experiments, found that during recovery from grazing, final leaf length was reduced by severe defoliation (Figure 3a). Leaf area index after defoliation was more affected by level of N supply than plant density (Figure 3b), and was accompanied by a transitory increase in specific leaf area (Figure 3c). From these studies Van Loo (1993) recognised that rate of canopy leaf area recovery after defoliation is limited by the density of tillers present and by their physical capacity to generate new leaf material. Bahmani (1999) termed this limitation morphological ceiling leaf area (MCLA) and explored the possibility of predicting seasonal change in tiller density (Davies, 1988) by comparing MCLA with a theoretical environmental limit to the leaf area that can be supported (Matthew *et al.*, 1995). If MCLA were greater than the environmental limit, self-thinning would occur.

More recently, there has been interest in defining events at the cellular level, in relation to changes in the leaf growth zone. With a single 5 cm defoliation, Schäufele and Schnyder (2000) found that the height of the leaf growth zone in *L. perenne* (cv. Vigor) was reduced two days after defoliation. In a study conducted by one of the authors (Dawson, with F. Gastal, INRA, France, unpublished) using the method of Schnyder et al., (1990), the distance from the leaf base was calculated as the point where the cell length was 95% of it's maximum value using a Richard's function. In this study, under non-limiting conditions, the height of the leaf growth zone in *L. perenne* (cv. Vigor) varied from 33 mm when cut at 9 cm height to 21 mm when cut at 3cm height (Table 1). *Festuca rubra* (cv. Agio) showed lesser, non-significant reductions. The height of the leaf growth zone was also greater in *F. rubra* than in the other species thus potentially exposing the developing meristem to the grazing animal. These data suggest there is not a common response strategy for different grass species and that *L. perenne* is more plastic in response o the leaf growth zone than some other grass species.

*(Please insert Table 1 near here)*

*Alternative leaf production strategies*

Robson (1969) has noted that there could be a range of strategies for producing the same amount of leaf, through variation in leaf appearance rate ($A_L$), leaf elongation rate (LER), and leaf elongation duration (LED). On selection of experimental breeding lines of *F. arundinacea* with contrasting high and low leaf elongation rates, it quickly became apparent that high LER was associated with low site filling (Zarrough *et al.,* 1984). Similarly, high LER and low tillering have been linked in *F. arundinacea* by Robson (1967), and Allard *et al.* (1991), in wheat (Bos and Neuteboom, 1998), and in contrasting New Zealand *L. perenne* cultivars, 'Grasslands Ruanui' and 'Ellett'. ('Grasslands Ruanui' has a comparatively short leaved, small tillered growth habit and 'Ellett' is a more productive, longer leaved, larger tillered cultivar; Bahmani *et al.,* 2000). A schematic diagram of these interactions was presented by Bahmani (1999, Figure 4). Note that the interactions occurring within the plant (Figure 4) have much in common with those governing

plant-plant and plant-environment relations, discussed in the following paper (Lemaire, 2001).

In contrast with the above, when breeding lines of *L. perenne* were selected in France for long and short leaf length (Hazard and Ghesquière, 1995), the long-leaf-length line was found to have a higher tiller number in young plants than the short-leaf-length line, because of a high $A_L$. In addition, earlier commencement of tillering on the main tiller axis in the long leaf length line, may have contributed to this result (Bahmani, 2000). However, the short-leaf-length plants did have a higher site filling, which would be expected to lead to higher tiller number in time.

There is no clear consensus as to the preferred plant type. For the French long- and short-leaf *L. perenne* selection, the percentage of long-leaf-length plants in a mixture with short-leaf-length plants increased with time, and the increase was faster under a more lax defoliation (Hazard and Ghesquière, 1995). However, Bahmani *et al.,* (2000) suggested that high LER will normally be associated with increased tiller weight, and increased productivity, but at a cost of decreased persistence due to more intense interplant competition in the later stages of a regrowth cycle. A similar conclusion was reached when tetraploid and diploid cultivars of *L. perenne* were compared. The longer leaf length of the tetraploid was associated with a lower leaf appearance rate and a lower tiller number, compared with the diploid. (Van Loo, 1992; Van Loo *et al.*, 1992; Van Loo, 1993).

Little data is available for other species, but available evidence suggests wide intra- and inter-specific variation in leaf elongation strategy. New Zealand hill country grasses showed major between species differences in leaf elongation strategy (I. F. López, 2000, unpublished data) and the rhizomatous genotype of *F. arundinacea* mentioned below had a very different leaf elongation strategy from the non-rhizomatous type (Bryant, 1997; Table 2). As mentioned in discussing tiller axis structure, investigation of the ecological significance of such differences seems an interesting area for future study.

## True stem and rhizome formation

### *True stem*

An important consequence of phytomer turnover on the tiller axis is that elongation of the axis is unavoidable. Even in species categorised as tufted or of bunch grass form, elongation of the tiller axis cannot be ignored. In *L. perenne* for example, 30 to 40 new leaves are formed per year (Davies 1977) and, assuming the length of a phytomer on the tiller axis to be 0.3 to 0.5 mm, this would result in $10 - 20$ mm of true stem formation per tiller per year, even without internode elongation. In fact, vegetative internode elongation does occur and patches of a single genotype may attain a diameter approaching or exceeding a meter in older ryegrass swards through horizontal expansion of more successful individual plants with time (Harris *et al.*, 1979). This elongation must somehow be accommodated within the dynamics of the sward. In one experiment with *L. perenne*, the total length of true stem present ranged from 60 to 173 m m$^{-2}$, with greater quantity of true stem present under more laxly defoliated swards (Matthew *et al.*, 1989). Since *L. perenne* true stem has a dry mass around 1.0 mg mm$^{-1}$, the weight of true stem present was in the range $0.5 - 2.0$ t DM ha$^{-1}$.

True stem formation in a number of species has been extensively described in recent years (Korte and Harris, 1987; Brock and Fletcher, 1993; Vignolio *et al.*, 1994;

Brock *et al.,* 1996, 1997) and we will not comment further here. It is interesting to note, however, that the majority of the data have been presented on a per unit area or per plant basis, and further refinement of such studies to elucidate the position of true stem formation on the tiller axis and the timing in relation to other events would be useful.

In erect, larger tillered species, vegetative true stem formation is often assumed to contribute to tiller death through decapitation of apical meristems by grazing animals (e.g. Chapman *et al.*, 1984; Nabinger, 1997). However this factor may not always be as important as commonly believed. One recent study (Carvalho *et al.*, 2001) has shown that tillers of *Panicum maximum* frequently die from old age, before the growing point is elevated above defoliation height.

*Rhizomes*

Rhizomes[2] are not a departure from the fundamental pattern, but merely specialised implementations of it. The number of published studies on rhizomatous grass species within the last 25 years probably exceeds 200. Dong and Kroon (1994) and Dong and Pierdominici (1995) have suggested from a study of *C. Dactylon,,* which possesses both stolons (orthotropic shoots) and rhizomes, that rhizomes act as storage organs whereas stolon formation is concerned with foraging for light. More commonly, rhizomes are implicated in foraging for more favourable microhabitats (Macdonald and Leifers, 1993; Huber-Sannwald *et al.*, 1997; Kleijn and Van Groenendael, 1999), and rhizomes have also been identified as conferring stress tolerance (Humphrey and Pyke, 1998). A number of rhizomatous grasses can be particularly troublesome weeds (e.g. *Panicum repens, Elytrigia repens, Sorghum halepense, Imperata cylindrica*).

Studies of rhizome formation in *F. arundinacea*, a species with variable rhizome production, depending on growing conditions and genotype, include Porter (1958), Jernstedt and Bouton (1985), Bouton *et al.* (1992), Hume and Brock (1997), and Bryant (1997). The latter author followed expansion over four months from single tiller cuttings of rhizomatous and non-rhizomatous *F. arundinacea* genotypes under three defoliation regimes. Rhizome production was normally from older buds, and usually occurred on secondary rather than on primary tillers. Rhizome production was often limited to one or two rhizomes per tiller, despite additional buds being available. This was especially so under more severe defoliation. Perhaps coincidentally, rhizomatous and non-rhizomatous genotypes had very different leaf and tiller production strategies. The non-rhizomatous plants initially had higher tiller number per plant than non-rhizomatous plants, but only under a more lax defoliation. Later this difference disappeared (Table 2). Differences in leaf length (Table 2) reflect narrower leaves, a faster elongation rate and a less frequent leaf appearance interval in the rhizomatous genotype. Paradoxically, the rhizomatous genotype had the higher site usage (0.35 cf. 0.17), indicating that the energy demand of rhizome production does not necessarily compromise tillering ability. This illustrates again that the various interactions represented in Figure 4 have to be considered in terms of their overall effect on plant, and there is little predictive power from considering one process in isolation from the others.

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[2] The term *rhizome* is used here to indicate a specialised, underground, horizontal shoot, typically with achlorophyllous, scale-like leaves (Matthew *et al.*, 1999).

## Root growth

*Site and dynamics of root formation on the grass tiller axis*

By combining results of Yang *et al.* (1998) and Matthew and Kemball (1997) it is possible to form an overview of root formation as an event on the tiller axis. Tillers of *L. perenne* typically formed their first root four or five phytomers below the emerging leaf, and *F. arundinacea* tillers formed their first root five to seven phytomers below the first leaf (Yang *et al.,* 1998). In general the site of initiation of rapid root elongation corresponded with the site of leaf senescence, suggesting transfer of metabolites from senescing leaves to developing roots, or at least a signal for initiation of root elongation driven by products of leaf senescence. The final length of main axis or nodal (Russell, 1977) roots appeared to be attained about four phytomers below the site of initial root elongation, and accumulation of total length, including branches, appeared to cease about seven nodes below the site of leaf senescence (Matthew and Kemball, 1997).

Statistics from the latter study are instructive. The average root number per phytomer of around two (compared with an assumed number of four root initiation sites per phytomer, as for wheat, Klepper *et al.*, (1984) indicates a site filling ratio of around 50%, making root axis formation more plastic than tiller formation, but less plastic than leaf formation. The final root weight of around 20 mg per phytomer is indicative of an allocation to the root system of around 15-20% of DM accumulation, assuming leaf length (undefoliated potted plants) of 150 mm and specific leaf weight of 0.07 mg mm$^{-1}$. This percentage allocation to root growth is similar to values observed at high nitrogen supply (Van Loo *et al.*, 1992). The final root length of around 2.5 m per phytomer is approximately consistent with the value measured by Matthew (1992) of 82 km root m$^{-2}$ ground in laxly grazed field swards (assuming $6 \times 10^3$ tillers m$^{-2}$ and 6 rooted phytomers per tiller). In terms of the predictive measures of root system performance mentioned below (*Measuring root system performance)*, 82 km root m$^{-2}$ ground distributed 56 km in the 0-70 mm soil depth, 20 km in the 70-250 mm soil depth, and 6 km in the 250-600 mm soil depth equates to 8.0, 1.1 and 0.17 cm root cm$^{-3}$ soil, respectively. Alternatively, with a mean diameter of 0.25-0.3 mm (Matthew, 1992), the root area index (RAI) values for the root system would be 44-53, 16-19, and 4.7-5.7, for the three soil depths, respectively.

Also in this study, plants were destructively harvested 24 h after feeding $^{14}CO_2$ to trace allocation of photosynthesis products within the root system. Roots at the youngest rooted phytomer averaged 20 mm length, 2.8 mg DW, and accounted for more than 20% of total radiocarbon recovery. Roots at the 6$^{th}$ rooted phytomer averaged 2.27 m length (including laterals), 18.6 mg DW, and accounted for less than 10% of the carbon recovery from the root system. Specific activities in DPM[3] mg$^{-1}$ were therefore several hundred times higher in roots at the first rooted phytomer than in mature roots lower on the tiller axis. This raises the possibility that grass roots cease elongation and eventually die in response to diminishing carbon supply as ongoing phytomer development at the meristem increases their distance from the source of carbon supply. In these circumstances, it is possible that associated symbiotic fungi could materially prolong the life of a root if there was a mechanism to

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[3] DPM = disintegrations per minute

allow a modest contribution to the carbon supply of the root, from the associated symbiont.

This evidence for morphogenetic control of root development and of final root size needs to be reconciled with earlier reports of an annual root replacement cycle in *L. perenne* (Stuckey, 1941; Jacques, 1956). Mathematically, if we have 30 to 40 leaves produced on the tiller axis each year (Davies 1977), indicating the same number of phytomers, but only about 20 phytomers on the axis at any one time (Figure 1), then the notion of an annual crop of roots persisting until the next season in *L. perenne,* as described conceptually by Jacques (1956), is impossible.

However, the two perspectives of ongoing turnover as set out here, and annual renewal of the root system (Jacques, 1956) are not necessarily mutually exclusive. In a later study (Matthew, 1992) the rate of root formation in refilled cores was found to mirror seasonal rate of leaf accumulation above ground, but with the rate of root DM formation typically about 20% that of the leaf dry matter formation and with peaks of root formation activity after winter or summer drought preceding shoot formation activity by three to four weeks. Similarly, data from an upland field site in Scotland on an unimproved *Agrostis capillaris-F. rubra* pasture, suggest that the rate of new root production can drop from 4.6 roots per cm$^3$ per day in July to 0.4 roots per cm$^3$ per day over the winter .

Another point to be considered in analysing the dynamics of root formation is the delay between leaf and root formation at a given phytomer on the tiller axis (Matthew *et al.*, 1998). For example leaves appearing at an interval of 15 days in spring might be currently feeding root-forming phytomers that appeared at an interval of 25 days in winter, but in late autumn, leaves appearing in colder conditions at an interval of 20 days might be feeding root-forming phytomers that appeared at a shorter interval. While this calculation does not necessarily indicate a change in percentage allocation to the root system, it does show that the number of roots being fed by an individual leaf may change on a seasonal basis, perhaps by a factor of 2 (Matthew *et al.,* 1998). Depending on assumptions made, this could be a factor contributing to seasonal variation in root diameter, root vigour, final root length, and root system architecture.

*Root hair contribution*

There are numerous descriptive reports in the literature quantifying root hair density, length, and diameter on various root categories of a range of species (see e.g Dittmer, 1949; Reid, 1981), and an excellent review of information on root hair development and function is that of Hofer (1996). Here our interest is to consider the contribution of root hairs to the foraging effort of the grass plant. Dittmer (1937) is cited by Green *et al.* (1991), as reporting that root hairs increase the absorbing surface of roots by a factor of 5 to 18. Green *et al.* (1991), themselves reported a contribution of root hairs to total root length ranging from 1% in *Zoysia japonica* to 98% in *C. dactylon.* However, descriptive data on root hair length are generally not linked with whole-plant statistics in the same studies, or are from plants subjected to substantive manipulation for purposes of collecting the data. Data presented in the various studies are also extremely variable. To illustrate this, Table 3 gives root hair data for two studies on *L. perenne,* and some additional statistics derived from the data. These statistics are for a single root, assuming a 300 mm root axis with a 100 mm root hair zone. (The evidence on which this assumption is based is conflicting. Care (1999) reported root hairs present on almost the entire root length, although in that study

measurements were performed on roots approximately 10 days old. On the other hand, Hofer (1996) states the root hair zone of most roots is 10 – 40 mm.)

*(Insert Table 3 near here please)*

Table 3 confirms that root hairs contribute a large increase in absorptive area of roots, and shows that the proportional increase in total root length, and by inference, soil volume explored, is even larger. Also, the dimensionless area:volume ratio is much larger than that for a root axis without root hairs, which is in turn larger than that observed in the shoot system (Hernández Garay *et al.*, 1999). Notably, these increases in root length and surface area are achieved with only a marginal increase in root volume, therefore presumably a similarly small increase in carbon cost of construction. However, even though calculations (Table 3) show that root hairs can make an important contribution to the total root surface at low carbon cost, and selection for root hair length is feasible (Caradus, 1979, working with *Trifolium repens*), differences in nutrient uptake between cultivars of *Zea mays* in an experiment of Barber and Mackay (1986) were related to differences in topsoil root proliferation, and were not due to root hair characteristics.

*Mycorrhizal associations*

The prevalence of mycorrhizal fungi on the roots of agricultural plants is well known (Chapin, 1980; Krikun, 1991). These fungi, with their very fine hyphae, are capable of providing a substantial increase in capture of ions of low diffusivity, such as phosphate, and presumably at low energy cost to the host plant (Chapin, 1980). In this sense, they can contribute in a similar way to that outlined above for root hairs. Marschner and Dell (1994) indicate that 80% of plant P, as well as significant quantities of N, K, Zn and Cu, may be supplied by mycorrhizae. Wilson and Hartnett (1998) show that many rangeland grasses scarcely grow at all when deprived of mycorrhizal association. Transfer of nutrients such as P (Fischer Walter *et al.*, 1996) between neighbouring plants has been demonstrated and transfer of carbon also claimed, (e.g. Simard *et al.,* 1997), raising the possibility of subsidy to less competitive plants by this route. Even so, more productive grasses like *L. perenne* generally show an inconsistent and often small (Wilson and Hartnett, 1998) response to mycorrhizal association, and others argue it is likely that transferred carbon remains in the fungal hyphae, and is not actually transferred to the host grass (Robinson and Fitter, 1999). Thus we have here an issue of critical importance to our understanding of plant performance, but for which the facts remain uncertain.

*Root plasticity*

There are numerous observations suggesting root diameter in grasses is an important mechanism for adjustment to both reduction in carbon supply and nutrient supply. For example, Matthew (1992) observed a consistent (though non-significant) reduction in mean root diameter in harder-grazed swards, Mackie-Dawson (1999) found that root diameter was reduced significantly by a single defoliation to 40 mm height, and Fitter (1996) noted that younger root systems and those in nutrient-poor soils tend to have high specific root lengths, for example. Reduction in nutrient supply reduces total photosynthesis, but increases root:shoot allocation. In some cases root growth at low nutrient supply may even be larger than at high nutrient supply (Van

Loo *et al.*, 1992). This increase in root:shoot ratio occurs together with an increase in specific root length arising from a decrease in mean diameter, and can often mean that total root length is not greatly reduced, or can even be increased in less fertile situations (Fitter, 1996).

*Measuring root system performance*

The performance limits for the root system were neatly set out in De Willigen and Van Noordwijk's (1987) four quadrant diagram of plant productivity (Figure 5), adapted from an earlier three quadrant presentation by De Wit (1953). Development of ideas on how to measure root systems and conceptualise their performance is ongoing.

*(Please insert Figure 5 near here)*

Before commenting further, it should be noted that passive uptake of some nutrients (e.g. $Mg^{2+}$, $Ca^{2+}$) in the transpiration stream is a significant component of plant supply, while active transport across cell membranes is the dominant pathway for other nutrients (e.g. $NO_3^-$, $H_2PO_4^-$). Where uptake is by active transport, the situation is not fully analogous to that of light capture by leaves. Photons travel through the leaf canopy and leaves need only be positioned in the path of incoming photons, whereas roots involved in active uptake of nutrients must first grow towards and be positioned at the uptake site. As nutrients in the immediate proximity of the uptake site are depleted there arises the strategic option of continued uptake at that site, with supply by diffusion in the soil solution, versus moving the uptake activity after a time to a site where nutrients are not depleted. In short, any analysis aimed at predicting root-system performance should consider the potential for passive uptake, the optimum strategy for exploring a given volume of soil, the area presented for nutrient uptake, and the capacity for uptake sites to be relocated as nutrient depletion reduces the initial influx rate.

Turning to the data available, most early studies and many recent ones (e.g. Garwood, 1967; Caradus and Evans, 1977; Matthew, 1992; Stetson and Sullivan, 1998) either report data on root distribution in the soil profile or data that are essentially indices of seasonal root growth activity. While these data are helpful for some applications, there is little capacity for insight into nutrient uptake efficacy. It also took some time for an efficient method of measuring root length to be developed (Newman, 1966). Perhaps the simplest measure that allows some predictive power for root performance is root length per unit volume of soil, often reported in units of $cm\,cm^{-3}$. De Willigen and van Noordwijk (1987) summarise over 50 studies reporting root length density data for cereal crops and grasses. (Notably, all but one of these studies post-date publication of the root length counting algorithm.) Values ranged from 0.08 to 25.6 cm root $cm^{-3}$ soil, but it should be noted that because roots are much more prolific in upper regions of the soil profile, data presented in this way vary substantively depending on the sampling depth over which they are averaged. From their own experiments, these authors concluded that a root length density of at least 20 cm root $cm^{-3}$ soil is required before additional root length will not result in increased nutrient uptake.

More recently Fitter (1991, 1996) has argued convincingly that topological analysis has predictive capacity for root system performance. The topological extremes are a "herringbone" root system comprised entirely of first order branches and a maximally branched "dichotomous" architecture. The former is more costly to

construct in terms of carbon, but more effective at exploring a soil volume, and so is to be favoured where mobile resources are limiting plant growth. The dichotomous system is predicted to be more efficient in soils of low diffusivity. However, detailed measurement of topology is typically made on a fragment of the root system and is time consuming so there can be practical problems gaining an overview of events at the field level, even where differences in root branching pattern can be identified. Another approach has been the development of surface-area-based statistics, analogous to LAI in evaluating light harvesting efficiency. This approach was discussed by de Willigen and Van Noordwijk (1987) and pursued in detail by Care (1999).

*Shoot and root systems compared*

It is instructive to consider the similarities and differences between the root and shoot systems. The tiller apex is unique and generates new phytomers. Leaves and roots are respectively the light harvesting and nutrient gathering organs of phytomers, although they operate at different stages in the life span of the phytomer. The fact that there are approximately twice as many phytomers on the tiller axis bearing roots than bearing leaves indicates that axial roots have a longer turnover time than leaves, for *L. perenne*. However, leaves photosynthesise throughout their life span, whereas root hairs (which as we have seen above provide the majority of the surface area of the root system) are considered ephemeral (Hofer, 1996), and our understanding of the temporal and spatial dynamics of nutrient uptake has many gaps and uncertainties.

LAR, LED, $A_L$ and site usage statistics have been the subject of detailed study. Parallels reflecting axis root formation at each phytomer would be available but have only occasionally been reported (e.g. Hunt and Thomas, 1985; Matthew and Kemball, 1997, Yang *et al.*, 1998). As indicated above, leaf elongation zones are at the leaf base, conferring defoliation tolerance. Root elongation zones are at the root tip, and so facilitate soil penetration. The constraints of light and nutrient capture differ, such that root morphology emphasises surface area much more than does leaf morphology. Dimensionless area:volume ratio for a sphere is 10.63. For a single *L. perenne* tiller, a range of 40 –60 is typical (Hernández Garay *et al.,* 1999), and for the root system with root hairs, the ratio may approach or exceed 500 (Table 3). Particular types of branch root are under genetic control and are highly heritable. Selection for particular types of branch root has been proposed (Zobel, 1975; Zobel, 1996). There is no direct analogy for selection of leaf type, although plants may be selected for other leaf characteristics such as level of high molecular weight fructan for carbon storage (Waller and Sale, 2001).

**Application of component research in plant improvement**

Since many of the individual shoot and root development processes are interactive and mutually compensatory, it is not straightforward to isolate a particular plant character or growth strategy that will confer superior plant performance. In the final section of our paper we discuss the application of component research like that discussed above, to plant improvement. In the research programme considered, which spanned eight years, understanding of growth processes limiting regrowth was consolidated to identify selection criteria to be applied, possibilities for genetic improvement were explored, and economic implications of genetic improvement were evaluated.

*Considerations in deriving selection criteria*

To isolate selection criteria for plant improvement we need to consider the interactive effect of all the above processes working together. Growth processes in a dense crop with a high LAI are in essence independent of tiller density. This is particularly clear when looking at different species in the Poaceae that differ in tiller size. Across the family large differences in tiller size occur, ranging from (typically) one large tiller per plant in *Z. mays* to several smaller tillers per plant in a cereals such as *Triticum* spp and up to a few hundred tillers per plant in some turf grasses. Physiological relations at higher LAI, in the case of an even horizontal distribution of leaf area, are governed by the average light interception, photosynthesis, respiration, leaf and root death, and not so much by the number of tillers. Growth rates in these circumstances can be described by mass flow of assimilates per area as is shown in grass models for photosynthesis and growth (Johnson and Thornley, 1983; Lantinga, 1985), since at high LAI, growth is mostly source-limited.

When the LAI is low, however, tiller size and tiller dynamics are important. Two situations where this occurs are during the establishment of plants or swards, and during regrowth after defoliation.

Then, two aspects are different from the situation above, of higher LAI. First, leaf area increase is not solely governed by the current rate of net assimilate production, since leaf material and assimilates from the reserves in the stubble contribute to new leaf area growth. Second, the rate of leaf area production is in many cases not limited by the availability of assimilates (sugars and proteins) in the stubble, but by morphological limitations of the particular grass species such as a certain maximum leaf area extension per tiller and tiller density. The maximum leaf area expansion per tiller depends on the number of simultaneously expanding leaves, the maximum leaf extension rate, and leaf width. In *L. perenne* (Van Loo, 1993)*,* and probably in many other members of the Poaceae, a feature of leaf area expansion per tiller is that successive leaves are longer than the previous one. This pattern occurs on both older and younger tillers and is rather independent of external effects like cutting frequency and height except when the reserve level in the stubble is reduced considerably (Van Loo, 1993; Figure 3a). With drought, the leaf extension rates are reduced for all leaves on a tiller axis, but the pattern remains more or less the same; the first leaves on a tiller have lower rates of leaf area increase and lower final leaf length and width than leaves formed later on the same tiller axis (Van Loo, 1992).

Low nitrogen supply considerably reduces leaf area increase per tiller (Figure 3b), but again the pattern of an increase in leaf size and leaf area increase per tiller on a tiller axis with leaf number is similar on the main tiller as on secondary or tertiary tillers. This means that variation in leaf area increase after defoliation of the crops is to a large extent independent of light interception but determined by tiller density, the leaf elongation rate and specific leaf area (SLA).[4] SLA increases following defoliation (Figure 3c), and high SLA increases the rate of leaf area recovery. When nitrogen supply is not limiting, leaf area expansion rates are hardly limited by carbohydrate supply until the specific leaf area attains very high values of up to 600-700 $cm^2 g^{-1}$ in *L. perenne*. This maximum specific leaf area can function as an upper limit in modelling leaf area increase after defoliation. (Van Loo, 1993).

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[4] Specific leaf area is related to leaf width and inversely related to leaf thickness.

*Possibilities for genetic improvement*

Van Loo et al. (1998) using a hydroponic system showed that selection for tillering and leaf area increase after defoliation at low nitrogen supply is possible. Selection was carried out, to a certain extent independently, for root and shoot dry matter production, tiller number and leaf length and width of regrowth on the main tiller. The product of tiller number, leaf length extension rate and leaf width was taken as the increase in leaf area after defoliation (dLAI). The offspring of the selections was evaluated in the same way as the selections. The selection experiment showed that the investigated traits generally have a moderate to high heritability (Table 4).

*(Please insert Table 4 near here)*

*Effect of genetic improvement on nitrogen response and economics of dairy farming*

An extrapolation of the above information from the plant level to the farming level has been presented by Vellinga and Van Loo (1994). They used a physiological growth model to show that with the genetic variation found in nitrogen response in several components that at least a 5-10 % increase in dry matter yields over the range of nitrogen supply of 0 to 100 kg N/ha per cut was to be expected from development of new genotypes with a 10 % higher leaf weight ratio or a 20 % higher leaf area increase after defoliation. One interesting finding from the modelling exercise is that with a 10% increase in leaf weight ratio the absolute root production is only slightly decreased. This is because leaf weight is increased, and also total production, as a consequence of a higher light interception in early stages of regrowth.

Assessment of the financial return at the farm level arising from this improved plant performance was achieved using a farm economic model developed by the Research Station for Dairy Farming in Lelystad, the Netherlands, for extension services. This model has a standard grass production function depending on the nitrogen input. This function was increased by 10 % for the situation with improved grass cultivars. Required nitrogen, phosphorus and potassium inputs were calculated to reach the same grass production. In a nutrient balance module of the model, the effect was of improved cultivars on the nutrient surplus of the farm was calculated (i.e. import in fertilizer and concentrate minus export in milk and meat). This nitrogen surplus was reduced by 35 % with improved cultivars. Next, the reduction in grass production was calculated for a scenario where the same reduction in nitrogen surplus was achieved by reducing nitrogen application to exiting cultivars. In that scenario it was assumed the farmer bought extra forage to compensate for the reduced grass production. All calculations were carried out at the same total milk production (a standard milk quota per hectare), since it is most economic for a Dutch farmer to produce his full milk quota. Finally, the different scenarios were compared in terms of farm income. Table 5 shows that with cultivars selected for nitrogen use efficiency and rate of leaf area increase after defoliation, the nitrogen input may be reduced while the farm income per hectare increases. When compared at the same reduced nitrogen surplus, improved cultivars have an even greater advantage.

*(Please insert Table 5 near here.)*

This example illustrates successful application of detailed morphological and physiological information from component research in order to achieve improvement

in plant performance at the farm level. It also illustrates the complexity of investigation required in order to fully understand the factors limiting shoot development, and isolate selection criteria that will actually produce a beneficial result.

## Conclusions

- Consideration of growth processes as stages in phytomer development leads to useful insights. For example, eventual death of roots through reduction in assimilate supply, and seasonal increase in assimilate supply to individual roots in spring, are predicted.
- We have detailed component knowledge of individual growth processes, but we still have much to learn about the functional significance of alternative growth strategies.
- It is hard to find examples of the application of component research to plant improvement. The example given shows the logic used to identify high leaf elongation at low N level as a useful selection criterion, and demonstrates the potential benefit at farm level.
- We suggest that with current advances in analytical and other technologies, a renewed focus to ensure component research in forage plant morphogenesis is directed towards a practical outcome as illustrated here, could be very rewarding.

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**Table 1 -** Height of leaf growth zone (mm) after defoliation at 9 or 3 cm height above the stem base on three consecutive occasions, at 12-day intervals. From an experiment conducted in a growth room under a high N regime (8 mM N). (Dawson and Gastal, unpublished data.)

| Species | Cutting height (cm) | Height of leaf growth zone (mm) .Mean of 5 replicates | Standard deviation |
|---|---|---|---|
| *Lolium perenne* | 3 | 21 | 2.5 |
| *Lolium perenne* | 9 | 33 | 4.4 |
| *Dactylis glomerata* | 3 | 16 | 3.3 |
| *Dactylis glomerata* | 9 | 21 | 6.4 |
| *Festuca rubra* | 3 | 33 | 5.3 |
| *Festuca rubra* | 9 | 36 | 11.7 |
| *Festuca arundinacea* | 3 | 22 | 6.3 |
| *Festuca arundinacea* | 9 | 26 | 4.0 |

**Table 2 -** Tiller number per plant, at 84 and 126 days from planting a single rooted tiller, and length of longest leaf for rhizomatous and non-rhizomatous *F. arundinacea* genotypes, uncut (U), or subject to Lax (L) or hard (H) defoliation. Data of Bryant (1997).

| | Non-rhizomatous | | | Rhizomatous | | |
| --- | --- | --- | --- | --- | --- | --- |
| | U | L | H | U | L | H |
| Tillers per plant (84 d) | 104 | 77 | 50 | 79 | 64 | 49 |
| Tillers per plant (126 d) | 192 | 130 | 117 | 189 | 169 | 105 |
| Longest leaf (mm) | 191 | 147 | 71 | 364 | 232 | 113 |

**Table 3 -** Root hair counts and dimensions for *L. perenne*, with derived statistics indicating root hair contribution to total root area and volume, and dimensionless area:volume ratio.

| Measurement | *L. perenne* (cv. Aberystwyth S24)[1] | *L. perenne* (cv Grasslands Nui, low P)[2] | *L. perenne* (cv Grasslands Nui, high P)[2] |
|---|---|---|---|
| No. Root hairs mm$^{-1}$ root | 264 | 1369 | 1250 |
| Root hair length (µm) | 1120 | 145 | 132 |
| Root hair diameter (µm) | ~10 | 12.3 | 12.7 |
| Root axis diameter (µm) | Not available | 248 | 253 |
| Factor increase in length | 296 | 198 | 165 |
| % contribution to area[3] | 92 | 91 | 89 |
| % contribution to volume[3] | 11 | 10.7 | 9.6 |
| Dimensionless area:volume ratio[4] | 572 | 456 | 390 |

1. Data of Reid (1981). Number of root hairs per mm of root is based on an assumption that root hairs on one third of the root circumference were counted in observations made through glass viewing windows.
2. Data of Care (1999)
3. Based on formula for surface area of a cylinder, for a segment of root with root hairs over the entire segment, area of ends of root and root hairs ignored.
4. Area:volume ratios change with size of an object. Dimensionless area: volume ratio, (area)$^{3/2}$/volume is a useful measure of shape ("R" of Hernández Garay et al., 1999). For comparison, dimensionless area:volume ratio for a sphere is 10.63, for a cube is (6)$^{3/2}$ = 14.7, for a tiller typically 40-60, and for a root axis 300 mm long and 0.25 mm diameter without root hairs the dimensionless area:volume ratio is 61.

**Table 4 -** Mean ($\mu$) of original populations, coefficient of variation within populations($CV_P$), relative contrast between groups of selected plants (selection differential, S, % of mean of original populations), relative contrast between offspring of selected groups of plants (selection response, R, % of mean offspring) and realized heritability ($h^2_R$=R/S) of diploid (2n) and tetraploid (4n) populations. dLAI=initial leaf area increase after cutting (Van Loo et al, 1998).

| | $\mu$ | | $CV_P$ (% of T) | | S | | R | | $h^2_R$ | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 2n | 4n | 2n | 4n | 2n | 4n | 2n | 4n | 2n | 4n |
| Shoot DM (g per plant) | 1.07 | 1.01 | 41 | 32 | 86 | 81 | 47 | 30 | 0.55 | 0.37 |
| Root DM (g per plant) | 0.29 | 0.35 | 50 | 40 | 98 | 87 | 37 | 21 | 0.38 | 0.24 |
| Leaf weight ratio (%) | 79.6 | 74.8 | 5.3 | 5.5 | 9.6 | 10.8 | 5.5 | 2.9 | 0.57 | 0.27 |
| dLAI ($m^2\ m^{-2}\ d^{-1}$) | 0.070 | 0.079 | 49 | 37 | 101 | 96 | 63 | 42 | 0.62 | 0.43 |
| Leaf width (mm) | 2.89 | 3.31 | 13 | 13 | 20 | 32 | 17 | 6.2 | 0.88 | 0.19 |
| Leaf extension (mm $d^{-1}$) | 13.2 | 14.5 | 14 | 13 | 25 | 32 | 18 | 12 | 0.71 | 0.37 |
| Tiller number per plant | 10.6 | 7.6 | 40 | 36 | 111 | 81 | 63 | 34 | 0.57 | 0.41 |

**Table 5 -** Potential benefits of grass breeding for improved nitrogen use efficiency. Scenarios: A=current situation; B=improved N  use efficiency of grass cultivars, reduced N-input; C=N-surplus reduced to level of B. Milk production was equal for all scenarios at 400 000 kg milk for a farm of 28 ha (Vellinga and Van Loo, 1994).

|  | A | B | C |
|---|---|---|---|
| N-fertilisation (kg/ha/year) | 420 | 270 | 240 |
| N-efficiency grass | 0 | +10% | 0 |
| N-import (kg/ha/year) | 465 | 340 | 335 |
| N-export (kg/ha/year) | 85 | 85 | 85 |
| N-surplus (kg/ha/year) | 380 | 255 | 250 |
| Nitrogen use efficiency, N-export/N-import (%) | 18.3 | 25.0 | 25.4 |
| Animal nutrition costs (NLG/ha/year) | 1340 | 1400 | 1810 |
| N-fertisilation costs (NLG/ha/year) | 370 | 220 | 190 |
| Change in farm income compared to A (NLG/ha/year) | 0 | +120 | -275 |

NLG = Netherlands Guilder, 2.5 NLG = $1 US
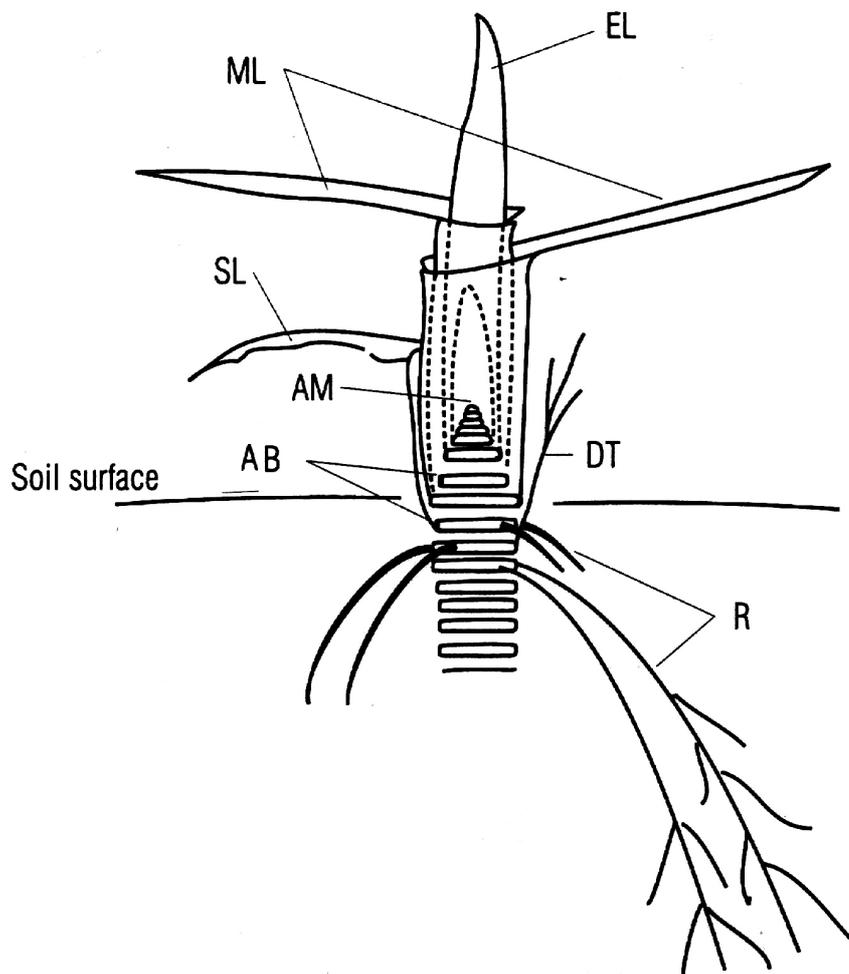
**Figure 1 -** Stylised diagram of a grass tiller showing arrangement of phytomers on the true stem. EL, elongating leaf; ML, mature leaf; AM, apical meristem; AB, axillary bud; R, root. The life cycle of an individual phytomer on the true stem is indicated by the progression of morphological development from top (younger phytomers associated with leaf production ) to bottom (older phytomers associated with root production). (see also Valentine and Matthew, 1999).
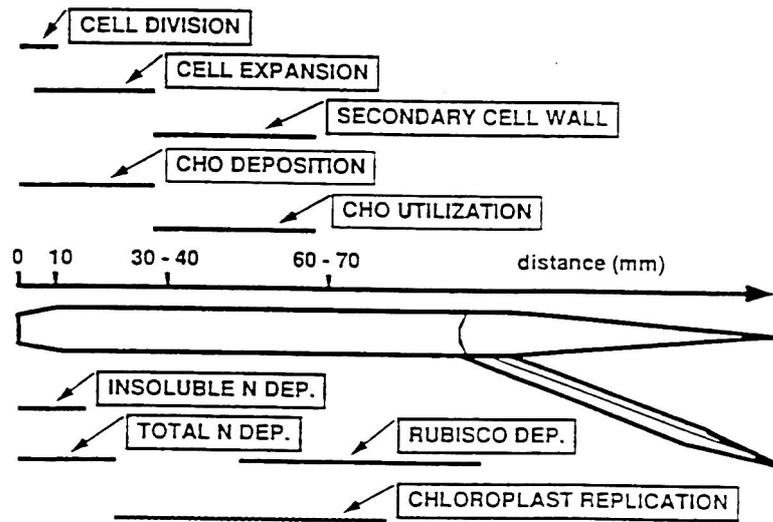
**Figure 2** - Position of growth zones and associated physiological processes during leaf expansion in *F. arundincaea*. (Skinner and Nelson, 1995; reproduced with permission of the editor, *Crop Science*.)
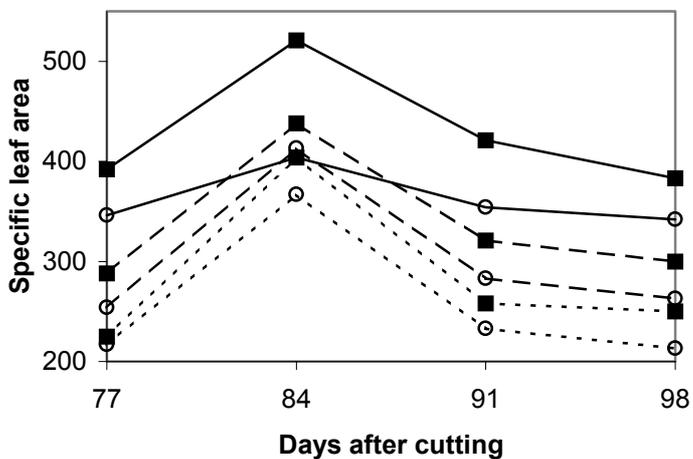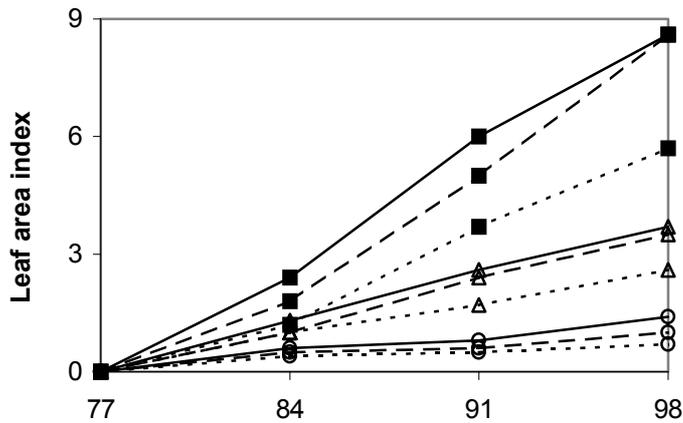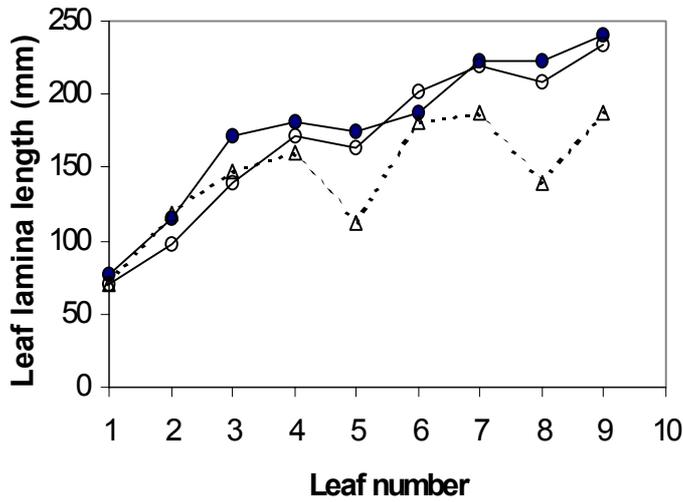
**Figure 3** - (a) Length of successive leaves on the main tiller of *L. perenne* cv. Wendy cut at 3-weekly intervals in a glass house experiment. Symbols indicate cutting height: triangle 25 mm, open circles 50 mm, closed circles 75 mm. Note that successive leaves are normally longer than their predecessor. Arrows indicate leaves cut while still expanding. (b) leaf area index, and (c) specific leaf area ($cm^{-2} g^{-1}$) for miniature swards in a growth cabinet. Symbols indicate a factorial combination of three plant densities and three nitrogen levels (D1, dotted line, 70 seeds $m^{-2}$; D2, dashed line, 280 seeds $m^{-2}$; D3, 1120 seeds $m^{-2}$; open circle, 1.7 g N $m^{-2}$; open triangle 6.7 g N $m^{-2}$; closed square 25.6 g N $m^{-2}$).
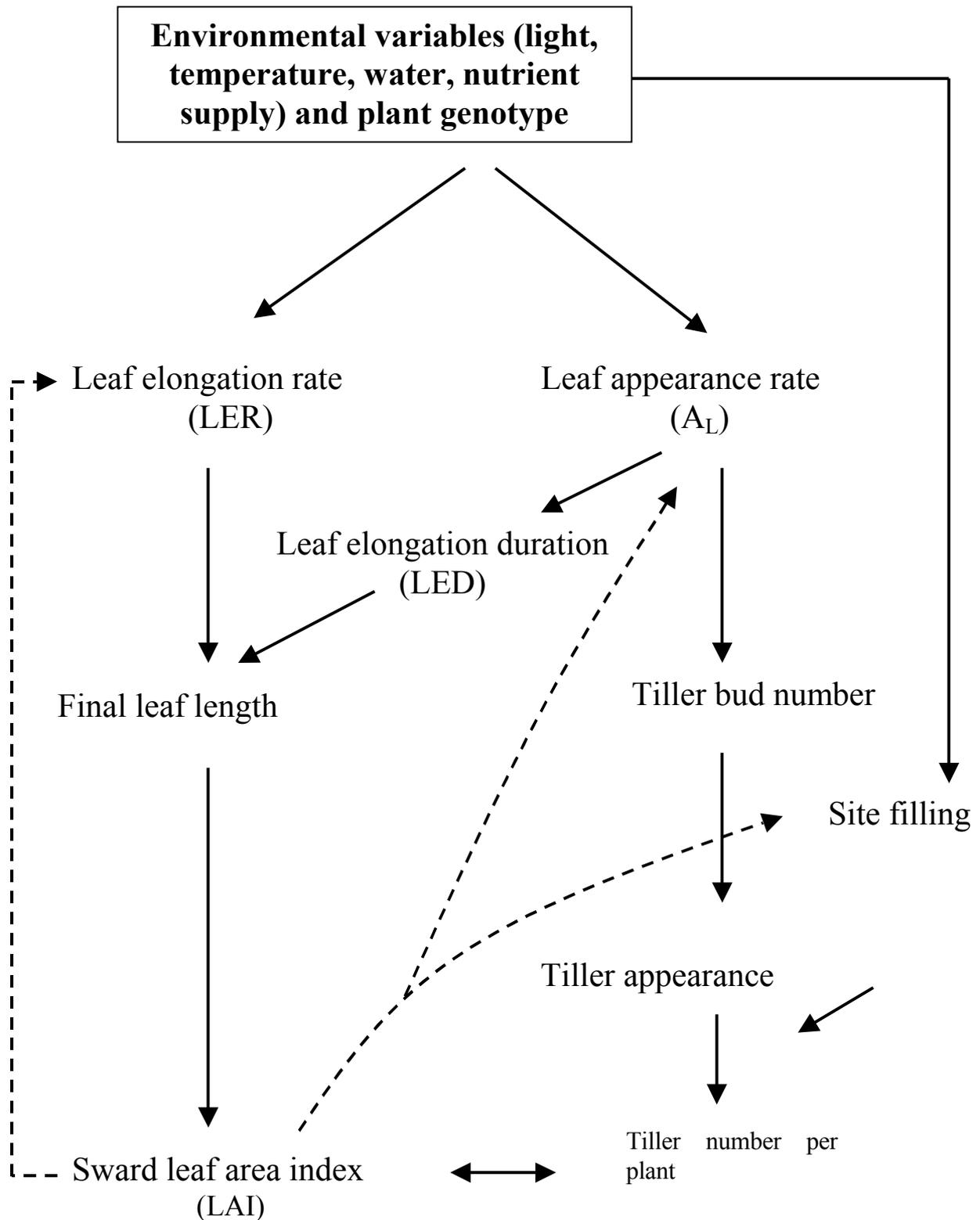
**Figure 4 -** Interrelationship between leaf elongation rate (LER), leaf elongation duration (LED), leaf appearance rate ($A_L$), tiller dynamics and LAI. (Bahmani *et al.*, 2000; reproduced with permission of the editor, Crop Science.)
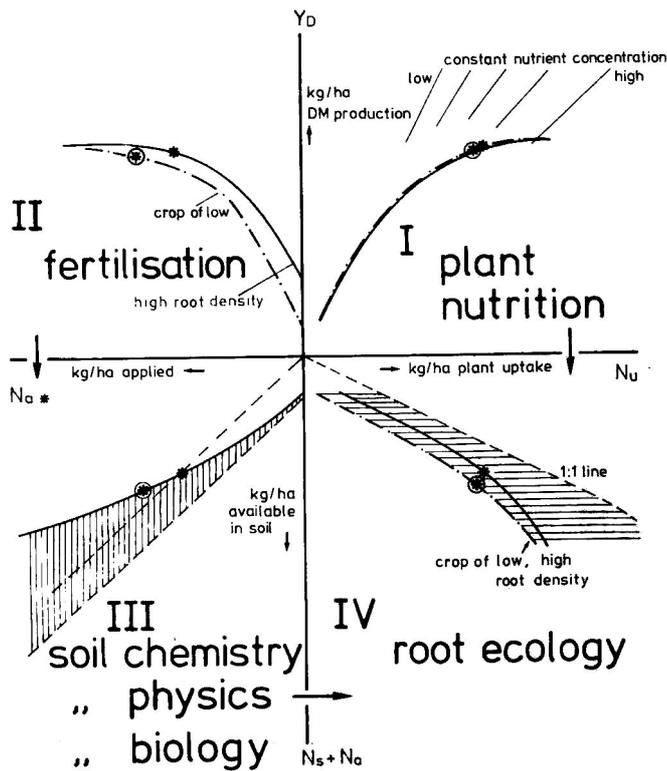
**Figure 5** - Four quadrant scheme for analysis of nutrient response in crops. The bottom left quadrant shows nutrient available to plants as a function of nutrient supplied, reflecting soil biology and soil chemistry factors. The bottom right quadrant shows plant uptake as a function of plant-available nutrient. (De Willigen and Van Noordwijk, 1987)