FACTORS INFLUENCING EAR INITIATION AND EAR EMERGENCE DEVELOPMENT OF PERENNIAL RYEGRASS CULTIVARS AT TWO DIFFERENT LATITUDES

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Abstract

The objective of this study was to define the relationship between ear initiation (EI) and ear emergence (EE) of perennial ryegrass cultivars at two latitudes. This investigation comprised three treatments (outdoor site at 54°N (CROSS'05), outdoor site at 50°N (MPK'06) and glasshouse at 54°N (CROSS'06)) on a common set of 40 cloned spaced plants of eight cultivars. EI date between MPK'06 and CROSS'05 was similar (+/- 1 day) while EI date at CROSS'06 was earlier (-16 days). Plants at MPK'06 had an EE date eight days earlier than plants at CROSS '05 and CROSS'06. The interval between EI and EE was longer at CROSS'06 (+19 days) and CROSS'05 (+6 days) compared to MPK'06. Later heading cultivars had shorter period between EI and EE than earlier heading cultivars. A strong relationship between plant EE and EI was found at Moorepark (r^2 =0.93) and Crossnacreevy (r^2 = 0.94). Predicting cultivar EI date is a key indicator of the timing of sward quality deterioration.

Keywords: perennial ryegrass, cultivars, ear initiation, ear emergence

Introduction

In Irish dairy production systems increased emphasis is being placed on ensuring that the price paid for milk reflects the market returns that can be obtained from that milk in terms of processed products (Kennedy, 2005). It is essential therefore, that milk composition, in particular protein content is maximised. With the onset of lower product prices and the rising production costs, a low cost quality feed must obtain these objectives. During the mid-season period high herd performance can be achieved from an unsupplemented grass based diet (O'Donovan *et al.*, 2004).

During spring, swards change from vegetative to reproductive growth and by the inflorescent period (May/June), the sward is predominately made up of reproductive tillers resulting in sward quality deterioration, which has a negative impact on milk production and milk composition. One of the first morphological signs before the transition to reproductive growth, occurs at the shoot apex where bud primordia develop in the axils of the older leaf primordia to give the shoot apex a 'double-ridge' appearance (Jones & Lazenby, 1988) which occurs during spring. Laredo and Minson (1975) established that the leaves of *Lolium perenne* (perennial ryegrass) had a 20% higher VDMI (voluntary dry matter intake) than the stem fraction even though the DM digestibilities were only slightly higher (67.3 v. 64.8%, respectively). Significant differences for green leaf proportion exist between cultivars with leaf proportions as low as 63% in mid-season and late heading cultivars tending to have a higher leaf content (Gilliland *et al.*, 2002).

While it has been previously documented that reproductive initiation is day length dependant and ear emergence is largely energy dependent, the interaction between growing conditions, genotypes and locations would be expected to provide a better understanding of the relative importance of each factor and could indicate potential strategies for controlling seed head development. The objective of this study was to investigate the effect of latitude and meteorological conditions on the timing of reproductive initiation and seed head development of eight perennial ryegrass cultivars.

Materials and Methods

Experimental Design and Management

The experiment was undertaken at two different latitudes in Ireland over two consecutive years; Northern Ireland Plant Testing Station, Crossnacreevy, Belfast (latitude 54°32'N) during 2005 and 2006, and Moorepark Dairy Production Research Centre, Fermoy, Co. Cork (latitude 50°07'N) during 2006. In 2004, 40 plants of each cultivar (Table 1) were established at 0.75m spacing in an outdoor site at Crossnacreevy. These were vernalised over winter and examinations began in spring 2005 (CROSS'05).

Table 1: Details of Lolium perenne cultivars assessed

25	Cultivar	26	Maturity level
27	**Aberdart**	**28**	**Intermediate**
29	**Fennema**	**30**	**Intermediate**
31	**Corbet**	**32**	**Intermediate**
33	**Aberavon**	**34**	**Late**
35	**Foxtrot**	**36**	**Late**
37	**Mezquita**	**38**	**Late**
39	**Melle**	**40**	**Late**
41	**Twystar**	**42**	**Late**

In the following autumn 2005, two clones of each plant were created by excising two tillers and transplanting them into multipot trays. One set of these plant clones were over wintered in a cool (frost free) glasshouse in multipots and then retained under controlled conditions in the glasshouse until all plants had initiated in spring (CROSS'06). These were then immediately transplanted to an outdoor site. The other set of tiller clones were transplanted at 0.75m spacing to an outdoor site in Moorepark in November 2005 and subsequently vernalised over winter. Examination of these plants began in parallel with the glasshouse experiment during the following spring of 2006 (MPK'06). In total therefore, this investigation comprised three treatments on a common set of 40 cloned plants for each cultivar. The treatments were ambient conditions at 54^{o}N in 2005 (CROSS'05), ambient conditions at 50^{o}N in 2006 (MPK'06) and glasshouse conditions at 54^{o}N in 2006 (CROSS'06).

Plant Measurements

Previous reproductive initiation data for three perennial ryegrass cultivars collected by Camlin (1977), were used to generate an 'ear initiation' (EI) versus 'ear emergence' (EE) regression coefficient. This was used as a guide to calculate an expected EI date for each cultivar in the present study, using their published ear emergence dates. Sampling for EI began in mid March prior to the expected EI date of the earliest cultivar. On alternate days one tiller was removed from each plant and examined under the microscope for reproductive budding as described by Sweet *et al*. (1991). Leaves were removed until the apex was visible under close examination. The presence of a double ridge on the apex indicated that the tiller had initiated or turned reproductive. Examinations continued until all plants had initiated. The mean EI date for each cultivar was then determined.

Critical day length, which is the minimum length of daylight required to trigger the growth of the reproductive apex, was subsequently calculated for each plant. Photoperiodic data at the time of EI were obtained by interpolation of the corresponding latitude (Fig 1) from a table compiled by (Lam, 12 Nov. 2006) who calculated the year-round hours of daylight at five degree latitude intervals. Ear emergence (EE) date was recorded, as the date when three seed heads had visibly emerged on a spaced plant Cooper (1952).

Plant energy requirements were calculated in terms mean daily temperature (>0^{o}C) and photosynthetically active radiation (PAR) from EI to EE. Photosynthetically active radiation is the amount of useable light energy received by a plant and is dependent on light intensity and day length. PAR is a direct measurement of radiation in the wave band 400-700nm measured in MJ $m^{2\,-1}$ day^{-1}.

Statistical Analysis

All statistical analyses were carried out using the statistical package SAS (SAS, 2002). Measurements were subjected to analysis of variance using the following model:

$$Y_{ij} = \mu + S_i + C_j + S_i X C_j + e_{ij}$$

where μ = mean; S_i = site effect (i = 1-3); C_j = cultivar effect (j = 1-8); $S_i X C_j$ = interaction of site and cultivar; e_{ijk} = residual error term.

A linear regression graph was drawn up for Crossnacreevy (54° 32' N) to determine the relationship (R^2) between EE and EI where the ten year average EE date was regressed on EI date (CROSS'05) for each cultivar.

Results and Discussion

Climatic Conditions

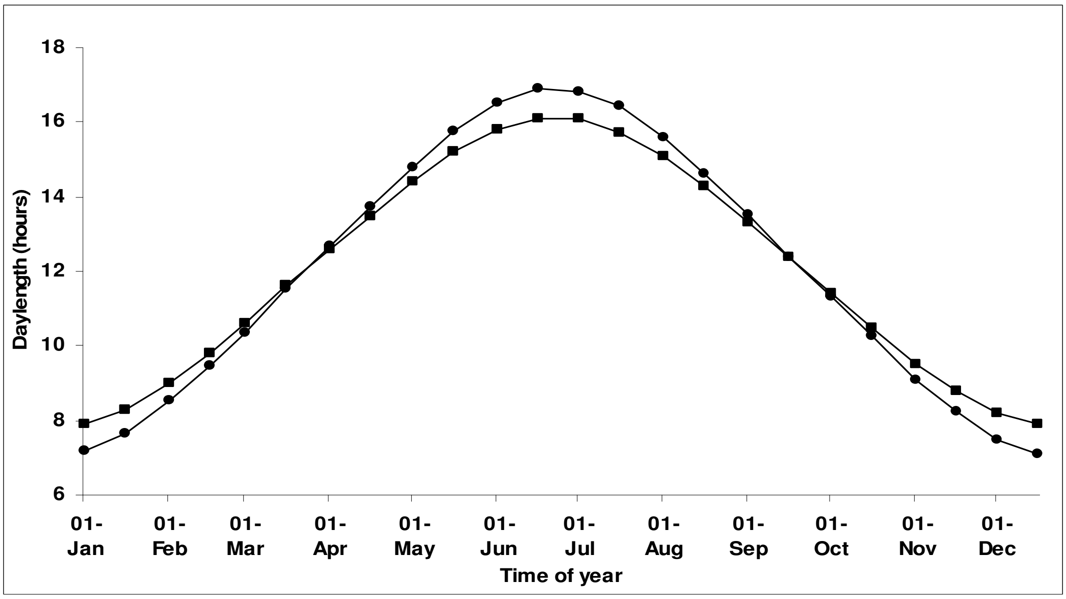
Table 2 shows the total monthly rainfall (mm) and average mean daily temperature (°C) for the three sites during January to June 2005 and 2006. Overall, from January to June, the driest and warmest conditions were in 2006 at Moorepark and the wettest and the coolest conditions were at Crossnacreevy in 2005 and 2006, respectively. These records show, therefore, that the differences in these two key climatic parameters were of sufficient magnitude to induce differential timing of any climatically influenced physiological development.

Table 2: Total monthly rainfall (mm) and mean air temperatures (°C)

43		44	CROSS'05			45	CROSS'06			46	MPK'06		
47		48	Total Rain fall	49	Mean air temp	50	Total Rainf all	51	Mean air temp	52	Total Rainf all	53	Mean air temp
54	Jan	**55**	**96.3**	**56**	**6.1**	**57**	**32.0**	**58**	**5.3**	**59**	**55.2**	**60**	**5.0**
61	Feb	**62**	**47.8**	**63**	**4.8**	**64**	**44.2**	**65**	**4.9**	**66**	**26.3**	**67**	**5.4**
68	Mar	**69**	**72.8**	**70**	**7.1**	**71**	**153.0**	**72**	**4.8**	**73**	**108.1**	**74**	**6.1**
75	Apr	**76**	**84.0**	**77**	**7.5**	**78**	**59.9**	**79**	**7.5**	**80**	**29.3**	**81**	**8.5**
82	May	**83**	**88.6**	**84**	**9.7**	**85**	**106.5**	**86**	**10.4**	**87**	**115.2**	**88**	**10.8**
89	June	**90**	**40.8**	**91**	**14.1**	**92**	**40.6**	**93**	**14.3**	**94**	**13.7**	**95**	**15.0**
96		**97**		**98**		**99**		**100**		**101**		**102**	
103	Mean	**104**	**78.1**	**105**	**8.2**	**106**	**72.7**	**107**	**7.8**	**108**	**58.0**	**109**	**8.5**

In addition to climatic variation, differences in latitude between the two experimental sites provided an additional factor in this investigation. Fig 1 shows the magnitude of difference in day length between the two trial sites caused by their difference in latitude. The southern site (Moorepark) has longer day lengths in the winter period than the northern site (Crossnacreevy), but this is reversed in the summer period. Production of this day length correction graph for these two sites allowed the influences of differences in accumulated climatic conditions at the two sites to be separated from the influences of differences in day length, so facilitating an assessment of which parameter EI and EE were most influenced.

Figure 1: Hours of daylight (day length) at Crossnacreevy (54°N) • and Moorepark (50°N) ▪



Ear Initiation

Table 3 shows the EI date and critical day length of each cultivar at each site. The average EI date between CROSS'05 and MPK'06 was similar (+/- 1 day) while the average EI date at CROSS'06 was much earlier; 16 and 15 days earlier than the EI date at CROSS'05 and MPK'06 respectively. There was a significant (P<0.001) site by cultivar interaction for EI date which was due to the large difference in the EI date (14 – 20 days) of each cultivar between the three sites. The average critical day length between CROSS'05 and MPK'06 was similar (+/- 0.4 hour) but was significantly less at CROSS'06 than CROSS'05 (-1.2 hours) and MPK'06 (-0.8 hours). Critical day length was significantly different (P<0.001) between sites however these differences were very small (≤ 1.2 hours) and so were in practical terms of little consequence. Data were sensitive to analysis due to the large number of replicate plants used. This can also be said of the significant (P<0.001) interaction between site and cultivar for EI critical day length, which was a result of a small yet significant range in day length hours (1.0 - 1.4) between cultivars at the three sites.

Table 3: Ear initiation dates and EI critical day lengths of eight test cultivars at three sites

	EI date				EI Critical day length (hours)			
Cultivar	CROSS '05	CROSS '06	MPK '06	Range (days)	CROSS '05	CROSS '06	MPK '06	Range (hours)
AD	30 Mar	15 Mar	4 Apr	20	12.7	11.5	12.8	1.3
FN	1 Apr	17 Mar	3 Apr	17	12.8	11.7	12.8	1.1
CB	13 Apr	29 Mar	17 Apr	19	13.6	12.6	13.5	1.0
AV	14 Apr	31 Mar	12 Apr	14	13.7	12.6	13.3	1.1
FX	20 Apr	4 Apr	17 Apr	16	14.2	13.0	13.6	1.2
MZ	22 Apr	6 Apr	18 Apr	16	14.3	13.1	13.7	1.2
ML	30 Apr	11 Apr	27 Apr	19	14.9	13.5	14.2	1.4
TR	2 May	12 Apr	28 Apr	20	15.0	13.6	14.3	1.4
Mean	*16-Apr*	*31-Mar*	*15-Apr*	*18*	*13.9*	*12.7*	*13.5*	*1.2*
SED	1.16				0.076			
S	***				***			
C	***				***			
S*C	***				***			

AD = Aberdart; FN = Fennema; CB = Corbet; AV = Aberavon; FX = Foxtrot; MZ = Mezquita; ML = Melle; TR = Twystar; EI = Ear initiation; S = site; C = Cultivar; SED = Standard Error of Difference, *** = P<0.001

While it is has been previously documented that photoperiod determines the initiation date (Evans, 1964), the effect of temperature during the early growth stages of the stem apex may have had a minor influence on EI. Temperature was not measured in the glasshouse however it can be safely assumed that temperatures in the glasshouse were higher than the outdoor conditions at Crossnacreevy in 2006. This may have accelerated EI at CROSS'06 compared to EI at the other two sites. According to Evans (1964) temperatures within the range of -6°C to about 14°C are required for vernalization, therefore it is safe to say that glasshouse temperatures were within this range or above the lowest threshold. According to Keatinge *et al.* (1979) increased temperature may stimulate initiation at an earlier stage by controlling the growth rate of the stem apex. Higher glasshouse temperatures may have therefore accelerated the growth of the stem apex, resulting in an earlier EI date at CROSS'06.

There was also a significant (P<0.001) difference in the EI date between cultivars at each site however prior to the commencement of the experiment cultivars were paired with similar heading dates thus pairs generally initiated together, which suggests a strong relationship between the EI and EE dates. All cultivars had a significantly lower critical day length requirement at CROSS'06 than the other two sites. Grass species vary in their day length requirements for inflorescence initiation. *Lolium perenne* is an obligate long-day plant (Evans, 1964), flowering only when the photoperiod exceeds a critical day length (Cooper, 1952; Cooper, 1960), while other species respond to short day length exposure. Work by Gangi (1983) has concluded that different cultivars of perennial ryegrass have different requirements for vegetative and reproductive growth and development.

Ear Emergence

As stated, day length is the most decisive component affecting inflorescence initiation. Once floral initiation is attained the subsequent rate of elongation of the fertile shoot and inflorescence development is controlled by spring temperatures, however for each cultivar there is a minimum time from ear initiation to ear emergence, under optimum temperature and photoperiod (Cooper, 1952).

Ear emergence was six days later at CROSS'05 than MPK'06 with CROSS'06 intermediate between these two sites (Table 4). Latitude had a large effect on the EE date as the rate of ear development is strongly influenced by temperature. Cooper (1952) demonstrated a close relation between spring temperatures and the date of ear emergence in perennial ryegrass. A transition to long days and higher temperatures is usually needed for heading and anthesis (Heide, 1994). There were large differences between latitude for temperature and light intensity, which will be discussed later. There was no significant difference in the EE date of six cultivars between MPK'06 and CROSS'06 however Fennema and Foxtrot were significantly (P<0.001) different. Plants at CROSS'06 were transplanted to an outdoor site after EI, and as the rate of ear development is largely influenced by spring temperature (Cooper, 1952), higher indoor spring temperatures prior to EI would have triggered an earlier EE date.

Table 4: Ear emergence (EE) dates and number of days between EI and EE of eight test cultivars

	EE date				EI – EE (days)			
Cultivar	CROSS '05	CROSS '06	MPK '06	Range (days)	CROSS '05	CROSS '06	MPK '06	Range (days)
AD	31 May	27 May	24 May	7	61	73	50	23
FN	29 May	28 May	23 May	6	58	72	50	22
CB	6 June	3 June	31 May	6	55	65	45	20
AV	9 June	5 June	2 June	7	56	67	50	17
FX	7 June	5 June	31 May	7	47	62	44	18
MZ	10 June	6 June	3 June	7	49	61	46	15
ML	16 June	11 June	9 June	7	47	61	43	18
TR	17 June	12 June	9 June	8	46	61	42	19
Mean	*7 Jun*	*4 Jun*	*1 Jun*	*6.9*	*52*	*65*	*46*	*19*
SED	1.48				1.40			
S	***				***			
C	***				***			
S*C	NS				***			

AD = Aberdart; FN = Fennema; CB = Corbet; AV = Aberavon; FX = Foxtrot; MZ = Mezquita; ML = Melle; TR = Twystar; EE = Ear emergence; EI = Ear initiation; S = site; C = Cultivar; SED = Standard Error of Difference, *** = P<0.001; NS = Non Significant

There was a significant (P<0.001) site by cultivar interaction for the number of days between EI and EE, which is due to the large difference in days between EI and EE (15 - 23) of each cultivar between the three sites (Table 4). CROSS'06 had significantly more (+13) days between EI and EE than CROSS'05, both of which are at the same latitude which is a result of an earlier EI date at CROSS'06 (-16 days). The southern site (MPK'06) had the shortest period between EI and EE (19 days less than CROSS'06) for the production of reproductive material. The number of days between EI and EE of several perennial ryegrass cultivars measured by Keatinge (1979) was between 50 to 70 days with later heading cultivars having a shorter period between EI and EE. A large difference existed between cultivars with later heading cultivars tending to have a shorter time interval between EI and EE than earlier heading cultivars. To increase sward quality late heading cultivars would therefore be more advantageous as the sward is in a reproductive growth mode for a shorter period than earlier heading cultivars.

Mean daily temperature (°C) and mean daily PAR were significantly (P<0.001) different between site and cultivar (Table 5). Mean daily temperature (°C) and PAR increased with cultivar maturity, that is, the later heading cultivars received more plant energy within a shorter period than earlier heading cultivars.

There was no significant difference in mean daily temperature and PAR between CROSS'05 and CROSS'06 during EI to EE; however both sites were significantly different to MPK'06, which had significantly greater values. Work by Hennessy (2005) has shown that greater mean daily temperatures increase the leaf appearance rate and leaf extension rate resulting in a greater leaf content and higher DM yields. Schapendont *et al.,* (1998) also agreed with this where an increase in temperature had a positive effect on yield and was obvious at more southerly latitudes. Johnson and Thornley (1983) found that an increase in the incident light flux density causes an increase in photosynthesis and hence greater yield. In conclusion, the southern site, MPK'06 had a greater mean daily temperature and greater mean daily radiant exposure (PAR), both of which have a positive impact on leaf content and DM yield. Later heading cultivars also had higher values than earlier heading cultivars during a shorter period (EI – EE).

Table 5: Daily mean energy requirements between EI and EE of eight test cultivars

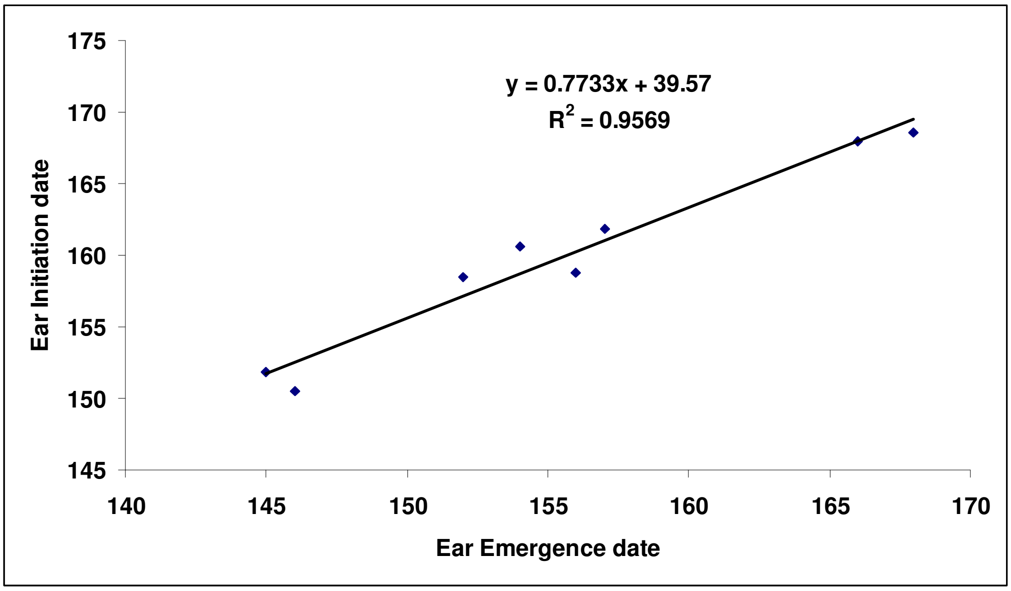
	Daily mean temperature (°C)				Daily mean PAR (MJ m^{2-1} day^{-1})			
Cultivar	CROSS '05	CROSS '06	MPK '06	Range	CROSS '05	CROSS '06	MPK '06	Range
AD	8.9	8.4	10.1	1.7	6.7	6.1	8.9	2.8
FN	8.9	8.9	10.1	1.2	6.8	6.2	8.7	2.5
CB	9.8	9.5	11.0	1.5	7.1	7.0	9.4	2.4
AV	10.0	9.6	10.9	1.3	7.2	7.2	9.4	2.2
FX	10.4	9.8	11.0	1.2	7.5	7.3	9.4	2.1
MZ	10.4	10.1	11.5	1.4	7.4	7.4	9.8	2.4
ML	11.2	10.9	12.1	1.2	7.4	7.7	11.0	3.6
TR	11.2	11.0	12.5	1.5	7.6	7.7	11.0	3.4
Mean	*10.1*	*9.8*	*11.2*	*1.4*	*7.2*	*7.1*	*9.7*	2.6
SED	0.154				0.121			
S	***				***			
C	***				***			
S*C	NS				***			

AD = Aberdart; FN = Fennema; CB = Corbet; AV = Aberavon; FX = Foxtrot; MZ = Mezquita; ML = Melle; TR = Twystar; EI = Ear initiation; EE = Ear emergence; PAR = Phototsynthetically active radiation; S = site; C = Cultivar; SED = Standard Error of Difference, *** = P<0.001; P<0.05

Relationship between EI and EE date

A linear regression line was drawn up to demonstrate the EI to EE relationship at Crossnacreevy using outdoor plant EI date data (CROSS'05) and the ten year average EE date (personal communication) for each cultivar. A strong relationship between plant EE and EI was found at Crossnacreevy (R^2 = 0.96; Fig. 2). Given such a strong relationship, the regression line and/or predicted equation of the EE/EI correlation can be used to determine the EI date for any perennial ryegrass cultivar using a known EE date at the corresponding latitude.

Figure 2: Relationship between ear emergence (EE) and ear initiation (EI) of eight cultivars at Crossnacreevy (54° 32' N) based on ten year average EE date



Conclusion

Maintaining high quality herbage is imperative in increasing animal output and performance mid-season. A good understanding of sward physiological changes throughout the growing season and the factors affecting these changes is vital in minimizing herbage deterioration. Large variation for plant initiation exists between cultivars which is largely influenced by latitude and day length. Predicting cultivar EI date will determine when swards change from vegetative to reproductive growth. Day length is the principal factor influencing plant initiation and therefore cannot be controlled; however by combining this information on the timing of plant initiation date with appropriate spring grazing management may help reduce sward quality deterioration mid season. In Ireland the Irish recommended cultivar list evaluates cultivars on DM yield, yet no information on sward quality is available, a factor which has a substantial impact on animal intake and production. Sward quality reduction is associated with increasing sward maturity; therefore cultivar heading date is the only indicator of cultivar sward quality. The date of ear initiation is the date when growth changes from vegetative to reproductive and there is a rapid increase of poorly digestible reproductive material in the sward. Predicting the EI date of various cultivars is a key indicator of the timing of sward quality deterioration, and this information can be incorporated into a sward management plan so as to improve herbage quality mid season. Cultivar choice may also have a positive effect on mid-season sward quality as later heading cultivars tend to have a shorter period (EI-EE) for the production of reproductive material.

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