

Growth, Development and Yield Determination in Barley

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Introduction

In a typical spring barley the accumulation of dry mass (growth) commences slowly with the emergence of the coleoptile and increases exponentially until physiological maturity (Fig. 1). During that interval crop growth is characterized by an orderly sequence of ontogenic events (development), such as coleoptile emergence, floral initiation and anthesis (Fig. 2). These events precipitate the coordinated initiation, appearance and growth of tissue structures (such as leaves, stems, spikes and grain) characteristic of the mature plant. The timing of developmental events, together with rates of tissue structure initiation and appearance, determines the manner in which accumulating dry mass is partitioned into those structures and, to the proportion stored as grain (Figs. 1 & 2). Cultivar and growing season conditions impact on developmental progress, on growth and the manner of its partitioning. From an analysis of the latter the determination of yield involves three component steps. These are:

- The development a vegetative foundation for future yield determination over the vegetative phase.
- The translation of that vegetative foundation, over the pre-anthesis stage of the reproductive phase, to actual yield potential at the time of anthesis.
- The realization of yield potential over the post-anthesis stage of the reproductive phase.

This paper quantifies the numerous factors contributing to the accumulation and partitioning of dry matter among commercially available barley cultivars differing substantially in their phenology and in their agro-ecological regions of adaptation in Western Australia.

Materials and Methods

Plant growth and developmental progress were examined by frequent sampling from five replicated field trials over four growing seasons. All trials were sown in the interval of late May/early June under conditions of high soil fertility and at a density of 100 plants m⁻². At a wheatbelt location in 1994 and 1995 heavy opening rainfall ensured a fully charged soil profile at the time of sowing. With limited winter rainfall in 1994 soil moisture deficiency intensified from the time *cv.* Stirling was approaching anthesis. The 1995 season was very different. Persistent winter rainfall resulted in saturated soils until shortly before anthesis in *cv.* Stirling. With ample soil moisture reserves, and below average temperatures thereafter, physiological maturity occurred a month later. To overcome the confounding of soil moisture related problems, the 1996 and 1997 trials were located on the UWA Field Station in Perth (a coastal location) where, on a free draining soil with the availability of irrigation and higher but less extreme temperatures, the inherent potential of cultivars was more fully expressed.

Results

a. Development of vegetative foundation for future yield

During the vegetative phase, from sowing (S) to coleoptile emergence (CE) and CE to floral initiation (FI), the barley plant initiates its total complement of leaves and primary tillers (Fig. 2). The mean duration of this phase varied with cultivar and to a greater extent with season (Table 1). Variation in temperature and radiation, together with cultivar differences in the timing of FI and leaf sizes, were considered the primary factors responsible for mean cultivar differences recorded for canopy development (LAI), shoot numbers and dry mass at FI.

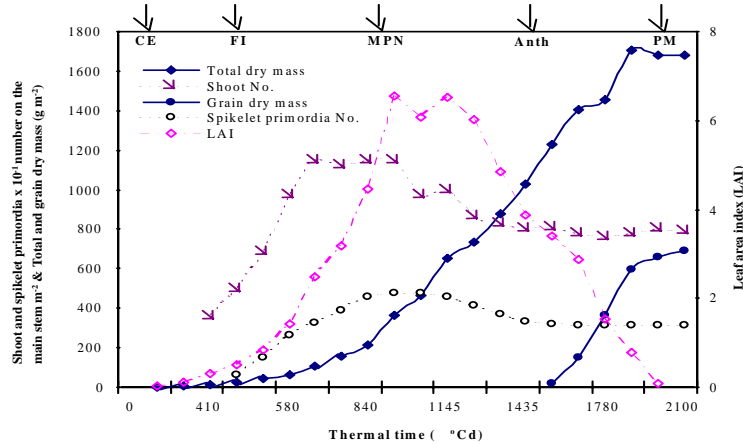


Figure 1: The seasonal pattern of shoot and spikelet primordia production and survival, leaf area index expansion and senescence, dry matter accumulation and grain growth of a crop of barley *cv.* Stirling grown under non-limiting conditions at Perth, Western Australia in 1996. CE = coleoptile emergence, FI = floral initiation, CSE = commencement of stem elongation, MPN = maximum primordia number, Anth = anthesis, PM = physiological maturity.

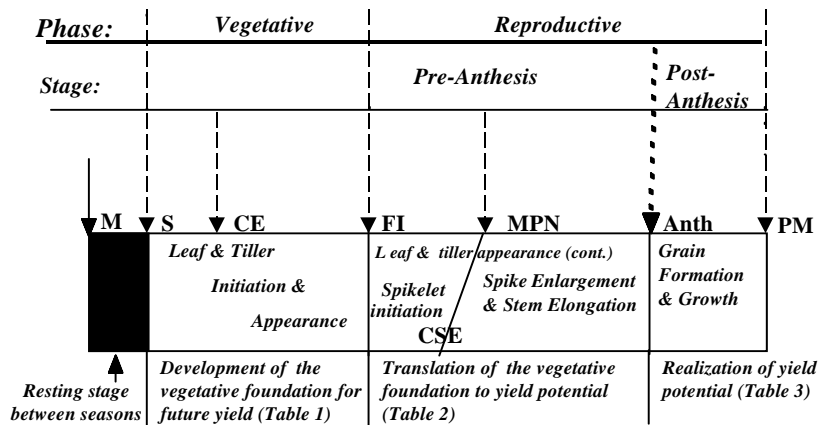


Figure 2: Life-cycle of a typical spring barley plant: S = sowing, CE = coleoptile emergence, FI = floral initiation, CSE = commencement of stem elongation, MPN = maximum primordia number, Anth = anthesis, PM = physiological maturity.

(Adapted from Boyd, 1996)

b. Translation of vegetative foundation to actual yield potential at anthesis

The interval from FI to anthesis comprises two sub-stages. During the first (FI to MPN = maximum primordia number) spikes are formed and, during the second (MPN to Anthesis), those spikes grow in size concurrently with the elongation of the stem internodes subtending them (Fig. 2). Mean cultivar differences in the duration to FI (vegetative phase) expanded over the interval from FI – Anthesis and, unlike seasonal differences, were significantly correlated with one another (Table 2). Mean leaf area indices, shoot numbers and dry masses increased slowly during spike formation but exponentially thereafter (Fig. 1), with variation due to seasons greater than variation among cultivars. Similar comments apply to the rates of stem elongation and tiller appearance but not, spikelet primordia number. The imbalance between the exponential increases in LAI (= assimilate supply) and growth (= assimilate demand) generated competition between and within plants and tillers, restricting the number of fertile spikes and spikelets at anthesis to about 60% of the maximum formed; irrespective of dry mass (Fig. 1 and Table 2). Seasonal, but particularly, cultivar differences in dry mass at FI were reflected in dry mass at anthesis; indicating dominant influences of cultivar, temperature and radiation on dry matter accumulation over the pre-anthesis stage.

Table 1 : Season and cultivar means for measures of thermal durations ($^{\circ}\text{Cd}$), leaves, shoot and dry mass over the vegetative phase (S – FI). It is over this interval that the vegetative foundation for future yield is established. Temp = mean for temperature, PTQ = photo-thermal quotient, S = sowing, CE = coleoptile emergence, FI = floral initiation, LN = leaf number on the main stem, LAI = leaf area index, DM = dry mass.

<i>Variation</i> <i>due to:</i>	Temp $^{\circ}\text{C}$	PTQ MJ/ $\text{m}^2 \cdot ^{\circ}\text{C}$	Duration ($^{\circ}\text{Cd}$)			LN FI	LAI FI	Shoot/ plant FI	DM g/m^2
			S - CE	CE - FI	S - FI				
Seasons									
1994	12.2	0.8	102	358	460	5.0	0.68	4.9	36.0
1995	10.7	0.7	110	276	387	4.0	0.38	3.7	18.0
1996	13.6	0.6	120	306	426	4.2	0.49	3.3	22.3
1997a	15.6	0.6	117	390	506	4.6	-	4.5	30.1
1997b	15.5	0.6	108	406	514	5.2	-	5.3	57.9
Cultivars									
Unicorn	13.9	0.6	113	307	420	4.0	0.28	3.4	23.4
Stirling	13.5	0.7	111	338	450	4.7	0.50	4.0	28.6
Harrington	13.0	0.7	111	350	460	4.8	0.74	4.6	42.3
Skiff	13.4	0.7	110	393	503	4.9	0.38	5.3	40.8

c. Realization of actual yield potential at the time of maturity

In the interval from anthesis to maturity grains form and grow in size (Figs. 1 and 2). The duration of this interval varied minimally with cultivar but greatly with season. Plant dry mass doubled, with contributions from current photosynthesis supplemented by the translocation of stored reserves as canopy senescence increased (Fig. 1 and Table 3). Seasonal and cultivar differences in dry mass at maturity was strongly correlated with dry masses at anthesis but not, with either grain yield or harvest index. This reflex the influence of temperature, evaporative demand and soil moisture availability on the realisation of potential yield.

Conclusions

- Relative to growing season duration the timing of anthesis is a major factor determining the adaptation of cultivars and their classification into developmental groupings. Although correlated with the duration to FI, cultivar differences in the timing of anthesis were significantly greater due to subtle variation in the duration of sub-stages over the interval from FI to Anthesis.
- Developmental differences within cultivar groupings were inconsistently expressed due to interactions with transient and unpredictable variations in seasonal weather conditions. Such differences are of value in retrospectively explaining cultivar differences in performance but, of limited value as selection criteria or for predictive purposes.
- With results of any single trial reflecting specific adaptation to the seasonal weather conditions experienced, selection in early generations is therefore opportunistic, with recommendations unreliable unless replicated over a realistic number of seasons.

References

- Boyd, W. J. R. (1996): In: Barley genetics VII. Proc. 7th Int. Barley Genet. Symp., Saskatoon, Canada. pp. 276-283
- Jalal Kamali, M. R. (1999): Ph. D. Thesis (submitted), The University of Western Australia. pp. 380.

Table 2: Season and cultivar means for measures of thermal durations ($^{\circ}\text{Cd}$), leaves, shoot and spikelet, and dry mass over the spike formation stage (FI - MPN) and spike/stem growth (MPN – Anth) sub-stages. It is over these intervals that the vegetative foundation at FI is translated into actual yield potential at anthesis. Temp = mean for temperature, PTQ = photo-thermal quotient, S = sowing, FI = floral initiation, MPN = maximum primordia number, Anth = anthesis, LN = leaf number on the main stem, LAI = leaf area index, RCE = rate of canopy expansion ($\text{LAI}/^{\circ}\text{Cd}$), TI = tiller interval ($^{\circ}\text{Cd}/\text{tiller}$), TS = tiller survival (%), DM = dry mass.

<i>Variation due to</i>	Temp $^{\circ}\text{C}$	PTQ $\text{MJ}/\text{m}^2 \cdot ^{\circ}\text{C}$	Duration ($^{\circ}\text{Cd}$)			LN MPN	Canopy		Shoot/plant			RSE $\text{mm}/^{\circ}\text{Cd}$	Spikelet		DM g/m^2		
			FI - MPN	MPN - Anth	S - Anth		LAI	RCE $\times 10^2$	TI	No	TS		No.	SS	MPN	Anth	
Seasons																	
1994	12.7	1.3	294	374	1128	8.3	2.8	1.02	84	7.2	56	-	-	223	709		
1995	11.0	1.0	292	466	1144	7.3	1.6	0.37	100	5.0	75	-	-	123	427		
1996	13.7	0.7	428	559	1414	8.7	4.8	1.35	36	8.7	64	1.8	45	65	261	782	
1997a	13.2	1.0	413	519	1439	8.7	-	-	54	9.0	59	1.6	43	61	260	830	
1997b	12.4	0.9	396	527	1380	9.2	-	-	45	9.6	55	1.4	46	64	439	1013	
Cultivars																	
Unicorn	12.3	0.9	318	460	1198	7.7	2.6	0.95	63	7.5	63	1.9	46	62	208	623	
Stirling	12.5	0.9	364	490	1290	8.7	2.8	0.84	67	7.4	67	1.6	41	63	249	750	
Harrington	12.6	1.0	399	467	1305	8.9	4.0	1.40	70	7.1	61	1.5	50	67	338	840	
Skiff	12.6	1.1	368	543	1395	8.4	2.0	0.59	59	9.5	57	1.2	45	61	263	781	

Table 3: Season and cultivar means for measures of thermal durations ($^{\circ}\text{Cd}$), leaves, shoot and spikelet, and dry mass over the post-anthesis interval (Anth – PM). It is over this intervals that the potential yield at the time of anthesis is translated into realizeable yield at maturity. Temp = mean for temperature, PTQ = photo-thermal quotient, S = sowing, AA = awn appearance, Anth = anthesis, LN = leaf number on the main stem, MLAI = maximum leaf area index, RCS = rate of canopy senescence ($\text{LAI}/^{\circ}\text{Cd}$), MShn = maximum shoot number, PT = primary tiller, FShn = fertile shoot number, DM = dry mass, GY = grain yield, HI = harvest index.

<i>Variation</i> <i>due to</i>	Temp °C	PTQ MJ/m ² .° C	Duration ($^{\circ}\text{Cd}$)		LN AA	Canopy		Shoot number/plant			DM (g/m ²)	GY (g/m ²)	HI (%)
			S - PM	Anth - PM		MLAI	RCS x 10 ²	MS hn	PT	FShn			
<i>Seasons</i>			-	-	-	-	-	-	-	-	-	-	-
1994	21.6	1.50	1657	528	12.0	5.36	0.91	10.2	4.0	5.5	1234	472	38
1995	14.2	1.48	1826	683	11.0	2.49	0.30	5.5	3.2	4.2	1050	503	48
1996	15.0	1.27	1983	569	12.3	7.24	0.83	9.8	4.7	6.2	1433	653	43
1997a	15.9	1.27	2117	679	11.8	-	-	10.3	4.0	6.0	1653	615	38
1997b	15.9	1.28	2020	640	12.0	-	-	11.6	-	6.5	1718	670	39
<i>Cultivars</i>													
Unicorn	14.1	1.25	1812	614	11.3	4.91	0.60	9.0	4.0	5.5	1335	582	45
Stirling	16.8	1.38	1925	635	12.0	4.83	0.64	9.3	3.9	5.9	1410	559	40
Harrington	17.0	1.40	1938	634	11.8	5.49	0.75	8.3	3.9	5.0	1466	604	40
Skiff	17.5	1.40	2007	612	11.8	3.48	0.52	11.0	3.8	6.0	1445	594	43