GRAIN GROWTH WITHIN OAT PANICLES

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Abstract

Mean individual grain weight of main stems from the forage oat (*Avena sativa*) 'Cashel' was 15% higher than from the milling oat 'Drummond', due to faster ($P<0.01$) grain growth rates for a similar growth duration (920 ^oCd). However, 'Cashel' had fewer ($P<0.01$) spikelets per panicle (22.4) than 'Drummond' (29.4). Primary grains also had faster ($P<0.01$) growth rates and were heavier ($P<0.01$) than secondary grains for both cultivars giving bimodal grain weight distributions. Floret and spikelet removal at anthesis showed mean grain weights could be increased by about 15% but the primary:secondary grain weight ratio was constant at 1.5. It was concluded that agronomic treatments are unlikely to reduce grain weight variability within oat crops. Selection for single grains per spikelet and increased spikelets per panicle may reduce variability in grain weight.

Keywords: Avena sativa, florets, spikelets

Grain growth of cereal crops occurs in three recognised phases. Post-anthesis there is a short lag phase, then an increase at a near linear rate to a maximum dry weight, or physiological maturity, followed by the maturation phase (6). The final grain dry weight within and between crops can be quantified in terms of differences in the duration of the lag and linear phases, and the rate of grain filling during the linear phase.

Grain weight is also dependent on environmental and genetic influences (10) and has been shown to differ at different spikelet positions within wheat (1) and barley (5) ears. However, in the absence of environmental stress the frequency distribution of individual grain weights from wheat (9) and barley (3) is approximately normal. In contrast, oats produce a bimodal distribution of grain weights with heavier primary than secondary grains (2). This bimodal distribution creates inefficiency in processing oat crops (4) and as seed, the smaller secondary grains have less seedling vigour and grain yield (11). Therefore, the first objective of this study was to identify the components of primary and secondary grain growth that cause different final grain weights. The second objective was to determine whether mean grain weights were altered by changing the sink demand with post anthesis removal of different proportions of florets and spikelets within oat panicles. This may allow physiologically based agronomic practices or plant breeding strategies to be identified to reduce grain size variability.

Materials and methods

A field experiment was sown on 20 September 1996 at Crop and Food Research, Lincoln, New Zealand (43^o, 36'S) in a Templeton silt loam. Two oat cultivars were sown to establish a population of 300 plants/m^2. Cashel is a tall early maturing cultivar used for winter forage. Drummond is a semi-dwarf, late maturing cultivar used for milling. Crop management aimed to maximise crop yield, with 90 kg N/ha^1 applied as Urea on 23 October and sprinkler irrigation as necessary to prevent moisture stress.

The experiment was a randomised complete block with two cultivars and three replicates. Plots were 1.5 m wide by 13 m long. Floret/spikelet removal was random within each plot.

Treatments

Floret removal involved cutting the ranchilla of the secondary floret (SF) or removing the anthers, stigma, lemma and palea of the primary florets (PF) within each spikelet. Within plots, four mainstem panicles were randomly selected, spikelet number counted, and a percentage of florets removed; 1) 100% PF / 0% SF, 2) 50% PF / 50% SF, or 3) 0% PF / 100% SF which left one grain per spikelet.

Spikelet removal at anthesis, involved randomly cutting 0, 25, 50 or 75% of the spikelets from the main stem panicle of four plants per plot, leaving two grains per spikelet. For ‘Cashel’ there was about 23 spikelets per panicle compared with 29 for ‘Drummond’. For ‘Cashel’, both treatments were applied when the anthers of the most developed (apical) spikelet had dehisced (anthesis), but was delayed 2-3 days for ‘Drummond’ to allow the base of the panicle to emerge.

Measurements

Primary and secondary grain growth was measured twice weekly from anthesis by cutting five main stems at ground level from each plot. Plants were separated into stem, leaves and grains and dried at 80 ^{o}C to constant weight. Harvests continued until physiological maturity when plants from the spikelet and floret treatments were also harvested.

Statistical analysis

Grain growth over thermal time, was analysed by fitting generalised logistic or Gompertz functions with the Maximum Likelihood Program (8). From the functions, maximum grain weight (MGW), mean growth rate over the linear phase (5 - 95% of MGW), and the duration of the lag (0 - 5% of MGW) and linear phases were derived. Analysis of variance was used to compare cultivar, replicate and grain class on these parameters.

Results and discussion

The time course of grain growth had lag, linear and maturation phases (Fig. 1), which was consistent with previous studies for other cereals (6). Logistic curves fitted the observed data to within 3 mg throughout the linear phase for both cultivars and grain classes. MGW of both primary and secondary grains from ‘Cashel’ was about 15% heavier than those from ‘Drummond’ (Table 1).

The heavier grains from ‘Cashel’ resulted from higher ($P<0.01$) growth rates for a similar grain filling duration (Table 1). This was consistent with the mechanism reported for grain size differences for wheat (6). However, in contrast to wheat there was also a difference ($P<0.01$) in the MGW of grains from primary and secondary florets from both oat cultivars (Table 1). The primary grains were about 33% heavier than the secondary grains, giving a primary:secondary grain weight ratio of about 1.5, consistent with those previously calculated (11). The difference in final grain weight was almost entirely due to the faster ($P<0.01$) growth rates of primary grains (Table 1). The implication was that the bimodal grain weight distribution (2) resulted from differences in grain growth rates and not the duration of growth. Indeed, the duration ($t_b = 0$) from anthesis to physiological maturity was similar for both primary and secondary grains of each cultivar (Table 1).

Reducing grain number to one per spikelet did result in increased grain weights. Removal of all primary or secondary florets increased the remaining grain weights by about 5 mg (Table 2). Given that all plants reached anthesis and were harvested at the same time, the increase in final grain weights can also be attributed to increased grain growth rates and not differences in duration. The implication was that under optimal conditions the untreated plants failed to achieve their maximum potential grain weight.

The 50% PF/ 50% SF treatments produced an equal magnitude of increase in grain weight, leaving the grain weight ratio unchanged at 1.5. The symmetry of this response suggests the grain weight distribution remains bimodal with only a change in mean grain weight. Crampton *et al*. (2) observed this effect for spring and autumn sown crops.

The maximum increase in primary and secondary grain weight from spikelet removal was about 4 mg for 50% spikelet removal (Table 3). For this treatment grain number per panicle was the same as in the floret removal treatments and analogous to the 50% PF/ 50% SF treatment except there were two grains per spikelet. The grain weight ratio was unchanged at 1.5 indicating equal compensatory growth for primary and secondary grains in response to the reduced panicle sink.

The response of grain weight to spikelet removal was quadratic with lower ($p<0.01$) grain weights at 75% spikelet removal than at 50% removal. A similar decline in grain weight at 60-80% spikelet removal has been related to a reduction of the overall sink capacity of the panicle relative to other plant organs (*eg*. tillers) leading to a reduced allocation of assimilates (7).

Conclusions

The heavier primary grain weights resulted from higher growth rates for both a milling and forage oat cultivar. Reducing the sink capacity of the panicle by floret or spikelet removal increased mean individual grain weights. However the grain weight ratio was unaffected. Thus, there was no indication from this physiologically based study that agronomic practices could be used to manipulate grain weight distributions. Therefore, a monomodal grain weight distribution, with minimal variability would only result from plants containing a single grain per spikelet. The implication was that cultivars should be selected for a single large grain per spikelet. To maintain grain yield it may also be necessary to increase spikelet number per panicle or other yield components such as panicles per unit area.

Acknowledgments

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Table 1: Derived parameters from logistic functions fitted to grain growth data against thermal time ($t_b = 0$) for 'Cashel' and 'Drummond' oats.

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?	?	?	?	?	?
Cultivar	Grain class	Maximum grain weight (mg)	aGrain growth rate (mg/oCd)	Growth duration (^{o}Cd)	
?	?	?	?	lag phase	linear phase
Cashel	Primary	48.2_a	0.065_a	236_a	669_a
?	Secondary	32.2_c	0.044_b	235_a	653_a
Drummond	Primary	39.9_b	0.050_b	225_a	724_a
?	Secondary	26.1_d	0.034c	233_a	716_a
?	S.E.	0.46	0.0030	14.1	48.7

aMean growth rate over the linear phase (5-95% of maximum grain weight)

Values within a column with a letter subscript in common are the same based on l.s.d tests (α = 0.5).

Table 2: Mean weight of primary (1^{o}) and secondary (2^{o}) grains after removal of primary (PF) and secondary (SF) florets of 'Cashel' and 'Drummond' oats.

?	?	?	?	?
Florets removed (%)	Cashel		Drummond	
	1^{o}	2^{o}	1^{o}	2^{o}
0	44.4_a	29.0_c	39.2_b	25.2_b
100PF	------	34.8_a	-------	29.7_a
50PF/50SF	49.9_a	33.1_b	45.5_a	29.8_a
100SF	49.1_a	------	45.3_a	-------
S.E.= 0.50	?	?	?	?

Values within a column with a letter subscript in common are the same based on l.s.d.tests (α = 0.05).

Table 3: Mean weight of primary (1°) and secondary (2°) grains after removal of spikelets of ‘Cashel’ and ‘Drummond’ oats.

?	?	?	?	?
Spikelets removed (%)	Cashel		Drummond	
	1° 2°		1° 2°	
0	44.4c	29.0_{b}	39.2_{b}	25.2_{b}
25	46.4_{b}	30.9_{ab}	42.1_{a}	27.5_{a}
50	48.5_{a}	32.4_{a}	43.5_{a}	29.0_{a}
75	46.5_{b}	31.3_{a}	41.9_{a}	27.7_{a}
S.E.= 0.59	?	?	?	?

Values within a column with a letter subscript in common are the same based on l.s.d.tests (α = 0.05).

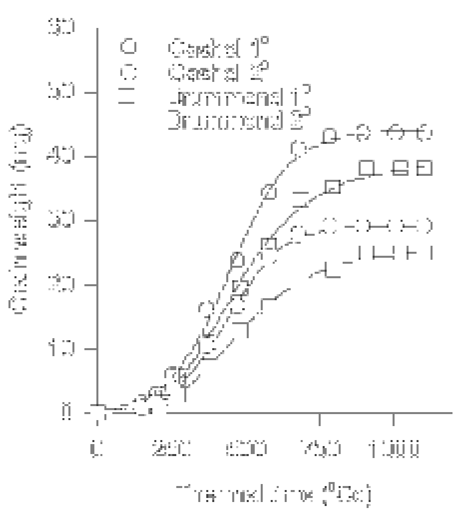

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Figure 1: Mean grain weight and fitted curves for primary and secondary grains of ‘Cashel’ (o ,•) and ‘Drummond’ (M ,N) oats over thermal time. Curves shown are functions fitted using MLP.