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Duration of vegetative and generative development phases in oat cultivars released since 1921

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Abstract

Genetic yield improvements in oat (*Avena sativa* L.) cultivars grown at high latitudes have resulted from marked changes in harvest index and yield components. This study was designed to investigate whether such changes have entailed alterations in duration of different developmental phases: vegetative, generative and grain filling phases and pre-anthesis generative sub-phases such as pre-fertile, pre-abortion, fertile pre-abortion, fertile and abortion sub-phases. We tested 14 oat cultivars released between 1921 and 1988 and 6 breeding lines. Ten randomly sampled plants of each oat entry were collected every 3–4 d (18 times) from seedling emergence until pollination, and apical developmental stages were determined on the most advanced spikelet. Cumulated degree-days (Cdd) for each critical developmental stage and component phases were determined (5 °C as a base temperature). At each measurement the number of leaves, green leaves and tillers on main shoot, apex length (mm) and height to the uppermost node, and stipule (cm) were recorded. Phyllochron (°C d leaf^{-1}) and relative elongation rates (RER) for height characterising traits were calculated. Grain filling was the only period altered by breeding, while no consistent effects on duration of vegetative and generative pre-anthesis phases and sub-phases were detected. Different developmental phases were interrelated: in some cases cultivars with similar duration of pre-anthesis phase, however, differed in duration of some pre-anthesis sub-phases. Their duration was not, however, consistently associated with measured growth and yield parameters. Likely long days that make the northern growing conditions exceptional and unique, substantially narrowed the differences among oat entries in duration of different developmental phases, thereby making their role also less critical in yield determination contrary to the situation in the main global temperate cereal production regions.

Keywords: Apex; Developmental phase; Double-ridge; High latitude; Long day; Oat; Phenology; Phyllochron; Tillering; Year of release; Yield; Yield components

1. Introduction

The substantial achievements of breeding for improved grain yield in cereal crops have been demonstrated to result from marked alterations in traits associated with improved harvest index (HI) such as shortened straw and increased number of grains per head (Austin et al., 1980; Martiniello et al., 1987; Siddique et al., 1989; Peltonen-Sainio, 1990; Calderini et al., 1995). It is evident that such changes entail simultaneous changes in cereal growth dynamics, although this has not been thoroughly studied. These changes include those in relative duration of critical developmental phases as well as alterations in the rate of organ appearance and growth. For example, Riggs et al. (1981) found that the pre-anthesis period of modern barley (*Hordeum vulgare* L.) cultivars was shortened with coincident reduction in final leaf number and rate of leaf emergence. Abeledo et al. (2004) demonstrated that some 50 years of barley breeding in Argentina resulted in higher numbers of tillers with enhanced rate of tiller appearance, although no differences in final leaf number or time of onset of tillering were recorded. Phyllochron of the modern cultivars differed from that of older ones for initial leaves, but only when low nitrogen rates were applied. Abeledo et al. (2004) also demonstrated that for barley increased tillering recorded in modern cultivars was attributable to increased accumulation of intercepted radiation at the jointing phase.

Tillers play only a modest role in grain yield production in oat (*Avena sativa* L.) when grown at high latitudes (Peltonen-Sainio and Järvinen, 1995). Vegetative tillers sustaining early canopy closure are produced despite the high seeding rates used to enhance uniculm performance (Peltonen-Sainio, 1997). At high latitudes long days do not only inhibit tillering through

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strengthening apical dominance (Michael and Beringer, 1980), but they also favour development of cereals. Hence, due to the short growing season and intensive development and growth (Peltonen-Sainio et al., 2003) the scope for, and contribution of, alterations in development and growth dynamics may differ from those at lower latitudes. As marked yield improvements have been demonstrated in oat under northern growing conditions (Rekunen, 1988; Peltonen-Sainio, 1990; Slafer and Peltonen-Sainio, 2001), this study of 20 oat entries aimed at investigating the possible, earlier unnoticed breeding effects on duration of major development phases (vegetative, generative and grain filling) and further sequenced generative sub-phases (pre-fertile, pre-abortion, fertile pre-abortion, fertile and abortion sub-phases) and evaluating the possible concomitant changes in leaf and tiller traits and major yield components.

Sequencing developmental and growth patterns of crops is very useful for many purposes as recently summarised by McMaster et al. (2005). In this study, the sequencing of the phases based on detection of the critical apical developmental phases (Fig. 1): double-ridge stage marked transition from vegetative phase to generative phase, initiation of stamen primordia transition to fertile phase, initiation of stigmatic branches onset of floret abortion (i.e., reduction in total floret number in panicle, Peltonen-Sainio and Peltonen, 1995) and pollination transition to grain filling phase.

2. Material and methods

2.1. Plant material and experimental design

Field experiments were conducted in 1989 and 1990 at the Viikki Experimental Farm of the University of Helsinki (60°13′N), Finland, i.e., under long days typical for northern growing conditions. Plant material evaluated included 14 oat cultivars released between 1921 and 1988 [Bred Landrace (1921), Esa (1922), Karhu (1985), Kyrö (1959), Osmo (1921), Pellervo (1935), Pol (1974), Puhti (1978), Ryhti (1970), Sisu (1948), Svea (1976), Veli (1981), Virma (1988), Vouti (1982)] and six unreleased breeding lines (Hja 76416, Hja 76420, Hja 78033, Hja 78156, Hja 80090, Hja 80326). Of these, Veli is still among the most popular cultivars grown in Finland, while none of the breeding lines have been released. Typically the older cultivars were characterised as the most long-strawed. However, none of the newer and shorter cultivars carried *Dw* dwarfing genes.

Plots of 10 m^2 (8 m × 1.25 m) were sown on 28 April 1989 and 1990. Sowing density was 500 viable grains per square meter and soil type was sandy clay. Plots were fertilised at sowing with complete nutrient fertilisers resulting in 80 kg N/ha. Weeds were controlled with MCPA [(4-chloro-2methyl-phenoxyl) acetic acid] at a rate of 700 g ha^{-1} applied after double-ridge stage of the apex. The experiments were conducted in a randomised complete block design with four replicates in 1989 and three in 1990.

2.2. Sampling, measurements and analysis

After seedling emergence at intervals of 3–4 d or more frequently when appropriate until pollination stage, 10 randomly sampled plants per entry were collected from replicated plots and pooled. Apical developmental stage of each main shoot was determined on the most advanced spikelet of the developing inflorescence by using descriptive scales of Waddington et al. (1983), Åfors et al. (1988, ref. Peltonen-Sainio, 1999). By this means a total of some 2500 apical samples were analysed per year. Altogether 18 different apical developmental stages were detected. Simultaneously, the number of emerged tillers (senescent and live), leaves and green leaves were counted and heights from the soil to the uppermost detectable node (not necessarily visible)

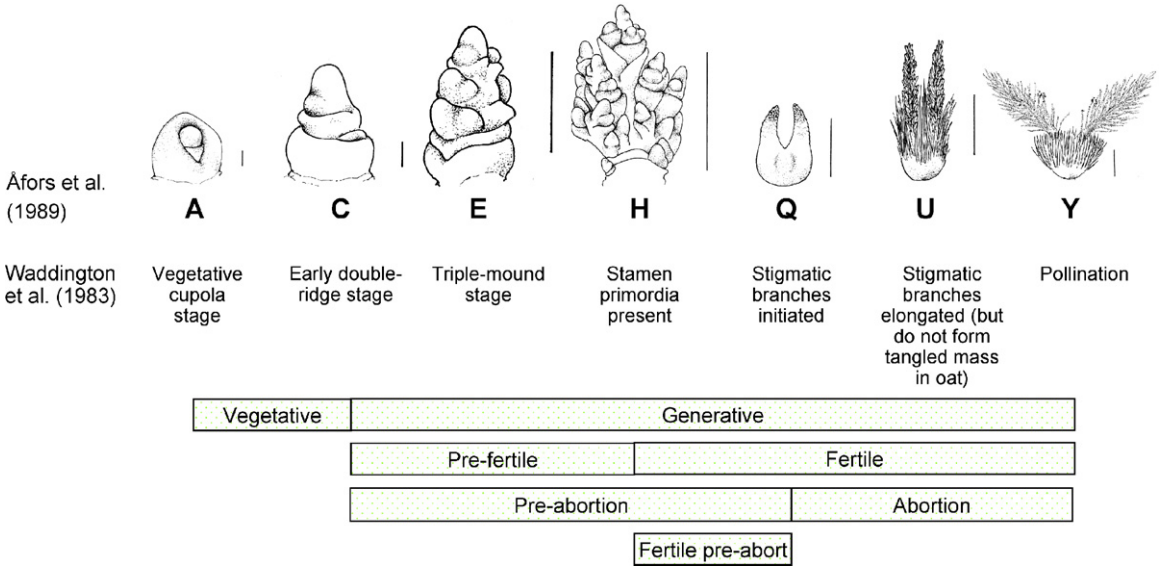

Fig. 1. Critical apical development stages of oat, corresponding with codes by Åfors et al. (1988, ref. Peltonen-Sainio, 1999), descriptions by Waddington et al. (1983), and sequencing of pre-anthesis development phases and their sub-phases used in this study. Vertical lines in right hand side of each drawing of apical development stage indicate following dimensions: 0.1 mm for A and C, 0.5 mm for E and Q and 1.0 mm for H, U and Y. Drawings from Frederik Stendahl.

and stipule (i.e., where leaf laminae turn to leaf sheath) were measured.

Each entry was considered to have reached the specified developmental stage on the sampling day if 50% of plant samples were at least at that stage or at a slightly advanced stage. From the total of 18 detected apical developmental stages, the most critical stages (C, E, H, Q, U and Y, see Fig. 1) used for determining different growth phases were also the ones that are not quickly passed, being thereby relatively easier to detect frequently. In the cases when the critical developmental stages occurred between sampling dates interpolation was done on the basis of their frequency in the preceding and subsequent samplings in proportion to occurrence of the other apical stages. Cumulated degree-days (Cdd) for each of the critical developmental stages were determined by using 5 °C as a base temperature (Kontturi, 1979; Kleemola, 1991). In this study pre-anthesis development was sequenced into a vegetative and a generative phase, the latter was further sequenced into a pre-fertile and a fertile sub-phase and the latter further subdivided into a pre-abortion and abortion sub-phases (Fig. 1). In the case of oat, anthesis refers to pollination because protrusion of stamens is not detectable. In addition, duration of grain filling and growing time until maturity (oat stands turned to yellow) were determined and converted to °C d. The ratios (°C d/°C d) between vegetative phase and growing time, generative phase and growing time, grain filling period and growing time, vegetative phase and grain filling, as well as generative phase and grain filling, were calculated.

Phyllochron (mean °C d leaf^{-1}) was calculated for each oat entry from the two-leaf stage until emergence of flag leaf by dividing the cumulated degree-days for that time period by the number of emerged leaves on the main shoot. The maximum number of leaves, the highest number of green leaves and the total number of (vegetative) tillers on the main shoot were counted and timing was converted to cumulated degree-days. Maximum leaf to maximum tiller number ratio (°C d/°C d) was calculated for each entry in both years.

At each measurement the mean apex length (mm) was calculated for each entry. Polynomial regressions, explaining 99–100% of apex length by cumulated degree-days, were used to interpolate the apex length at each critical apical development stage. To achieve this, the data were often divided into two parts and analysed separately, i.e., into early and later apical stages, to get a coefficient of determination of one. The same procedure was applied when interpolating the height from soil surface to the uppermost node (cm) and stipule (cm), and the distance from the uppermost node to stipule (cm). Relative elongation rate (RER) for main shoot apex, stem up to the uppermost node and stipule, and the distance from the uppermost node to stipule were calculated for the main pre-anthesis developmental phases of each oat entry by applying the general procedure for calculating relative growth rate:

$$\frac{\ln(x_{\text{phase}}) - \ln(x_{\text{previous phase}})}{\text{Cdd}}$$

where Cdd represents cumulated degree-days for each developmental phase.

Variation among oat entries in duration of developmental phases and in leaf, tiller, stem and yield formation traits was illustrated by measuring statistical parameters such as minimum, maximum, standard deviation (S.D.), median and quartile range in addition to annual mean. The genotypic correlations between year of cultivar release and duration of different developmental phases and leaf, tiller, RER and yield formation traits were estimated using linear regressions. Furthermore, all the possible linear and polynomial relationships between the measured and interpolated (ca. 100) traits were evaluated through scatter diagrams. In cases where some relationships between traits were identified visually, linear trends were generally the most appropriate to demonstrate the relationship. Polynomial functions failed to improve significantly the coefficients of determination in comparison with linear regression.

Prior to harvesting, plant samples were collected from each plot (from two times half meter row) and the following 'yield components' were recorded: plant phytomass (g plant^{-1}), plant vegetative phytomass (g plant^{-1}), HI (%) and number of grains per plant. Grain yield was measured after harvest (g m^{-2} at 15% grain moisture). Mean Cdd (°C d) for production of 1 g of grain yield per square meter was calculated by dividing grain yield by cumulated degree-days required for grain filling. Similarly Cdd needed for production of 1 mg of phytomass and vegetative phytomass as well as set of single filled grain was calculated by dividing the trait by degree-days used for the period of their formation. The data on grain yield and 'yield components' per plot basis were subjected to analysis of variance. Only year was characterized as random and oat entry as fixed factor. When differences between the age groups (oldest and newest) in duration of developmental phases were tested, four cultivars in both age groups were regarded as replicates within both years as the original samples for detection of developmental phases were always pooled over replicates. Analysis of variance was calculated by using SAS PROC MIXED (Littell et al., 1996).

3. Results

3.1. Variation in main developmental phases

The growing seasons were similar with respect to number of days from sowing to maturity. The growing time of the earliest and latest maturing oat entries differed by 105 °C d (Table 1), indicating potential for genotypic variation in duration of different pre-anthesis developmental phases. Indeed, duration of the pre-anthesis phase among genotypes ranged from 456 to 495 °C d. In every case the median for each developmental phase was near the mean indicating normality of distribution of the data. Comparison of quartile range to that between minimum and maximum duration of each developmental phase demonstrated that in many cases half of the tested oat entries were relatively close to the mean, while the other half scattered at larger extent. When further sequencing (Fig. 1) the pre-anthesis phase, duration of the vegetative phase ranged by 27 °C d depending on entry (corresponding to 2 d), while

Table 1
Variation among oat entries ($n = 20$) in duration of different developmental phases and their sub-phases shown as cumulated degree-days (Cdd, °C d)

Developmental phase	Mean	Minimum	Maximum	S.D.	Median	Quartile range[a]
Total growing time (GT)	953	889	994	27	954	938–970
Pre-anthesis	470	456	495	11	469	463–477
Vegetative (VEGE)	146	134	161	7	147	142–149
Generative (GENE)	324	308	341	10	322	317–331
Pre-fertile	60	43	76	8	61	55–66
Fertile	264	243	288	11	263	257–272
Pre-abortion	175	164	191	8	171	169–183
Abortion	150	140	172	8	148	143–153
Fertile pre-abortion	114	91	130	12	114	107–124
Grain filling (GF)	483	427	526	25	486	475–497
Phase to phase ratio						
VEGE/GT	0.153	0.143	0.174	0.008	0.153	0.147–0.156
GENE/GT	0.341	0.320	0.365	0.013	0.341	0.332–0.348
GF/GT	0.506	0.477	0.529	0.015	0.506	0.500–0.514
VEGE/GF	0.304	0.280	0.364	0.023	0.297	0.286–0.311
GENE/GF	0.678	0.606	0.770	0.044	0.680	0.645–0.698

[a] Quartile range indicates the range of the oat entry means from lower quartile to upper quartile, i.e., half the oat entries are within the shown range.

generative pre-anthesis phase ranged by 33 °C d (about 3 d) (Table 1). The duration of the vegetative phase was about 15% of the entire growing time, generative pre-anthesis phase 34% and the grain filling period 51%.

Dividing the generative pre-anthesis developmental phase into sub-phases (Fig. 1) indicated that most variation occurred among entries for duration of pre-fertile and fertile pre-abortion phases (Table 1). The pre-fertile phase was the shortest of the sub-phases measured. Some variation, though more modest was detected in duration of pre-abortion, fertile and abortion phases. Total variation among entries was detected when shown as difference between minimum and maximum for different phases and sub-phases compared to their S.D. As variation in pre-abortion phase was less relative to its two sub-phases, pre-abortion and fertile pre-abortion, prolonged duration of the other sub-phase evidently corresponded with shortened duration of the counterpart phase.

3.2. Variation in measured traits

Only modest variation in maximum number of leaves and maximum number of green leaves was recorded (Table 2). The total number of leaves ranged from six to seven, with an average of 6.6 over years, while the highest number of green leaves was 6.7. Phyllochron averaged 78 °C d leaf^{-1} with a range of 68–87 °C d leaf^{-1}. The maximum green leaf number was reached on average at 336 °C d with marked varietal variation of 58 °C d when measured over years. Even more substantial variation among oat entries was detected in timing of maximum tiller number: earliest and latest entries differed by 205 °C d. However, variation in tiller number was relatively modest, ranging from 1.4 to 2.2. Tillering was slightly more favoured in 1990 ($P < 0.001$, when analysed by having four cultivars in both age groups, the oldest and newest, as replicates within both years). Timing of maximum tiller number compared to that of maximum leaf number (i.e., tiller/leaf synchrony) varied among oat entries (Table 2), as 0.74 was the lowest and 1.59 the highest value while S.D. was 0.22. Tiller/leaf synchrony did not consistently associate with other studied parameters.

The oat entries studied expressed similar yielding capacity during the 2 years of the study: grain yield ranged significantly from 442 to 606 g m^{-2} in 1989 and from 403 to 682 g m^{-2} in 1990 depending on entry (Table 3). In 1989 eight more grains were set per panicle on average and also mean value for HI was higher than in 1990.

When characterising the general trends in rate of dry matter accumulation by measuring mean Cdd per unit of yield and major yield components, differences among oat entries were

Table 2
Variation among oat entries ($n = 20$) in leaf and tiller traits measured at pre-anthesis

Leaf and tiller trait	Mean	Minimum	Maximum	S.D.	Median	Quartile range[a]
Phyllochron (°C d leaf^{-1})	78	68	87	5	79	75–81
Maximum leaf no.	6.6	6.2	7.1	0.2	6.7	6.5–6.8
Maximum green leaf no.	6.1	5.7	6.5	0.2	6.1	5.9–6.3
Maximum tiller no.	1.8	1.4	2.2	0.2	1.8	1.6–1.9
Cdd for maximum green leaf no. (°C d)	336	307	365	19	331	319–352
Cdd for maximum tiller no. (°C d)	351	231	436	61	354	307–395
Tiller/leaf synchrony (°C d/°C d)[b]	1.01	0.74	1.59	0.22	1.00	0.85–1.15

[a] Quartile range indicates the range of the oat entry means from lower quartile to upper quartile, i.e., half the oat entries are within the shown range.
[b] Tiller/leaf synchrony indicates the coincidence between the timing of maximum tiller number compared to that of leaf number.

Table 3
Variation among oat entries ($n = 20$) in grain yield and 'yield components' and mean for the four oldest and newest cultivars in 1989 and 1990

Trait	*P*-value			Mean (minimum–maximum)		1989		1990	
	Year	Entry	Year × entry	1989	1990	Oldest	Newest	Oldest	Newest
Grain yield (g m^{-2})	0.424	<0.001	<0.001	520 (442–606)	493 (403–682)	469	547	453	507
Phytomass (g $plant^{-1}$)	0.771	0.002	0.083	2.69 (1.92–3.17)	2.52 (2.04–3.89)	2.67	2.80	2.51	2.45
Vegetative phytomass (g $plant^{-1}$)	0.134	<0.001	0.045	1.69 (0.79–1.42)	1.08 (0.80–1.83)	1.19	1.18	1.10	1.01
Grains (no. $plant^{-1}$)	0.001	<0.001	0.166	44 (32–54)	36 (28–49)	43	47	36	37
Harvest index (%)	<0.001	<0.001	0.390	57 (52–60)	52 (47–56)	56	58	51	52
Cdd for grain yield g^{-1} m^{-2} (°C d)	0.040	<0.001	<0.001	0.88 (0.74–1.05)	1.06 (0.77–1.27)	0.99	0.80	1.87	1.01
Cdd for mg phytomass $plant^{-1}$ (°C d)	0.116	0.008	0.275	0.35 (0.30–0.45)	0.39 (0.26–0.47)	0.36	0.33	0.40	0.40
Cdd for mg vegetative mass $plant^{-1}$ (°C d)	0.046	0.007	0.073	0.42 (0.34–0.60)	0.44 (0.26–0.58)	0.41	0.41	0.42	0.46
Cdd for set of single fertile grain (°C d)	0.001	<0.001	0.019	7.7 (6.4–11.0)	8.8 (6.6–11.2)	7.9	7.1	8.8	8.8

All correlation coefficients for year of cultivar release and measured traits were not different at $P > 0.05$ ($n = 14$ individual data points in both years), except Cdd for grain yield ($r = -0.64^{*}$).

detected. Grain number was a major determinant of panicle yield ($r_{1989} = 0.84^{***}$; $r_{1990} = 0.93^{***}$). As fewer grains were produced for filling in 1990, more degree-days for set of a single non-aborted, filled grain were used (Table 3). Similar trends were found in yield and other 'yield components', except phytomass, when comparing accumulation rate between years.

3.3. Plant breeding effects on development and growth

Changes in oat development brought about by plant breeding were studied in two ways: by measuring correlation coefficients between year of release and a particular trait and through comparing the means of the four oldest and four newest oat cultivars tested. The correlation coefficients between year of cultivar release and measured developmental and growth indicating all traits were statistically non-significant. Regarding duration of different developmental phases, none of them was associated with year of cultivar release (Table 4). However, it appeared that plant breeders had shortened the entire length of the growing period in oat, when the group of four oldest cultivars was compared with that of the four newest ($P < 0.010$). The difference between these two groups was 34 °C d, which corresponds to 3–4 d on an average. Modern oat entries also tended to have shorter pre-abortion ($P = 0.094$) phases and grain filling periods ($P = 0.056$, Table 4).

No effects of plant breeding on leaf and tiller traits were detected (Table 5). Maximum leaf number was the only trait that tended to be slightly reduced, but not significantly ($P = 0.164$) when groups of old and modern cultivars were compared. Also no consistent effects of plant breeding on apex length and relative elongation rate (RER) were recorded when measured at different pre-anthesis developmental sub-phases (data not shown).

Grain yield and major yield components of modern cultivars were greater in 1989 when growing conditions were more favourable (Table 3). As length of the growing time of modern cultivars were shortened, they tended to have higher grain filling rate.

Table 4
Differences in duration of developmental phases and their sub-phases shown as cumulated degree-days (Cdd, °C d) between the groups of the four oldest (released in 1921, 1921, 1922 and 1935) and newest (1981, 1982, 1985 and 1988) cultivars studied over years

Developmental phase	Oldest	Newest	*P*-value for year[a] (difference in means for years)	*P*-value for age group[a]
Total growing time (GT)	972	938	<0.001 (48)	0.010
Pre-anthesis	472	474	0.002 (22)	0.889
Vegetative (VEGE)	151	150	0.897	0.844
Generative (GENE)	321	324	0.004 (21)	0.740
Pre-fertile	56	59	0.400	0.658
Fertile	265	264	0.031 (16)	0.933
Pre-abortion	178	171	0.003 (18)	0.094
Abortion	143	153	0.343	0.175
Fertile pre-abortion	122	111	0.066	0.231
Grain filling (GF)	499	464	<0.001 (70)	0.056
Phase to phase ratio				
VEGE/GT	0.156	0.160	0.105 (0.008)	0.493
GENE/GT	0.331	0.345	<0.001 (0.040)	0.112
GF/GT	0.513	0.494	<0.001 (0.047)	0.182
VEGE/GF	0.305	0.326	0.003 (0.045)	0.333
GENE/GF	0.650	0.703	<0.001 (0.142)	0.141

All correlation coefficients for year of cultivar release and measured phases were not different at $P > 0.05$ ($n = 14$ individual data points averaged over years).
[a] Analysed by having four cultivars in both age groups (oldest and newest) as replicates within both years, no significant year × age group interaction occurred.

Table 5
Differences in leaf and tiller traits measured at pre-anthesis between the groups of the four oldest and newest cultivars studied over years

Leaf and tiller trait	Oldest	Newest	*P*-value for year[a] (difference in means for years)	*P*-value for age group[a]
Phyllochron (°C d leaf^{-1})	75	77	<0.001 (18)	0.570
Maximum leaf no.	6.9	6.6	0.567	0.164
Maximum green leaf no.	6.1	6.0	0.006 (0.4)	0.782
Maximum tiller no.	1.9	1.8	<0.001 (0.5)	0.768
Cdd for maximum green leaf no. (°C d)	327	338	0.912	0.436
Cdd for maximum tiller no. (°C d)	366	357	0.600	0.863
Tiller/leaf synchrony (°C d/°C d)[b]	0.95	1.00	0.475	0.702

All correlation coefficients for year of cultivar release and measured traits were not different at $P > 0.05$ ($n = 14$ individual data points averaged over years).
[a] Analysed by having four cultivars in both age groups (oldest and newest) as replicates within both years, no significant year × age group interaction occurred.
[b] Tiller/leaf synchrony indicates the coincidence between the timing of maximum tiller number compared to that of leaf number.

3.4. Associations between duration of main developmental phases and measured traits

The longer the pre-anthesis phase, the longer also was the generative phase ($r = 0.78^{***}$), but not the vegetative phase ($r = 0.43^{ns}$). Regarding its associations with component sub-phases, no single dominating phase was recorded that contributed to the length of the pre-anthesis phase. Rather many of the sub-phases seemed to contribute only modestly to the length of the pre-anthesis phase (not shown). A prolonged pre-anthesis period was associated with higher vegetative phytomass in 1989 ($r_{1989} = 0.58^{**}$), but not in 1990 ($r_{1990} = 0.28^{ns}$), and not at all with grain yield ($r_{1989} = 0.09^{ns}$; $r_{1990} = -0.02^{ns}$).

Prolongation of the vegetative phase occurred at the expense of other developmental phases as it was correlated positively with vegetative to growing time ratio ($r = 0.84^{***}$). The longer vegetative period resulted in higher total number of leaves, especially in 1990 ($r_{1989} = 0.27^{ns}$; $r_{1990} = 0.77^{***}$), while no other consistent effect on leaf and tiller growth, apex and stem elongation and yield components was recorded. Prolongation of the generative pre-anthesis phase occurred most clearly at the expense of the grain filling period as it correlated with generative phase to grain filling period ratio ($r = 0.55^{*}$).

In contrast, the prolongation of the growing time from sowing to maturity was strongly associated with the length of the grain filling period ($r = 0.91^{***}$). Hence, prolonged grain filling period did not occur at the expense of any of the pre-anthesis growth phases, but was independent of them. Length of grain filling period was not controlled or determined by development and growth occurring during the pre-anthesis period as no associations between measured traits and duration of grain filling were detected.

4. Discussion

Yield improvement in cereals grown at high latitudes cannot be achieved through extending the growing time. This is because the growing season is naturally short, starting when snow melts and the fields can support agricultural machinery. It terminates when autumn rains are too heavy to allow successful harvest and when temperatures decrease below a critical level (Mukula and Rantanen, 1987). Spring sown oat is able to cope with the extreme demand of being harvested within about 4 months of sowing, as long days considerably enhance pre-anthesis development (Bleken and Skjelvåg, 1986; Peltonen-Sainio and Pekkala, 1993). Transition from vegetative to generative phase occurs already at the two-leaf stage of oat, i.e., double-ridges initiate when about 150 °C d are accumulated. Even with such an extremely short vegetative period, some variation among oat entries in the length of the vegetative period occurred (Table 1), but this was not attributable to plant breeding intervention (Table 4). The recorded difference, ranging from 134 to 161 °C d implies that while some entries reached double-ridge stage, the most advanced were already at triple-mound stage or glume primordia were initiated in their apices (Peltonen-Sainio and Pekkala, 1993). Despite some variation (Tables 1 and 2), duration of the vegetative phase was not consistently associated with any of the measured leaf and tiller traits, except for total leaf number and then only in 1990.

Grain number was the major determinant of oat grain yield in this study, in agreement with earlier studies of oat and other cereals (Fischer, 1985; Slafer and Andrade, 1989; Peltonen-Sainio, 1991; Garcia del Moral et al., 2003). Therefore, especially the latter half of the period of spikelet and floret initiation is of paramount importance for determining yield potential (Fischer, 1985; Kirby, 1988; Slafer et al., 1990; Miralles and Slafer, 1999). In particular a longer period of stem elongation was demonstrated to be the avenue to further improving yield potential by promoting higher numbers of fertile florets per head (Miralles et al., 2000; Slafer et al., 2001; Abeledo et al., 2003; Gonzalez et al., 2003). Reorganising the relative lengths of developmental phases is an alternative, especially when related to differences in photoperiod sensitivity (Slafer, 2003). In general, such an approach is interesting also for growing conditions where early maturity is essential without compromise such as in northern Europe. However, as long days considerably enhance apical development, the differences among entries in length of the development phases and sub-phases remained modest (Table 1). Hypothetically, even relatively small differences in duration of the most critical development phases may correspond to 2–3 d difference and may be important, because within even a short time, apical development may change by several stages (Peltonen-Sainio

and Pekkala, 1993). However, this was not demonstrated to be the case in our data on oat.

Our results indicated that in oat entries adapted to high latitudes, reorganisation of the relative duration of different major developmental phases through plant breeding and thereby improving oat productivity has not been exploited to date (Table 4). Genetic gains in grain yield (Rekunen, 1988; Peltonen-Sainio, 1990) that result from increased grain set and HI (Peltonen-Sainio, 1991) were also recorded in this study, especially when comparing the four oldest and four newest cultivars (Table 3). It is likely that under these extreme long day conditions all the differences in duration of each phase and sub-phase were restricted to differences in earliness, especially as it is likely that spring oat does not require vernalisation. Photoperiod is likely to be the key factor explaining both the recorded minor differences in duration of developmental phases and also the lack of association with oat productivity. Namely, Abeledo et al. (2003) demonstrated not only larger differences in duration of developmental phases but also their consistent contribution to yield determination in barley. Furthermore, Slafer (2003) have summarised that future alternative to raise grain yield in barley and wheat is through utilising genotypic differences in their photoperiod sensitivity, which was not true regarding the oat entries studied here.

Grain filling was the only phase that tended to be altered by breeding (Table 4). When comparing the four oldest cultivars with the four newest ones, duration of grain filling was shortened by 35 °C d, which corresponds to 3–4 d. This was, however, not due to differential plant pathogen effects. Parallel shortening of the growing time in modern cultivars has evidently improved yield stability and broadened adaptability because in Finland oats are now cultivated from 60 to 64°N. Such parallel reduction in growing time and grain filling period, while grain yield has been concomitantly increased, resulted from enhanced dry matter accumulation into grains, i.e., increased grain filling rate especially in 1989 (Table 3). Harvest indices were exceptionally high in this study, more than 50% in older cultivars and even exceeding 60% in some breeding lines.

Different development phases were interrelated. Oat entries with similar duration of pre-anthesis phase differed in duration of different pre-anthesis sub-phases. Generative pre-anthesis phase varied by some 33 °C d, but also the far shorter sub-phases, pre-fertile and fertile pre-abortion phases that varied most among oat entries, did so by some 33–39 °C d (Table 1). Regarding plant breeding effects, the pre-abortion phase tended to be slightly shorter in the four modern than in the four older cultivars (Table 4), but again the differences were quite negligible and the modern cultivars were delayed in their development only about 1 d at that particular time (Peltonen-Sainio and Pekkala, 1993).

In conclusion, the results of this study indicated that even though plant breeding has changed plant stand structure, 'yield components' and grain yield – and all these while simultaneously shortening the growing time – duration of the main developmental phases and pre-anthesis sub-phases has not been altered consistently in oat entries adapted to the extreme long day conditions typical for northern Europe. Only growing time was shortened through reducing the duration of grain filling.

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