Segmental Morphology of Perennial Ryegrass (*Lolium perenne* L.): A Study of Functional Implications of Plant Architecture

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Abstract

This thesis investigated the structural and functional implications of segmental organisation of two hydroponically grown perennial ryegrass (*Lolium perenne* L.) cultivars, Alto and Aberdart in spring and autumn, for around 90 days in each season. The objectives included describing tiller axis morphology, studying leaf and root turnover pattern in a phyllochron (leaf appearance interval) time scale, and studying root-shoot and tiller-tiller functional relations. In the Spring experiment a total of 15 – 16 segments or phytomers developed, 10 – 11 of which bore roots. In the Autumn experiment, a total of 22 – 23 phytomers developed, 17 – 18 of which bore roots. New leaves appeared more frequently in autumn and achieved significantly greater final leaf length, dry weight and lamina area through a significantly faster rate of leaf extension, though with significantly shorter elongation duration compared to spring leaves. However, autumn leaves had significantly longer life span and lower specific leaf area. The individual leaves achieved maximum photosynthetic capacity between 12.5 and 14.8 days after appearance. The individual root-bearing phytomers in autumn bore a significantly higher number of roots (2.4) than in spring (1.7). At successively more developed phytomers root main axis length, root dry weight, root length including branches, surface area and volume increased linearly up to phytomer 6 – 7 for both of the cultivars in both seasons whereas dry matter deposition rate per phytomer per day and mean root diameter decreased gradually. Branching to quaternary order was observed during root development. Principal component analysis of root morphology data detected statistically significant morphological variation between genotypes of each cultivar but the basis for differentiation was not visually evident. Roots older than 10 leaf appearance intervals in autumn decreased gradually in volume while still increasing in total branch length. This was interpreted as evidence of root death in some branches while the remainder continued elongation. Tiller root:shoot ratio varied seasonally, possibly mediated by faster leaf than root appearance rate at successive phytomers in spring, and *vice-versa* in autumn. Excision of adult daughter tillers significantly reduced number of root-bearing phytomers of the main tiller which indicated slower new root appearance rate at the main tiller. A significant proportion of root derived N and assimilated C from daughter tillers was translocated to the main tillers and this may explain why daughter tillers remain smaller in size than their parent tillers. Evidence for a proposed oscillation of N concentration within the tiller axis of *Hordeum vulgare* L. linked to N uptake by successive developing leaves was also examined. A weak N concentration oscillation was detected, with the highest concentration just prior to each leaf appearance event. Evaluation of ryegrass root morphology from a segmental perspective, though logistically challenging, has provided previously unavailable information on the time course of root mass accumulation and of root branching. This methodology could be used in future to further explore the carbon economy of the root system and the factors that limit final root size.

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Dedication

I dedicate this thesis to my beloved mother

Ferdousi Begum

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Glossary of Abbreviations

A_{lf}	Leaf appearance interval/phyllochron
A_{lg}	Ligule appearance interval
ANOVA	Analysis of variance
A_{rt}	Root appearance interval/rhizochron
C	Carbon
C:N	Carbon-nitrogen ratio
CER	CO_2 exchange rate
CRD	Completely randomized design
d	Day(s)
d	Maximum net photosynthetic rate
de	Delay between leaf and root appearance at the same phytomer (node)
DM	Dry matter
DMD_p	Dry matter deposition rate per phytomer
$RL/RV^{1/3}$	Dimension corrected root length:root volume ratio
$RSA/RV^{2/3}$	Dimension corrected root surface area:root volume ratio
DT	Daughter tiller
DT-	Daughter tiller excised plants
DT+	Plants with two oldest daughter tillers
DTL	Daughter tiller labelled plant (refers to stable isotope labelling)
DW	Dry weight
EL	Elongating/emerging leaf
Exp	Experiment
f	A measure of curve-width of the log-normal curve in log-days
FLL	Final leaf lamina length
g	Leaf age when maximum net photosynthetic rate occurs
GDD	Growing degree days
Geno	Genotype
GLM	Generalized linear model
IGER	Institute for Grassland and Environmental Research
L	Leaf
LA	Leaf area
LA_i	Leaf area of the individual leaves
LA_t	Leaf area per tiller
LAR	Leaf appearance rate

LDW	Leaf dry weight
LDW_i	Leaf dry weight of the individual leaves
LDW_t	Leaf dry weight per tiller
LDW_{DT}	Leaf dry weight of the two daughter tillers
LED	Leaf elongation duration
LER	Leaf elongation rate
LLS	Leaf life span
LW	Leaf lamina width
MES	2-(*N*-morpholino) ethanesulfonic acid, a pH stabilizer
MT	Main tiller
MTL	Main tiller labelled plant
N	Nitrogen
NEL	Number of visible elongating leaves per tiller
NLA	Number of leaf appearance events
NLL	Number of live leaves per tiller
NP	Number of phytomers per tiller
NPr	Number of root-bearing phytomers per tiller
NPR	Net photosynthetic rate
NR_t	Number of roots per tiller
p	Probability value
P (numeral)	Phytomer position using the emerging leaf as the reference point
PAR	Photosynthetically active radiation
PC	Principal component
PCA	Principal component analysis
PPFD	Photosynthetic photon flux density
Pr	Root-bearing phytomer using the youngest root as a reference point
PrAR	Root-bearing phytomer appearance rate
PVC	Polyvinyl chloride
R	Root
RA	Root axis
RAL	Root main axis length
RCBD	Randomized complete block design
RD	Root diameter
RDW	Root dry weight
RDW_i	Root dry weight of the individual roots
RDW_P	Root dry weight per phytomer
RDW_t	Root dry weight per tiller

RL	Root length
RL_i	Individual root length
RL_P	Root length per phytomer
RL_t	Root length per tiller
R_P	Number of roots per phytomer
RSA	Root surface area
RSA_i	Root surface area of the individual roots
RSA_P	Root surface area per phytomer
RSA_t	Root surface area per tiller
RT	Root tips
RT_i	Number of root tips of individual roots
RT_P	Number of root tips per phytomer
RV	Root volume
RV_i	Root volume of the individual roots
RV_P	Root volume per phytomer
SDW_t	Dry weight of leaf sheaths per tiller
SE	Standard error
SEM	Standard error of mean
SL	Senescing leaves
SLA	Specific leaf area
SRL	Specific root length
SRSA	Specific root surface area
SRV	Specific root volume
TADW	Tiller axis dry weight
TAR	Tiller appearance rate
T_{base}	Base temperature for GDD calculations
TD	Tissue density
TPA_t	Total photosynthetic assimilation per tiller
T_{max}	Maximum temperature
T_{min}	Minimum temperature
Treat	Treatment
YR	Young roots
$\delta^{13}C$	Carbon isotope mass ratio (^{13}C:^{12}C) per mill (‰)
$\delta^{15}N$	Nitrogen isotope mass ratio (^{15}N:^{14}N)