〔韓作誌(Korean J. Crop Sci.) 40(3) : 285~296(1995)〕

Longitudinal Root Anatomy, Cell Dynamics, and Physiological Cell Responses in Root Growth Zones of Two Tall Fescue Genotypes at Two Nitrogen Levels

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톨페스큐 뿌리生長部位의 縱的解剖構造, 細胞力學 및 生理的 反應에 대한 窒素效果

宋凡憲* · 커티스 제이 넬슨**

ABSTRACT : Anatomical studies of sink tissues are required for better understanding the biological plant growth system and energy metabolism. Kinematics of root growth zones of two genotypes of tall fescue (*Festuca arundinacea* Schreb.) receiving 50 or 200 ppm N were determined. Longitudinal anatomy and cell dynamics of root growth zones were studied and calculated. The root growth zone is organized similarly to the leaf growth zone which has cell division, elongation, and maturation zones, but the root growth zone is only about 3.0 mm long compared to 25 to 30 mm for the leaf growth zone. The root cap extends about 0.4 to 0.5 mm from the apical initial, while the cell elongation zone for both cortical and metaxylem cells extends about 3.3 mm from the apical initial for both genotypes and N levels.

Root cap cells elongate from an initial length of about 5 μm long to a final length of about 40 μm before being sloughed. Initial lengths of cortical and metaxylem cells were about 8.5 μm and 13.0 μm, respectively. Elongation of cortex and metaxylem cell showed sigmoidal curves with final lengths of about 120 μm for cortex cells and 650 μm for metaxylem cells. Initial size and final size for both types were not affected by N level, but cell fluxes and cell elongation rates of cortical and metaxylem cells were about double in low N. Cell production rates were about 5 to 6 times higher in cortical cells than in metaxylem cells. Differences in N caused a larger change in cell production rate, duration of cell elongation, and relative cell elongation rate than did the genotypes. These data indicate that N application affects root growth longitudinally by changing cell production rate and elongation rate.

Key words : Root, Cell, Nitrogen, Anatomy, Tall fescue

Plant growth is based on cell division, expansion, and maturation. In both experimental[2,16] and theoretical[6,8,18] works, careful delineation of spatial and temporal aspects of growth has permitted a better understanding

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of functioning of meristems and elongation regions[19].

Growth in root apices has been described from two different viewpoints, spatial description and referential description[6,20]. In spatial description of growth, variables are expressed as functions of position in space, or in time. This viewpoint is complemented by the referential description, in which variables are expressed as functions of some reference position, and of time. The referential description is used to describe the behavior of cells, or growths of cells. Therefore, a satisfactory model for root growth should consider spatial and referential aspects of growth[3,7].

In monocot roots, cell division is restricted to an apical meristem, and cell elongation occurs both in and distal to the meristem, the 'elongation zone' region of the growing organ[19]. The root can be conceived as a single column of cells with three successive zones ; the meristematic zone, where cell division occurs, the elongation zone, where cells undergo longitudinal enlargement, and the maturation zone, where elongated cells differentiate and produce secondary cell wall[4]. Root tips contain a growth zone distal to the apical initial, which gives rise to the root cap, and a proximal growth zone, which produces the root proper. Cells within the proximal zone are arranged in longitudinal files, and growth occurs as the result of cell production and cell expansion[3].

Each cell file or tissue within the root acts in a specific way, largely independent of its neighbors. For example, in *Vicia faba,* mid-cortex cells divide seven times and then elongate and mature, whereas metaxylem cells divide only five times before elongation and maturation[2]. In *Pisum sativum,* cell divisions in the root meristem region are entirely restricted to two cylinders, one composed of the inner root cap, epidermis, and outer cortex, and other composed of the inner cortex cells, pericycle and vascular tissue[16]. In *Allium cepa,* cell division is most active in the cortical region between 450 and 1,850 μm, and in the stele between 550 and 1,850 μm[11]. These studies indicate that the cell division activity is tissue specific.

Root growth is also affected by environmental factors such as temperature[14] and water stress[17,22]. Increases in temperature caused two- to three-fold increases in growth velocity, growth strain rate, and biomass deposition rate in the primary root of maize. Temperature had small effects on root diameter, length of the growth zone, and fresh weight and dry weight density[14]. When water stressed, root growth was reduced and the elongation zone was shortened. In well-watered seedling, the longitudinal strain rate was maximum at the middle of the growth zone, but when water stressed, the maximum strain rate decreased and moved to a more apical region[17].

In tall fescue (*Festuca arundinacea* Schreb.) and monocotyledonous species, the leaf growth zone contains regions of cell division, elongation, and maturation which are located at the base of elongating leaves and are enclosed within a whorl of encircling leaf sheaths[5,24]. Leaf growth in grasses is predominantly unidirectional, parallel with the longitudinal axis of the leaf[13]. Epidermal cell divisions occur at approximately 1 to 2 mm above the ligule[13,23], whereas mesophyll cell divisions occur to about 10 mm distal from the ligule. MacAdam et al[13] observed the ratio of mesophyll cells to adjacent epidermal cells was 1:1 near the leaf base, while the ratio was 1:10 to 15 at the distal portion of

leaf growth zone. Nitrogen fertilization increased leaf elongation rate due mainly to an increase in cell production. Nitrogen did not affect final size of epidermal cells or relative cell elongation rate [13,21,25].

These results suggested that root anatomy in more detail should evaluate as affected by nitrogen fertilization and compare root anatomy with leaf anatomy with respect to growth rates. Our long-term goal is to simulate growth mechanisms and energy metabolism to better understand the relationships between source and sink. The main objectives were 1) to observe the anatomy of the root growth zone and to compare it with the leaf growth zone, 2) to examine cell dynamics and kinematics of the root growth zone, and 3) to evaluate effects of N on root anatomy of two genotypes of tall fescue.

Materials and Methods

1. Plant materials and growth conditions

Tall fescue genotypes were used, one selected for high yield per tiller(HYT) and one for low yield per tiller(LYT). Vegetative tillers (6 cm long) of the two genotypes, having similar diameter of the leaf whorl, were sampled from plants growing in the greenhouse. Selected tillers were removed from surrounding tillers, and planted in flats that were 50 cm long × 30 cm wide × 10 cm deep and filled with sand to a depth of 8 cm. Flats were placed in the greenhouse, and watered daily. After one week the HYT plants had produced 3 to 4 roots and the LYT plants 2 to 3 roots.

Rooted tillers were removed from the flat and rinsed free from sand. Tillers were selected for uniformity in size and number of roots, then transferred to hydroponic culture in the controlled environment growth chamber. Conditions were a 14-h photoperiod of 400 μmol m^{-2} s^{-1} PPFD, 21℃ constant temperature, 70% relative humidity.

Each pot of one liter volume, 11 cm × 15 cm deep, was used for one vegetative tiller. Based medium was Hoagland's nutrient solution modified for N content. Levels of N were 50 and 200 ppm with the ratio of NH_4^+ : NO_3^- being 35 : 65. The solution was changed weekly. Air was bubbled continuously through the solution in each pot to supply oxygen. Pots of the two genotypes, two N treatments, and six replications were located randomly in the growth chamber. Plants remained vegetative throughout the experiment.

2. Anatomical techniques

1) Tissue sampling

Root growth of two tall fescue genotypes grown with low and high N levels maintained a near constant rate at 4 or 5 days after solution culture. During steady-state growth, the apical 7 mm of roots were excised and placed in FAA solution for 48 h.

2) Dehydration and imbedding

The tissue was dehydrated by treating sequentially with water:95% ethanol:t-butanol (5:4:1) for 2 h; water:95% ethanol:t-butanol (3:5:2) for 8 h; water: 95% ethanol:t-butanol (1.5:5.:3.5) for 1 h; 95% ethanol:t-butanol (4.5:5.5) for 1 h; 100% ethanol:t-butanol (1:3) for 1 h; 100% t-butanol

for 1 h; and 100% t-butanol overnight. For sectioning, tissue was infiltrated with t-butanol:paraffin oil (1:1) for 1 d at 58℃, then the pure paraffin was changed once daily for 2 d at 58℃. Casting occurred on day 3 or thereafter.

3) Sectioning and staining

Imbedded tissue was sectioned longitudinally, 10 μm thick, with a model 820 Spencer Microtome (American Optical Cooperation). Thus, the root cap was included in the samples near the tip. Sectioned tissue was mounted on microscope slides, and stained with 1% safranin-O in 95% ethanol for 5 min. Tissue was destained using water for 3 min, followed by 70% and 95% ethanol, each for 3 min. The tissue was then stained with 1% Fast Green in 95% ethanol for 5 seconds and destained in two baths of 100% ethanol for 3 min each, a 1:1 mixture of xylene and pure ethanol for 3 min, and finally pure xylene for 5 min. Cover slips were applied.

4) Cell length measurement

Longitudinal sections were observed with a Dialux 20EB Microscope connected to an Image Analysis System, Master Piece Plus, containing a television camera and monitor. Profiles of root cap cells from the apical initial were measured with the Image Analysis System attached to a MacIntosh IIx computer. Images for cortex and metaxylem cell profiles were also captured with the Image Analysis System. Cortex cell length was measured at 0.25 mm distance intervals with the Image 1.28 program of the MacIntosh IIx until 2 mm distal from the apical initial, and at 0.5 mm intervals distal to 2 mm until cells reached their final size. Metaxylem cell length was also measured at 0.5 mm distance intervals until cells reached their final size. At each position cell lengths of six cortical cells and three metaxylem cells were measured.

3. Growth analysis

The root cap, epidermal, cortical, and central cylinder cells were divided and elongated from near the root apical initial, called the apex of the root proper[19]. Growth rates were calculated using the relationship between cell length and distance from the apical initial. It is assumed in this study that length of the root cap remains constant, i.e. is in steady state because the root cap cells divide near the apical initial, elongate, and slough off when they reach a certain length.

Velocity of displacement (Vx) of cortical and metaxylem cells were determined from the following equation[4,8,19]:

$$Vx = RER \frac{Lx}{Lf}$$

where:

Vx ($mm\ h^{-1}$) = displacement velocity at position x mm from the apical initial

RER ($mm\ h^{-1}$) = root elongation rate,

Lx (μm) = cell length at x mm position from the root apical initial

Lf (μm) = final length of cortical or metaxylem cells.

Time of cell elongation (tx) was estimated from following equation[13,15]:

$$tx = \frac{S}{Vx}$$

where:

tx (h) = time of cell elongation

S (μm) = distance of cell movement in the growth region

The time value which corresponds to each distance from the root apical meristem represents the velocity of cell elongation. A curve of the reciprocal of velocity, i. e. time as a function of distance, allowed us to determine cumulative time for any distance within the elongation zone. The natural logarithm of cell length at each distance was plotted against cumulative time. The relative cell elongation rates of cortex and metaxylem cells were calculated as the slope from the linear regression of natural logarithm of cell length versus time[13,15].

The cell flux (Fx) was calculated according to the following equation[19]:

$$Fx = \frac{RER}{Lf}$$

4. Statistical analysis

The data were analyzed statistically. Means were compared with LSD values between genotypes, nitrogen levels, and the interaction effect of genotype and nitrogen if the F-test indicated a significant difference at $P<0.05$.

Results and Discussion

1. General root anatomy

From the root apical meristem, often called the apical initial, root cap cells divided and elongated forward (Fig. 1). The initial cell length was about 8 μm, whereas the final cell length was about 40 μm (Fig. 2). Cells appeared to reach maximum size, but were then sloughed off. The length of the root cap, from the apical initial to the root tip, where root cap cells were being sloughed off, was about 0.4~0.5 mm. Root cap cells showed similar anatomy and growth patterns for both genotypes and for both nitrogen levels.

Cortex, metaxylem, and epidermal cells elongated at different rates and had different final lengths at maturity (Fig. 1,2). Metaxylem cells reached about 650 μm, cortex cells about 120 μm, and the epidermal cells were shortest, reached about 40 to 50 μm long. The cell division zone was considerably longer for epidermal and cortical cells than for metaxylem cells (Fig. 2).

Metaxylem cells began elongation near the apical initial, whereas cortical cells continued active division for 1.0 mm or more before elongation began (Fig. 2). The root cap had the 3 to 4 layers of cells near the apical initial that were dividing, and then the cells elongated. Root cap cells which were located outside were sloughed off (Fig. 2).

Cell division zones of the epidermis, cortex, and metaxylem cells were different. Metaxylem cells stopped dividing near the apical initial, whereas cortex cells continued to divide until about 1.0 mm distance from apical initial and epidermal cells continued division beyond 1.0 mm. These results are similar to previous studies[11,12,26] which show cell types differ and the vascular conducting elements stop dividing closer to the body/cap junction[16].

Cortex and metaxylem cells in wheat roots begin elongation at a distance of not less than 0.9 and 0.4 mm, respectively, from the root tip. Initial cell length of both cells was similar, about 10 μm, but final cell lengths of cortex were about 220 μm and metaxylem about 800 μm long[10]. In *Allium cepa* L, final cell size of cortex and metaxylem was about 400 μm and 1,400 μm, respectively, while initial lengths of both cell types were similar[4].

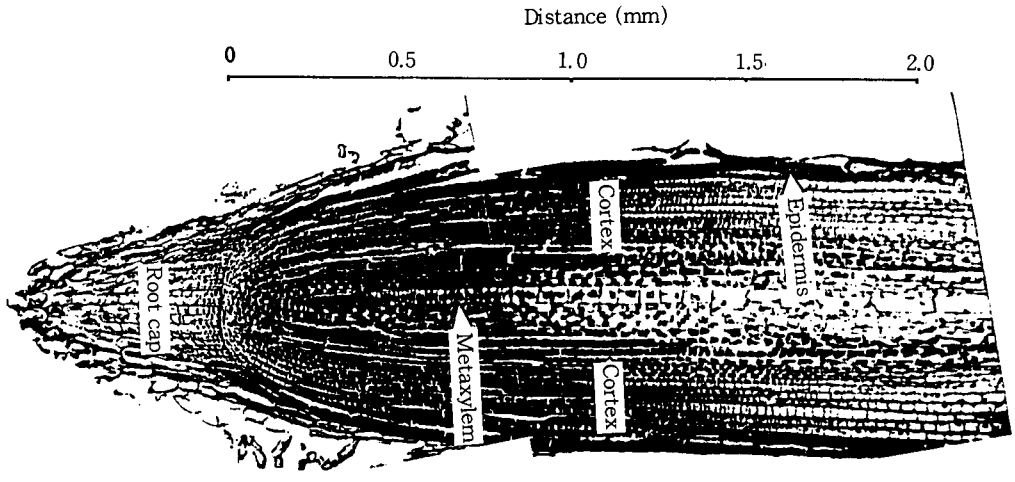

Fig. 1. Longitudinal section through the root tip of tall fescue. Note the metaxylem cell begin elongation close to the apical initial, whereas cortical cells continue active division for 1.0 mm or more before elongation begins. Note also that the epidermis becomes less distinct as distance from the tip increases. Photograph is about 100X. The root is from the LYT genotype grown with 50 ppm N. Two separated images of the same section were combined to show the distance gradient.

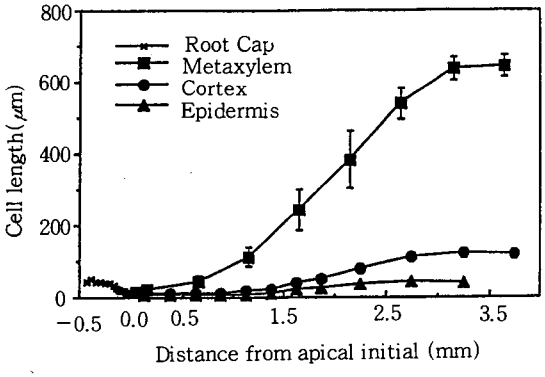

Fig. 2. Length of root cap cells and major cell types in the root proper increase with distance from the apical initial. Data are means with standard deviation (n=6) for the LYT genotype at high N.

Our data are similar, in that final cell lengths of root cap cell (about 40 μm), cortex (about 120 μm), and metaxylem (about 650 μm) were different, although the initial cell lengths of each cell type was quite similar. Further, final cell lengths for each cell type were similar for the two genotypes and two N levels, although both genotype and N level affected root growth rate. Thus, initial and final cell sizes within a species show less variation than among different species[4,10]. Further, root growth is more dependent on cell flux and rates of cell elongation than on initial or final cell size.

2. Cell dynamics and tissue kinematics.

Initial length of cortical cells was slightly longer at 50 ppm N than at 200 ppm N (Table 1), but final cell length was not affected by genotype or N, and averaged about 125 μm, Conversely, both initial and final cell length of metaxylem cell were similar for genotypes and N levels, but initial cell lengths were 40 to 60% longer than cortical cells, and final cell lengths of metaxylem were about five times those of cortical cells.

Root elongation rate of both genotypes at

Table 1. Parameters of cell dynamics and tissue kinematics of root growth of two tall fescue genotypes fertilized with two N levels

Geno.	N	RER	ICL		FCL		CF		TCE		RCER		RGZ
			CC	MC	CC	MC	CC	MC	CC	MC	CC	MC	
	ppm	mm h^{-1}	.....		μm	.....	Cells h^{-1}		h		μm h^{-1}		mm
HYT	50	0.57	9.9	13.5	119	657	4.8	0.9	21	35	0.16	0.13	3.2
	200	0.31	8.6	14.0	122	638	2.6	0.5	44	63	0.10	0.07	3.2
LYT	50	0.52	8.7	12.5	127	655	4.1	0.8	21	39	0.20	0.12	3.2
	200	0.25	8.1	11.5	124	666	2.0	0.4	43	82	0.11	0.06	3.2
LSD	Geno	NS	0.7*	NS	NS	NS	0.3**	0.07*	NS	10*	0.02**	NS	NS
(0.05)	N	0.2**	0.7*	NS	NS	NS	0.3**	0.07**	1.2**	10**	0.02**	0.04**	NS
	G*N	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

RER (Root elongation rate), ICL (Initial cell length), FCL (Final cell length), CF (Cell flux), TCE (Time of cell elongation rate), RGZ (Root growth zone), CC (Cortical cell), and MC (Metaxylem cell). NS: non-significant, *: significant at $P<0.05$, **: at $P<0.01$.

50 ppm N was nearly double that at 200 ppm N, due largely to increased cell flux and faster cell elongation with low N (Table 1). Cell flux of cortical cells was about five times higher than that for metaxylem cells. Both cortex and metaxylem cells took nearly twice as long to elongate to their final cell length with 200 ppm N than with 50 ppm N, which was also reflected in the relative cell elongation rates. Thus, the faster root elongation rate at 50 ppm N occurred because nearly twice as many cells were produced per hour, but they elongated nearly twice as fast, so the number of cells elongating within the growth zone and the length of the growth zone were similar to those at 200 ppm (Fig. 3). This means that the cell "turnover rate" in the growth zone at 50 ppm N is much faster than at 200 ppm N.

Cortical cell length increased in a sigmoidal manner, beginning about 1.0 mm from the apical initial (Fig. 3).

Low N caused a continuation of cell division and a stimulation in cell elongation, whereas cell growth at the distal portion of the growth zone and final cell length were not affected by N levels. In general, genotypes had similar cell elongation rates (Table 1) and final cell lengths (Fig. 3). Previous reports[13,15] suggested that the nature of cell elongation was best expressed as an exponential function.

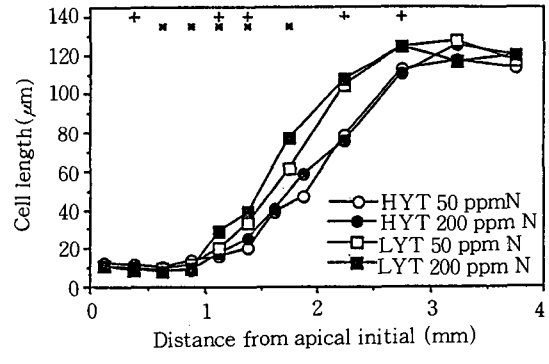

Fig. 3. Cortical cell profiles in root growth zones of two tall fescue genotypes grown at two N levels. + : significant for genotypes at $P<0.05$. * : significant for N levels at $P<0.05$.

$$C_t = C_o e^{rt}$$

where:

C_t = cell length (μm) at time t

C_o = initial cell length (μm) before elongation begins

r = relative cell elongation rate (μm h^{-1})

t = time of cell elongation rate (h)

Cell elongation rate was calculated by plotting the natural logarithms for cell length vs. time of cell elongation and fitting a linear regression. Relative cell elongation rate (RCER) for root cortical cells was higher with low N than with high N in both genotypes (Fig. 4). Interestingly, cell expansion was much slower until cell length reached about 40~45 μm long, then expansion rate was suddenly increased and cells quickly reached final length. About 75% (HYT) to 80% (LYT) of the total cell elongation time was consumed before cortical cells reached 40~45 μm long with high N. RCER of the LYT genotype was similar to that for the HYT genotype at both N levels (Fig. 4).

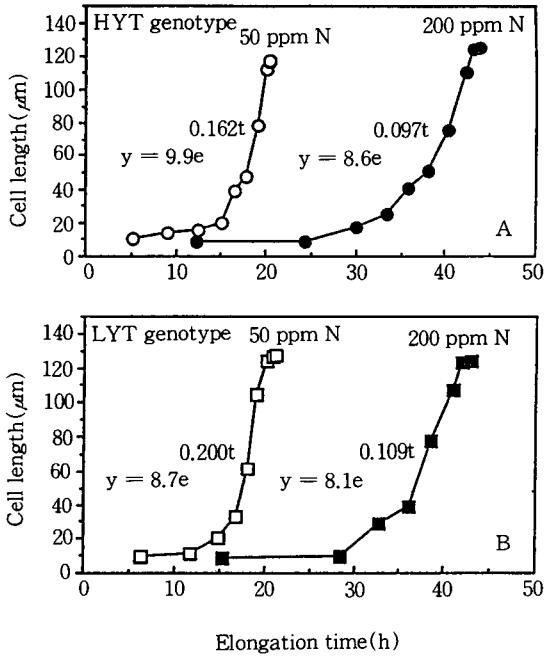

Fig. 4. Relative cell elongation rates for cortex cell of two tall fescue genotypes, HYT (upper) and LYT (lower), receiving two N levels. Cell length data were fitted with an exponential function to estimate cell elongation rate.

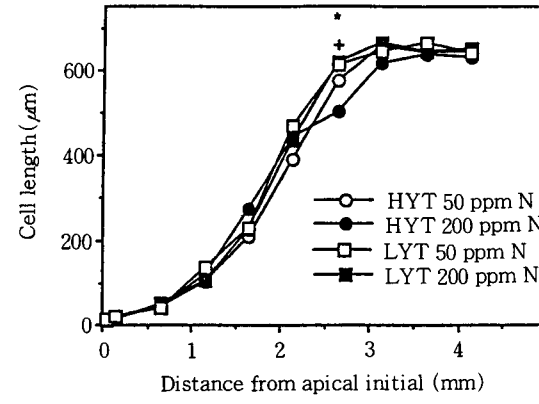

Fig. 5. Metaxylem cell profiles in root growth zones of two tall fescue genotypes grown at two N levels. + : significant for genotypes at $P<0.05$. * : significant for N levels at $P<0.05$.

In contrast with cortical cells, metaxylem had a shorter cell division zone, and much longer final cell length (Fig. 5). Again, however, neither N level nor genotype had a significant effect on cell length profiles in the growth zones or final cell size. The RCERs calculated for metaxylem cells were 25 to 57% lower than those for cortical cells (Fig. 6). Generally, N effects on RCER of metaxylem cells were similar to those for cortex cells.

Cell production rates were higher with low N than with high N. Further, the faster RCERs in the root growth zone with low N suggested the wall expansion rate was higher than with high N, i.e. wall yielding properties may have been changed. It is concluded that the stimulation of root growth with low N level was due to increased cell production and a more rapid cell elongation rate. This suggests a more rapid cell production and elongation, both factors, contribute to rapid cell turnover in the

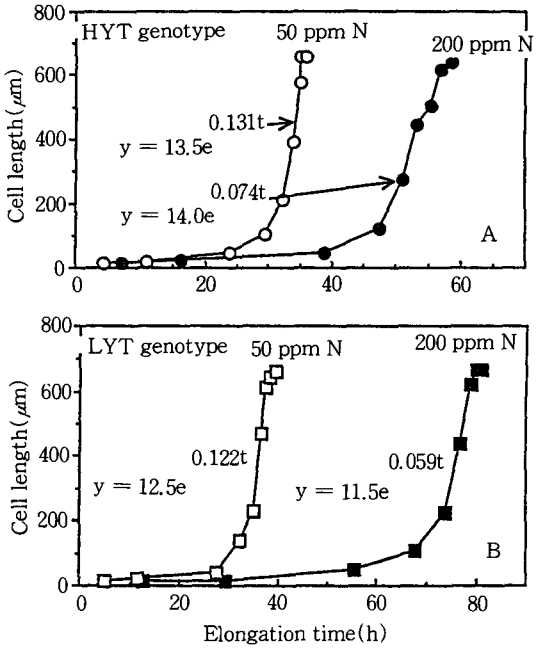

Fig. 6. Relative cell elongation rates for metaxylem cell of two tall fescue genotypes, HYT (upper) and LYT (lower), receiving two N levels. Cell length data were fitted with an exponential function to estimate cell elongation rate.

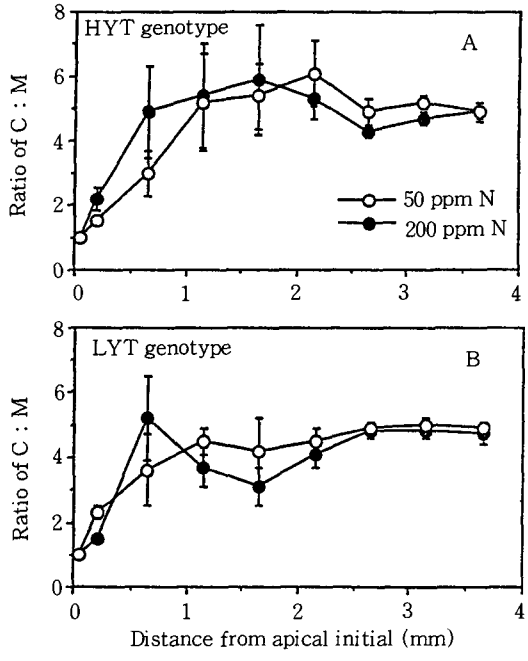

Fig. 7. Ratios of cortex cells to metaxylem cells in the root elongation zones of two tall fescue genotypes, HYT (upper) and LYT (lower), Fertilized with two N levels. Data are means with standard deviation (n=3).

growth zone. This is coincidence with the previous result that stimulation of leaf growth with high N is due mainly to increased cell production[9].

The ratios of cortical cells to metaxylem cells (C:M) at positions along the root elongation zone were investigated (Fig. 7).

The ratio for both genotypes was 1.0 near the root tip, then increased quickly to be about 5:1 at 1.0 mm distance, which was maintained through the remainder of the growth zone and into the non-growing tissue beyond 3.0 mm. Increase in the C:M ratio appeared faster at high N than at low N level (Fig. 7), but the overall effect was that cell production was nearly 5 times faster for cortex compared with metaxylem cells. Thus, root growth shows parallels to leaf growth where mesophyll cell divisions continue while adjacent epidermal cells elongate.

The data compare closely with that of Barlow[1], however, in that the C:M ratio increased to about 5. His data showed metaxylem cells divide five times, whereas cortical cells divide seven times. Assuming the first five divisions occurs together the C:M ratio would be expected to increase to 4 following the two additional divisions in the cortical cell files. Our calculated rates are near 5. It is not understood why growth rates of the metaxylem and cortex cell are not identical; especially near the end of the

growth zone (last 5 to 10 hours) where cell division should not occur and the cells might be growing in synchrony.

In summary, most N in the root growth zone is utilized to increase root cell production, using the photosynthate imported from the source, when N is limited in root environments. Additional carbohydrate remains in the root growth zone and is utilized as substrate for synthesis of cell wall materials. On the other hand, some N is utilized for cell production in the root growth zone through using carbohydrate imported from the source, when N is sufficient in root environment. The extra N is translocated to the shoot as NO_3^-, amino acids, and C-N compounds to stimulated leaf growth. Therefore, root growth rate is faster in low N level than that in high N level.

摘　　要

본 시험은 톨페스큐의 잎과 뿌리伸長 및 同化産物의 貯藏利用樣相과 관련하여 뿌리生長點部位의 縱的인 解剖學的 考察을 통해 細胞分裂, 伸長, 그리고 成熟速度등 細胞力學 및 細胞의 生理的 反應에 대한 窒素의 效果를 究明하고자 遂行하였다. 공시품종은 莖當 收量性이 높은 HYT 품종과 莖當 收量性이 낮은 LYT 품종이었으며, 이들은 葉伸長 및 分蘖性 등 生理的 特性이 다른 품종이다.

1. 根冠, 表皮細胞, 皮層細胞, 導管細胞로 크게 구분되는 뿌리생장부위는 약 3.2 mm로 잎생장부위(약 25~30 mm)보다 훨씬 짧았으며, 根冠部位는 약 0.4~0.5 mm였다.
2. 根冠細胞의 경우, 分裂時 크기는 약 5 μm, 最終크기는 약 40 μm였으며 皮層細胞와 導管細胞의 분열시 크기는 각각 8.5 μm와 13.0 μm, 최종 크기는 각각 120 μm와 650 μm로 큰 차이가 있었다.
3. 뿌리生長部位의 皮層細胞와 導管細胞의 分裂直後 또는 最終크기는 질소시용수준에 영향을 받지 않았으나, 細胞伸長速度는 질소시용수준에 영향을 받아 높은 질소수준(200ppm)에서 보다 낮은 질소수준(50ppm)에서 약 2배 정도 빨랐다.
4. 뿌리細胞의 分裂速度는 窒素의 영향을 받아 피층세포의 경우 50ppm N 수준에서 시간당 약 4.5 세포, 200ppm N 수준에서는 시간당 약 2.3 세포 였으며, 導管細胞의 경우는 각각 시간당 0.9 세포와 0.6 세포 였다.
5. 뿌리세포가 分裂後 최대로 伸長하기까지의 時間은 피층세포의 경우 50 ppm N에서 약 21 시간, 200 ppm N에서 약 43 시간이 所要되었으며, 導管細胞의 경우는 각각 약 37 시간과 73 시간이 소요되었다.
6. 뿌리生長部位의 皮層細胞와 導管細胞의 比率을 調査한 結果, 細胞 分裂部位에서는 1:1이었으나, 細胞伸長部位에서는 그 比率이 增加해 生長點으로부터 1.0 mm 位置에서 5:1로 증가해 계속 維持되었다.
7. 뿌리生長에 대한 窒素의 效果를 分析해 볼 때, 窒素는 뿌리細胞의 크기보다는 細胞分裂과 細胞伸長速度에 크게 영향함을 알 수 있었다.

Literature Cited

1. Barlow, P.W. 1976. Toward an understanding of the behaviour of root meristems. J. Theor. Biol. 57:433-451.
2. Barlow, P.W. 1987. Cellular packets, cell division and morphogenesis in the primary root meristem of *Zea mays* L. New Phytol 105:27-56.
3. Bertaud, D.S., P.W Gandar, R.O. Erickson, and A.M. Ollivier. 1986. A simulation model for cell growth and proliferation in root apices. I. Structure of the model and comparisons with observed data. Ann. Bot. 58:285-301.
4. Carmona, M.J. and A. Cuadrado. 1986.

Analysis of growth components in *Allium* roots. Planta 168:183-189.
5. Esau, K. 1965. Plant anatomy. John Wiley & Sons, New York.
6. Gandar, P.W. 1980. The analysis of growth and cell production in root apices. Bot. Gaz. 141:131-138.
7. Gandar, P.W. 1983. Growth in root apices. I. The kinematic description of growth. Bot. Gaz. 144:1-10.
8. Gandar, P.W. and A.J. Hall. 1988. Estimating position-time relationships in steady-state, one-dimensional growth zones. Planta 175:121-129.
9. Gastal, F., C.J. Nelson, and J.H. Coutts. 1992. Leaf growth of tall fescue: the role of nitrogen nutrition. Proc. 14th Meeting of European Grassland Federation (in press).
10. Hejnowicz, Z. and P. Brodzki. 1960. The growth of root cells as the function of time and their position in the root. Acta Soc. Bot. Polon. 26:625-644.
11. Jensen, W.A. and L.G. Kavaljian. 1958. An analysis of cell morphology and the periodicity of division in the root of *Allium cepa*. Am. J. Bot. 45:365-372.
12. Luxova, M. and A. Murin. 1973. The extent and differences in mitotic activity of the root tip of *Vicia faba* L. Biol. PL. 15:37-43.
13. MacAdam, J.W., J.J. Volenec, and C.J. Nelson. 1989. Effects of nitrogen on mesophyll cell division and epidermal cell elongation in tall fescue leaf blades. Plant Physiol. 89:549-556.
14. Paphlavanian, A.M. and W.K. Silk. 1988. Effect of temperature on spatial and temporal aspects of growth in primary maize root. Plant Physiol. 87:529-532.
15. Pearen, J.R. 1991. The relationship of growth and maintenance respiration of leaf growth in tall fescue. Ph. D. Dissertation. Univ. of Missouri-Columbia.
16. Rost, T.L, T.J. Jones, and R.H. Falk. 1988. Distribution and relationship of cell division and maturation events in *Pisum sativum* (Facaceae) seedling roots. Am. J. Bot. 75:1571-1583.
17. Sharp, R.E., E.K. Silk, and T.C. Hsaio. 1988. Growth of the maize root at low water potentials. I. Spatial distribution of expansive growth. Plant Physiol. 87:50-57.
18. Silk, W.K. 1984. Quantitative description of development. Annu. Rev. Plant Physiol. 35:479-518.
19. Silk, W.K., E.M. Lord, and K.J. Eckard. 1989. Growth patterns inferred from anatomical records. Plant Physiol. 90:708-713.
20. Silk, W.K. and R.O. Erickson. 1979. Kinematics of plant growth. J. Theor. Biol. 76:481-501.
21. Song, B.H. 1993. Carbon and nitrogen economy, respiration rates, and dry matter partitioning in two tall fescue genotypes. Crop Production and Improvement Technology in Asia:187-204.
22. Spollen, W,G. and R.E. Sharp. 1991. Spatial distribution of turgor and root growth at low water potentials. Plant Physiol. 96:438-443.
23. Volenec, J.J. and C.J. Nelson. 1981. Cell dynamics in leaf meristems of contrasting tall fescue genotypes. Crop Sci. 21:381-385.
24. Volenec, J.J. and C.J. Nelson. 1984a. Carbohydrate metabolism in leaf meristems of tall fescue. I. Relationship to genetically altered leaf elongation rates. Plant Physiol. 74:590-594.

25. Volenec, J.J. and C.J. Nelson. 1984b. Carbohydrate metabolism in leaf meristems of tall fescue. Ⅱ. relationship to leaf elongation rates modified by nitrogen fertilization. Plant Physiol. 74:595-600.
26. Webster, P.L. 1980. Analysis of heterogeneity of relative division rates in root apical meristems. Bot. Gaz. 141:353-359.