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# Cross-sectional Cell Anatomy and Physiological Growth Responses of Cells in Root Growth Zones of Two Tall Fescue Genotypes at Two Nitrogen Levels

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# 톨페스큐 뿌리生長部位의 橫的 解剖構造 및 細胞生長의 生理的 反應에 대한 窒素效果

宋凡憲* · 커티스 제이 넬슨**

**ABSTRACT** : Anatomical and physiological studies of sink tissues are required for better understanding the biological plant growth system and energy metabolism. Anatomy of root growth zones of two genotypes of tall fescue (*Festuca arundinacea* Schreb.) receiving 50 or 200 ppm N were determined, Cross-sectional anatomy and cells responses of root growth zones were observed and examined.

Rapid radial root expansion occurred within the first 1.0 mm from root apex, and then increased gradually for both genotypes and N levels. Another increase in diameter occurred at high N after cell elongation slowed near 3.0 mm. Area of the central cylinder cell increased rapidly near the root apex. However, it then decreased again about 1.0 to 1.5 mm from the apex, perhaps because of pressure from the rapid increase of root diameter due largely to an increasing proportion of cortex and epidermis or hypodermis in the distal portion of the root growth zone. Root area from the apical initial to 6.0 mm distal consisted of 10 to 18% epidermis or exodermis, 67 to 79% cortex, and 10 to 22% vascular cylinder cells containing cambium cells (6 to 20%) and xylem cells (0.8 to 2.5%). These data indicate that N application affects root growth radially by increasing mainly cortex cell area, with less effect on epidermis and central cylinder cells.

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

Root growth is inhibited by increment of nitrogen application, while leaf growth is stimulated[18]. Root growth zones from the apical initials are consisted of root cap, epidermis, root cortex, and vascular or central cylinder. Each cells has specific growth characteristics longitudinally and radially through cell division, elongation, and maturation. The root cap is situated at the tip of roots. It protects the root promeristem of the growing root into soil. The epidermal cells of roots are thin-walled and are usually devoid of cuticle, although sometimes the outermost cell walls undergo cutinization[16]. At the cer-

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tain distal from the apical initial, the epidermal cells become thick and contain lignin or dark-colored substances[2].

The cortex of the root consists mainly of parenchyma cells. The root cortex is usually wider than the stem cortex and therefore it plays a larger role in storage. The innermost layer of the cortex constitutes the endodermis possessing the Casparian strips in the anticlinal cell walls. In that part of root where the primary vascular system is starting to mature, Casparian strips appear in radial and cross walls of the endodermal cells. These strips develop about 20 mm further from the root tip and are not merely wall thickenings but integral parts of the primary wall and the middle lamella in which suberin and lignin are deposited[1]. The Casparian strips prevent inward flow of water and nutrients through the apoplast.

The cortex of the root has mainly been existed as parenchyma cells between the innermost layer beside endodermis and the outermost layer below epidermis or exodermis. The arrangement of the cortex cells is in radial rows, at least in the inner layers, or the cells of two adjacent concentric layers are arranged alternately. The radial arrangement is dependent on the result of the way in which the cells divide during the formation of the cortex. Repeated periclinal divisions increase the number of cell layers in a radial direction, whereas anticlinal divisions add to the periphery and length of the cortex. The cell that undergo periclinal divisions are the inner cortical cells and the innermost layer of the cortex differentiates to form the endodermis after the periclinal divisions are completed[13,14].

The formation of aerenchyma cells in roots developed at 5 cm from the root tip by enhancing hypoxia, whereas no aerenchyma was observed in aerated roots. Development of aerenchyma tissue in roots may reduce shoot and root growth caused by the lack of oxygen in the root growth zone[6]. Under drought conditions, some plant species such as desert succulents also develop air-filled spaces in their roots; the cortical cells can be rehydrated after soil rewetting, although lacunae remain. The effect of air-filled spaces in the root cortex on water and nutrient uptake has not still been understood clearly[11]

Schizogenous intercellular spaces, which appear in the early ontogenetic stages, are very usual in the root cortex. Large air canal are common in the root cortex and a lacunae cortex may also be found in roots of some dicotyledonous plants[4]. The lacunae, called an internal air space, are formed both schizogenously and lysigenously. They develop preferentially in roots in which the cortical cells, as seen in cross-section, are arranged in radial rows[7].

The vascular cylinder occupies the central portion of the root. It is more clearly delimited from the cortex in roots than in the stem, because of the presence of the endodermis. The primary vascular tissue is surrounded by a region of cells which is termed the pericycle. The pericycle generally consists of one or more layers of thin-walled parenchyma cells. It is in direct contact with the protophloem and protoxylem and can already be distinguished prior to the lignification of the protoxylem elements[3].

Tracheary elements in the root mature centripetally and therefore the xylem is exarch, i.e. the protoxylem is situated on the outer side of the metaxylem. The differentiation of the phloem is also centripetal so that the protophloem is closest to the peri-

cycle, while the metaphloem is closest the axis of the root. The number of protoxylem in the root is expressed by the terms of monoarch, diarch, triarch, and polyarch, respectively. Diarch roots are found in *Lycopersicon, Nicotiana, Beta, Raphanus, Daucus,* and *Linum.* In *Pisum* the root is triarch, while in *Vicia* tetraarch. Polyarch arrangement is characteristic of adventitious roots of monocotyledons. A correlation exists between the diameter of the vascular cylinder and the number of protoxylem groups. When the diameter of the vascular cylinder is large, a pith is usually present and the number of protoxylem group is large. Variations in these features may be found even within the same plant[3,20].

Root growth both longitudinally and radially is affected by environmental factors such as temperature[12], water stress[17], oxygen supply in the root zone[5], and nitrogen application[18]. Longitudinal growth responses of roots including the cell division, elongation and maturation with different factors have been investigated and observed much more than did radial growth responses.

Previous our research results suggested that N application affected shoot and root growth differently; N addition stimulates shoot growth, while N addition inhibits root growth through affecting by cell production rates and cell elongation rates. Our long-term goal is to simulate growth mechanism and energy metabolism to better understand the relationship between source and sink. The main objectives were 1) to examine the anatomy of root growth zone cross-sectionally, 2) to evaluate the radial growth of each cells of root growth zone, and to investigate the N effects on anatomy and physiological cell responses of root growth zone of two tall fescue genotypes.

## Materials and Methods

### 1. Plant materials and growth conditions

Tall fescue (*Festuca arundinacea* Schreb.) genotypes were used, one was the high yield per tiller (HYT) which has rapid leaf growth rate and other was the low yield per tiller (LYT) which has slow leaf growth rate. Vegetative tillers (6 cm long) of the two genotypes, which have similar diameter of the leaf whorl, were planted in flats that filled with sand. 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 $\mu$mol $m^{-2}s^{-1}$ PPFD, 21℃ constant temperature, and 70% relative humidity. Each pot of one liter volume was used for one vegetative tiller. Base medium was Hoagland's nutrient solution modified for N content. Levels of N were 50 and 200 ppm with ratio of $NH_4^+$:$NO_3^-$ being 35:65. The solution was changed weekly. Oxygen was supplied to the solution in the each pot through bubbling the air. 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 the 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 (1.5:5.5:3.5) 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-buthanol: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

Imbeddedtissue was sectioned transversely, 10 $\mu$m thick, with a model 820 Spencer Microtome (American Optical Cooperation). Transverse sections were taken at 0.25, 0.5, 0.75, 1.0, 1.5, 2.0, 2.5, 3.0, 4.0, 5.0, 6.0 mm distances from the root apex. Thus, the root cap was included in the samples near the tip. Sectioned tissue was mounted on microscope slides, and stained with 1% safranin-0 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) Tissue area measurement

Radial growth patterns were determined by measuring cross-sectional areas of epidermis or hypodermis, cortex, and central cylinder cells using a Dialux 20EB Microscope. Images for measuring the area of epidermis, cortex, and vascular cylinder cells containing metaxylem and procambium, were captured onto a floppy disk with the Image Analysis System. Areas of each cell types were measured, beginning at 0.5 mm intervals from the apical initial to 3 mm distal, and with 1 mm intervals from 3 mm to 6 mm distal. Photographs showing transverse sections were taken using Kodak technical pan film (ESTAR-AH Base) with a Leitz Varioorthomat DIAPLAN Microscope.

#### 3. 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

Roots consist largely of epidermis, cortex, and central cylinder cells containing cambium, xylem, and phloem cells. Diameter of the root proper, i.e. without root cap, increased rapidly from near the apical initial to 1.0 mm distance, due largely to increased areas of central cylinder, epidermal, and especially cortical cells (Fig. 1). The rapid increasen root diameter in this particular zone was similar for both genotypes and N treatments, with area of epidermal cells being the only tissue that was affected by genotypes or N levels (Table 1). Cortex cells had the lar-

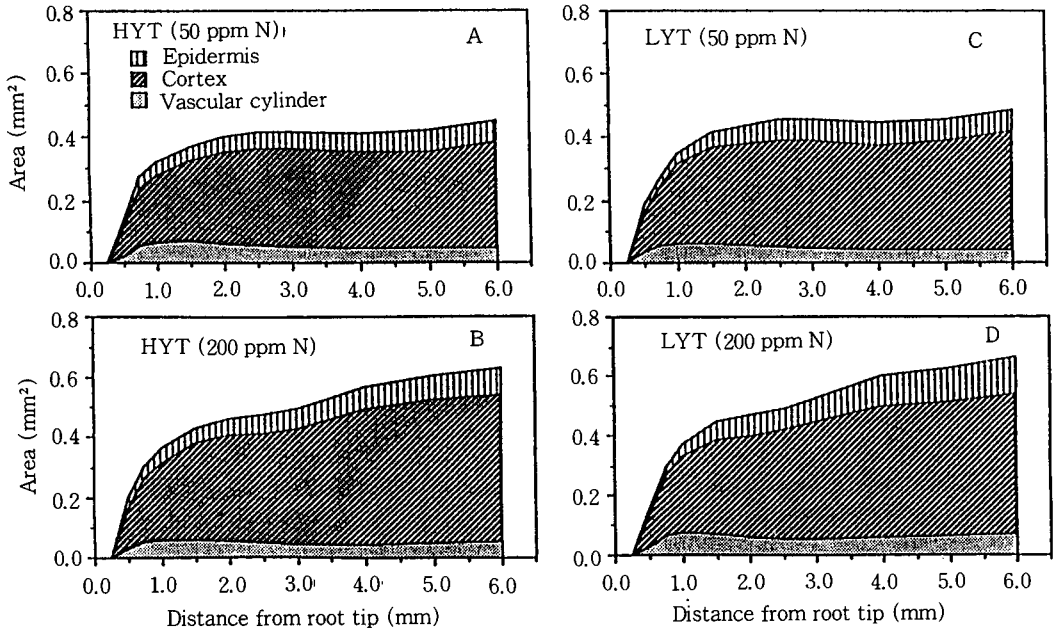


**Fig. 1.** Changes in cross-sectional areas of epidermis, cortex, and vascular cylinder cells containing procambium and metaxylem cells at positions within the elongation zone. The two tall fescue genotypes were grown at 50 or 200 ppm N. Data are plotted from the apical initial, i, e. the root cap in about 0.4 mm long.

gest influence on root diameter in the basal of root growth zone. Anticlinal cell divisions couldn't observe in the cortex, or an increase in cortical cell layers (averaged: about 10.0) beyond 0.5 mm from root tip (Fig. 3). This meant that the increase in cortex tissue and root diameter was caused by radial expansion of individual cortex cells rather than an increase in cortical cell layers.

Radial growth decreased a little between 1.0 and 2.0 mm from the apex (Fig. 1) at the same time active cell elongation commenced. Interestingly, the area of the central cylinder, which contained procambium and metaxylem cells (Fig. 2), decreased largely due to decreased the area of cambium cells because the area occupied by metaxylem cells increased continuously to about 3.0 mm from the apex in both genotypes and both N levels. Beyond 3.0 mm, where elongation growth stopped, root diameter was increased much more with high N than with low N (Fig. 1), due mainly to renewed lateral enlargement of cortex cells and, to a lesser degree, the epidermis or hypodermis.

These radial growth appear separated in space or time in that radial growth predominates at distances less than 1.0 mm, longitudinal growth predominates between 1.0 and 3.0 mm, then radial growth occurs again. There are numerous reports about cortical cell senescence at later stages of root development[8,9,19]. Cortex senescence is determined based on the presence or absence of nuclei. This root cortex death (RCD)' correlates with failure of cells to plasmolyze and with failure to respond to invasion by parasites. It begins in the epidermis and progresses from the outer to the inner cortex. The inner most cell layer remains nu-

cleate over most or all of the root length[8]. Our result showed that cortex cells appeared to coalesce at about 3.0 to 4.0 mm from the root tip, perhaps about eventually forming one large cell.

Severe deficiency of nitrogen and calcium enhances the rate of RCD, while less severe deficiencies have little effect on RCD even though both root and shoot growth were reduced[9]. Robinson[15] argued that RCD could be beneficial if mineral nutrients are remobilized from senescing cells to support new root growth, but they found no direct evidence for this. Conversely, RCD could be detrimental if it reduced the efficiency of nutrient capture behind the root tip[9].

Central cylinder cells occupied about 20% of cross-sectional root area about 1.5 mm from the root apex, then decreased to about 7 to 10% of the total area at the distal end (3.0 mm) of the root growth zone (Fig. 2A, B). The central cylinder cells in the HYT genotype, often called the vascular cylinder, increased sharply in cross-sectional area during the first 1.0 mm, while cortical cells were actively dividing, then decreased in area from the middle of the root growth zone (1.5 mm) until the end (3.0 mm) of growth zone (Fig. 2A). The proportional area of metaxylem cells in the central cylinder gradually increased from the root apex to about 0 mm, with little change thereafter.

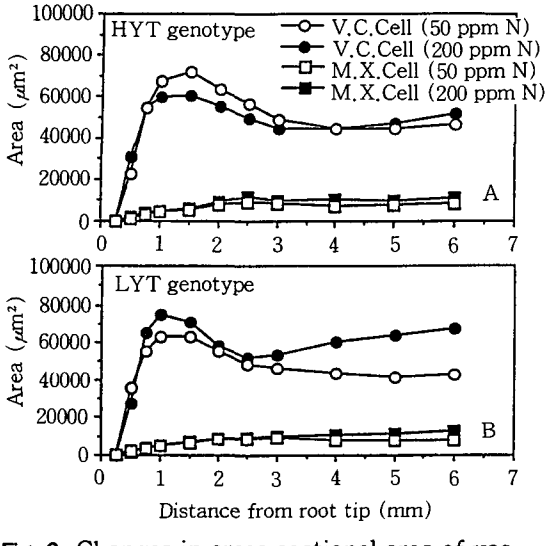


**Fig. 2.** Changes in cross-sectional area of vascular cylinder and metaxylem cells in elongating roots of two tall fescue genotypes grown at two N levels. V. C.=vascular cylinder cell; M.X.= metaxylem cell.

Genotypes were similar in area of the central cylinder (Fig. 2A,B). The cross-sectional area of central cylinder near the 1.0 mm position showed an interaction effects between genotypes and N levels (Table 1). Beyond the root growth zone, high N caused a larger area of vascular cylinder, compared with low N (Fig. 2A, B). No explanation or interpretation is known.

At about 0.5 mm distance from root tip, cortex cell files (about 10.0) had been determined, and metaxylem cells were discernible in the vascular cylinder (Fig. 3A). At about 1.0 mm, root diameter was larger due to increased areas of cortex and vascular cylinder tissues. Metaxylem cells were enlarging (Fig. 3B). At about 2.0 mm distance (Fig. 3C), root diameter was larger due to expanding cortex cells, but the layers of cortex were not increased. On the other hand, the area of vascular cylinder tissue was reduced (Fig. 3). At about 4.0 mm distance, radial root growth was increased slightly from the 3.0 mm distance, due to further lateral expansion of cortex cells and an increased proportion of hypodermis tissue, which was probably formed from outer layers of cortex. Cortex cells near the central cylinder remained small, while cells near the middle and outer edges of the cortex markedly

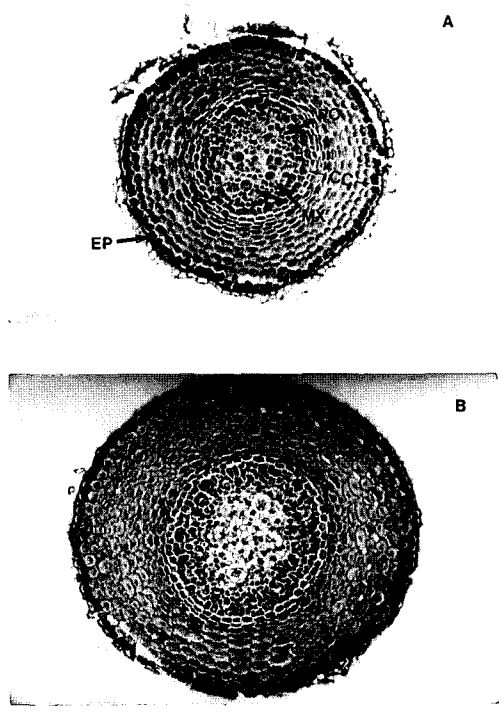


Fig. 3. A,B. Cross-section through the elongating root. Note the vascular cylinder containing the procamblum and metaxylem cells is located inside a clear pericycle. The number of central cylinder cell is fixed and the epidermis is clearly discernible. Photograph is about 100X. This root is from the LYT genotype with 50ppm N. A:0.5 mm distance from the root tip. B:1.0 mm from the root tip. (P:pericycle, MX:metaxylem, PC:procambium cells, CC:cortical cells, EP:epidermal cells)

expanded (Fig. 3D).

At about 6.0 mm distance, radial root growth was only increasing slightly by increasing the areas of cortex and hypodermis. Cells near the middle of the cortex appeared to be joining together as cells greatly enlarged. It appears that 2 or 3 cells were combined together to produce one large cortical cell (Fig. 3E).

The LYT genotype had more epidermal or hypodermis area near the apex than did the HYT genotype, and high N plants had more epidermis or hypodermis than did the low N plants. Similar to the genotype effect, N increased the epidermal area, especially near the root apex and beyond the root elongation zone (Table 1). High N had its biggest effect

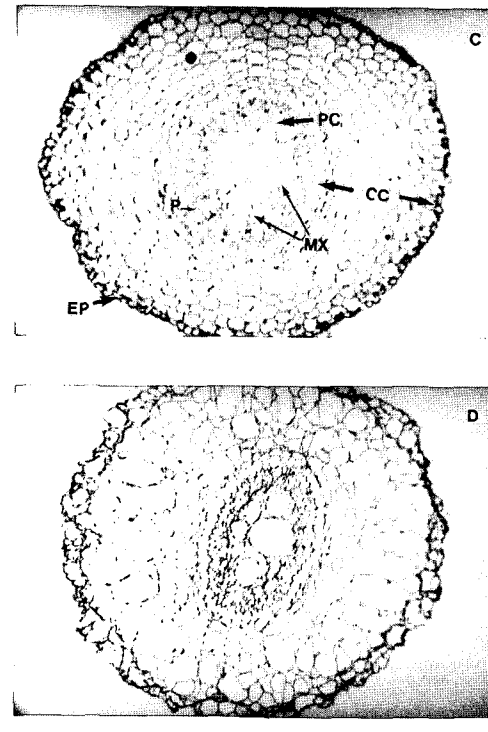


Fig. 3. C,D. Cross-section through the elongating root. Note the vascular cylinder containing the procambium and metaxylem cells is surrounded by cortex. Photograph is about 100X. This root is from the LYT genotype with 50 ppm N. C: 2.0 mm distance from the root tip. D: 4.0 mm from the root tip. (P:pericycle, MX:metaxylem, PC:procambium cells, CC:cortical cells, EP:epidermal cells)

Table 1. Variance analysis of volumetric changes of epidermal. cortex, vascular cylinder, procambium, and metaxylem cells at positions within the elongating roots. The two tall fescue genotypes had been grown with two N levels

| Effect | Factor | Distance from root tip (mm) | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 0.5 | 0.75 | 1.0 | 1.5 | 2.0 | 2.5 | 3.0 | 4.0 | 5.0 | 6.0 |
| Genotype | Total area | NS | NS | NS | NS | NS | NS | NS | NS | NS | NS |
| | Epidermis | ** | * | * | NS | NS | NS | NS | NS | NS | NS |
| | Cortex | NS | NS | NS | NS | NS | NS | NS | NS | NS | NS |
| | V. Cylinder | NS | NS | NS | NS | NS | NS | NS | NS | NS | NS |
| | Procambium | NS | NS | NS | NS | NS | NS | NS | NS | NS | NS |
| | Metaxylem | NS | NS | NS | NS | NS | NS | NS | NS | NS | NS |
| Nitrogen | Total area | NS | NS | NS | * | * | NS | NS | ** | ** | ** |
| | Epidermis | ** | NS | * | * | NS | NS | * | ** | ** | ** |
| | Cortex | NS | NS | NS | NS | NS | NS | NS | ** | ** | ** |
| | V. Cylinder | NS | NS | NS | NS | NS | NS | NS | NS | * | * |
| | Procambium | NS | NS | NS | NS | NS | NS | NS | NS | * | * |
| | Metaxylem | NS | NS | NS | NS | NS | NS | NS | * | * | ** |
| Geno*Nit | Total area | ** | NS | NS | NS | NS | NS | NS | NS | NS | NS |
| | Epidermis | ** | NS | * | * | NS | NS | NS | NS | ** | ** |
| | Cortex | * | NS | NS | NS | NS | NS | NS | NS | NS | NS |
| | V. Cylinder | * | NS | ** | ** | * | * | NS | NS | * | NS |
| | Procambium | * | NS | ** | ** | * | NS | NS | NS | NS | NS |
| | Metaxylem | * | NS | NS | NS | NS | NS | NS | NS | NS | NS |

NS: non-significant; *: significant at $P<0.05$; **: significant at $P<0.01$.

beyond the elongation zone (about 3.0 mm) where all tissues had increased volume compared with those at low N.

The volume of central cylinder cells was reduced in the middle of root growth zone although root diameter actually increased due to cortical and epidermal cell expansion. It appeared the metaxylem cells were expanding, indicating the pith cambium was decreasing in cross sectional area. The forces in place to cause this are unknown, but one could speculate that lateral cell expansion of the cortex and epidermis was crushing the procambium cells in the central cylinder.

The number of cortical cell files was not changed from near the apical initial to the end of root growth zone. The cells in the middle 2 or 3 layers of cortex started to expand or swell at about 2.0~3.0 mm distance from the root tip. Beyond the root growth zone, several expanded cortical cells seemed to be combined together to produce one large cortical cell. But, the inner most cortical layers still existed as thin cells compared to the outer cortex cells which expanded radially in order to increase the circumference of the root. The epidermal cell layer began to slough off at about 2- to 3- mm from the root initial, and a hypodermis was formed from the outer cell layers of cortex. Nitrogen did not affect lateral expansion of cortical cells, but addedc N increased the volume of hypodermis.

Developmental anatomy and the influence of N differs markedly between the root and leaf[10]. In the longitudinal root growth, metaxylem cells in the vascular cylinder differen-

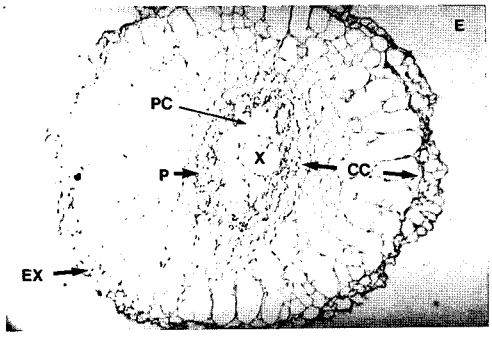


Fig. 3. E. Cross-section through the elongating root at 6.0 mm distance from the root tip. Note the central cylinder has well-developed metaxylem cells. but little procamblum, and some of the outer cortex cells appear to have coalesced. Photograph is about 100X. This root is from the LYT genotype with 50 ppm N. (P:pericycle. X:xylem, PC:procambium cells, CC:cortical cells, EX:exodermis)

tiate first near apical initial to the end of cell elongation zone, cortex cells second at about 1.0 mm distance from the apical initial, and epidermal cells last. On the other hand, root diameter depended on radial growth of epidermis or exodermis, cortex, and vascular cylinder increased rapidly to about 1.0 mm distance from the apical initial due mainly to cortical cells, which do not start to elongate yet. Beyond 1.0 mm distal from the apical initial, root diameter increased gradually due to exodermis and cortex.

It is concluded that N affects leaf and root growth differently; high N stimulates leaf growth due mainly to increased cell production rate and cell elongation rate with little effect on final cell size, whereas low N stimulates root growth by increasing cell production rate and cell elongation rate. Radial root growth near the tip depends largely on expansive growth of cortex and vascular cylinder cells to increase root diameter, then cortex and other cells elongate. But at the end of root growth zone, cortex and epidermis or hypodermis again expand radially to increase the cross-sectional area of the root.

## 摘　　要

본 시험은 톨페스큐의 葉과 뿌리生長 및 炭水化物의 貯藏移動 양상과 관련하여 뿌리 생장부위의 橫的 解剖構造 考察을 통해 表皮細胞, 皮層細胞, 및 通導組織細胞들의 橫的 伸長과 이들 세포의 생리적 생장반응에 대한 질소효과를 구명하고자 수행하였다. 공시품종은 莖當 收量性이 높은 HYT 품종과 경당 수량성이 낮은 LYT 품종이었으며, 이들은 잎과 뿌리伸長 및 分蘖性등 生理的 特性이 다른 품종이었다.

1. 뿌리 생장부위의 橫的 伸長은 첨단 뿌리 生長點으로부터 약 1.0 mm이내에서 表皮細胞, 通導組織細胞, 및 특히 皮層細胞에 의해 橫的伸長이 이루어지며, 1.0 mm 이후에는 서서히 이루어지다가 3.0 mm 部位에서 제2차 橫的伸長이 이루어졌다.
2. 뿌리의 제2차 횡적 신장은 주로 피층세포의 신장에 의해 이루어졌으며, HYT와 LYT 품종간에는 뚜렷한 차이가 없었으나 窒素水準間에는 차이를 보여 200 ppm N 수준에서 뿌리의 횡적 신장이 뚜렷하였다.
3. 뿌리의 횡적 신장에 가장 크게 영향을 미치는 皮層細胞의 경우, 뿌리 생장점으로부터 0.5 mm 이후 횡적 細胞分裂이 발견되지 않아 피층세포의 횡적 분열보다는 주로 횡적 신장에 의존됨을 알 수 있었다. 또한 뿌리 생장점으로부터 3 mm 이후 피층세포들이 서로 합쳐져 큰 피층세포들을 생성되었는데, 6 mm 부위에서는 아주 큰 피층세포들이 外部層에 많이 생성되었다.
4. 通導組織細胞의 경우 뿌리 생장점으로부터 1

mm 부위까지 급격한 횡적 신장을 보였으며, 그 이후 3 mm까지는 감소하다가 다시 서서히 증가하였다. 뿌리 生長點으로부터 1 mm 부위까지 급격한 橫的 伸長시 品種과 窒素水準間에 차이를 보여 HYT품종은 50 ppm N 수준에서, LYT 품종은 200 ppm N 수준에서 높은 횡적 신장을 보였으나, 3 mm 이후에서는 두 품종 모두 200 ppm N 수준에서 넓은 통도조직세포를 가졌다.

5. 뿌리 생장점으로부터 약 6 mm 부위까지 뿌리의 횡적 신장에 관여하는 세포들의 비율을 조사한 결과, 表皮細胞는 약 10~18 %, 피층세포는 약 67~79 %, 그리고 通導組織細胞는 약 10~22 %가 뿌리 直徑에 관여하는 것으로 나타났다.

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