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Elongation Angle of Nodal Roots and Its Possible Relation to Spatial Root Distribution in Maize and Foxtail Millet*

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Abstract : The elongation direction of nodal roots is a key parameter analyzing the root distribution of cereal crops. Elongation angle, which is represented by degrees of deflection from the vertical (plant axis), was measured on the nodal roots that appeared from each internode of isolated individuals of maize (cv. Gold-dent 1106, cv. Nagano 1) and foxtail millet (cv. Toranoo, cv. Rikuu 8). A greater or lesser elongation angle implies that a nodal root elongates in a more horizontal or vertical derection, respectively. In maize, the elongation angle was less on nodal roots that appeared from upper internodes than on those from lower internodes. In foxtail millet, the elongation angle of nodal roots was conspicuously great on middle internodes. Along the axis of a nodal root, the elongation angle of foxtail millet increased nearest the base and decreased towards the tip. It is clear that the degree of plagiogravitropism of the nodal roots of both maize and foxtail millet varies according to internode number. Some distinct differences were observed between cultivars in root distribution patterns in soil as well as in the elongation angle, that is, the maize and foxtail millet cultivars whose nodal roots had lesser elongation angles developed a vertically orientated root system. The elongation angle of nodal roots is an useful parameter for characterizing the shape of a rooting zone in soil.
Key words : Elongation angle, Nodal root, Plagiogravitropism, Root distribution, Root length density, Root system, *Setaria italica* Beauv., *Zea mays* L.

トウモロコシとアワにおける節根の伸長角度と根系分布：中元朋実・下田和雄・松崎昭夫（東京大学農学部附属農場）

要　旨：トウモロコシ２品種（ゴールドデント 1106，長野１号）とアワ２品種（虎の尾，陸羽８号）の孤立個体を対象に，節間位別に節根（１次根）の株近傍における伸長角度と土壌中の根系の２次元的な分布を調査した．伸長角度は節根の伸長方向が鉛直線となす角と定義した．したがって，伸長角度が大きい（小さい）ことは節根がより水平あるいは横（垂直あるいは下）方向に伸長することを意味する．トウモロコシの２品種では，節根出現直後の伸長角度は上位の節間から出現する節根ほど小さかった．また１本の節根の先端方向へ向かって伸長角度は減少したが，その減少程度は上位節間の節根で著しかった．これらの原因により，節根の最終的な伸長角度は上位節間の節根ほど小さかった．一方アワにおいては，中位節間の節根で伸長角度が顕著に大きかった．また，いずれの１本の節根についても，伸長角度は基部近傍で一旦増加しその後先端に向かって減少した．このように，アワとトウモロコシでは特徴が異なっていたが，ともに主として節根の由来する節根の位置によって程度の異なる傾斜重力屈性を示すことが明らかになった．トウモロコシ，アワそれぞれについて品種を比較した場合，伸長角度がより小さいすなわち節根がより鉛直下方向に伸長するとみられる品種（ゴールドデント 1106，陸羽８号）では，株の直下あるいは斜下方向での根長密度が高かった．根系の分布を規定する要因として節根の伸長方向が重要であり，それを伸長角度として定量的にとらえることが有用と考えられる．
キーワード：アワ，傾斜重力屈性，根系，根系分布，根長密度，伸長角度，節根，トウモロコシ．

A knowledge of root spatial distribution is essential to understand the ecology of a root system, that is, the uptake of water and nutrients, the competition with neighbouring plants and so forth. Recent studies revealed the two- or three-dimensional root distribution of maize by determining root length density[3], by studying nodal root trajectories[5], or modeling root systems[4]. In either study, the elongation direction of nodal roots plays an improtant role analyzing root distribution. The elongation direction and other similar characteristics are also well studied in rice[7].

This study is intended to show elongation pattern of nodal roots shortly after their appearance, where the elongation direction is considered to be determined genetically rather than environmentally, and examine its signifi-

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cance to root spatial distribution, comparing some cultivars of maize and foxtail millet. The elongation direction of nodal roots is intensively investigated on successive internodes.

Materials and Methods

The experiment was conducted at the Experimental Farm of The University of Tokyo, in 1989. The soil is a volcanic ash of the Kanto loam type (Humic Andosol). Chemical fertilizer (10 g N, 15 g P, 13 g K per m^2) was applied on the soil surface before sowing. On 8 May two maize cultivars (*Zea mays* L. cv. Gold-dent 1106, cv. Nagano 1) and two foxtail millet cultivars (*Setaria italica* Beauv. cv. Toranoo, cv. Rikuu 8) were sown. Each plant was grown nearly singly, i.e. with 1.8 m interrow and 0.9 m interhill space. Weeds were completely removed during their growth. Gold-dent 1106 reached heading on 26 July, Nagano 1 on 27 July, Toranoo on 23 July and Rikuu 8 on 7 August. These cultivars produced no tillers (suckers) and the mean number of leaves per plant was 21.4 (Gold-dent 1106). 23.0 (Nagano 1), 20.3 (Toranoo) and 22.8 (Rikuu 8). During the growth period (8 May-31 July) rainfall amounted to about 510 mm and mean soil temperature in 10 cm depth was 21.1°C.

Ten days after heading about twenty medium-sized plants per cultivar were cerefully excavated and washed with water, so that all nodal roots were visible. Since most nodal roots developed cortical sclerenchyma or hypodermis, they were rigid enough to maintain their original three-dimensional trajectories, at least, within some distance from the base. The trajectory of a nodal root was, as a rule, on the vertical plane which included the plant axis. A projection of trajectory on the vertical plane was obtained by tracing it on a transparent plastic board. Since this method could be applied only to the fully rigid part of nodal roots, the projection obtained was limited to within the basal 5—20 cm of nodal roots according to rigidity. From the projection, an elongation angle, which was defined by degrees of deflection from the vertical (plant axis), was measured on every 1 cm length of a nodal root (Fig. 1). With the aid of the elongation angle the elongation direction of nodal roots could be investigated in detail or quantitatively. Although the elongation angle varied from 0 to 90 degrees in most cases, there were also some nodal roots which had negative elongation angles (the root elongated towards the plant axis) or greater than 90 degrees (the root elongated upwards). Each nodal root chosen at random for the study was identified, that is, from which internode it appeared. Location of internodes and nodal roots was numbered according to the conception of 'shoot unit'[2,8], the internode and the nodal roots between (N-1)th and Nth leaves being numbered N. A seminal root was not taken into consideration because it was doubtful whether it retained its original trajectory after sampling because of the flexibility of mesocotyl.

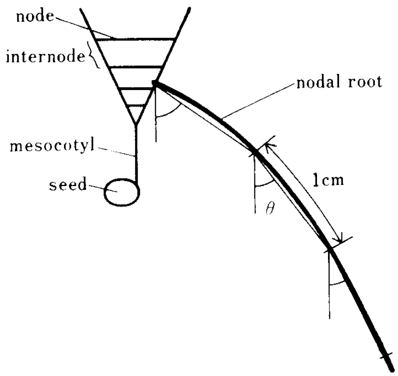

Fig. 1. Elongation angle of nodal roots.
Elongation angle (θ), which is defined by degrees of deflection from the vertical, is measured on each 1 cm length of a nodal root.

Also, ten days after heading a trench was excavated and two vertical soil profiles which included the plant axis (60 cm deep and 40 cm wide) were made around each of the four plants per cultivar. Soil samples with 100 cc metallic cylinders were collected from seventeen spots on each profile (dots in Fig. 3). After separating roots which appeared fresh and light in color from soil and debris, the root length was determined on a personal computer system[3]. The authors are afraid that in foxtail millet the root length was considerably underestimated because many fine roots were too thin (<0.05 mm in diameter) for the system to measure. Mean root length density (cm. cm^{-3}, root length per unit volume of soil) was calculated from eight samples at each spot and the two-dimensional root distribution was obtained by drawing contour lines.

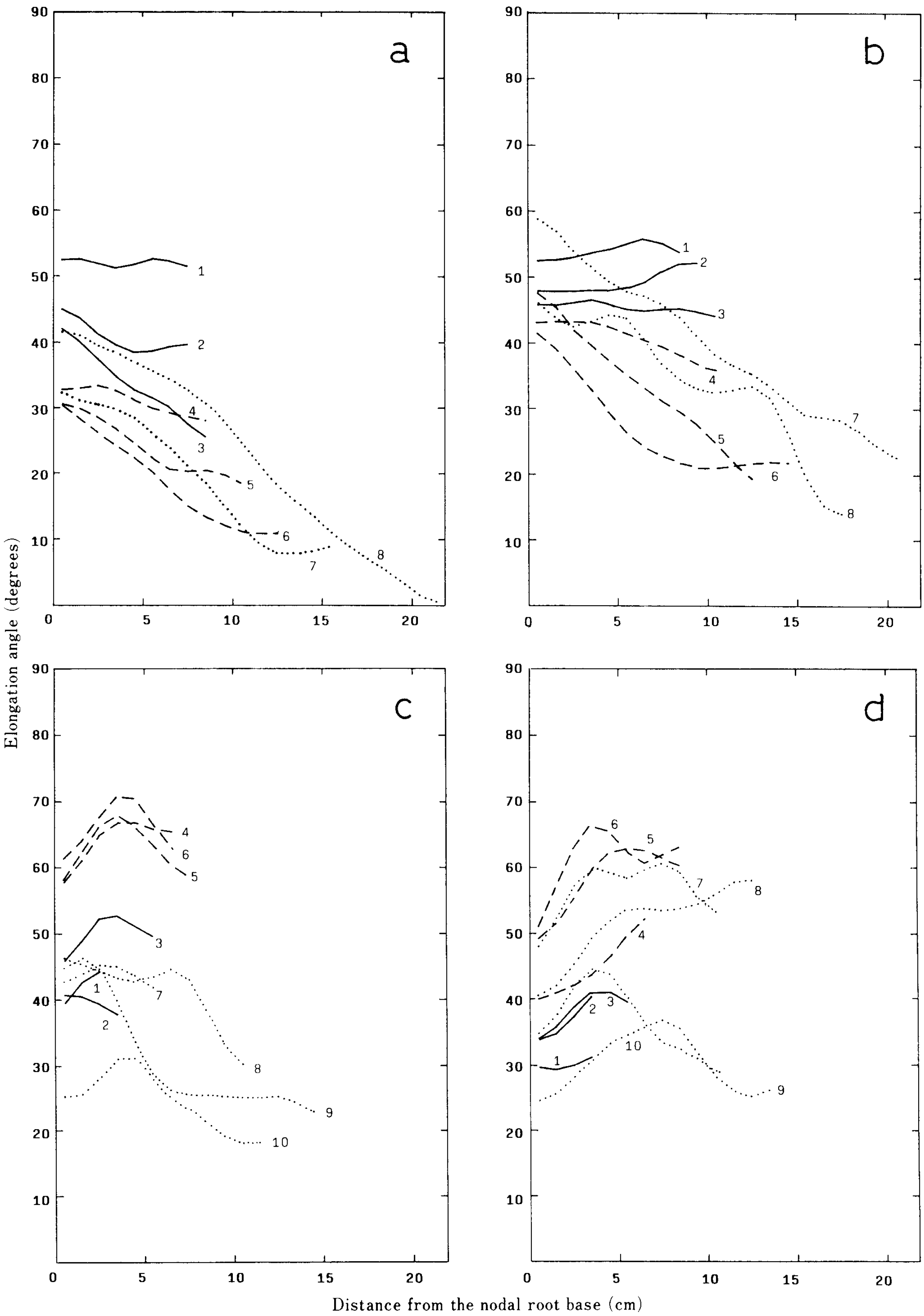

Fig. 2. Elongation angle along the nodal root axis.
Each number in figures indicates a nodal roots number (=internode number). **a** : maize cv. Gold-dent 1106, **b** : maize cv. Nagano 1, **c** : foxtail millet cv. Toranoo, **d** : foxtail millet cv. Rikuu 8.

Table 1. Estimated standard deviation of the elongation angle of nodal roots on each internode (degrees).

Cultivar	Internode No.	Distance from the base (cm)					Sample size
		0−1	5−6	10−11	15−16	20−21	
Maize							
Gold-dent 1106	1	12	14				39
	2	10	13				25
	3	10	13				40
	4	10	9				45
	5	9	9	11			52
	6	10	9	7			56
	7	14	10	8	4		27
	8	13	16	13	9	6	33
Nagano 1	1	11	10				45
	2	13	12	14			55
	3	14	13				52
	4	14	16	8			70
	5	15	13	10			51
	6	14	11	10			20
	7	16	16	9	10	8	28
	8	11	15	12	14		10
Foxtail millet							
Toranoo	1	12					14
	2	17					17
	3	14	12				22
	4	13	18				26
	5	15	16				19
	6	14	14				20
	7	9	15				12
	8	20	24	19			17
	9	14	14	11			21
	10	11	20	13			10
Rikuu 8	1	11					13
	2	12					15
	3	12	14				20
	4	13	14				31
	5	17	14				23
	6	18	15				22
	7	17	21	21			12
	8	20	21	17			21
	9	20	27	18			15
	10	18	24	14			10

Results and discussion

1. Elongation angle

The elongation angle of nodal roots on each internode is shown in Figure 2 and estimated standard deviations at some positions in Table 1. Though the standard deviations were rather great, there were distinct tendencies for the elongation angle to change along the axis of nodal root according to the internode number.

(1) Maize

In both cultivars the initial elongation angle, which was measured at the most basal part (0 -1 cm) of nodal roots, decreased with inceasing internode number (Fig. 2a, b). This means that the nodal roots on upper internode were orientated more vertically than those on lower internodes. Some nodal roots on upper

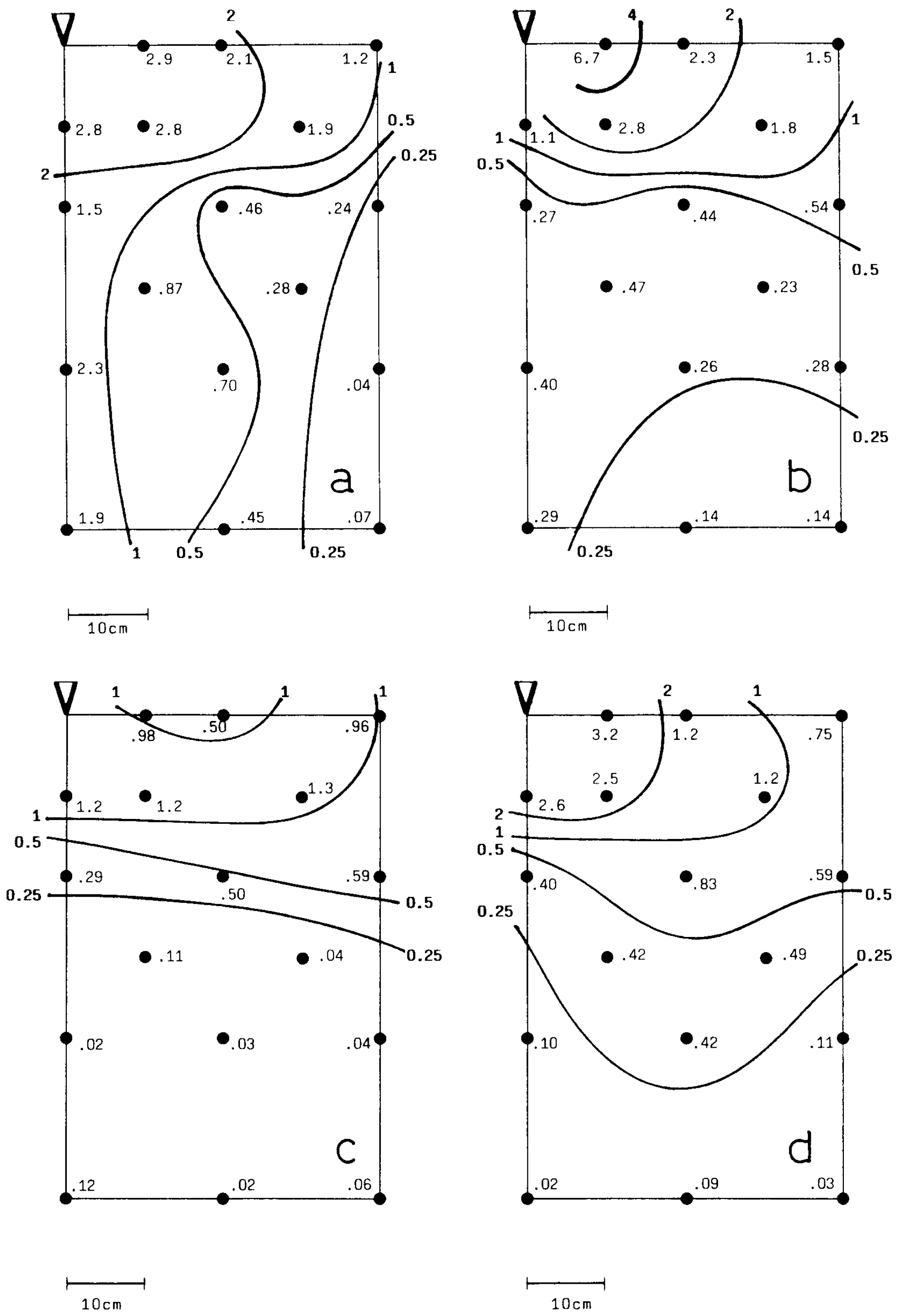

Fig. 3. Root length density on the vertical profile at ten days after heading.
The plant stands on the upper-left corner of each figure. Samples are taken from the seventeen spots which are at intervals of 10 or 20 cm. Mean root length density (cm cm^{-3}) at spots and contour lines are shown. **a** : maize cv. Gold-dent 1106, **b** : maize cv. Nagano 1, **c** : foxtail millet cv. Toranoo, **d** : foxtail millet cv. Rikuu 8.

internodes, however, had great initial elongation angles (nodal roots 8 of Gold-dent 1106, 7 of Nagano 1) and started growing somewhat horizontally. The elongation angle of maize decreased acropetally (towards the tip), and more rapidly on upper internodes than on lower internodes. Nodal roots on upper internodes constantly changed their elongation directions to downwards. The elongation angles of some nodal roots seemed to reach

Table 2. Mean number of nodal roots and estimated standard deviation on each internode.

Cultivar	Internode number										
	S[1)]	1	2	3	4	5	6	7	8	9	10
Maize											
Gold-dent 1106	1.0	3.4	2.4	3.3	4.1	6.7	11.8	13.8	17.8		
SD[2)]	−	0.6	0.5	0.6	0.9	1.3	1.4	1.5	0.5		
Nagano 1	1.0	4.3	4.7	4.4	5.8	7.4	10.7	14.3	18.5		
SD	−	0.6	0.6	1.3	0.8	1.0	1.9	1.7	2.0		
Foxtail millet											
Toranoo	1.0	2.2	2.7	3.5	4.2	4.7	6.2	7.0	10.0	14.3	15.5
SD	−	0.7	0.5	0.5	0.4	0.5	0.5	0.8	1.0	2.4	2.1
Rikuu 8	1.0	2.6	3.4	3.6	4.0	4.8	6.6	7.3	8.3	10.0	13.5
SD	−	0.5	0.8	0.8	0.8	0.7	0.8	0.5	0.5	2.0	2.8

1) Seminal root, 2) Standard deviation.

definite final values (e.g. nodal roots 2, 6, 7 of Gold-dent 1106, 6 of Nagano 1), which were less on upper internodes than on lower internodes. This result was in accord with the results of more macroscopic studies that the nodal roots which appeared on upper internodes were more vertical than those on lower internodes[1,5]. The authors can therefore conclude that the nodal roots of maize show a various degree of plagiogravitropism according to internode number.

Comparing the two cultivars, it was obvious that Gold-dent 1106 had less elongation angles than Nagano 1, that is, Gold-dent 1106's nodal roots elongated more vertically.

(2) Foxtail millet

In foxtail millet two cultivars had similar features, which were completely different from maize. The initial elongation angle of nodal roots was conspicuously great on middle internodes (nodal roots 4, 5, 6 of Toranoo, 5, 6, 7 of Rikuu 8), namely, the nodal roots on middle internodes appeared horizontally (Fig. 2c, d). It is noteworthy that on almost every internode the elongation angle of nodal roots increased at the basal part of a root and then changed to decreasing at some position on a root axis, that is, each nodal root altered its elongation direction first more horizontally and after that more vertically. The nodal roots of foxtail millet therefore have complicated gravitropic reaction, which also depends on the position of the internode.

Rikuu 8 had less initial elongation angles and developed nodal roots more vertically than Toranoo.

(3) Standard deviation

Estimated standard deviations of root elongation angle in maize varied about from 10 to 15 degrees, in foxtail millet about from 15 to 25 degrees (Table 1). These rather great standard deviations might show that several nodal roots which appeared on the same internode could elongate in diverse directions. Though it is known that soil temperature affects nodal root trajectories[6], it remains to be shown to what extent the nodal roots on a same internode have a genetic capacity to change their elongation direction.

2. Distribution pattern of root in soil

(1) Maize

Gold-dent 1106 had a root system which developed well in the vertical direction (Fig. 3a). The region which had root length density higher than 1 cm. cm^{-3} reached the depth of 60 cm right under the plant. Contour lines were rather vertical in a 20—60 cm soil layer. At 20 cm in depth and 20 cm from the plant axis Gold-dent 1106 seemed to have a 'gap' in its rooting zone, where the root length density was lower than in a subjacent soil layer. Such a gap was first observed in another Gold-dent type cultivar (Gold-dent 1103)[3]. The authors believe that the main factor which gives rise to a gap like this is a remarkable difference in the elongation direction between nodal roots on lower internodes and those on upper internodes. In Fig. 2a, it was noticed that there was a somewhat great change of the elongation angle between nodal roots 3 and 4 (more clearly between nodal roots 3 and 5).

In contrast with Gold-dent 1106, Nagano 1 had horizontally orientated contour lines (Fig. 3b). Root length density right under the plant was significantly lower in Nagano 1 than in Gold-dent 1106. There was little difference in the number of nodal roots between the two cultivars (Table 2), and consequently the discrepancy of root distribution pattern was due to the difference of the elongation angle mentioned above, that nodal roots of Nagano 1 tended to elongate more horizontally than those of Gold-dent 1106. The authors considered that the elongation direction of nodal roots, which was successfully represented by the elongation angle, determined a rough outline of the root system.

(2) Foxtail millet

Showing horizontally orientated contour lines, the root length density of Toranoo decreased downwards (Fig. 3c). As compared with Toranoo, Rikuu 8 developed its root system more obliquely or vertically (Fig. 3d). The difference of root distribution between the foxtail millet cultivars also seemed to be related to the difference of the elongation angle between the two cultivars, since they had a similar number of nodal roots on each internode (Table 2). The authors believe that the elongation angle is an important parameter determining root distribution patterns in foxtail millet as much as in maize. It needs no saying that there are also some other morphological parameters which are not easy to measure under field conditions but have a great influence on the root distribution of cereal crops, e.g. the length of nodal roots and the number and length of branch roots. Our results suggests that there is a possibility of predicting root spatial distribution to some extent with the elongation angles, which are easily measured nearest the crown.

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* In Japanese with English summary.