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Growth Regulation of Dark-grown Dwarf Barley Coleoptile by the Endogenous IAA Content

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Growth curves of dark-grown coleoptiles of 11 isogenic coleoptilar dwarf strains of barley (*Hordeum vulagare* L.. cv. Akashinriki: uzu, 5, 77, 97, 105, 125, 131, 133, 136, 145 and 148) were simulated with a logistic equation and the endogenous IAA contents of the barley strains were determined. Growth analysis of the dwarf barley coleoptiles revealed that the final coleoptile length was correlated with the growth rate on the 2nd day after germination ($r=0.897$), when the growth rate was about maximum. The endogenous IAA content of the barley strains, measured fluorometrically, indicated that on the 2nd day, the dwarf strains contained less endogenous IAA than the normal strain. The IAA content on the 2nd day was correlated to the growth rate on the 2nd day ($r=0.907$, except for strain 145) and the final coleoptile length ($r=0.933$, except for strains 77 and 145). The correlation, however, was not significant on the 3rd day. These results suggested that the dwarfism of the dark-grown coleoptiles of the barley strains examined is primarily controlled by the endogenous IAA content.

Key words: Barley (dwarf) — Growth analysis — *Hordeum vulgare* — IAA (endogenous content) — Logistic equation.

Most of physiological studies of dwarf plants have been focused on the role of gibberellins (Brian and Hemming 1955, Phinney 1961, Ogawa 1962, Suge and Murakami 1968, Goto and Esashi 1973, Perez et al. 1974). However, the dwarfism has not always been explained only by the deficiency of gibberellins (Phinney 1961, Radley 1970, Wylie and Ryugo 1971, Suge 1972, Kuraishi 1974a). Gibberellins do not aid the overcoming of stunted growth in dwarf wheat coleoptile (Ricard and Nitsch 1958) and dwarf barley coleoptiles (Suge 1972, Kuraishi 1974a). Furthermore, the growth of dark-grown plants is insensitive to exogenously applied gibberellins (Lockhart 1958, Lockhart and Gottschall 1959, Wakloo 1975). These results suggested that gibberellins are not a major cause of dwarfism of coleoptiles grown in the dark.

Kuraishi (1974a) has indicated that the dark-grown coleoptile of a dwarf barley strain (uzu) results from its abnormal auxin biosynthesis and its smaller auxin quantities are due to the low enzymic activity of converting tryptophan into tryptamine. The uzu strain cultivated in central and western regions in Japan has a recessive semi-dwarf gene, called uzu. Konishi (1977) induced many dwarf barley strains, which were isogenic except for their different single-recessive dwarf genes, by treating a normal type of Akashinriki with ethyl methanesulfonate. He described their agronomic characteristics, but no physiological studies of these dwarf strains have yet been carried out.

Abbreviations: T_i, time of the inflection point of the growth curve; T_c, growth-continuing period; V_i, growth rate at the inflection point; V_2 and V_3, growth rate of the coleoptile on the 2nd and 3rd day, respectively; L_0, initial coleoptile length; V_0, initial growth rate.

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In our preliminary experiment, only strains with dwarf characteristics in the dark-grown coleoptiles were selected from these dwarf strains.

The present study was undertaken to clarify the characteristics of the growth patterns of dark-grown coleoptiles of the dwarf barley strains with a logistic equation and to investigate the role of the endogenous IAA content of coleoptiles on the growth of dwarf coleoptiles.

Materials and Methods

Plant materials—Seeds of 12 barley strains (*Hordeum vulgare* L. cv. Akashinriki), i.e., a normal type and 11 isogenic dwarf types, ten of which had been induced to form by ethyl methanesulfonate, were kindly supplied by Dr. Konishi of the Institute for Agricultural Biology, Okayama University. The barley seeds were soaked for 4 hr in water, germinated for 20 hr on petri dishes (9 cm in diameter) at 26±1°C in the dark, then transplanted in sand or 0.75% agar at 26±1°C in the dark.

Simulation of the growth of barley coleoptiles by a logistic equation—After transplantation, the lengths of about 15 coleoptiles of each strain were measured twice a day under dim green light.

The following simple logistic equation (Richards 1969) was applied to describe the growth of each coleoptile length,

$$L=\frac{H}{1+e^{A-Bt}}$$

where L is the coleoptile length at time t, H is the upper limit of L, and A and B are constants. These three logistic constants of each coleoptile were calculated with a least squares method. All calculations were carried out with a microcomputer (Apple, J-II plus).

Extraction and measurement of IAA content—The IAA content of coleoptiles with first leaves was extracted by the method of Atsumi et al. (1976). The sample was homogenated with a homogenizer (IKA-Werk, Ultra-Turrax TP 19/19 S2) in 200 ml of $(NH_4)_2SO_4$ aqueous solution (80% saturation at 0°C, pH 3.5 with tartaric acid). The homogenate was extracted three times with the same volume of methylene chloride. The combined CH_2Cl_2 solution was dried under vacuum aspiration, then stored at −20°C in the dark until use.

The dried material was dissolved in 1 ml methanol and centrifuged at 1,500×*g* for 5 min to remove salt. The concentrated sample was streaked on Whatman 3MM filter paper (2 cm wide) and the paper was ascendingly chromatographed with the solvent system of 2-propanol : ammonia (16.5 N) : H_2O (10 : 1 : 1, v/v) at room temperature in the dark until the solvent front reached ca. 17 cm from the streaked line. The paper was dried, and then the portion of Rf 0.2 to 0.6 (average Rf range for IAA) was cut and eluted for 6 hr with 5 ml of methanol. A 1-ml portion of the methanol solution was pipetted out and added to 0.5 ml of methanol solution containing 0, 0.1, 0.2 or 0.3 nmol of IAA. After the methanol had been evaporated under reduced pressure at 50°C, IAA was converted into indolo-α-pyrone as described by Knegt and Bruinsma (1973) and the turbid solution with impurities of the plant material was cleaned by adding glacial acetic acid as described by Kamisaka and Larsen (1977). The fluorescence of the indolo-α-pyrone formed was measured with a spectrofluorometer (Hitachi, MPF-4). Excitation and emission wave lengths were 440 and 490 nm, respectively. The unknown IAA content was determined with the reference line as described by Stoessl and Venis (1970).

Results

Growth analysis of dwarf barley coleoptiles—Fig. 1 shows the growth curves of the dark-grown coleoptiles of 12 barley strains. No coleoptile growth of the dwarf strains exceeded that of the

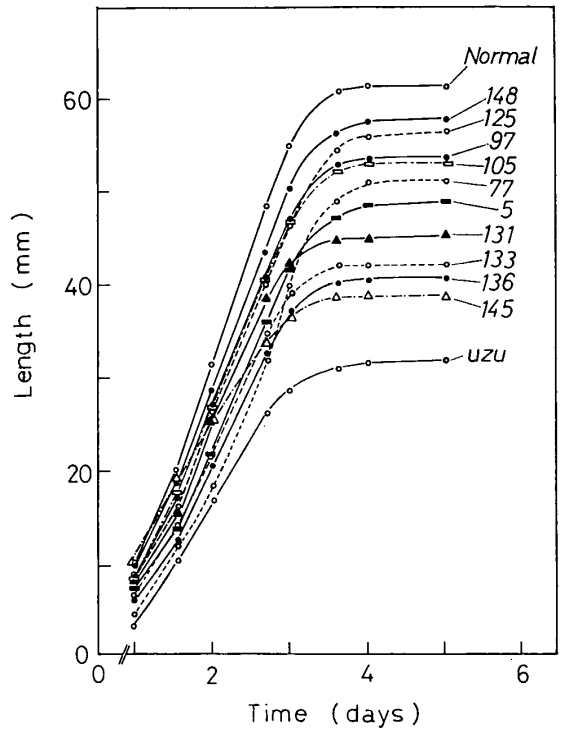

Fig. 1 Growth curves of coleoptiles of 12 barley strains grown in the dark. The coleoptile lengths were measured twice a day from the 1st day to the 5th day after germination. Mean values of measured coleoptile lengths are given. Number of coleoptiles measured: Normal and uzu, 14 each; strains 5 and 77, 10 each; strain 105, 12; all other strains, 15.

normal strain throughout their growth periods. The growth of these strains could be substantially simulated by the simple logistic equation (Richards 1969). The degree to which the coleoptile lengths matched the measured ones was calculated with the logistic equation. All values of the squares of the correlation coefficients (r^2) between the measured and calculated lengths were greater than 0.982, indicating that 98.2% of the measured lengths could be explained by the logistic equation.

Table 1 Three constants of the logistic equation simulating the growth of barley coleoptiles and the calculated initial length

Strain	H (mm)	A	B ($\times 10^2$ /hr)	L_0 (mm)
Normal	63.2±1.1	3.58±0.05	7.59±0.11	1.74±0.08
148	59.3±0.5*	3.41±0.05	7.06±0.12*	1.93±0.10
125	58.6±0.6*	3.11±0.03*	6.29±0.08*	2.50±0.06*
97	54.7±0.6*	3.48±0.07	7.26±0.14	1.70±0.11
105	54.4±0.8*	3.43±0.03	7.22±0.10	1.72±0.06
77	53.3±1.3*	3.98±0.07*	7.09±0.19	0.99±0.07*
5	49.9±0.6*	3.82±0.04*	7.56±0.17	1.08±0.04*
131	45.6±0.4*	3.41±0.05	7.99±0.09*	1.47±0.06*
133	42.8±0.3*	3.72±0.06	8.60±0.14*	1.04±0.06*
136	41.6±0.4*	3.65±0.05	7.86±0.09	1.07±0.05*
145	39.1±0.9*	2.94±0.05*	7.57±0.18	1.99±0.10
uzu	32.2±0.3*	3.91±0.09*	8.43±0.19*	0.67±0.06*

The measured coleoptile lengths (cf. Fig. 1) were simulated with a simple logistic equation, and three logistic constants (H, A and B) were calculated with a least squares method (see **Materials and Methods**). L_0 (initial coleoptile length) $= H/(1+e^A)$.

* significantly deviated from the normal value at the 1% level.

Table 1 shows the three constants of the logistic equation (H, A and B) and the calculated initial length of the coleoptile (L_0). The final coleoptile length (H) of all the dwarf strains was significantly lower than that of the normal strain ($\alpha<0.01$). The B values of strains 5, 77, 105, 136 and 145 did not significantly deviate from the normal value. These dwarf strains are presumed to be of the same group as the normal one in terms of the B parameter according to the F-test ($\alpha<0.01$). Since the B parameter is the coefficient of the growth, strains 125 and 148 with B values that were significantly lower than normal, seem to display dwarfism due to the low coefficient of growth. Of the dwarf strains examined, the uzu and 125 strains had H, A and B values significantly different from those of the normal strain. Strains 97, 105 and 136 differed from the normal one only in the H value.

Since the visible coleoptile did not emerge from the seed at t=0, the initial coleoptile length (L_0) was calculated. The L_0 is equal to $H/(1+e^A)$. The L_0 values of the dwarf strains except strain 125 were not significantly greater than that of the normal. The time of the inflection point of the logistic growth curve (T_i), and the time when the coleoptile length attained 95% of the final coleoptile length (T_c) were calculated (Table 2). T_i and T_c were mathematically equal to A/B and (A+2.94)/B, respectively. T_i is the time when the coleoptile grows at the maximum growth rate (V_i). T_c could be regarded as the growth-continuing period. These parameters were more or less associated with A and B.

With two exceptions (strains 77 and 145), T_i of the barley strains studied was around 48 hr, indicating that they grew at their maximum growth rates on the 2nd day. The order of the strains for the T_i values is almost the same for the T_c values. Strains 77 and 125 grew for longer periods and the uzu, 131, 133 and 145 strains ceased their growth in the early growth stage.

The results in Tables 1 and 2 seem to depict some particular characteristics of each dwarf strain. The uzu strain had the smallest H and L_0 values and its A and B values were significantly greater than the normal ones, suggesting that the growth pattern was quite different from the normal one. Strain 77 had the largest A, T_i and T_c values. Although it was the dwarf strain in terms of H, it grew slower but for a longer period. Strain 125 had smaller H, A and B values than normal and had one of the largest T_c and L_0 values, suggesting that it also had quite a

Table 2 T_i and T_c values of barley coleoptiles

Strain	T_i (hr)		Strain	T_c (hr)	
77	56.3*±0.8	(+9.1)	77	98.1*±1.9	(+11.9)
5	50.7*±0.8	(+3.5)	125	96.4*±1.1	(+10.2)
125	49.5 ±0.6	(+2.3)	148	90.2*±1.1	(+4.0)
148	48.3 ±0.5	(+1.1)	5	89.8 ±1.6	(+3.6)
97	48.0 ±0.9	(+0.8)	97	88.8 ±1.4	(+2.6)
105	47.6 ±0.6	(+0.4)	105	88.4 ±1.1	(+2.2)
Normal	47.2 ±0.8	(0.0)	Normal	86.2 ±1.2	(0.0)
136	46.5 ±0.6	(−0.7)	136	84.0 ±0.8	(−2.2)
uzu	46.4 ±0.4	(−0.8)	uzu	81.5*±0.9	(−4.7)
133	43.4*±0.6	(−3.8)	131	79.6*±0.6	(−6.6)
131	42.7*±0.4	(−4.5)	145	78.4*±1.9	(−7.8)
145	39.1*±1.0	(−8.1)	133	77.7*±0.9	(−8.5)

T_i, time at the inflection point of the growth curve; T_c, time when the coleoptile length attained 95% of the final coleoptile length. Figures in parentheses represent differences of T_i or T_c values of dwarf strains from those of the normal type.

* significantly deviated from the normal value ($\alpha<0.01$).

Table 3 Growth rates of barley coleoptiles

Strain	V_i (mm/hr)	V_2 (mm/hr)	V_3 (mm/hr)	V_0 (mm/hr)
Normal	1.20 ±0.02	1.18 ±0.02	0.55 ±0.03	0.127 ±0.005
148	1.05*±0.02	1.04*±0.02	0.22*±0.02	0.131 ±0.004
97	0.99*±0.02	0.99*±0.02	0.49 ±0.03	0.117 ±0.006
105	0.98*±0.01	0.98*±0.01	0.49 ±0.02	0.119 ±0.003
77	0.94*±0.03	0.87*±0.03	0.69*±0.03	0.068*±0.003
5	0.94*±0.02	0.93*±0.03	0.52 ±0.02	0.079*±0.002
131	0.91*±0.01	0.87*±0.02	0.29*±0.01	0.131 ±0.003
125	0.92*±0.01	0.92*±0.01	0.58 ±0.02	0.151*±0.003
133	0·92*±0.02	0.88*±0.01	0.27*±0.07	0.086*±0.004
136	0.82*±0.01	0.81*±0.01	0.34*±0.01	0.081*±0.003
145	0.74*±0.01	0.64*±0.02	0.22*±0.02	0.141 ±0.005
uzu	0.68*±0.01	0.67*±0.01	0.25*±0.01	0.054*±0.004

V_i, growth rate at the inflection point of the growth curve, defined as $H \cdot B/4$; V_2 and V_3, growth rate on the 2nd and 3rd day, respectively; V_0, initial growth rate, defined as $L_0B(1-L_0)/H$.
* significantly deviated from the normal value ($\alpha<0.01$).

different growth pattern. Strain 133 had the largest B and the smallest T_c values. Strain 133, because of its high B value, attained the final coleoptile length in an early growth stage. Strain 145 had the smallest A and T_i values and one of the smallest T_c values. The dwarfism of this strain seems to be due to the small A parameter. Although the physiological importance of parameter A is not clearly understood, this parameter affected the T_i and T_c values in strain 145.

Table 3 shows the four growth rate parameters (V_i, V_2, V_3 and V_0) calculated from the logistic equation. V_i is the growth rate at the inflection point of the growth curve (i.e., the maximum growth rate), V_0 is the initial growth rate at $t=0$, and V_2 and V_3 are growth rates on the 2nd and 3rd day, respectively. V_i and V_0 are mathematically equal to $BH/4$ and $L_0B(1-L_0/H)$, respectively. All the V_i and V_2 values of the dwarf strains were significantly lower than the normal ones.

Table 4 shows the correlation coefficients among the growth parameters shown in Tables 1, 2 and 3. Among the H, A and B parameter, H was negatively correlated to B. Since only five strains had B values different from the normal one, the negative correlation might be due to

Table 4 Correlation coefficients among growth parameters calculated on the basis of the logistic equation

	H	A	B	L_0	V_0	V_i	V_2	V_3	T_i
A	−0.171								
B	−0.727*	0.438							
L_0	0.595	−0.878*	−0.737*						
V_0	0.513	−0.907*	−0.547	0.950*					
V_i	0.909*	0.017	−0.379	0.360	0.369				
V_2	0.897*	0.050	−0.372	0.341	0.337	0.980*			
V_3	0.845*	0.183	−0.755*	0.272	0.095	0.677	0.669		
T_i	0.499	0.557	−0.501	−0.166	−0.369	0.355	0.375	0.872*	
T_c	0.680	0.132	−0.831*	0.273	0.040	0.401	0.415	0.937*	0.896*

Correlation coefficients were calculated from the data shown in Tables 1, 2 and 3.
* significant correlation ($\alpha<0.01$).

Table 5 Endogenous IAA content of barley strains

Strain	IAA content (pmol/g fr wt)	
	2nd day	3rd day
Normal	235±34	61±16
97	217±21	58± 9
145	208±32	19± 3
148	196±39	43± 5
105	185±25	75± 4
125	178±17	42± 4
131	139±15	67± 3
133	138±11	69±27
5	127±42	32± 8
136	117±26	45± 9
77	89±23	87± 2
uzu	54±14	44± 7

these dwarf characteristics. Although V_i is equal to BH/4, it could be correlated directly with the H parameter (r=0.909). The close correlation may be due to the smaller variations of the B value than those of the H value. It implied that the maximum growth rate at the inflection point (V_i) determined the final coleoptile length and physiological factor(s) controlling the maximum growth rate was involved in the final coleoptile length, i.e., dwarfism. V_2 was correlated with V_i (r=0.980) and H (r=0.897), and V_3 was correlated with T_c (r=0.937), H (r=0.845) and T_i (r=0.872).

The A parameter was correlated with the parameters representing the initial growth characteristics (L_0 and V_0). The B parameter was correlated negatively with L_0, V_3 and T_c, in addition to H. L_0 was correlated with V_0 (r=0.950) as expected, since V_0 is equal to $L_0B(1-L_0/H)$ and B and L_0/H do not vary as largely as L_0. The correlation between T_i and T_c suggested that the growth-continuing period was largely determined by the time of the inflection point which was defined as A/B.

IAA content in barley strains—The endogenous IAA contents in the 2- and 3-day-old coleoptiles

Table 6 Correlation between the endogenous IAA content and growth parameters

Parameter	IAA (2)	IAA (3)
H	0.632	0.289
A	−0.695	0.455
B	−0.298	0.048
L_0	0.802*	−0.261
V_0	0.832*	−0.215
V_i	0.606	0.413
V_2	0.573	0.371
V_3	0.200	0.359
T_i	−0.277	0.411
T_c	0.031	0.234

* significant correlation at the 1% level.
IAA (2), endogenous IAA content on the 2nd day. IAA (3), endogenous IAA content on the 3rd day.

with first leaves are shown in Table 5. On the 2nd day, the normal and uzu coleoptiles contained the largest and the smallest IAA contents, respectively. However, on the 3rd day, the IAA content of each barley coleoptile remarkably decreased, especially in strain 145, where the level decreased to less than 1/20 of that on the 2nd day. One exception was strain 77 which had about the same IAA content on both the 2nd and the 3rd days.

Table 6 shows the correlation between the endogenous IAA content and growth parameters. The endogenous IAA content on the 2nd day was correlated with the L_0 and V_0 parameters. When the data for strain 145 was removed from the calculation, a highly significant correlation was obtained between the IAA content on the 2nd day and parameters V_1 ($r=0.848$) and V_2 ($r=0.906$). Since parameter H was correlated with parameter V_1, the IAA contents were plotted against the corresponding H values (Fig. 2). This clearly revealed that the dwarf barley strains, except strains 77 and 145, displayed coleoptilar dwarfism due to the deficiency of the endogenous IAA content on the 2nd day. The correlation between the IAA content and the H parameter of the barley strains, except strains 77 and 145, was 0.933.

Fig. 3 shows the relationship between the IAA content (pmol/g fr wt) and the growth rate of the coleoptile. On the 2nd day, the correlation was significant at the 1% level ($r=0.907$) when the data of strain 145 was removed from the calculation. This correlation was also significant when the IAA content was expressed as pmol/coleoptile ($r=0.912$). On the 3rd

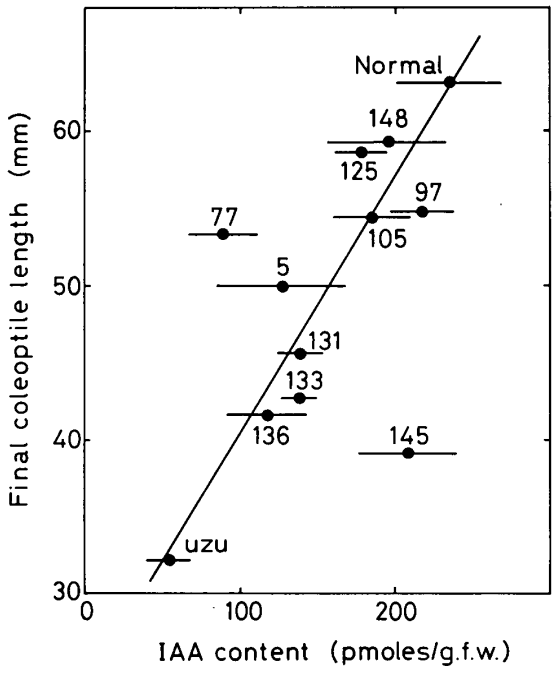

Fig. 2

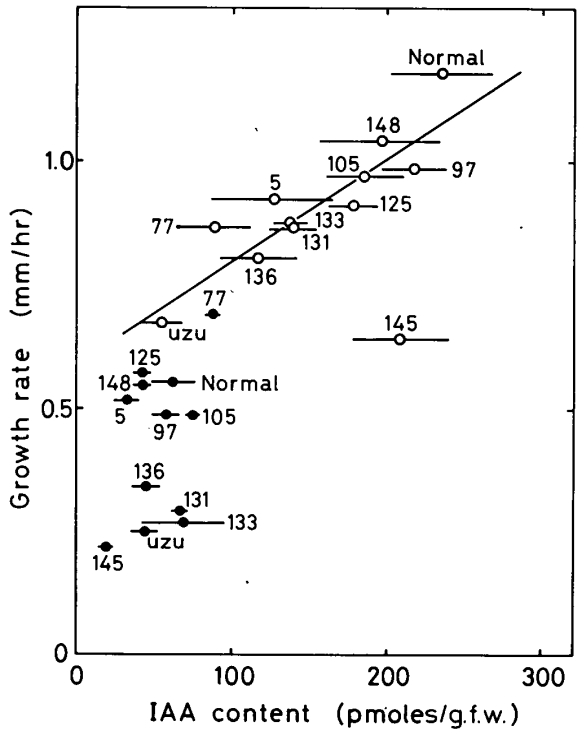

Fig. 3

Fig. 2 Relationship between the endogenous IAA content on the 2nd day and the final coleoptile length of 12 barley strains. The IAA content of 12 barley strains on the 2nd day (cf. Table 5) were plotted against the corresponding final coleoptile length (cf. Table 1). Horizontal lines represent standard errors of IAA contents. The regression line and the correlation coefficient were calculated on the basis of the data, excluding those for strains 77 and 145 ($r=0.933$).

Fig. 3 Relationship between endogenous IAA contents and coleoptile growth rates of 12 barley strains. Open circles, IAA content and growth rates on the 2nd day; closed circles, those on the 3rd day. Horizontal lines represent standard errors of IAA contents. The regression line and the correlation coefficient were calculated on the basis of the data excluding those for strain 145 ($r=0.907$).

day, however, the correlation between the IAA content and the growth rate and other parameters of the coleoptile was not significant at the 1% level (Table 6).

Discussion

Most mathematical studies on plant growth with the logistic equation have been carried out on the basis of the increase in dry weight, leaf area or cell number (Richards 1969). Our results on the simulation of coleoptile growth of 12 barley strains with the simple logistic equation clearly demonstrated that the elongation growth of the plant cell can be substantially simulated by this equation.

The endogenous IAA contents of dark-grown dwarf barley coleoptiles were determined to clarify the role in the growth of dwarf coleoptiles. A good correlation was obtained between the IAA content and the growth rate or the final coleoptile length, when the data of one or two strains were removed from the calculation. This result suggested that the endogenous IAA content of the coleoptile around the inflection time regulates the growth rate and thus finally determines the dwarfism of the coleoptile. The correlation between V_i and IAA content suggested that the IAA content was involved in multiplication of the H and B parameters. Although we calculated the relative growth rate (RGR) for the coleoptile elongation, RGR could not be correlated with the IAA content nor the H value. Thus, IAA content expressed as pmol/g fr wt or pmol/coleoptile seems to regulate the absolute growth rate.

Although L_0 is the calculated initial coleoptile length, it was correlated with the IAA content on the 2nd day. We presumed that the physiological activities on the initial growth stage might reflect the IAA level on the 2nd day.

Kuraishi (1974a, b) indicated that the stunted growth of the uzu strain resulted from the lower auxin content, which is of about the same order as our results measured fluorometrically. Since the lower auxin content in the uzu coleoptile was due to the low activity of the enzyme converting tryptophan into tryptamine, the dwarfism of the isogenic dwarf barley strain used here also probably resulted from the decline of some enzymic activity involved in the IAA biosynthesis.

Although dwarfism due to abnormal IAA metabolism under the *light* condition has rarely been reported (van Oberbeek 1938, Lantican and Muir 1969), our results strongly suggested that the endogenous IAA content of the *dark*-grown coleoptiles plays an important role in the dwarfism.

An exceptional case was strain 145, which showed lower growth rate on the 2nd day in spite of its high content of IAA. The factors causing dwarfism are probably not only the shortage of IAA in the coleoptile but some other unknown one(s). Growth analysis also supported this idea in that strain 145 was the dwarf strain associated with the lowest A parameter of the logistic equation.

Although V_3 was significantly correlated with H ($r=0.845$), the correlation between the IAA content and V_3 was not significant. This fact led us to assume that physiological factor(s) other than the endogenous IAA content is involved in limiting coleoptile growth in the later growth stage after the inflection point of the growth curve. The decreasing osmotic pressure and/or increasing cell wall pressure may retard the coleoptile growth in spite of the relatively high level of IAA, since most of the growth rates of the barley strains on the 3rd day were below the regression line of the correlation between the IAA content and the growth rate on the 2nd day. Alternatively, the decreasing IAA content below some critical point may have resulted in changes in the osmotic pressure and/or cell wall pressure leading to the cessation of coleoptile growth.

In the normal barley strain, the noncellulosic sugar content of the cell wall per unit length

remarkably decreases after the inflection point of the growth curve (Sakurai and Masuda 1978). Since the decrease in the noncellulosic glucan content is assumed to be involved in the decrease of the cell wall viscosity leading to cell wall loosening (Sakurai et al. 1979), it is likely that the cell wall loses its viscosity, leading to the increase in the cell wall pressure.

The cell wall analysis and mechanical properties of the cell wall of these dwarf strains will be published in another paper.

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