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Effects of Lodging on Dry Matter Production, Grain Yield and Nutritional Composition at Different Growth Stages in Maize (*Zea mays* L.)

Mineo MINAMI and Akio UJIHARA
(*Faculty of Agriculture, Shinshu University, Ina, Nagano 399-45, Japan*)
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Abstract : To analyze the mechanism of damage to yield of maize by lodging, root lodging (RL) and stalk lodging (SL) were mechanically induced at four growth stages, and their effects on canopy architecture, dry matter and grain yield, and nutritional composition were investigated. Except for RL 15 days before silking, a decrease of dry matter and grain yield by treatment was observed. An uneven distribution of leaves in the narrow spaces of lodged canopy reduced the net assimilation rate (NAR). Increased reduction of the NAR occurred as the treatment stage advanced, more so by SL than by RL. Crop growth rate (CGR) correlated closely with the NAR. These results indicated that due to lodging, a reduction of the NAR was correspondingly the primary cause of a reduction of the CGR, and of subsequent yield reductions. Reduction of leaf area also decreased the CGR. Translocation of assimilates from foliage to ear was not inhibited by lodging. Being lowest by SL at silking, grain yield correlated with the number of grains per ear. It was concluded that lodging at silking decreased the number of grains per ear and caused the most serious damage to grain yield. All treatments caused a change in the nutritional composition of ear and foliage.
Key words : Dry matter production, Grain yield, Growth analysis, Light-intercepting characteristics, Lodging, Maize, Nutritional composition.

生育時期別の倒伏処理がトウモロコシの収量と品質に及ぼす影響：南　峰夫・氏原暉男（信州大学農学部）
要　旨：倒伏がトウモロコシの収量と品質に及ぼす影響とその機構を解明するために，絹糸抽出期をはさんで4回，ころび型倒伏（RL）と折損型倒伏（SL）処理を行ない，個体群構造の変化と乾物生産，子実収量との関係，および栄養組成の変化について解析した．倒伏処理後の植物体は種々の程度に姿勢を回復したが，草高の低下により縮小された狭い群落空間内に葉群が不均一に分布しており，受光態勢の悪化による NAR の低下が認められた．植物体の姿勢の回復は生育時期が進むほど，また SL 処理区の方が悪く，絹糸抽出期15日前の RL 処理区を除いて乾物および子実収量の減少が認められた．CGR は NAR と高い正の相関関係を示し，倒伏による乾物生産量の減少は受光態勢の悪化による NAR の低下に起因していた．倒伏処理による茎葉から雌穂への同化産物の転流の阻害は認められなかった．子実収量は絹糸抽出期の SL 処理で最低となり，一穂当り粒数と正の相関を示した．一穂当り粒数の減少は RL，SL ともに絹糸抽出期の処理で最大となり，子実収量については絹糸抽出期の倒伏が最も大きく影響すると考えられた．倒伏処理による栄養成分組成の変化が全処理区でみられ，植物体全体では粗繊維の増加と粗脂肪の減少が認められた．
キーワード：栄養組成，乾物生産，子実収量，受光態勢，生長解析，倒伏，トウモロコシ．

Although much progress has been made in breeding of lodging resistance in maize[10,22], modern cultural practices of higher planting density and extravagant use of chemical fertilizers accelerate lodging. According to Zuber and Kang[26], lodging still accounts for annual yield losses of 5—25% in the United States. Furthermore, lodging causes difficulties in harvesting and changes the quality of grain. Therefore, lodging is still one of the most important problems in maize culture and breeding of lodging resistant maize genotypes is needed[2,5].

A decrease of grain yield due to lodging has been reported in many cereal crops[8,20]. In rice plants, such a loss of grain yield is ascribed to the disturbance of photosynthesis by the detrimental effect on light-intercepting characteristics, the inhibition of absorption of nutrients and water, as well as the inhibition of a translocation of assimilated materials to the grain[12,13].

Lodging of maize plants occurs at various growth stages from before silking to maturity, with two types of lodging (i.e. root lodging and stalk lodging). The former is caused from root pruning without damaging the stalk and the latter from the breakage of stalk.

In the present study, to analyze the mechanisms of decrease in dry matter and grain yield due to lodging, the effects of artificial damages induced by root lodging treatment and stalk lodging treatment at different growth stages on the change of canopy architecture, as well as the effects on dry matter and grain production was investigated. The change of the nutritional composition of ear and foliage due to lodging treatment was also investigated.

Materials and Methods

The commercial hybrid variety, P3382 (Pioneer Hibred Co.) was planted on May 15, 1985 at the Experiment Farm of the Faculty of Agriculture, Shinshu University, Ina, Nagano, with 0.9 m spacing between rows and 0.2 m between hills (55,660 plants/ha). Fertilizers were applied at rates of 60-120-90 kg/ha of N-P-K as basal dressing and additional N of 60 kg/ha was applied at the ear initiation stage as a top dressing. Each plot consisted of 6 rows 5 m long in two replicated blocks.

Root lodging (RL) and stalk lodging (SL) treatments were made by hand at 15 days before silking (RL1, SL1), mid-silking (RL2, SL2), and at 15 and 30 days after silking (RL3, SL3 and RL4, SL4). Plants were perpendicularly leveled to the ground at more than 60 degrees in RL plots. In SL plots, stalks were broken at the third internode below the uppermost ear-born node where natural stalk breakages were frequently observed[18]. Plants were lodged uniformly alout 60 degrees west from the north in north-south rows.

Plant posture recovery after treatments was recorded for 20 plants per plot. After the last treatment, leaf area and relative illuminance were measured from the ground to the canopy top by 0.3 m intervals. The former was measured with an automatic leaf area meter (Hayashi Denko Co.) for 5 plants, and the latter with a luxmeter (Lichtmeβ Technik Co.) at 40 locations, half of which were 0.3 m from hills on both sides of the rows and the rest were at the center between hills in the rows.

Changes in dry matter weight and leaf area for 5 plants were measured 15 days after treatment and growth parameters were calculated.

At maturing stage, dry matter yield and grain yield were measured for 5 and 20 plants per plot, respectively.

Nutritional composition, (i.e. the content of crude protein, crude fat, crude fiber, crude ash and nitrogen free extract) of ear and foliage was analyzed by the authorized methods of the Ministry of Agriculture, Forestry and Fisheries[1].

Results

1. Effects on canopy architecture and light-intercepting characteristics

Maize plants treated with RL rose up in the lower part of the stalk and recovered their upright posture in the upper part of the plants, but the extent and number of days needed for recovery of their upright posture differed according to the treated growth stages. As the growth stage advanced, recovery of the erect posture of the plant became slower and less prominent. Though plants treated 15 days before silking (RL1) stood nearly perpendicular within a few days, those treated 30 days after silking (RL4) rose up only slightly. Plants treated with SL also stood up but slower and less prominently than those with RL at the same growth stage (Fig. 1).

Changes of plant posture were accompanied with leaf area reduction. Leaf area was evidently smaller in RL2 and all SL plots than in the control. In contrast with increasing in the control, the treatments at the silking stage caused even leaf area reduction (Fig. 2). This resulted from the inhibition of leaf area development and acceleration of senescence of leaves in lower position.

As a result, vertical distribution of leaf area density and relative illuminance in the canopy were changed as shown in Fig. 3. Vertical distribution of leaf area density in the canopy of RL1 was nearly the same as that in the control, and leaf area density was largest in the middle strata. But in the other plots, leaves distributed more in the lower strata. Especially in SL3 and SL4, almost all leaves stood within 60 cm above the ground.

Consequently, relative illuminance in the canopy was drastically altered. Though relative illuminance descended gradually from the canopy top to 90 cm above the ground and was nearly constant at less than 60 cm in the control and RL1, relative illuminance descended straight from the canopy top to the ground in the other plots. Except for RL4, the average relative illuminance at the ground was higher in the treated plots than in the control (Fig. 3).

Fig. 4 shows frequency distribution of rela-

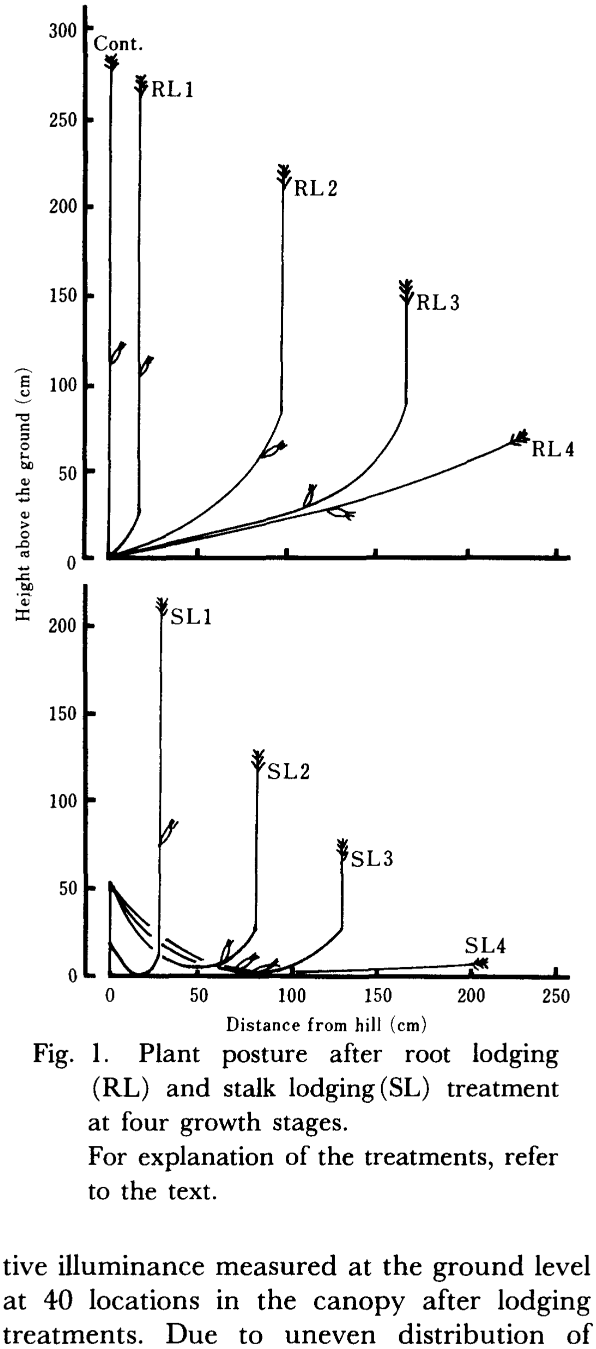

Fig. 1. Plant posture after root lodging (RL) and stalk lodging (SL) treatment at four growth stages.
For explanation of the treatments, refer to the text.

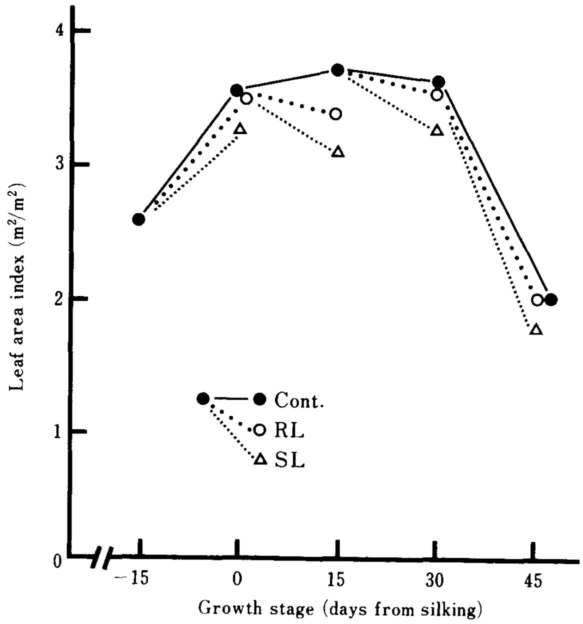

Fig. 2. Effect of root lodging (RL) and stalk lodging (SL) treatment on leaf area index at four growth stages.

tive illuminance measured at the ground level at 40 locations in the canopy after lodging treatments. Due to uneven distribution of leaves in the canopy, relative illuminance varied from less than 10 to nearly 100% in RL3 and all SL plots, where much of the light reached directly to the ground without interception by leaves resulting in higher average relative illuminance. On the other hand, relative illuminance at the ground was uniformly low in RL1 and RL2 as well as in the control.

Furthermore, a significant linear regression of relative illuminance according to logarithmic scale on cumulative leaf area index was recognized in RL1 and RL2, and their extinction coefficients[19] were smaller than that in the control (Fig. 5). These facts indicated that leaves also recovered their erect position and that their higher average relative illuminance at ground level resulted from their smaller leaf area and extinction coefficients.

In RL4, plants covered the space from 0 to 60 cm above ground (Fig. 3), so that relative illuminance at ground level was uniformly low (Fig. 4).

2. *Effect on dry matter production*

Dry matter weight in the control was maximum at the last sampling date (i.e. the yellow ripening stage). This pattern of dry matter accumulation was the same as previously reported by several authors[4,11,15].

The effect of RL and SL treatments on dry matter production in 15 days after treatments are shown in Fig. 6. An increase of total dry matter weight was not affected by RL1, RL2 and SL1 but was significantly inhibited by the other treatments. The damage to dry matter production by treatments became more serious as the treated stage advanced and was greater by SL than by RL. In contrast to an increase in the control, no increase or decrease of total dry matter weight was observed in RL4 or SL4.

Except for RL4 and SL4, the effects of RL and SL on ear dry matter were the same for total dry matter. Despite the absence of an increase of total dry matter weight, ear dry weight increased after the RL4 and SL4 treatments. This fact illustrated that an increase of ear dry matter weight was derived from translocation of assimilates stored in foliage.

As a result, except for RL1, final total dry matter yield at maturing stage was significantly decreased by the treatments (Fig. 7). SL had a greater decreasing effect than RL at the same growth stage. Except for RL1 and SL1, ear dry matter yield decreased, being lowest in SL3. Foliage dry matter yield was decreased by all treatments. Late RL caused a greater decrease than early RL, and SL1 caused a smaller decrease than the other SL.

To evaluate the cause of a decrease of dry matter production, growth parameters 15 days after treatment were calculated (Table 1).

Crop growth rate (CGR), relative growth rate (RGR) and net assimilation rate (NAR) were not significantly lowered by RL1, RL2 and SL1 but were remarkably reduced by the other treatments. While leaf area ratio (LAR) was not affected by the treatments, detrimen-

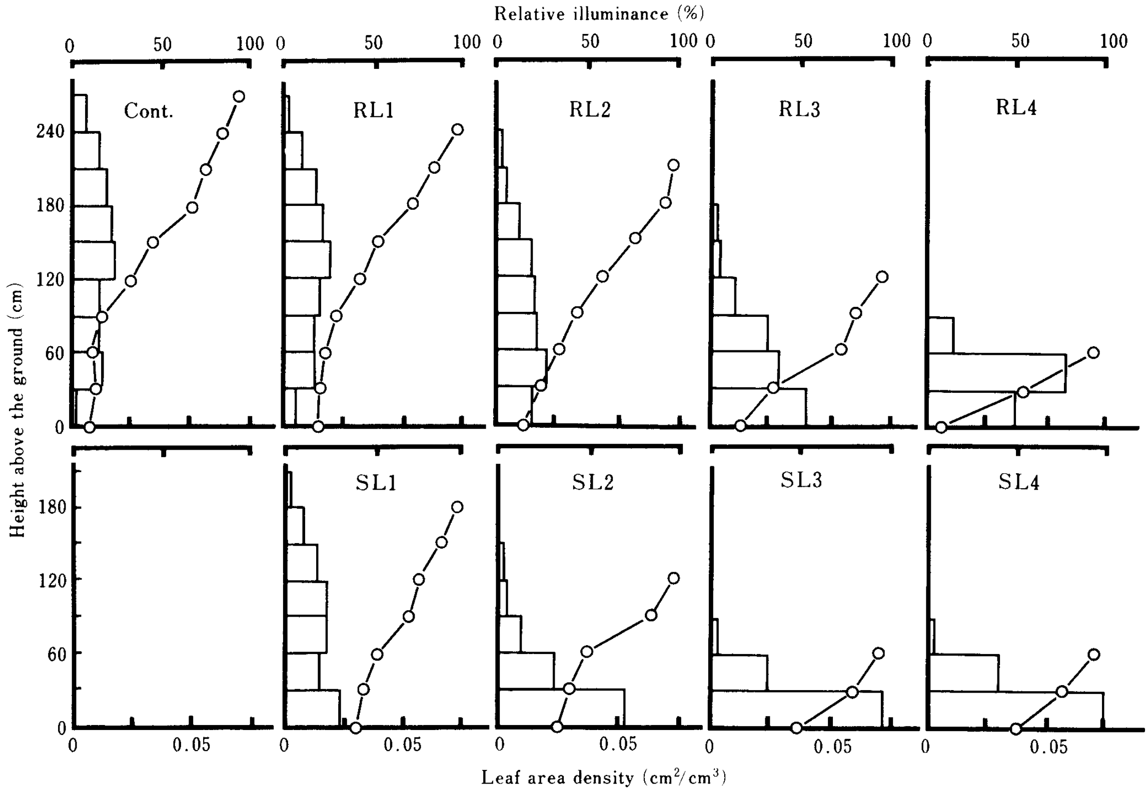

Fig. 3. Vertical distribution of leaf area density and relative illuminance after root lodging (RL) and stalk lodging (SL) treatment at four growth stages.

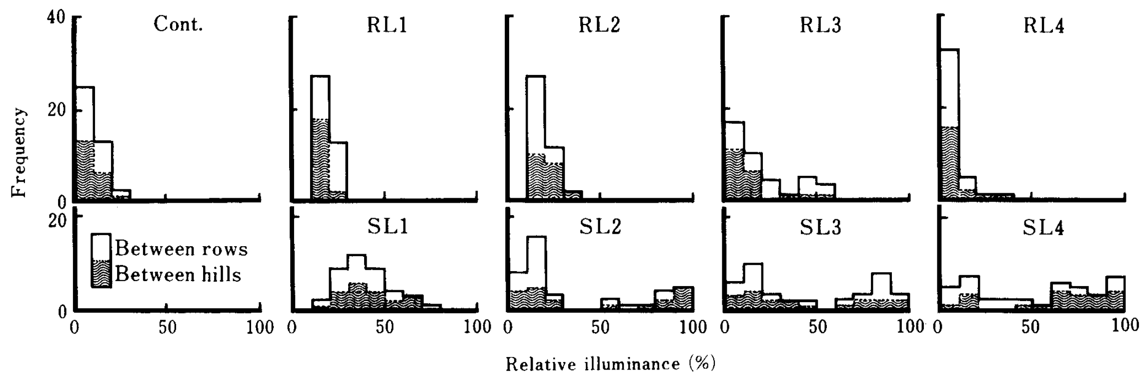

Fig. 4. Frequency distribution of relative illuminance at the ground in the canopy after root lodging (RL) and stalk lodging (SL) treatment at four growth stages. Relative illuminance was measured at 20 locations between hills and 20 locations between rows, respectively.

tal effects on these parameters increased as the growth stage advanced, and more so by SL than RL.

A reduction of dry matter production (CGR) by the treatments was due to low photosynthetic activity (NAR) since a highly significant correlation between CGR and NAR (r=0.979***) was observed.

Except for RL1, the CGR 15 days after treatment to maturing stage was higher than the CGR in 15 days after treatment, but was still lower than the control. In RL1, plants regained their erect position as in the control, and recovered dry matter productivity (CGR) entirely, as before treatment (Fig. 8). This demonstrated that CGR improved by recovery of the upright position of plants.

3. Effects on grain yield and yield components

Grain yield and yield components are shown in Table 3. Except for RL1, grain yield was significantly reduced by the treatments. The reduction of grain yield ranged from 15 to 28%, being larger in SL than RL at the same growth stage, though the difference was not significant.

The number of florets per ear was observed at the silking stage in RL1 and SL1, which were the treatments 15 days before silking (Table 2). Both RL1 and SL1 had little effect on the floret development of ears. A small but significant decrease in the number of florets

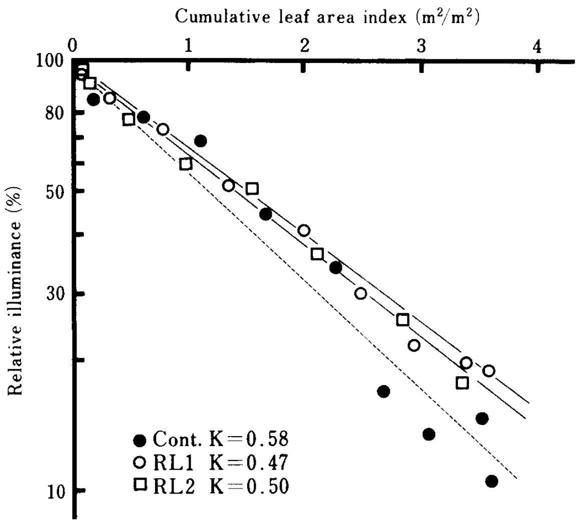

Fig. 5. Relationship between cumulative leaf area index and relative illuminance in the canopy after root lodging (RL) treatment.
K=extinction coefficient.

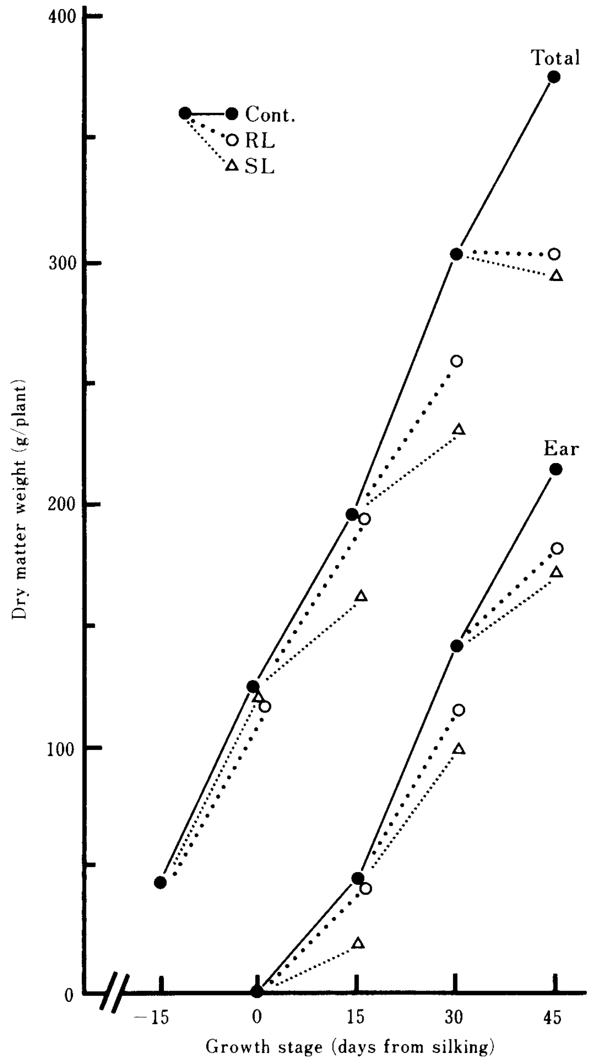

Fig. 6. Dry matter production in 15 days after root lodging (RL) and stalk lodging (SL) treatment at four growth stages.

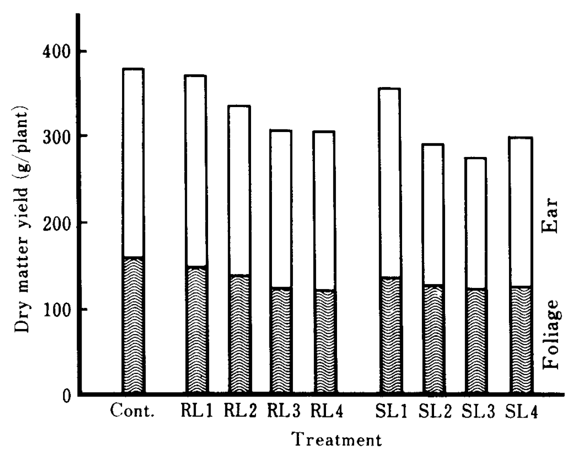

Fig. 7. Effect of root lodging (RL) and stalk lodging (SL) treatment on dry matter yield at four growth stages.

Table 1. Effects of root lodging (RL) and stalk lodging (SL) treatment on growth parameters in 15 days after treatment at four growth stages.

Growth parameter	Treatment	Growth stage (days from silking)			
		−15	0	15	30
Crop growth rate	Cont.	30.501	27.104	39.872	26.880
(g/m²/day)	RL	27.552	26.432	23.184	−0.227
	SL	28.075	14.037	12.208	−3.397
Relative growth rate	Cont.	0.0697	0.0303	0.0287	0.0141
(g/g/day)	RL	0.0654	0.0297	0.0181	−0.0001
	SL	0.0661	0.0174	0.0101	−0.0020
Net assimilation rate	Cont.	10.068	7.510	10.955	9.821
(g/m²/day)	RL	9.113	7.580	6.385	−0.083
	SL	9.553	4.228	3.519	−1.317
Leaf area ratio	Cont.	76.982	41.604	27.081	15.301
(cm²/g)	RL	78.550	42.212	27.865	17.570
	SL	76.853	41.907	29.598	17.943

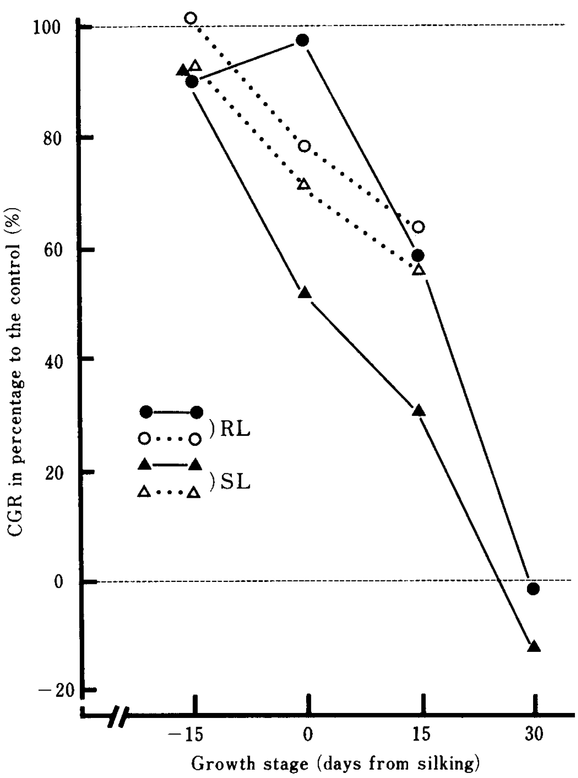

Fig. 8. Effect of root lodging (RL) and stalk lodging (SL) treatment on crop growth rate (CGR) in 15 days after treatment (●, ▲) and since 15 days after treatment to maturing stage (○, △), at four growth stages.

per row with no decrease in the number of rows resulted in only a slight decrease in the number of florets per ear. Therefore, it is believed that a reduction of grain yield in SL1 resulted from the detrimental effect on the development of fertilized florets.

The number of grain rows per ear was not significantly decreased by treatment. On the other hand, the number of grains per row decreased significantly in RL2, SL1, SL2 and SL3, being smallest in RL2 and SL2. Similar results were obtained for the number of grains per ear which significantly correlated with the number of grains per row ($r=0.959^{***}$). Except for RL1 and SL1, the 100 grain weight was significantly decreased by the treatments, with the lowest 100 grain weight occurring in SL4 (Table 3).

Grain yield, which is composed of the 100 grain weight and the number of grains per ear, correlated significantly with the number of grains per ear ($r=0.834^{**}$) but not with the 100 grain weight ($r=0.339$). From these results, grain yield loss by treatment was due to the reduction of the number of grains per ear resulting from reduction of the number of grains per row.

4. Effects on nutritional composition

The nutritional composition of ear and foliage was altered by all treatments (Table 4). In foliage, an increase of crude fiber (CF) and corresponding decrease of nitrogen free extract (NFE) were observed in all treatments. The degree of alternation was greater in the later treatments. An increase of crude protein (CP) in SL and crude fat (EE : Ether extract) in RL was observed. In ear, increase of CF was recognized to be the same as in foliage but

Table 2. Effect of lodging treatment 15 days before silking on floret development of ear.

Treatment	First ear			Second ear		
	No. of rows /ear	No. of florets /row	No. of florets /ear	No. of rows /ear	No. of florets /row	No. of florets /ear
Control	14.0a[1)]	55.7a	781a	14.2a	51.6a	732a
Root lodging	14.8a	52.3b	772a	14.7a	51.1a	750a
Stalk lodging	14.4a	52.4b	751a	14.5a	49.6a	720a

1) Figures followed with same letter are not significantly different by Duncan's multiple range test (P=0.05).

Table 3. Effects of root lodging (RL) and stalk lodging (SL) treatment on grain yield and yield components at four growth stages.

Treat-ment	Grain yield (g/plant)[1)]	100 grain weight (g)[1)]	No. of grains /ear	No. of grains /row	No. of rows /ear
Cont.	193.5a[2)]	28.2b	688.0ab	47.6a	14.5a
RL1	192.9a	27.5bc	709.0a	46.6ab	14.6a
RL2	162.9bc	25.8de	615.1cd	42.8bc	14.2a
RL3	161.2bc	24.8 ef	653.1abc	45.2ab	14.3a
RL4	164.7b	25.3def	664.3abc	46.8ab	14.3a
SL1	158.4bc	29.5a	582.4de	40.9cd	13.9a
SL2	139.4c	26.6cd	534.8e	38.6d	13.9a
SL3	153.2bc	25.5de	626.9bcd	45.1bc	13.9a
SL4	161.5bc	24.1f	671.9abc	46.4ab	14.5a

1) Water content is adjusted to 15%.
2) Figures followed with same letter are not significantly different by Duncan's multiple range test (P=0.05).

little or no increase of NFE was observed. Except for SL2 and RL2, CP increased in SL but decreased in RL, so that CP content was higher in SL than in RL. EE was remarkably decreased by all treatments, especially by later treatments. Crude ash (CA) decreased in all treatments and was higher in SL than in RL. As a whole plant, increase of CF and decrease of EE were recognized in all treatments and changes were larger in SL than in RL. Furthermore, a decrease of CA in RL and NFE in SL, and an increase of CP in SL were observed, respectively. Other definite tendencies were not observed.

Discussion

In this experiment except for RL1, RL and SL treatments decreased dry matter yield and grain yield (Fig. 7, Table 3) and this decrease was related with the ability of the plants to recover their erect position. The ability of the plants to recover erect position became less as the growth stage advanced. Laude and Pauli[17)] reported that wheat that was artificially lodged before heading or within one week thereafter regained erect position, but its ability to maintain it decreased after heading. These results are ascribable to the progressive hardening of the stalk and cessation of the internode elongation after heading.

Corresponding to the change of plant posture, canopy architecture and light-intercepting characteristics were disturbed. Uneven distribution of leaves in the narrow space of lodged canopy caused mutual shading and low light-interception and consequently resulted in low NAR. Furthermore, reduction of leaf area index (LAI) caused low CGR (NAR × LAI).

According to Warren Wilson[24)], the ideal canopy that realizes maximum photosynthesis of a community has a structure in which all of the light is equally intercepted by all leaves, but lodging resulted in an adverse change of

Table 4. Effects of root lodging (RL) and stalk lodging (SL) treatment on nutritional composition of ear and foliage at four growth stages (% in dry matter).

Treatment	CF[1]	CA	CP	EE	NFE
		==== Foliage ====			
Cont.	25.60	5.64	5.58	0.63	62.57
RL1	28.78	5.77	5.65	0.69	59.10
RL2	28.87	5.32	5.36	0.77	59.69
RL3	31.17	5.26	5.54	0.73	57.30
RL4	30.71	5.66	5.67	0.81	57.15
SL1	29.40	6.53	6.23	0.98	56.86
SL2	33.16	6.71	5.67	0.56	53.90
SL3	33.66	5.41	5.85	0.77	54.31
SL4	32.94	6.00	6.10	0.42	54.54
		==== Ear ====			
Cont.	4.18	1.83	7.15	5.94	80.83
RL1	4.31	1.45	7.02	4.59	82.63
RL2	4.68	1.58	7.41	4.81	81.52
RL3	4.57	1.39	6.56	3.62	83.87
RL4	4.82	1.38	6.60	3.74	83.46
SL1	4.98	1.51	7.62	4.32	81.57
SL2	4.60	1.68	7.13	4.43	82.16
SL3	6.10	1.79	7.76	3.73	80.61
SL4	5.86	1.75	7.44	4.01	80.93

1) CF : Crude fiber, CA : Crude ash, CP : Crude protein, EE : Crude fat (Ether extract), NFE : Nitrogen free extract.

canopy architecture.

It was concluded that the detrimental effect of lodging on photosynthesis increases as growth stages progress, and is more significant by SL than RL.

In spite of the above conclusion, final dry matter yield is determined by the quantity of dry matter produced before and after treatment. Dry matter yield was higher in SL4 than in SL3 and did not differ between RL3 and RL4 because dry matter accumulated prior to the treatment was higher in SL4 and RL4 than in SL3 and RL3 (Fig. 6).

Besides productivity of dry matter, the grain yield is determined by the ability to translocate assimilates from foliage to grain. Hitaka and Kobayashi[12,13] observed the inhibition of translocation of assimilates to grain in lodged rice plants, while an increase of translocation of assimilates from stalk to grain was found in maize when photosynthesis was restricted by leaf defoliation[9,14] and frost damage[7]. In the present study, an increase of ear dry matter weight and the corresponding decrease of foliage dry matter weight were observed in RL4 and SL4 (Fig. 6). This fact showed that the translocation of assimilates from foliage to ear is not hindered by lodging treatments.

Grain yield was lowest in SL2 and closely correlated with the number of grains per ear. The number of grains per ear was smallest in RL2 and SL2 which were treated at silking (Table 3). Because the first few days after fertilization is the critical period that decides whether the fertilized ovules develop or abort[3,15], a short supply of assimilates due to lodging at silking causes abortion of fertilized ovules in the upper part of ear and following grain yield reduction. Therefore, it is thought that lodging at silking has the most detrimental effect on grain yield through the reduction of the number of grains per ear.

The changes of the nutritional composition of grain and/or foliage by cultural practice and stress such as N application and leaf clipping[21], root pruning by corn rootworm[16], and soil water deficit[23] were reported in maize. An increase of CP content in the ear after SL treatment was observed in this experiment (Table 4). An increase of CP content in grain by artificial lodging was also reported in wheat[17,25] and barley[6]. But the increase of CP content was accompanied by a reduction of grain yield per plant, so that CP yield per plant or per unit land area was reduced by lodging.

It should be noted that nutritional composition was also altered by RL1 which did not affect dry matter and grain yield.

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* In Japanese with English summary.

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