Characterization and preliminary evaluation of factors for early growth in sugarcane *(Saccharum officinarum)*

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ABSTRACT

Sugarcane has a very slow growth during the early part of its life. An experiment was conducted under field conditions to identify, characterize, and evaluate traits that could improve its productivity during this phase. Two sugarcane cultivars, Ni9 and NiF3, were used. They were planted at an average of 4.16 plants m^{-2} normal density (HD) and 6.25 plants m^{-2} high density (HD). The cultivars were sprayed with GA_3 to modify the canopy structure, and the growth characteristics were analyzed. For dry matter production and leaf characteristics, differences between the treated and control plants were significant in most of the traits studied at 1 month after the treatment. In the later stages, the differences between the treatment and the control were not significant, but the differences between Ni9 and NiF3ND and between NiF3ND and NiF3HD were significant. Within the canopy structure, leaf area concentration and leaf area index (LAI) were greater in the control of the cultivars, resulting in reduced light penetration. In the treatments with a relatively lower LAI and even distribution of leaf area, light penetration was greater. Ideal traits proposed for higher productivity in the early growth phase in sugarcane include moderately tall plant, long and large leaf, even distribution of leaf area in the canopy, maximum but not excessive number of tillers, and greater dry matter allocation for leaf development.

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RÉSUMÉ

ABOAGYE, L. M., TERAUCHI, T. & MATSUOKA, M.: *Caractérisation et évaluation préliminaire des facteurs pour la croissance première en canne à sucre* (Saccharum officinarum). La canne à sucre a une croissance très lente pendant sa période de première croissance. Une expérience s'est déroulée sous les conditions du champs pour identifier, caractériser et évaluer les traits qui pourraient améliorer sa productivité pendant cette phase. Deux variétés de canne à sucre Ni9 et NiF3 étaient utilisées. Elles étaient plantées à 4.16 et 6.25 plantes m^{-2}, respectivement pour densité normale (ND) et haute densité (HD) et pulvérisées avec GA_3 pour modifier la structure de voûte et les caractéristiques de croissance analysées. Sur le plan de la production de matière sèche et les caractéristiques foliaires, il y avait des différences considérables entre les plantes traitées et les plantes de contrôle dans la plupart de traits étudiés à un mois après le traitement. Aux dernières étapes il n'y avait pas des différences considérables entre le traitement et le contrôle mais il y avait des différences considérables entre Ni9 et NiF3 ND et entre NiF3 ND et NiF3 HD. A l'intérieur de la structure de voûte, il y avait plus grande concentration de surface foliaire et l'index de surface foliaire (LAI) dans le contrôle des variétés résultant en une pénétration reduite de lumière. Dans les traitements avec LAI relativement plus faible et la distribution égale de surface foliaire, il y avait plus grande pénétration de lumière. Les traits idéaux proposés pour la productivité plus élevé à la phase de première croissance en canne à sucre comprennent: plante modérément élevée, de feuille longue et large; distribution égale de surface foliaire dans la voûte et un maximum mais pas un nombre excessive des talles et plus grande allocation de matière sèche pour le développement foliaire.

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Introduction

The basic principle of crop productivity, the production of dry matter, is a cumulative effect of several factors. The identification, characterization, and evaluation of the crop's inherent physiological and morphological traits would enable the synthesis of a crop type for maximum productivity. Sugarcane (*Saccharum* species) is a long-seasoned crop which matures between 12 and 18 months, depending on the time of planting. Crop duration can be shortened by high density planting (Nose *et al*., 1989). Several production technologies have been developed ranging from agronomy, breeding and adaptability, but some basic pertinent problems that would enhance rapid development such as ideal plant height, leaf and plant morphology, and the number of tillers remain unresolved.

Varieties have been developed that could withstand adverse environmental conditions (Shimabuku, 1997). However, information on factors that would enhance growth in the early phase and thus shorten the growing period is scanty. Growth rate in sugarcane during the early phase is slow compared to other crops (Ehara, Ysuchiya & Takamura, 1994; Terauchi *et al*., 1999; Terauchi & Matsuoka, 2000). Growth rate during the early growth phase has been increased by planting at a higher density for optimum leaf area index (LAI) and maximum crop cover to intercept solar radiation, and thus accelerate the growth phase (Aboagye *et al*., 1993). Planting and harvesting in autumn improves initial growth and early soil coverage, and thus minimizes the soil runoff during the rainy season (Sugimoto, 1999, 2000).

Sugarcane planting at higher population invariably produces greater number of stalks per unit area. Depending on the tillering ability, many tillers do not reach maturity, due most probably to less light interception at the base of the canopy and the intense competition for the limited environmental resources (Shimabuku & Higa, 1977a, 1977b). Furthermore, most sugarcane stalks have small stalk diameter, which predisposes the crop to natural calamities such as typhoons. Tiller removal enhances growth and productivity, but it is labour demanding (Terauchi *et al*., 2001). High density planting resulted in higher productivity in the early stage, but the net yield was low due to excessive leaf area and greater number of tillers (Shimabuku, 1997). The manipulation of tillers to produce an optimum number of acceptable size, encouraging early growth by planting at high density so as to use the available environmental resources for growth, and avoiding conditions that hinder growth and ripening would improve the overall productivity through sound management practices.

In sugarcane, the relation between LAI at the early growth stage and yield is positive among several varieties. However, this yield was reduced in cultivars with greater LAI than the average in the early growth stage. Thus, an optimum LAI exists for optimum yield in sugarcane (Shimabuku *et al*., 1982). Though the positive relation between LAI and yield in the early phase is greater, the value of leaf area duration (LAD) was high. This suggests the maintenance of LAI with greater efficiency through the canopy structure. The benefit of LAI is dependent on the time of planting. Furthermore, the correlation between the co-efficient of extinction and LAI is positive when sugarcane is planted in October, but negative when planted in July (Shimabuku & Higa, 1977a). Thus, adopting better management practices in manipulating the canopy structure through planting at a higher population and controlling the number of tillers would enhance the productivity of sugarcane.

The objectives of this study were to manipulate the agronomic and morphological features that may enhance productivity, especially, in the early growth phase; to control and maintain optimum tillers for higher productivity by characterizing two sugarcane cultivars with different tillering ability, through agronomic and chemical manipulation of the canopy structure; and to analyze possible effects that would enhance early growth, thus, improving the overall productivity in sugarcane.

Materials and methods

Location

The experiment was conducted under field conditions at the Japan International Research Centre for Agricultural Sciences, Okinawa Subtropical Station, Ishigaki, Japan, located at 24° 21'N and 124° 21' E and 33 m above sea level. The soil is reddish yellow with the following physico-chemical properties: *p*H of 5; available N, 2.4 mg/kg; available P, 51.0 mg/kg; exchangeable K, 86.2 mg/kg; water holding capacity of 35.6 per cent; silt, 17 per cent; clay 14 per cent; and bulk density of 1.29 g/cm². The temperature ranged from 16.5 to 31.5 °C with a relative humidity between 67 and 88 per cent and irradiance of 2.7 to 26.2 mJ/m²/day.

Planting materials, experimental design, and cultural practices

Two sugarcane varieties, Ni9 and NiF3, with different characteristics were used. The Ni9 variety has thin stalks, narrow leaves, and profuse tillering ability. The NiF3 variety has thick stalks, broad leaves, and produces few tillers. The planting materials were prepared from 1-year-old sugarcane stalks of both varieties with one bud per sett (Fig.1). The setts were pre-sprouted in plastic boxes under continuous mist of water for 1 week. Uniform germinated setts were selected and planted on 11 April 2001. The Ni9 variety was planted at the normal density (ND) of 120 cm inter-row and 20 cm intra-row. NiF3 was planted at the ND of 80 cm inter-row and at high density (HD) of 20 cm intra-row. The final population at ND was 41,600 plants ha^{-1} and at HD 62,500 plants ha^{-1}. The randomized complete block (RCB) design was used with three replications. Before the planting of the setts, 80 kg/ha each of calcium/silica fertilizer and a long- term fertilizer 22:8:8 (N:P:K) were applied. Standard cultural practices were adopted throughout the cultivation period.

Growth hormone application

The knapsack was used to spray gibberellic acid at a concentration of 100 ppm, 1 month after planting when the plants were at the average leaf stage of four, to the ND and HD stands of both varieties to modify the canopy structure and to control the tillers.

Dry matter production

One month after planting and thereafter every month (from May to August), five plants per treatment were sampled. The stalk height was determined from ground level to the point of attachment of the fully expanded leaf on the main stalk. The number of leaves (dead and fresh), leaf length, leaf width (at the broadest part), the number of all other stalks (considered as tillers) and stalk diameter (at the middle part) were measured for the main stalk (first sprouted shoot) and the tillers. The leaf area was measured with the automatic leaf area metre (Hayashi Denko AAM-8) and the leaf area index determined. The leaves and stalks were oven dried at 80 °C for 72 h to determine the dry weight.

Fig. 1. Single bud setts of sugarcane.

Relative light intensity, leaf area, leaf and stalk dry weight with plant height

Three plants per treatment were selected and the leaves and stalks of the main stalk and tillers were clipped off in each layer of 20 cm of the stalk height of the sprayed plants (treatment) and unsprayed plants (control). The leaf area per layer was measured with the automatic leaf area metre. The leaves and stalks were oven dried at 80 °C for 72 h to determine the dry weight. Photosynthetic active radiation (PAR) within the canopy was determined in each 20-cm layer of plant height by measuring five points in each layer with LICOR quantum sensor (LI 190SA) to determine the relative light intensity.

Results

Effect of GA_3 on morphological characteristics and dry matter production at the early growth stage (first 3 months after planting, i.e. 7th June 2001)

Table 1 shows the effect of GA_3 4 weeks after the treatment. On the main stem, with the exception of the number of leaves which showed no significant differences, plant height, leaf length, width and total dry weight showed significant differences between the two cultivars and the treatments within a cultivar. In the leaf width, differences between the treatments in Ni9 and between and among the treatments in NiF3 were not statistical. In the tillers, GA_3 reduced the number of tillers especially in Ni9 as compared to the less tillering NiF3. In the plant height within a treatment, the differences between the treatments in a cultivar were not significant. However, the differences between Ni9 and NiF3 at the ND were significant, but not between the NiF3 ND and NiF3 HD. With the exception of NiF3 HD, the total dry weight at ND of NiF3 and Ni9 in both the control and treatment cultivars had significant differences.

Changes in total leaf area, leaf and stalk dry weight with time

Fig. 2 shows the changes in the total leaf area, leaf and stalk dry weight with time in the early growth phase. The total leaf area was lowest up to June in the treatments of Ni9 and NiF3 at ND. The total leaf area was greatest in the control of NiF3 at ND and HD. Though the total leaf area was low in the control of Ni9, it recorded a higher LAI in July. Generally, the treated plants had lower leaf area than the control. For leaf dry weight, similar trends were observed. The leaf dry weight was higher in the treatment and control of NiF3

TABLE 1

Effects of GA_3 on Some Morphological Traits and Dry Matter Production, 1 Month After Treatment

Treatment	*Main stem*					*Tillers*		
	Plant height (cm)	*Leaf number*	*Leaf length (cm)*	*Leaf width (cm)*	*Total dry weight (gm^{-2})*	*Number*	*Plant height (cm)*	*Total dry weight (gm^{-2})*
Ni9 CND	26.0	7.6	106.3	2.2	50.8	3.4	8.1	17.9
Ni9 TND	32.6	7.9	117.5	2.1	63.3	0.5	6.1	5.9
NiF3 CND	31.0	8.0	108.3	2.7	76.5	2.4	19.0	53.6
NiF3 TND	38.1	8.2	113.4	2.6	94.3	1.7	18.5	26.4
NiF3 CHD	31.0	7.2	101.8	2.6	104.4	2.2	17.1	66.4
NiF3 THD	39.4	7.8	111.0	2.6	139.5	1.9	20.0	60.9
LSD (0.05)	3.72	NS	8.62	0.19	12.45	0.63	4.97	17.7

CND: control normal density; TND: treatment normal density; CHD: control high density; THD: treatment high density.

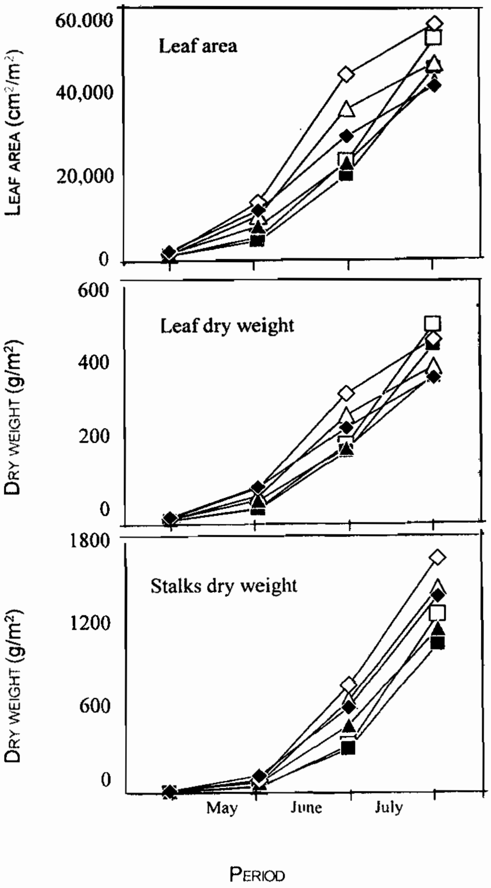

Fig. 2. Changes in total leaf area, leaf and stem dry weight.

☐ : Ni9 C; ■ : Ni9 T; △ : NiF3 C; ▲: NiF3 T; ◇ : NiF3 C(HD); ◆: NiF3 T(HD); HD: high density.

HD in early June. In July, the leaf dry weight was exceedingly greater in the control and treatment of Ni9 as well as in the control of NiF3 HD. The stalk dry weight was lowest in the treatment of Ni9 and greatest in the control of NiF3 at ND and HD.

Evaluation of leaf characteristics in the early growth phase

Table 2 shows the leaf characteristics in the early growth phase (1st August 2001). The leaf length was highest in both the treatment and the control of Ni9 and lower in the control of the HD of NiF3. The differences between the cultivars were significant, but not within the treatments of the cultivars. Whereas it was highest in the control of Ni9, it was lowest in the control of NiF3. For the leaf width, the differences between the cultivars were statistical; however, no differences were recorded between the treatments in a cultivar. The leaf width was greatest in the control of both Ni9 and NiF3 (in both densities) and lower in the treatments. For the leaf thickness, the difference in the treatments of the cultivars was not statistical. In the specific leaf area, the control had greater specific leaf weight as compared to the treatment. It was highest in NiF3 HD and lowest in Ni9. The differences between the two cultivars were statistical, but not between the control and the treatment in a cultivar.

Evaluation of some structural components in the early growth phase

Table 3 shows the evaluation of some agro-morphological characteristics of the two cultivars. In the main stalk of Ni9 and NiF3 HD, the treatment was greater than the control. The differences between the cultivars were statistical, but not between the treatments of a cultivar. In the tillers, the reduction in the stalk height of the treatments was considerable. The number of green leaves on the main stalk of Ni9 and NiF3 ND was greater than that of the control. In the tillers, the treatments had less leaves. In NiF3 HD, the control had greater number of green leaves on the main stalk. The differences between the number of green leaves on the main stalk were significant, but not on the tillers. The number of dead leaves on the main stalk and tillers of the control was greater than that of the treatments, with statistical differences in the number of dead leaves on the tillers but not on the main stalk.

In the number of tillers and the main stalk thickness, the differences between the treatments were statistical, with a reduction in the number of tillers in the treatment of NiF3 (ND and HD), but

TABLE 2

Evaluation of Leaf Characteristics of the Two Sugarcane Cultivars 3 Months After Treatment

Treatment	*Leaf length (cm)*	*Leaf width (mm)*	*Leaf thickness (mm)*	*Specific leaf area* $(cm^2\ g^{-1})$
Ni9 CND	159.5	35.9	0.23	106.4
Ni9 TND	153.6	33.9	0.23	103.8
NiF3 CND	133.5	52.7	0.22	122.1
NiF3 TND	137.3	51.9	0.23	117.3
NiF3 CHD	129.5	52.9	0.21	122.8
NiF3 THD	136.8	51.1	0.23	120.5
LSD (0.05)	8.9	3.6	0.02	17.4

TABLE 3

Evaluation of Some Structural Components of the Two Sugarcane Cultivars

Treatment	*Stalk height (cm)*		*No. of green leaves*		*No. of dead leaves*		*No. of tillers*	*Main stalk thickness (mm)*
	Main stalk	*Tillers*	*Main stalk*	*Tillers*	*Main stalk*	*Tillers*		
Ni9 CND	168.6	112.9	10.9	8.3	2.8	5.4	4.1	21.8
Ni9 TND	179.6	90.7	15.0	6.9	2.4	4.2	4.5	21.2
NiF3 CND	201.5	100.7	15.2	8.5	2.6	5.1	2.0	28.4
NiF3 TND	197.5	95.8	15.9	8.0	1.3	1.4	1.3	24.2
NiF3 CHD	202.1	105.9	14.7	8.9	3.5	5.0	1.3	27.3
NiF3 THD	205.4	73.3	14.3	9.5	2.9	2.1	0.7	24.7
LSD (0.05)	14.9	32.9	3.2	NS	NS	2.0	1.2	2.1

not in Ni9. In the main stalk thickness, the differences between the stalk thickness in Ni9 were not statistical. In NiF3, differences were observed between the control and treatment at both densities.

Evaluation of leaf area, leaf and stalk dry matter production in the early growth phase

Table 4 shows the leaf area and dry matter production in the leaves and stalks on 1st August 2001. Generally, in the leaf area of the main stalk, the differences within the treatments of a cultivar were not significant. However, the differences between the ND and the HD in NiF3 were significant. Thus, intra-varietal response was minimal for the treatments. The differences between the cultivars and density of NiF3 were statistical. Generally, the reduction of the leaf area of the tillers of the treatments was greater as compared to the control, especially in the NiF3 high density. The LAI was highest in the control of NiF3 HD and lowest in the treatment of NiF3 HD. The differences in the LAI were not significant for the treatments or cultivars.

The total dry weight was highest in the control of NiF3 HD and lowest in the treatment of Ni9. The differences among the treatments were statistical, but not between the treatments of a cultivar. The main stalk dry weight was greatest in NiF3 HD and lowest in the Ni9 control. In the tillers, Ni9 had the greatest tiller dry weight in the control and the treatment. The NiF3 HD treatment had the lowest dry matter in the tillers. The differences between the control and treatment of Ni9 and NiF3 HD were significant, but not between the treatments in the HD of NiF3.

TABLE 4

Characterization and Evaluation of Leaf Area and Dry Weight of the Sugarcane Cultivars

Treatment	*Leaf area*			*Total dry weight*				
	Main stalk (cm^{2}m^{-2})	*Tillers* (cm^2 cm^{-2})	*LAI*	*Total* (gm^{-2})	*Main stalk* (gm^{-2})	*Tillers* (gm^{-2})	*Dead leaves* (*ms)(gm^{-2})	*Dead leaves* (*T)(gm^{-2})
Ni9 CND	14803.6	37818.2	5.26	1738.53	575.37	1636.08	21.17	28.78
Ni9 TND	15825.6	29747.0	4.55	1476.23	603.83	872.43	23.18	11.20
NiF3 CND	26712.6	20582.8	4.72	1820.52	1139.10	681.37	9.92	18.70
NiF3 TND	26428.5	16148.5	4.26	1513.33	1073.20	440.13	5.27	6.84
NiF3 CHD	37460.2	19332.1	5.61	2102.83	1499.40	603.51	31.38	33.56
NiF3 THD	37204.0	5956.7	4.31	1736.90	1591.77	145.13	27.09	9.17
LSD (0.05)	4674.9	12864.9	NS	325.21	199.40	301.88	13.83	9.79

*ms : main stalk; *T : tillers.

The dry weight of the dead leaves on the main stalk was lowest in the treatments of NiF3 (ND and HD). However, the differences between the treatment and control of Ni9 as well as between the treatments of NiF3 at ND and HD were not significant. In the tillers, the dry weight of the dead leaves was greater in the control of all the cultivars and treatments, with statistical differences. The control of NiF3 HD had the greatest dead leaves and the treatment of NiF3 ND had the least.

Leaf area, leaf and stalk dry weight distribution with stalk height

Fig. 3 shows the total LAI, leaf and stem dry weight, and the relative light intensity of the cultivars and treatments. The control of Ni9 had the greatest LAI of 6.76, which was concentrated near the top of the canopy. In the treatment of Ni9, with about half the LAI of the control, light penetration of the canopy was greater as a result of increasing LAI towards the bottom of the canopy as compared to the control. In the control of NiF3 ND, the concentration of LAI was at two levels. This, together with its LAI of 4.6, reduced light penetration in the canopy. The treatment of NiF3 ND had LAI of 3.68, and though it had greater LAI near the top of the canopy, the lesser LAI resulted in greater light penetration of the canopy as compared to the control. In NiF3 HD, the concentration of LAI was at most levels of the canopy of the control, especially near the top, with an LAI of 5.28. This resulted in the rapid reduction of solar radiation in the canopy. In the treated plants, the concentration of leaves was sparse in the canopy, resulting in greater light penetration.

Discussion

The production of adequate morphological and structural components for effective growth and development has been elucidated by several authors (Shimabuku & Higa, 1977b; Allen & Scott, 1980; Isoda, Nakaseko & Gotoh, 1984; Aboagye *et al.*, 1994). In this study, the plant structures, and their effect on growth and dry matter production, were modified mainly through the tillers and pronounced few weeks after the treatment with GA$_3$. For total dry matter production and leaf area, the control plants had greater values than the treatment (Tables 1 and 4). Considering the production of dry matter in specific organs, GA$_3$ had a greater effect on the total dry matter in the early phase, but it was less effective during

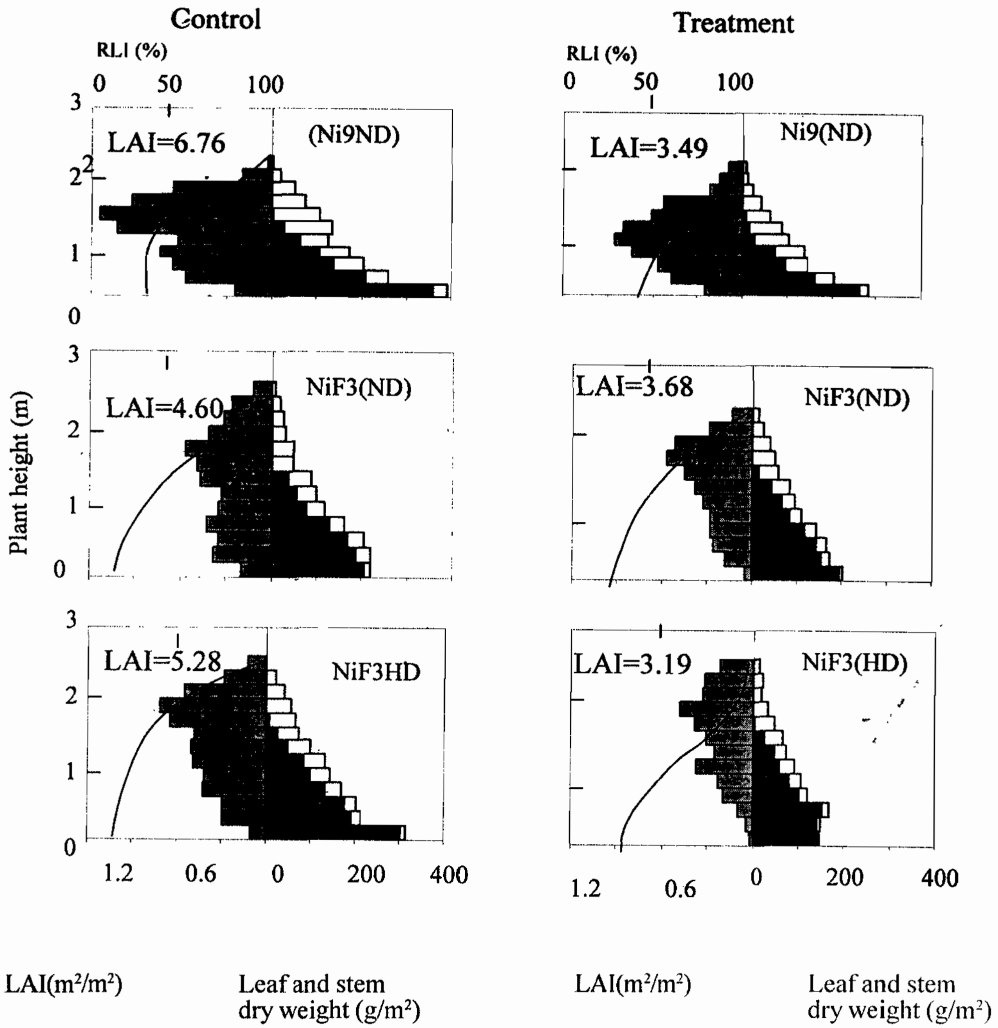

Fig. 3. Canopy structure, leaf area, leaf and stem dry weight, and light interception.

■ : leaf area index ☐ : leaf dry weight ■ : stem dry weight

ND : normal density HD : high density RLI : relative light intensity

the latter growth phases. This corroborates with studies by Tanimoto & Nickel (1967) on commercial varieties of sugarcane in which the effect of GA_3 lasted for about 4 weeks. The transient action of GA_3 requires repeated application for effective modification of plant structures and the production of dry matter.

In this study, GA_3 increased plant height and leaf length, implying that greater dry matter was allocated to these organs. Greater plant height and longer leaf length would have little effect on dry matter production at this stage, since greater leaf area through broader leaves is more advantageous in intercepting greater solar radiation than longer, flexible leaves which intercept less light. Taller plant height is less advantageous in the early growth phase, since the LAI is less and unlikely to cause mutual shading. Dry matter production during the early growth phase has been ascribed to greater leaf area in several crops (Watson, 1952, 1958; Davis & Maack, 1991). This implies that sugarcane cultivars that can develop greater leaf area as in the NiF3 HD (Fig. 2) would produce greater dry matter during the early growth phase through greater allocation of dry matter to the leaves at the expense of tiller development.

The tendency was that the longer the leaf, the narrower its leaf width (as in Ni9), and the broader the leaf, the shorter the leaf length (as in NiF3). Improving the specific leaf area by developing shorter and broader leaves had been recognized (Terauchi & Matsuoka, 2000). Invariably, longer and narrower leaves would allow greater light penetration than the shorter and broader leaves. The characteristic nature of the sugarcane stalk as well as the flexible and narrow leaves may permit solar radiation penetration, if not excessive (Williams, Loomis & Lepley, 1965; Isoda *et al.*, 1994). The main stalk, with its sparing distribution of leaves, would not have any adverse effect on light interception by the tillers, and a short plant height is ideal.

However, the combined effect of the number of tillers and height would have a pronounced effect on dry matter production due to the dense canopy that would cause mutual shading. The greater demand for assimilates to maintain excessive and unproductive tillers would reduce the overall dry matter production. Irrespective of the stage of development (early or rapid), the dry matter partitioning to the tillers of the control was greater as compared to the treatment. This further shows that the production of few but productive tillers at a relatively short time would improve the overall productivity per stand, since each tiller would contribute towards dry matter production as compared to the protracted development of tillers.

In the early growth phase, the broader leaves with the tendency to be horizontal would intercept greater amount of solar radiation as compared to the longer and thinner leaves which would intercept less radiation as in Ni9. But this would be more advantageous during the late growth period when the canopy is dense and the photosynthetic structures would be contributing effectively towards the production of assimilates due to greater light penetration. On the other hand, most of the leaves with broad width would not be contributing towards the production of assimilates.

Ideally, during the early growth period in sugarcane, allocation of dry matter to the leaves should be maximum. The sinks (stalks) should have minimum dry matter allocation during the early growth stage and maximum in latter growth stages to develop greater sink capacity to accumulate assimilates for improved, sustainable, and maximum productivity through the development of optimum number of tillers. Tentatively, sugarcane productivity at the early growth stage would depend on greater dry matter allocation for leaf development, short stalk height, few tillers, higher source capacity (LAI) and later, greater sink activity.

In this study, most of the traits examined could be greatly influenced by the environment. To validate the data, further studies must be conducted by using several varieties with different tillering ability and also timing of the GA_3 treatment so as to reach a definite logical conclusion. Table 5 shows the comparative ideal characteristics in the early and late growth stages and their effects on productivity. These could be used to develop ideal types for maximum productivity in the early growth phase of sugarcane.

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TABLE 5

Comparative Ideal Characteristics at the Early and Rapid Growth Stages in Sugarcane

Component	*Early growth phase*		*Rapid growth phase**	
	Ideal character	*Effect on productivity*	*Ideal character*	*Effect on productivity*
Plant height	Short	Greater dry matter for leaf growth and increased LAI, less to stems	Tall	More effective for increased light penetration and greater stem dry weight
Leaf morphology	Broad and long	Maximum LAI, maximum light interception	Narrow and long	Optimum LAI, greater flexibility, deeper light penetration and interception
Leaf size	Large	Greater light interception	Small	Improved light penetration
Leaf inclination	Horizontal	Improved light interception due to less dense canopy	Erect	Improved light penetration in dense canopy with greater LAI
Leaf area concentration in the canopy	Even distribution	Greater light penetration	Increased LAI towards base of canopy	Reduction of mutual shading with greater light penetration and interception
Specific leaf area	Maximum**	Rapidly attainable greater leaf area	Optimum	Regulation of light penetration
Number of tillers	Optimum	Improved dry matter production	Minimum	Maximum dry matter production to main stem and tillers

Source: *Shimabuku & Higa (1977a, b); Shimabuku *et al.* (1982); **Terauchi & Matsuoka (2000).

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