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Adaptive Strategy and Its Agronomic Implications in Tall Fescue (*Festuca arundinacea* Schreb.)

2. The Relationship between Plant Type and Productivity under the Different Cultural Conditions

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It was shown from the previous paper[24] that the plant type, few large tillers or many small tillers, was of particular importance in adaptation to natural environmental conditions. On the other hand, such a plant type also plays important roles in the agricultural conditions. Perennial herbage grasses generally are grown under various cultural conditions, grazing or hay, monoculture or mixture, and ley or permanent pastures. Therefore, high productivity under one cultural conditions is not necessarily consistent with that under another cultural conditions. In this paper, therefore, the relationship between productivity and the plant type was investigated under the three cultural conditions, pure swards at complete light interception, regrowth after defoliation and mixed swards at incomplete light interception.

A. Potential sward productivity

A large variation in productivity of grass swards at complete light interception has been found between genotypes[16,28,29], cultivars[11] and species[9]. These differences in productivity are due to the differing efficiency in utilization of light energy, which is mainly determined by the pattern of light distribution through the canopy and hence by canopy structure rather than by photosynthetic capacity of individual leaves. And the canopy structure is closely associated with the plant type[11]. In this section, the relationship between canopy structure and productivity at complete light interception was examined during the vegetative growth stage.

Materials and methods

Materials examined were 14 populations of tall fescue including 5 cultivars (Kentucky 31, Kenwell, Demeter, Yamanami, Hokuryo) and 9 natural populations (Bn501, Bn853, Bn670, Bn947, Bn759, Bn948, Bn949, It77428, It77450). 8-m^2 plots (2m x 4m) of each population were established in the field by sowing in May 1980. Plots were broadcast sown at the rate of 2.5g (approx. 1200 seeds) per m^2. A randomized block layout was used incorporating two replications. Fertilizer was applied at the equivalent rates of 60kg N, 60kg P_2O_5 and 75kg K_2O per hectare during the first year and 70, 60 and 125kg during the second year. In the first seeding year the resulting swards were

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cut to approx. 5cm when all intercepted more than 90% of the total incoming light energy. Measurements were made on the primary swards during the first full harvest year.

Samplings were made three times at about 2 weekly intervals after the commencement of growth in spring (14 April). After herbage was cut from the sampling site, 25 x 25cm, at the soil level, leaf blades were separated from the stems, and then leaf blade area was determined. Weights of leaf blades and stems were determined after drying at 80℃ for 48 hours. Tillers were counted and average weight per tiller (including leaf blades) was calculated. At the same time, canopy height, tiller angle, leaf angle, leaf length, leaf width and relative light intensity below the canopy were measured at each sampling.

Results

Table 1 shows the correlation coefficients between CGR, NAR, MLAI, the number of tillers, the mean tiller weight, K and DW in 14 populations at 2 and 4 weeks. Because LAI ranged from 1.5 to 4.2 and all swards did not attained 90% interception of the incoming light energy at 4 weeks CGR correlated significantly with MLAI ($r=0.67^{**}$), but not with NAR ($r=0.16$). At this stage, the number of tillers was associated with both the growth rate and the DW because of a high positive correlation between the number of tillers and MLAI ($r=0.84^{**}$).

On the other hand at 6 weeks, CGR correlated with NAR ($r=0.85^{**}$), but not with MLAI ($r=0.02$) because LAI ranged from 4.5 to 7.8 and all swards intercepted more than about 90% of the incoming light energy. At this stage swards with large tillers tended to show high growth rate and high productivity as shown in the positive correlation of mean tiller weight to CGR ($r=0.82^{**}$) and to DW ($r=0.83^{**}$). These high positive correlations may be due to low K value and hence the effective distribution of incoming light energy through the canopy for the large tiller types.

Table 2 shows the correlation coefficients between K, the mean tiller weight, the number of tillers and five morphological characters. At 4 weeks there was not any significant correlation. At 6 weeks, however, K, the mean tiller weight and the number of tillers correlated highly with canopy height, tiller and leaf angle. These correlations show that a sward with large tillers tended to show a high canopy, erect tiller and leaves, and thus more efficient light distribution through the canopy. We[23] also reported that during reproductive growth stage, a sward with large tillers also tended to show high productivity because of the effective distribution of incoming light through the canopy.

B. Regrowth after defoliation

In contrast with swards under the infrequent cutting system, the swards under the grazing system remain at incomplete light interception. Thus, a rapid regrowth after defoliation may become important in attaining high productivity. The present section aims to examine the variation of regrowth after cutting and factors associated with it in genotypes of tall fescue.

Materials and methods

Materials used were fifteen genotypes which were derived from two cultivars (Kentucky 31 and Hokuryo) and three natural populations (Bn853, Bn949, It77450). Three genotypes were randomly

Table 1. Correlation coefficient between CGR, NAR, MLAI, the number of tillers, the mean tiller weight, extinction coefficient (K) and dry matter weight (per m²) in 14 populations at 4 (above) and 6 weeks (below) after the spring recovery

	(1)	(2)	(3)	(4)	(5)	(6)	(7)
(1) CGR		.16	.67**	.68**	.07	−.68**	.86**
(2) NAR	.85**		−.61*	−.39	.37	.16	−.29
(3) MLAI	−.02	−.52		.84**	−.23	−.71**	.92**
(4) Number of tillers	−.70**	−.65*	.20		−.52	−.63*	−.83**
(5) Mean tiller weight	.82**	.51	.27	−.84**		.34	−.02
(6) Extinction coefficient	−.74**	−.66*	.09	.73**	−.74**		−.64*
(7) Dry matter weight	.68**	.24	.64*	−.41	.83**	−.51	

* = significant at 5% level; ** = significant at 1% level.

Table 2. Correlation coefficients between extinction coefficient (K), the mean tiller weight (MTW), the number of tillers (NOT) and 5 morphological characters at 4 and 6 weeks after the spring recovery

	4 Weeks			6 Weeks		
	K	MTW	NOT	K	MTW	NOT
Canopy height	−.31	.52	−.37	−.85**	.82**	−.77**
Tiller angle	.15	.21	−.44	−.60*	.71**	−.77**
Leaf angle	−.02	−.16	−.25	−.42	.55*	−.64*
Leaf length	.08	.42	−.52	−.47	.52	−.68**
Leaf width	−.18	.13	−.17	−.34	.42	−.55*

chosen from each population. Each genotype was divided into single tillers and each tiller was planted in a paper pot (5cm diameter by 5cm deep) filled with sandy loam, peat and vermiculite on August 16, 1982. Plants were allowed to grow for 34 days and then transplanted into an experimental field on September 20, 1982. A randomized block layout was used with two replications. Spacing was 50cm apart in rows with inter-plant spacing of 25cm, and one row consisted of thirteen plants. Prior to the transplanting, 30kg N, 75kg P_2O_5 and 45kg K_2O per hectare were applied. In the second year (1983), cuttings were made three times (24 May, 22 June and 24 July). At each cutting, the plants were cut at 5 cm above soil level and the plant DW and the number of tillers were measured. Fertilizer was applied at the rate of 20kg N, 50kg P_2O_5 and 30kg K_2O in the early spring and 10kg N and 10kg K_2O per hectare after each cutting.

Investigation of regrowth was started from the third cutting (24 July) and samplings were carried out four times at intervals of 10 days. At each sampling plants were cut at the soil level and plant DW, number of tillers and leaf area were recorded. Measurements were made on two plants per replication in each genotype. Plant fraction of 3cm stem base was removed for the measurement of WSC. WSC was determined in the same manner as described in the previous paper[24].

In addition, the leaf elongation rate (LER) was determined by measuring the length of young growing leaf blades for 20 days at intervals of two days. Four measurements of each genotype were recorded per replication. The leaf elongation rate was estimated by the regression coefficient of leaf length on time, because it is known that the rate of leaf growth is nearly linear[26].

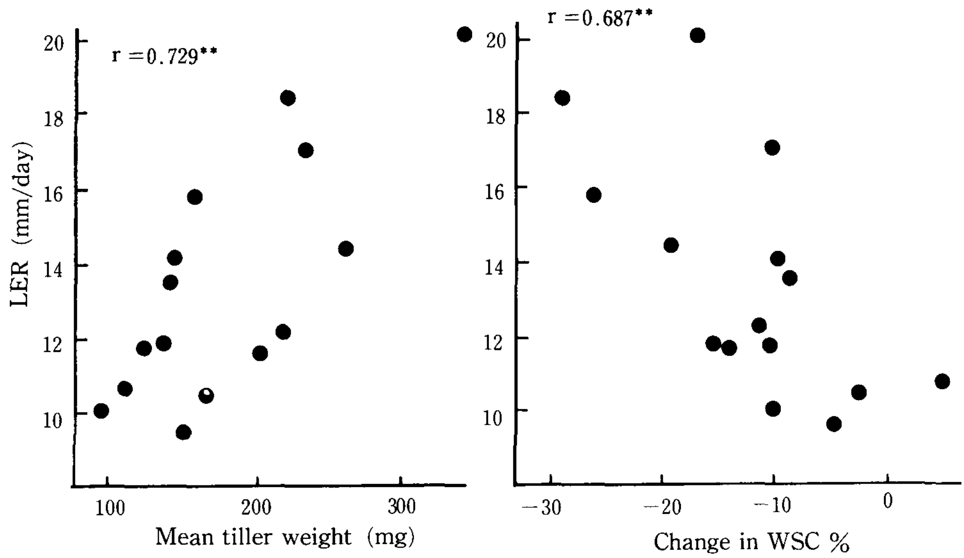

Fig. 1 Relations of leaf elongation rate (LER) to mean tiller weight before cutting and changes in water soluble carbohydrate (WSC)% during the subsequent 10 days after cutting.

Table 3. Multiple regression analysis for number of tillers per plant (X_1) and leaf elongation rate (X_2) on leaf area per plant (Y) at 10, 20 and 30 days after defoliation

Days after defoliation	Multiple regression equation	Coefficient of determination
10	$Y = 0.8679X_1 + 0.2908X_2$	0.779
20	$Y = 0.6190X_1 + 0.5662X_2$	0.664
30	$Y = 0.5696X_1 + 0.6026X_2$	0.723

Note. Multiple regression coefficients were obtained after standardization.

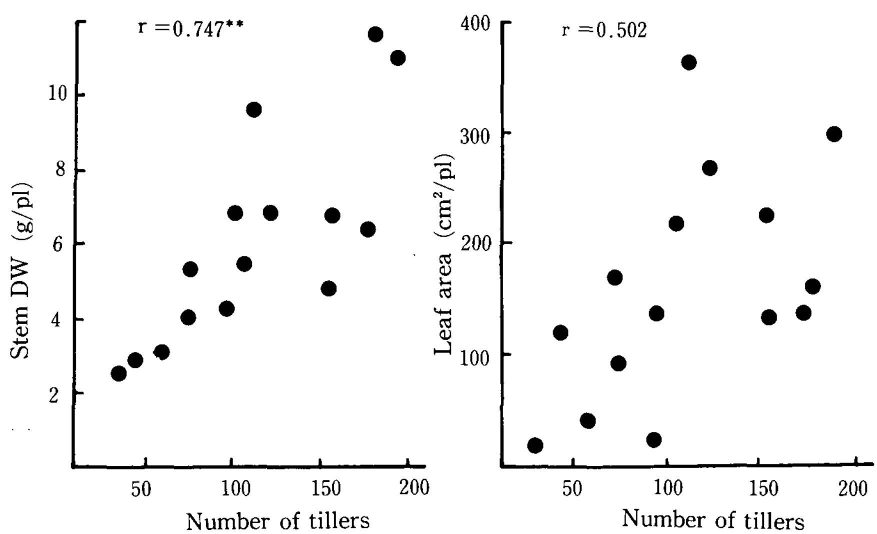

Fig. 2. Relations of number of tillers per plant to stem DW and leaf area remaining after cutting.

Results

In this experiment, the leaf area was used as the measure of regrowth, because it represents the photosynthetic capacity of a plant as well as the main part of yield in regrowth. The leaf elongation showed almost linear increase. However, there was a large variation in the LER among genotypes, ranging from 9.5mm/day to 20.2mm/day.

Figure 1 shows the relations of the LER to mean tiller weight before cutting and the changes in the WSC percent from the time of cutting to the subsequent ten days. The LER correlated positively with the mean tiller weight, but negatively with the changes in the WSC percent. These results indicate that genotypes with large tiller tended to have higher LER and to utilize more carbohydrate reserves to support rapid leaf growth than those with small tillers.

The leaf area after cutting is mainly determined by the product of the number of tillers and growth rate of each tiller. The latter is nearly represented by LER. Table 3 shows the effects of the number of tillers and the LER on the leaf area. Multiple regression analysis was applied at each of ten, twenty and thirty days after cutting. At all three stages, the two variables explained about 70% of variance in the leaf area among genotypes, as shown by coefficient of determination. Whereas, standard regression coefficients of two independent variables showed marked changes with the course of time. At the early stage of regrowth, the standard regression coefficient was high for the number of tillers, but low for the LER. As time passed, however, the contribution of the LER to the leaf area increased, but that of the number of tillers decreased. These results suggest that although the number of tillers is of marked importance in the early stage of regrowth, the LER becomes progressively important in determining productivity as the time passes.

It is well known that regrowth in the early stage after cutting is supported by the leaf area remaining after cutting (residual leaf area) and carbohydrate reserves[2]. The amount of carbohydrate mainly depends on the carbohydrate content and the volume of stored tissues. In temperate grasses, the carbohydrates are mainly reserved in the stem base rather than the root[1]. Figure 2 shows relations of the stem DW and the leaf area remaining after cutting to the number of tillers at the cutting. The stem DW and leaf area showed positive correlations with number of tillers. It is supposed from these results that the plants with many small tillers have more carbohydrates available for regrowth after cutting than those with few large tillers, as a result of photosynthesis of large residual leaf area and the large volume of stored tissue remaining after cutting, and thus the plants with many small tillers show rapid leaf growth in the early stage of regrowth. In conclusion, in the early stage after cutting, the number of tillers is of considerable importance for regrowth due to the amount of carbohydrate reserves available for regrowth, but as time passes, the tiller size becomes more important for regrowth due to leaf elongation rate.

C. Performance in the mixed cultures

Herbage grasses are usually grown in association with another herbage species in pastures. But, populations which are very productive under the pure swards do not necessarily show high productivity under the mixed swards[4]. Thus, the competitive ability becomes important in determining the productivity of component species in mixed swards. In this section, the variation of performance of six tall fescue populations in association with orchardgrass and white clover was examined.

Materials and methods

Pure sward and the three kinds of mixed swards were established in each of six cultivars of tall fescue. The mixtures were made up of tall fescue and orchardgrass (OG mixture), tall fescue and white clover (WC mixture) and tall fescue, orchardgrass and white clover (OG+WC mixture). The cultivars used were Fawn, Yamanami, Kyushu-6, Kentucky 31, Hokuryo and 50 : 50 seeds mixture of Kentucky 31 and Hokuryo (KY+HK) for tall fescue, Okamidori for orchardgrass, and Grassland Huia for white clover. The experiment was laid out as a split plot design incorporating two replications, with the associated species as the main plot, and tall fescue cultivars as the subplot. Each plot (3m×4m) was broadcast sown May 5, 1983 at the following seeding rate: 40kg/hectare for tall fescue in the monoculture, 20kg/hectare for each of tall fescue and orchardgrass in OG mixture, 35kg/hectare for tall fescue and 5kg/hectare for white clover in WC mixture, and 17.5kg/hectare for each of tall fescue and orchardgrass and 5kg/hectare for white clover in OG and WC mixture. Three cuttings (4 July, 8 August and 28 September) were taken in the first year (the established year), five (25 May, 20 June, 26 July, 26 September and 20 October) in the second year and the four (24 May, 9 July, 9 August and 18 September) in the third year. Fertilizer was applied at the equivalent rates of 40kg N, 100kg P_2O_5 and 60kg K_2O per hectare before sowing in the first year, 40kg N, 100kg P_2O_5 and 60kg K_2O in early spring and 10kg N and 10 kg K_2O after each cutting in the second and the third year.

Measurements were made at the last cutting time in each of three years. In the second year, however, measurements were taken at each time of the cutting on the monoculture and OG mixture. After herbage was cut from each (25x25cm) of the five sampling sites at the soil level in each plot, each component species of the mixture was separated and weighed after drying at 80℃ for 48hr. Number of tillers of tall fescue was also counted at each plot.

Results

Table 4 shows DW, the number of tillers and the mean tiller weight of each cultivar of tall fescue in monoculture in the first, the second and the third years. There was not any significant difference in DW between cultivars throughout the three years. Hokuryo was very productive in the first year, but became the least productive in the second and the third years. Hokuryo also had fewer larger tillers throughout the three years than another cultivars, although differences were not significant in some years. The mixture of KY+HK tended to show intermediate characteristics between both cultivars.

Table 5 shows the DW per plot of each tall fescue cultivar in the three mixed plots in the first, the second and the third years. Significant differences were found in OG mixture and WC mixture in the second and the third years. But, there were no significant differences in OG+WC mixture in all of the three years. Hokuryo showed the least values in the all mixed plots throughout the three years. As a result of analysis of variance for DW of three years, there were highly significant differences between cultivars, but no significant difference in the interaction between cultivar and association. These results suggest that the order of the productivity of six cultivars in the mixture does not change by the associated species.

Table 6 shows the correlation coefficients of relative yield of tall fescue cultivars in OG mixture with DW, the number of tillers and the mean tiller weight in monoculture in each sampling time. There were not consistent correlations between the relative yield and the DW in monoculture, although correlations tend to be positive except the first year. Whilst, the relative yields correlated positively with number of tillers but negatively with mean tiller weight at all sampling time, although all correlations were not necessarily significant. These results suggest that the plant type is also related to the competitive ability, and cultivars with many small tillers tend to have higher competitive ability than those with few large tillers.

Table 4. DW, number of tillers and mean tiller weight in pure plots in the first (1983), the second (1984), and the third (1985) years

	DW (g/plot)			Number of tillers (/plot)			Mean tiller weight (mg)		
	1st	2nd	3rd	1st	2nd	3rd	1st	2nd	3rd
Fawn	19.1	12.6	13.9	160	197	183	119	64	76
Yamanami	23.1	13.1	13.4	182	185	175	128	72	79
Kyushu-6	21.1	11.9	14.6	132	178	207	160	69	71
Kentucky 31	20.0	11.3	14.6	171	218	204	117	52	71
Hokuryo	23.3	8.9	11.9	135	135	122	177	66	98
Ky 31+Hokuryo	23.9	11.9	14.0	148	206	178	164	58	79
LSD (5%)	NS	NS	NS	23	NS	34	39	NS	NS

Table 5. DW of six cultivars of tall fescue in association with orchardgrass (OG), white clover (WC) and orchardgrass and white clover mixture (OG+WC) in the first, second and third years

	OG (g/plot)			WC (g/plot)			OG+WC (g/plot)		
	1st	2nd	3rd	1st	2nd	3rd	1st	2nd	3rd
Fawn	10.9	5.0	6.3	18.2	12.3	14.3	6.0	4.2	4.4
Yamanami	5.2	4.7	5.1	14.9	10.4	14.5	5.7	3.3	5.5
Kyushu-6	10.1	4.2	5.2	21.0	11.7	15.7	5.1	2.7	4.0
Kentuky 31	9.3	5.5	5,3	16.1	13.3	13.5	4.8	3.6	4.6
Hokuryo	2.3	0.7	1.1	13.5	5.5	10.6	3.6	0.8	0.8
Ky31+Hokuryo	9.0	4.0	3.9	15.0	10.7	16.0	4.6	3.1	4.3
LSD (5%)	NS	1.8	2.1	NS	2.5	2.0	NS	NS	NS

Table 6. Correlation coefficients of relative yield of tall fescue in association with orchardgrass to DW, number of tillers and mean tiller weight in pure plot in each sampling time

	1st	2nd year					3rd
	year	1st	2nd	3rd	4th	5th	year
DW	−0.79	0.09	0.03	0.82*	0.16	0.75	0.76
Number of tillers	0.08	0.61	0.53	0.99**	0.34	0.93**	0.81
Mean tiller weight	−0.54	−0.92**	−0.30	−0.48	−0.46	−0.40	−0.86*

Discussion

Morphological characters affect the canopy structure and hence the productivity of the sward at complete light interception in herbage grass species. Rhodes[18,19,20,21] indicated the significance of the combinations of some morphological characters in determining the productivity of swards in ryegrass. Nelson[13] and Zarrough and Nelson[27] showed that tiller size was closely associated with productivity and regrowth in swards of tall fescue. The present study also confirmed that morphological characters, particularly tiller size, were of considerable importance in controlling the productivity at complete light interception. Swards with large tillers ensure the effective distribution of the incoming light energy within the canopy and hence a low K value. Thus, it is concluded that the swards with few large tillers are more productive at complete light interception than those with small many tillers because of the efficient light interception within the canopy.

However, when swards remain at incomplete light interception, the canopy with the large tiller size dose not represent its superiority. In fact, when swards were subjected to the frequent cutting Hokuryo with few large tillers showed low productivity. Particularly this trend was evident in the early stage of regrowth. On the other hand, swards with many small tillers showed good regrowth after defoliation, because of relatively large amount of carbohydrate reserves available for regrowth, as shown in the present experiments. Thus, at frequent cutting condition, plant with many small tillers may have an advantage than those with few large tillers.

Furthermore, when plants are grown in association with another species, the growth rate in the early stage of regrowth seems to have considerable effects on the subsequent growth. Under the competitive conditions, slow growth rate in the early growing stage may cause serious suppression by the other component species[3,5,6]. Zarrough[28] reported that the plant with few large tillers showed lower productivity in association with birdsfoot trefoil relative to monoculture than that with many small tillers. In this experiment Hokuryo showed the lowest value of relative yield in all mixtures, which is measure of competitive ability. The relative yield correlated positively with the number of tillers but negatively with the mean tiller weight of monoculture. The competitive ability of herbage grass was affected by many factors[8,12,17]. However, it has been frequently reported that the number of tillers was closely related to competitive ability in herbage grasses[7,10,15,17,25].

Herbage species are grown under various cultural conditions, high fertilizer application or low fertilizer application, ley (short year grassland) or permanent grassland, conservation system (hay and silage) or grazing system and monoculture or mixture etc. However, the characteristics which give the high productivity in one cultural condition do not necessarity agree with those in another cultural conditions, as shown in the present experiments. Generally speaking, relatively larger proportion of reproductive growth and larger tiller size seem to be favoured under the conditions of monoculture and conservation system. On the contrary, high tillering rate and relatively larger proportion of vegetative growth may be favoured under the conditions of mixture and grazing system.

The cultural conditions of herbage species can be roughly classified into two categories in terms of the magnitude of management by human beings, intensive cultivation and extensive cultivation, although there are a series of continuous forms between the both extremes. The former is more similar to the cultural conditions of field crops and is more likely to be under the combination of high fertilization, conservation system, monoculture and frequent grassland renovation. On the other hand, the latter is more similar to the conditions of natural grassland, and is more likely to be under the combination of low fertilization, grazing system, mixture and less or no pasture renovation. If there is less or no disturbance by man, the grassland ecosystem proceeds to the course of succession. As the stage of succession proceeds, the changes in structural and functional characteristics in ecosystem appear, and generally, net production of grasslands decreases but the stability of it increases[14]. Therefore, it can be said that intensive cultivation such as much fertilization and frequent renovation keep the grassland ecosystem young stage of succession to maintain the high productivity. Thus, selection pressure acts differently on plants in the young stage and in the mature stage of succession. High growth rate may be favoured in the former environment but high protection (high competitive ability and high resistance to grazing etc.) may be favoured in the latter one[14].

In past breeding of herbage grasses, emphasis was placed on the productivity under the spaced planting condition. Populations selected under this condition may have an advantage in the intensive cultural conditions. However, there is a possibility that the plants fit for this condition are replaced by another species and become extinct in the old grassland which are subjected to extensive management. In this respect, breeding in the herbage species should be considered in close relation to the cultural conditions in which the population will be grown. Adaptive strategy is "a set of coadapted traits, designed by natural selection, to solve the particular ecological problem"[22]. Thus, the concept of adaptive strategy can just apply to the breeding and cultural practice of herbage grasses, which are grown in the contrasting environmental conditions. And this is likely to enable us to utilize and manage the grassland ecosystem more efficiently and properly. For this purpose, further understanding of interaction between herbage species and various environmental factors in grassland ecosystem will be required.

Summary

1. The relationship between the plant type and productivity was investigated under the three cultural conditions, pure sward at infrequent cutting, regrowth after cutting and mixed sward at frequent cutting.

The morphological characteristics, particularly tiller size were closely associated with the productivity of sward at complete light interception, and swards with large tillers showed the more efficient distribution of the incoming light energy within the canopy, and thus higher productivity than those with small tillers.

2. The number of tillers was of particular importance for the regrowth after cutting, because plants with many small tillers could utilize more carbohydrate reserves available for regrowth than those with few large tillers. Plants with few large tillers became progressively productive because of their high leaf elongation rate.

3. The plant type was also important in determining the productivity under the mixed swards, and cultivars with many small tillers tended to have higher competitive ability and thus higher

sward productivity than those with few large tillers. Thus, the desirable characteristics differed between cultural conditions, and large tiller size conferred the high productivity at complete light interception, but it conversely brought about low productivity in mixed swards at frequent cutting.

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トールフェスクの適応戦略とその農業的意義

2．異なる栽培条件下における草型と生産性の関係

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摘　要

本報では，3つの異なる栽培条件下におけるトールフェスクの生産力と草型の関係を検討した。

(1)・潜在的草地生産力：　トールフェスク14品種，系統について単播草地を造成し，2年目の早春における乾物生産特性について調査した。単播少回刈取り条件下では，分げつサイズの大きな草地ほど高い生産力を示した。これは大きな分げつで構成された草地ほど群落構造がすぐれ，光が群落内に効率的に透過するためであった。

(2)・刈取後の再生：　トールフェスクの15遺伝子型を圃場に個体植え条件で栽培し，刈取り後30日間の再生を検討した。茎数型の遺伝子型は，茎重型のものより，刈取後に残る茎の部分が多いため，再生により多くの可溶性炭水化物を利用でき，再生初期では有利であった。しかし，茎重型の遺伝子型は葉の伸長速度が高いため，生育が進むにつれ，次第に高い生産力を示すようになった。

(3)・混播条件下での収量性：　トールフェスク6品種をオーチャードグラス，白クローバー，オーチャードグラス＋白クローバの3種類の混播多回刈条件下で3年間調査した。一般に，茎数型の品種が茎重型の品種より多収を示した。これは，競争力が分げつ数と正の相関関係にあり，生育の経過とともに，茎数の少ない茎重型の品種は草地内での構成割合が低下していくためであった。

(4)・以上の結果，多収をもたらす形質は栽培条件によって異なるため個々の管理条件に適した品種を育成し，利用することが重要と指摘できる。一般に，採草条件では茎重型が，放牧条件では茎数型が有利となった。