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ADAPTIVE STRATEGY AND ITS AGRONOMIC IMPLICATIONS IN TALL FESCUE (*FESTUCA ARUNDINACEA* SCHREB.)

1. LIFE HISTORY, DRY MATTER ALLOCATION AND ADAPTIVE STRATEGY

Shuichi SUGIYAMA
Experiment Farms, Faculty of Agriculture,
Hokkaido University, Sapporo, 060 Japan

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Contents

I. Variation in life history characteristics of natural populations

Natural selection does not act on only one stage in the lifetime of a individual, but on the whole process of lifetime, from birth through reproduction to death. In this respect, studies of life history are particularly important in understanding the adaptive mechanism of an organism. In fact, the theoretical and experimental studies of adaptive strategy have been focused on the variation of life history in plants as well as animals[61,63,65].

Life history and morphology of temperate grasses are rather simple and the main events in the life cycle are considered to be germination, seedling establishment, reproduction, seasonal pattern of growth and overwintering. In this chapter, variations in life history characteristics in natural populations of tall fescue were examined in relation to environmental conditions of collection sites.

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A. Classification of natural populations.

Many characteristics of organisms are not independent but are generally interconnected. Thus principal component analysis is a good method for classification, because it enables us to evaluate the variations of many characters synthetically. In this section, natural populations were classified by principal component analysis and results were further analysed in relation to environmental variables in collection sites.

Materials and Methods

As shown in Table 1, the materials used were 19 natural populations

TABLE 1. The place, latitude and altitude of origin and the estimated mean temperature in January

Population	Country	Locality	Latitude	Altitude (m)	Temperature	Meteorological site
1. Bn 501	France	Sestiron	44	500	2.5	Nimes
2. Bn 502	France	Sestiron	44	550	2.2	Nimes
3. Bn 505	France	Tallard	44	875	0.8	Nimes
4. Bn 509	France	Chorges	45	800	−1.5	Lyon
5. Bn 853	France	Mattaincourt	48	290	0.3	Nancy
6. Bn 860	France	Lonqueville	49	250	0.3	Nancy
7. Bn 945	France	Esbarres	46	120	2.6	Lyon
8. Bn 670	U. K.	Butingford	51	42	4.2	London
9. Bn 271	Tunisia	Grombalia	35	—	11.0	Tunis
10. Bn 272	Tunisia	Bou Ficha	35	—	11.0	Tunis
11. Bn 759	Italy	Monsei	43	1250	−0.3	Genova
12. Bn 760	Italy	Monsei	43	1250	−0.3	Genova
13. Bn 764	Italy	Passo di Teglia	43	1387	−1.1	Genova
14. Bn 765	Italy	Rezzo	43	900	−1.8	Genova
15. Bn 767	Italy	Bormio	46	1250	−6.1	Bolzano
16. Bn 772	Italy	Cavalese	46	900	−4.0	Bolzano
17. Bn 947	Switzerland	Saviese	46	870	−1.6	Geneva
18. Bn 948	Switzerland	Mayons de la Dzou	46	1276	−4.0	Geneva
19. Bn 949	Switzerland	Vex	46	1200	−3.7	Geneva
Kentucky 31	USA	Lexington	38	—	−1.3	Dayton
Hokuryo	Japan	Sapporo	43	50	−5.8	Sapporo

Mean tempepature in January was estimated by making altitudinal correction of climatic data in the meteorological site.

derived from Europe and North Africa, and two cultivars, Hokuryo and Kentucky 31. Hokuryo was bred in the Hokkaido Agricultural Experimental Station in Sapporo, Japan, and Kentucky 31 was bred in the Kentucky Experimental Station, Lexington, USA. Both cultivars were bred by using local strains near the breeding sites as the original breeding materials.

Table 1 also shows the locality, latitude, altitude and the mean temperature in January of the collection sites in each population. The mean temperature in January was estimated from those in meteorological stations presented in Table 1, by making altitudinal correction at the standard lapse rate of 0.6°C for 100 m. However, these should be considered as approximate estimates rather than the precise measures. The latitudes in natural populations range from 35°N of the populations from Tunisia to 51°N of that from U. K. The experimental site, Sapporo, lies at 43°03′N. Thus, all natural populations except two from Tunisia come from higher latitudes than Sapporo. There were also large altitudinal variations among populations, ranging from 42 m of populations from U. K. to 1378 m of that from Italy. All three Swiss populations belong to the Alps regions. But the Italian populations can be separated into two locations by their regions of origin, the Italian Alps (15, 16) and the Ligurian Apennine (11, 12, 13, 14).

The seeds of each population were individually planted in paper pots (3 cm diameter and 5 cm deep) filled with sandy loam, peat and vermiculite mixtures and allowed to grow for 45 days in a heated green house. After that, the plants were transplanted to an experimental field on 14 June, 1977. A randomized block layout was used with two replications. Spacing was 1 m apart in rows with inter-plant spacing of 50 cm, and one row consisted of 10 plants. Fertilizer was applied at the rate of 40 kg N, 60 kg P_2O_5 and 75 kg K_2O per hectare before transplanting in the first year and 70 kg N, 60 kg P_2O_5 and 125 kg K_2O in the second year.

In the year of sowing (1977), the number of heading plants was examined in all plants of each population. In the second year, the plant height was measured on 11 May. First heading date, the date on which the third inflorescence of each plant first appears at the mouth of the flag-leaf sheath, was recorded in all plants of each population. At the flowering time of each population, eight plants per replication were cut and five morphological characters, culm length, ear length, the rachis length, the number of spikelets per ear and the number of florets per spikelets were measured in the three representative reproductive tillers of each plant. The number of reproductive tillers was recorded in each plant and DW (dry matter weight) of reproductive and vegetative tillers were weighed after drying at 80°C for 48 h. The border plants in each population were allowed to grow till the ripening time and used for the measurement of 100 seeds weight. DW of aftermath was recorded on 25 August.

Results

The principal component analysis was applied on nine characters, culm length, mean reproductive tiller weight, number of florets per head, 100 seeds weight, plant height in spring, shoot DW at flowering time, DW aftermath, dry matter content at flowering time and the first heading date. Table 2 shows correlation coefficients among the characters used and factor loadings of the two components extracted from them. In the first component, shoot DW, first heading date, culm length, mean reproductive tiller weight and number of florets showed high positive values but 100 seeds weight had high negative value, and thus this component mainly represents the morphological characteristics related to tiller size and earliness in heading. The second component seems to represent productivity, because the plant height in spring and DW of aftermath showed high values.

TABLE 2. Correlation coefficients among main characteristics and principal components extracted from them

		(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	Component	
										Z1	Z2
(1)	Shoot DW at flowering	.59**	.81**	.76**	.65**	−.46*	−.22	−.31	−.12	.77	.40
(2)	First heading date		.77**	.86**	.73**	−.60**	−.53*	−.37	−.10	.88	−.08
(3)	Culm height			.88**	.79**	−.66*	−.35	.08	−.35	.92	.21
(4)	Mean reproductive tiller weight				.85**	−.71*	−.35	−.05	−.08	.95	.16
(5)	Number of florets per ear					−.73**	−.27	−.07	−.15	.88	.18
(6)	100 seeds weight						.50*	.23	−.30	−.81	−.24
(7)	DW of aftermath							.55*	−.60*	−.53	.74
(8)	Plant height in spring								−.26	−.16	.77
(9)	Dry matter content									.04	−.77
	Eigen value									4.9	2.1

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

Figure 1 shows the scatter diagram between the first and second component scores. The populations came to have larger tiller and ear size and to be later in heading with the increase in the first component score, and to

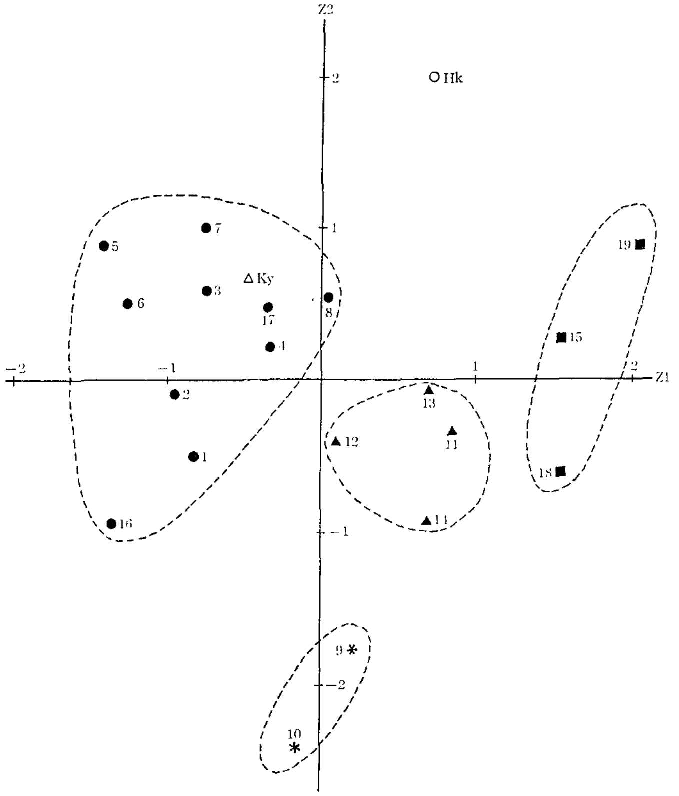


Fig. 1. Scatter diagram of 19 natural populations and 2 cultivars by the first and the second components.

● Lowland populations; ▲ Liguria populations; ○ Hokuryo;
■ Highland populations; * Tunisia populations; △ Kentucky 31.

be more productive in spring and summer with the increase in the second component score. The natural populations from similar regions of origin tended to take the similar positions in the scatter diagram. As for the first component, seven populations from France, one from U. K. and two from the Alps below 1000 m in altitude showed negative or small positive values. On the other hand, three populations from the Alps above 1000 m in altitude showed high positive value more than one. And four populations from the Ligurian Apennine took the intermediate values between these two groups. As to the second component which represents productivity, two populations from Tunisia showed particularly low values compared with another natural populations. With regard to the first and second component, 19 natural populations were classified into four groups as follows: Lowland group, seven populations from France, one from U. K. and two from Alps below 1000 m ; Liguria group, four populations from Ligurian Apennine ; Highland group, three populations from Alps above 1000 m ; Tunisia group, two populations from Tunisia. The cultivar, Kentucky 31 took the similar position to the Lowland group. And Hokuryo showed similar value to Liguria group in the first component, but particularly high value in the second component.

About 30% of the plants in the Tunisia populations were killed during winter, and the surviving plants were also subjected to the severe winter damage. Therefore, low winter hardiness accounts for the particularly low value of the second component in Tunisia populations. For this reason, two populations from Tunisia were excluded from the subsequent analysis.

There were large differences in morphological characteristics among three groups. Mean reproductive tiller weight, culm length, ear length, rachis length and number of florets per ear increased in the order of the Lowland populations, the Liguria populations and the Highland populations, as 1.09 g of mean of Lowland to 1.77 g of that of Highland in mean reproductive tiller weight, 117.5 cm to 146.3 cm in culm length, 21.8 cm to 35.4 cm in ear length, 7.8 cm to 16.2 cm in rachis length and 352 to 668 in number of florets per ear. However, 100 seeds size was lower in the Highland group (0.187 g) than the Lowland group (0.271 g).

Table 3 shows the correlation coefficients of the first component score and the eight morphological characters with three environmental variables, latitude, altitude and mean temperature in January in collection sites of each

TABLE 3. Correlation coefficients between some environmental variables and morphological characters in natural populations except those from Tunisia

	Latitude	Altitude	Temperature♯
The first principal component	−0.20	0.69**	−0.51*
Mean reproductive tiller weight	−0.16	0.62**	−0.45
Culm length	−0.26	0.71**	−0.60*
Ear length	−0.08	0.62**	−0.50*
Rachis length	−0.14	0.67**	−0.54*
Spikelets per ear	−0.05	0.64**	−0.64**
Florets per spikelet	0.21	−0.75**	0.76**
Florets per ear	−0.04	0.54*	−0.45
100 seeds weight	−0.08	−0.41	0.37

♯, The estimated mean temperature in January.

population. Although the latitude did not show any clear correlations with morphological characteristics, altitude and mean temperature in January showed generally high significant correlations. These correlations indicate that populations from high altitudes or severe winters tend to have larger tiller and ear size, longer rachis and more florets per ear than those from low altitudes or mild winters.

B. Variation in life history characteristics

It was shown in the previous section that natural populations from Europe could be classified into three groups mainly by morphological characteristics at flowering time. In this section, life history characteristics, germination, seedling growth and competitive ability, reproduction and seasonal pattern of growth were examined in the three groups, including Turkish populations from mountain areas over 1800 m.

Materials and Methods

Germination: Materials used were 13 natural populations and two cultivars; five from Lowland (Bn 501, Bn 670, Bn 853, Bn 772, Bn 947), two from Liguria (Bn 759 and Bn 765), three from Highland (Bn 767, Bn 948 and Bn 949) and three from Turkey (It 77420, It 77428 and It 77450) and cultivars, Hokuryo and Kentucky 31. These 15 populations were multiplied by allowing four genotypes from each of these populations to intercross in separate pollen-proof isolation house in 1979. The germination experiments were started from November 1, 1979. Fifty seeds of each population were placed in each of four petri dishes with moist filter papers. Half of them were kept at 25°C without any treatment. The rest, on the other hand, were placed in a refrigerator at 5°C for 14 days before being placed at 25°C. Records were taken every day for 30 days. Two measurements, germination rate and germination percentage, were calculated. Germination rate is the percentage of the germinated seeds for two days after the transfer to 25°C. The germination percentage is the percentage of germinated seeds after 30 days. The data were transformed to angles for the analysis of variance.

Seedling growth: Materials used were four populations from the Lowland, two from Liguria, one from the Highland, two from Turkey, and two cultivars, Hokuryo and Kentucky 31, as shown in Table 4. Three seeds of each population were sown in a pot (10 cm top diameter and 10 cm deep) filled with sandy soil in June 1982 and later were thinned to one plant. A randomized block design was used with five replications. The pots were watered every day and Robbins solution culture was applied once a month.

Harvests were made at 80 days (Sep.) after sowing. At each harvest the soil was washed from the root system and number of roots and of tillers were counted and then DW were determined after 80°C for 48 hr.

Competitive ability: The diallel competition experiment was made. Materials used were three natural populations from the Lowland (Bn 501), Liguria (Bn 759) and the Highland (Bn 767) and two cultivars, Hokuryo and Kentucky 31. Seeds of similar size in five populations were selected and were germinated on the moist papers in plastic dishes at 25°C. In June 1982, seeds which germinated on the same day were planted in plastic boxes 38 cm × 14 cm × 10 cm deep, filled with a heat-sterilized sandy soil. Sixty-five seeds (five rows with thirteen plants to one row) were planted in each box with inter-plant spacing of 3 cm. Each box contained either a monoculture of each population or a mixture of two populations. Each population in mixtures was planted at alternate sites. A randomized block layout was used with three replications. The boxes were watered every day and Robbins solution culture was applied once a month so that growth would not be limited by lack of water and mineral nutrients.

Harvest was made at 80 days after sowing. At the harvest plant was cut at soil level and then plant height, number of tillers and plant dry matter weight (DW) were measured in all plants. Thirty-three centre plants were used for the analysis.

Duration of reproductive growth: The following 12 populations were used for measuring the dates of heading, anthesis and ripening: five from the Lowland (Bn 501, Bn 509, Bn 853, Bn 772, Bn 947), three from Liguria (Bn 759, Bn 764, Bn 765), three from the Highland (Bn 767, Bn 948, Bn 949) and two cultivars (Hokuryo and Kentucky 31). Measurements were taken on 3-year-old plants which were the same as used in the previoussection. The dates of heading, anthesis and ripening were recorded on the same three tillers of each of five plants per replication in each population. The heading date is the date on which the inflorescence appears at the mouth of the sheath of the flag leaf and the anthesis and ripening dates are days of the first anthesis and the first ripening in the florets of the ear, respectively.

Reproductive effort: Except for two populations (Bn 947 and Bn 949) which showed heavy shattering, 15 natural populations in Table 1 were examined. Measurements were taken on 3-year-old plants used in the previous section. At the ripening time of each natural population, five plants per replication in each population were cut at the 5 cm above soil level, and the tillers of each plant were separated into vegetative and reproductive tillers. The representative 25 reproductive tillers of each plant were chosen and weighed after drying for 48 h at 80°C. After that ears were cut from culms and seeds were threshed from ears, and DW of seeds, ears and culms were recorded. DW of vegetative tillers were also measured.

Results

Germination: As a results of analysis of variance for germination rate and germination percentage, there were highly significant differences in both characters between populations and between treatments. Furthermore, the interaction between population and treatment was significant in both characters, suggesting that populations showed the different effects of low temperature pretreatment on seed germination. Figure 2 shows the germination rate and germination percentage of each population with and without low temperature pretreatment. Lowland populations showed higher germination rate without treatment and thus more rapid germination speed than another populations. On the other hand, some populations from Liguria, Highland and Turkey showed particularly low germination percentage (less than 50%) without treatment. But germination in these populations was enhanced by low temperature treatment.

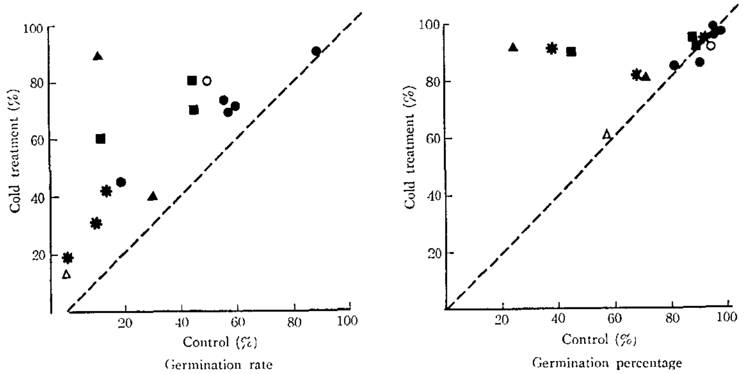


Fig. 2. Germination rate and germination percentage with and without cold pretreatment.

● Lowland populations; ▲ Liguria populations; ■ Highland populations; ✱ Turkish populations; ○ Hokuryo; △ Kentucky 31.

Seedling growth and competitive ability: Table 4 shows the mean values of shoot DW, root DW and root : shoot ratio at 80 days. Both cultivars showed lower root : shoot ratio than nine natural populations. Among the natural populations, populations from Lowland tended to show lower root : shoot ratio than those from Liguria, Highland and Turkey. There was a negative significant correlation between root : shoot ratio and mean temperature in January in the natural populations ($r=-0.859^{**}$). Thus natural populations from cold climates tend to have a larger root system relative to shoot system than those from warm climates.

As a result of ANOVA for diallel competition experiment, there was

TABLE 4. Root and shoot DW, number of roots and tillers, and root : shoot ratio at 80 days after seedling emergence in each population

		DW (g/pot)		Number of (/pl)		Root/ shoot
		Shoot	Root	Tillers	Roots	
1. Bn 501	Lowland	5.00	2.44	17.4	63.2	.492
2. Bn 853	Lowland	5.00	2.31	22.7	76.2	.462
3. Bn 670	Lowland	7.68	3.84	21.5	83.0	.499
4. Bn 772	Lowland	3.22	1.86	13.0	61.2	.577
5. Bn 759	Liguria	2.70	1.66	11.0	49.0	.614
6. Bn 765	Liguria	3.05	1.58	14.2	37.2	.516
7. Bn 767	Highland	4.55	2.65	14.7	68.0	.583
8. It 77428	Turkey	2.09	1.67	13.0	52.3	.797
9. It 77450	Turkey	1.78	1.54	10.8	46.4	.870
10. Kentucky 31		4.86	1.60	24.2	67.8	.330
11. Hokuryo		6.98	3.09	17.6	82.4	.443
LSD (5%)		3.38	1.32	8.7	29.0	.189

TABLE 5. Competition diallel table for plant dry matter weight in 5 populations. Monocultures shown in diagonal are presented in actual value (g/pl.), and mixtures are in difference between mixture and its corresponding monoculture. $t_{i.}$ and $t_{.i}$ are sum of the row and the column except for monoculture, respectively

	Bn 501	Bn 759	Bn 767	Hokuryo	Kentucky 31	$t_{i.}$
Bn 501	.739	.189	.012	.046	.064	.311
Bn 759	−.116	.738	.172	−.141	−.029	−.114
Bn 767	−.210	.174	.699	−.008	.136	.092
Hokuryo	.126	.364	.323	.807	.395	1.208
Kentucky 31	.297	.139	.257	−.009	.855	.684
$t_{.i}$	.097	.866	.764	−.112	.566	2.181

no significant difference in plant dry matter weight between populations in monoculture. However, populations differed significantly in general and specific competitive effects. Table 5 shows the result of a competition diallel of five populations of plant dry matter weight. The competitive ability $(t_{i.})$ decreased in the order of Hokuryo, Kentucky 31, Bn 501, Bn 767 and Bn 759. Cultivars had higher competitive ability than natural populations. Among natural populations those from the Lowland showed higher competitive ability

TABLE 6. Heading behavior in the sowing year, first heading date, reproductive effort and seasonal pattern of growth in each population

			% of heading plants	First heading date		Reproductive effort (%)	Growth rate (g/day)	
				Mean♯	Range		1st crop	Aftermath
1.	Bn 501		45	6.5	3/VI-13/VI	16.4	2.50	0.93
2.	Bn 502		40	3.0	25/V-10/VI	18.8	2.67	1.22
3.	Bn 505		67	8.4	6/VI-14/VI	15.5	2.90	1.15
4.	Bn 509		64	6.1	23/V-13/VI	14.0	3.73	1.00
5.	Bn 853	Lowland	65	4.4	28/V-10/VI	12.7	2.36	1.53
6.	Bn 860		70	3.1	25/V- 9/VI	15.9	3.29	1.20
7.	Bn 945		90	5.7	28/V-10/VI	16.8	4.04	1.04
8.	Bn 670		27	8.9	6/VI-13/VI	20.1	3.79	1.15
16.	Bn 772		85	6.7	3/VI-12/VI	14.3	1.69	0.77
17.	Bn 947		45	6.5	30/V-19/VI	—	3.46	0.93
	Mean		60	5.9		16.1	3.04	1.09
11.	Bn 759		40	15.9	12/VI-20/VI	10.8	3.82	0.67
12.	Bn 760		80	14.9	13/VI-17/VI	11.0	3.81	0.67
13.	Bn 764	Liguria	0	15.8	14/VI-19/VI	11.8	3.88	0.72
14.	Bn 765		20	15.3	12/VI-18/VI	12.6	2.85	0.61
	Mean		35	15.5		11.6	3.59	0.67
15.	Bn 767		10	19.7	18/VI-24/VI	10.1	4.02	0.87
18.	Bn 948	Highland	0	19.3	17/VI-25/VI	12.2	3.47	0.61
19.	Bn 949		10	18.4	17/VI-21/VI	—	3.97	0.77
	Mean		7	19.1		11.2	3.97	0.77
	Kentucky 31		55	0.6	23/V-11/VI	16.7	4.05	0.88
	Hokuryo		15	11.8	9/VI-16/VI	11.9	4.61	1.27

♯, days from June 1.

than those from Liguria and Highland.

Reproduction: Heading behaviour of the year of sowing is shown in Table 6. In all populations except for two (Bn 764 and Bn 948) from altitudes above 1200 m, some plants headed in the sowing year. This indicates that most populations do not have an obligate requirement for short day and low temperature for initiation and elongation of inflorescence. Generally, Lowland populations had a higher proportion of heading plants than Highland populations. A large variation was detected between Liguria populations in heading behavior of the sowing year. There was a significantly negative correlation between the percentage of heading plants and altitude ($r=-0.62^{*}$). Thus, natural populations from low altitude tended to head in the sowing year more freely than those from high altitude.

Table 6 also shows the mean and range of the first heading date of the second year in each population. There was a large difference in the mean of first heading date among natural populations, ranging from 3.1 June in Bn 860 to 19.7 June in Bn 767. Lowland populations headed earlier than Liguria and Highland populations. Furthermore, Lowland populations showed wider variation within a population than the others. There was negative correlation between mean and range in the first heading date, and thus early populations tended to be more variable in heading date than late populations.

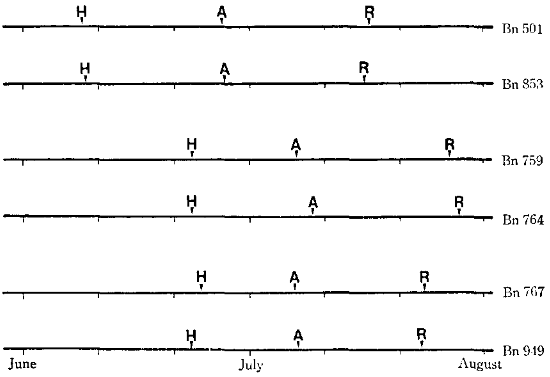


Fig. 3. Dates of heading (H), anthesis (A) and ripening (R) in the representative populations of Lowland (Bn 501 and Bn 853), Liguria (Bn 759 and Bn 764) and Highland (Bn 767 and Bn 949).

Figure 3 shows the date of heading, anthesis and ripening in the two representative populations of each group. Days from heading to anthesis were shorter in Liguria and Highland populations than in Lowland ones. Days from heading to anthesis correlated negatively with mean temperature from heading to anthesis. Thus, differences in the duration from heading to anthesis between populations may be mainly due to differences in temperature during this stage, although Highland populations showed a little shorter period than Liguria populations. On the other hand, Highland populations had a shorter period from anthesis to ripening than Liguria and Lowland populations. Days from anthesis to ripening did not clearly correlate with mean temperature during this period ($r=-0.34$), but significantly with 100 seeds weight ($r=0.74^{**}$). Therefore, small seed size of Highland populations contributes to complete reproductive growth more rapidly than Lowland and Liguria populations.

Reproductive effort (seed DW/shoot DW) is shown in Table 6. There was a negative correlation between reproductive effort and altitude in the collection sites ($r=-0.85^{**}$), showing that populations from high altitude (Liguria and Highland) had lower reproductive effort than Lowland populations. In addition, reproductive effort was negatively correlated with mean reproductive tiller weight ($r=-0.52^{*}$), although there was a large variation within Lowland group. Accordingly, low reproductive effort of Liguria and Highland populations is mainly due to their larger tiller size.

Seasonal pattern of growth: Since there was large difference in flowering time among populations. average growth rates (g/day/plant) were compared instead of dry matter weight. Average growth rate of each population, which are given in Table 6, was calculated by dividing DW of the first crop and aftermath by the length of each growing season. Marked differences were found among three groups. The average growth rates of the first crop were higher in Liguria (3.59 g/day) and Highland (3.97 g/day) than in Lowland (3.04 g/day). On the contrary, those of the aftermath were lower in Liguria (0.67 g/day) and Highland (0.77 g/day) than in Lowland (1.09 g/day). As a consequence, natural populations from Liguria and Highland tended to place more emphasis on the reproductive growth in spring rather than the subsequent growth in summer and fall. On the other hand, Lowland populations tended to maintain active growth after reproductive growth.

Discussion

Among natural populations, populations from Tunisia were markedly different from populations from Europe in the second principal component which represented the productivity. This was due to the low winter hardiness of Tunisia populations compared with European populations. Tunisia belongs to Mediterranean climate in which summer is hot and dry and winter is mild and moist, and the plant growth is restricted by the drought in summer. Plants adapted to the Mediterranean climates have to flower and set seeds before the dry season set in, to remain dormant during summer and to begin to grow after enough rain in fall. It has been reported[12,13,14,17,33,46,47,48] that Mediterranean populations in temperate grasses showed different developmental response from central and northern populations. Generally, Mediterranean populations show summer dormancy in the seeds, initiation and elongation of inflorescence in distinctly short photoperiod, active leaf and tiller development under the short photoperiod and low temperature and low cold tolerance.

On the other hand, natural populations from Europe markedly differed in the first principal component which mainly represents morphological characteristics at flowering time. This variation was closely associated with climatic conditions of place of origin. Particularly, distinct differences arose between low and high altitudinal populations from Alps regions in spite of the vicinity of their collection sites.

Besides morphological characters, there were large differences in life historical characteristics among these three groups, as shown in Table 7. Highland populations showed smaller seed size, slower germination, higher

TABLE 7. Main characteristics in three groups of natural populations

	Lowland	Liguria	Highland
Origin	France U. K. European Alps below 1000 m	Liguria Apennine	European Alps higher than 1000 m
Tiller size	Small	Intermediate	Large
Seed size	Large	Large	Small
Germination speed	Rapid	Slow	Slow
Dormancy	Absent	Present	Present
root : shoot ratio	Low	High	High
Competitive ability	High	Low	Low
Heading in the sowing year	Free	Variable	Less or no
Flowering time	Early	Late	Late
Duration of reproductive growth	Long	Intermediate	Short
Reproductive effort	High	Low	Low
Growth after reproduction	Active	Slow	Slow
Selection for	Competitive ability	Stress tolerance	Stress tolerance

root : shoot ratio, lower competitive ability, less free heading in the year of sowing, later in the heading, shorter duration of reproductive growth, lower reproductive effort and marked decrease in growth rate after reproduction than Lowland populations. Liguria populations showed generally intermediate features between the two groups.

The main limiting climatic factors of plant growth in central and northern Europe are low temperature during winter and the resultant short growing season. As altitude increases, winter generally becomes longer and more severe, and the growing season becomes shorter. In addition, plants become to be subjected to mineral nutrient stress with increase in altitude because of low microbial activity of the soil[24,25)]. On the other hand, plant density also changes along the altitudinal gradient. DOUGLAS[16)] reported that the plant density of *Mimulus primuloides* decreased with the increase of altitude, and that at low altitude plant size was reduced by severe intraspecific competition. ROCHOW[49)] found that altitudinal distribution of *Thlaspi alpestre* in the Rocky Mountains was partly limited by interspecific competition and infection by pathogens at low altitudes, but by low reproductive ability mainly due to the harsh climatic conditions at high altitudes. Thus, plant growth in low and high altitude may be controlled by different factors, mainly by physical factors in the high altitude and by biotic factors in the low altitude[4)].

The common features of plant populations adapted to high altitude or latitude have been well investigated by MOONEY and BILLINGS[40)], MCNAUGHTON[35)], BILLINGS and MOONEY[4)] and BLISS[7)] etc. Generally, northern or alpine plants tend to have the following characteristics : cold requirement for germination[40)], large root system relative to shoot system[4,40)], short duration of reproductive growth[35)], storage of large amount of carbohydrates in underground organs[39)], a prevailing vegetative reproduction instead of sexual reproduction[16)] and smaller seed size[3,54,57)]. Most of them were consistent with the characteristics of Highland populations. Thus, Highland populations seem to have been selected for the tolerance to severe winter and short growing season.

Northern Europe and the Alps were covered with glacial ice by about ten thousand years ago (pleistocene). As the glacial retreated, there occurred a colonization by species which had survived in the southern regions[8,56)]. Dispersal of seeds by wind, which is an important characteristics for colonizing ability, mainly depends on (i) the seed size, (ii) the height at which seed is released and (iii) specialized structures attached to the seed[27)]. Thus, small seed size and high culm characteristic of Highland populations may be advantageous to the colonization to new areas, although small seed size brings about lower competitive ability during early seedling stage, and high culm causes low reproductive effort.

Lowland populations may be subjected to a less severe winter but to heavy biotic pressures. In general, the competitive advantage seems to be mainly determined by the capture of resources[27]. Successful capture of resources depends on early germination[6,27,50], large seed size[5,27], a faster growth rate[27] and a longer period of growth[18,19,38]. Lowland populations had just these characteristics, a rapid germination, large seed size, faster growth rate during seedling growth due to a large allocation to the shoot system and a smaller decrease in growth rate after reproductive growth. In fact, these populations showed the highest competitive ability during seedling growth stage among the three groups of natural populations. Thus, Lowland population have been selected for the high competitive ability.

The organisms are usually subjected to two kinds of mortality, density independent mortality and density dependent one. The former are related to physical factors such as low winter temperature and extreme drought etc. On the other hand, the latter are caused by biological factors such as competition for resources and predation etc. In the environments imposing high density independent mortality such as temperate zones and the early stage of succession, a greater allocation of resources to reproductive activities and thus high fecundity are favoured (r strategy). On the other hand, in the environments imposing high density dependent mortality such as the tropics and the late stage of succession, a greater allocation of resources to non reproductive activities and thus high competitive ability are favoured (K strategy). And it has been frequently reported that the theory of r- and K-selection can be applied to many cases of ecological differentiation in plant populations[1,21,36,41,61].

However, it was not the case with natural populations in tall fescue, because they showed the different characteristics from those expected from the theory of r- and K-selection. Natural populations subject to high density independent mortality (Highland populations) showed not high, but low reproductive activity, and those subject to high density dependent mortality (Lowland populations) showed both high reproductive activities (free flowering in the sowing year and high reproductive effort) and high competitive ability. Thus, reproductive activity and competitive ability were not alternative characteristics in tall fescue, because the rapid rate of tillering seems to contribute to both high competitive ability and high reproductive effort. Instead, competitive ability and reproductive effort showed alternative relation with reservation of carbohydrate and root growth which may confer the high tolerance to harsh physical environments such as low temperature in winter, drought and low mineral nutrient (chapter III).

II. Variation in agronomic characteristics of cultivars

Natural populations have been screened to increase their fitness by natural selection. On the other hand, cultivars have been altered to improve their productivity by human being. Thus, there seems to be certain differences between cultivars and natural populations. In fact, the two cultivars, Hokuryo and Kentucky 31 showed lower root : shoot ratio, higher growth rate and higher competitive ability under the fertile soil conditions than natural populations, as shown in the previous chapter. In this chapter, therefore, it was examined what characteristics differ between cultivars and natural populations. Since the emphasis was placed on the comparison between cultivars and natural populations, the two species, tall fescue and meadow fescue (*Festuca pratensis* Huds.) were used in the experiments. Meadow fescue, diploid, is one of the progenitor species of tall fescue, and the both species show such a morphological similarity that they are hardly distinguished in the field.

A. Variation in morphological characteristics

A grass grows by repeating the production of new tillers and by developing each tiller. Since there is a generally negative correlation between rate of tillering and size of the tiller, two distinct plant types arise, a plant with many small tillers and one with few large tillers. Thus, this plant type is the most basic morphological characteristics for temperate grasses. In general, considerable variation in this plant type are detected between populations within the same species.

On the other hand, it was revealed in the previous chapter that morphological characteristics at flowering time were closely related to the climatic conditions of their places of origin and natural populations from high altitude or severe winter tended to have larger tiller than those from low altitude or mild winter. In this section, it was examined whether these climatic variation in tiller size is also observed among cultivars.

Materials and Methods

Materials used were 21 cultivars in tall fescue which were derived from six countries (two from Japan, one from Sweden, five from USA, six from Netherlands, six from France and one from U. K.) and 42 cultivars in meadow fescue which were derived from ten countries (one from Canada, two from

Finland, one from Norway, three from Sweden, three from W. Germany, twelve from Denmark, thirteen from Netherlands, one from Belgium, three from France and three from U. K.).

Seeds of each cultivar were individually planted in paper pot filled with sandy loam, peat and vermiculite mixture, and were allowed to grow for about 60 days. After that, plants were transplanted to an experimental field in 1970 for meadow fescue and in 1975 for tall fescue. A randomized block layout was used with two replications. Spacing was 50 cm apart in rows with inter-plant spacing of 25 cm. Fertilizer was applied at the rate of 40 kg N, 60 kg P_2O_5 and 75 kg K_2O per hectare in the first year and 70 kg N, 60 kg P_2O_5 and 125 kg K_2O in the second year.

At the flowering time of each cultivar, five plants per replication were cut at 5 cm above soil level, and culm length of the three representative reproductive tillers and the number of reproductive tillers in each plant were measured. Then, DW of reproductive tillers were weighed after drying at 80°C for 48 h.

Climatic data of each country were obtained from the World Climatic Table37). Although there are large differences in climatic conditions between locations even within the same country, climatic data of each country were in principle represented by those of capitals. However, those were not available in Netherlands and W. Germany, Utrecht and Berlin were used instead. Those of Japan were represented by Sapporo, because two Japanese cultivars were bred there.

Results

Table 8 shows the results of analysis of variance for culm length, mean reproductive tiller weight and the number of reproductive tillers in both species. There were significant differences in all three characters in tall fescue, but in two characters, culm length and mean reproductive tiller weight, in meadow fescue. For further analysis variance of cultivars was divided into between-countries and within-countries. Significant differences were evident in both between- and within-countries in all characters. But between-countries in all characters had larger variances than within-countries. These results suggest that tiller size and the number of tillers vary regularly according to the countries of origin rather than at random.

Table 9 shows the correlation coefficients of culm length, mean reproductive tiller weight and number of reproductive tillers with three environmental variables, latitude (LAT), mean temperature in January (JMT) and annual mean temperature (AMT) in each country. There were not any clear cor-

TABLE 8. Analysis of variance for culm length (CL), mean reproductive tiller weight (MTW) and number of reproductive tillers (NRT) in tall and meadow fescue

Source of variance	Tall fescue				Meadow fescue			
	df	Mean square			df	Mean square		
		CL	MTW	NRT		CL	MTW	NRT
Cultivar	20	72.1**	0.047**	1694**	42	64.4**	0.079**	1497
Between countries	5	73.7**	0.105**	2292**	9	146.9**	0.183**	
Within countries	15	71.5**	0.028**	1495**	33	41.9*	0.051*	
Replication	1	30.9	0.001	54	1	92.9*	0.052	5543
Error	20	11.2	0.007	373	42	22.8	0.029	1011

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

TABLE 9. Correlation coefficients between mean values of culm length (CL), mean reproductive tiller weight (MTW) and number of reproductive tillers (NRT) in each country, and latitude (LAT), mean temperature in January (JMT) and annual mean temperature (AMT) in tall and medow fescue

	Tall fescue			Medow fescue		
	CL	MTW	NRT	CL	MTW	NRT
LAT	−0.30	−0.05	−0.48	0.17	0.30	−0.31
JMT	−0.81	−0.69	0.59	−0.93**	−0.93**	0.41
AMT	−0.44	−0.66	0.90*	−0.84**	−0.84**	0.46

relations between three characters and latitude in both species. However, culm length and mean reproductive tiller weight negatively correlated with mean temperature in January and annual mean temperature in both species, although correlations were not significant in tall fescue. On the contrary, the number of reproductive tillers correlated positively with mean temperatures in January and annual mean temperatures.

Table 10 shows the mean values of culm length, mean reproductive tiller weight and the number of reproductive tillers in each country in both species. Figure 4 shows the relations of culm length to mean temperature in January. As shown in Table 10 and Figure 4, cultivars derived from cool countries tended to have few larger tillers than those from warm coun-

TABLE 10. Mean values of culm length (CL), mean reproductive tiller weight (MTW), number of reproductive tillers (NRT) and number of cultivars used (NOV) in each country, and mean temperature in January (JMT), anual mean temperature (AMT) and latitude (LAT) of representative cities in each country

Countries	Tall fescue				Meadow fescue				Cities	LAT	JMT	AMT
	NOV	CL	MTW	NRT	NOV	CL	MTW	NRT				
Canada	—	—	—	—	1	125	1.59	161	Ottawa	45°20′	−11.1	5.3
Finland	—	—	—	—	2	119	1.63	128	Helsinki	60°19′	−6.8	4.4
Japan	2	121	0.97	102	—	—	—	—	Sapporo	43°00′	−5.8	7.8
Norway	—	—	—	—	1	121	1.60	152	Oslo	59°56′	−4.7	5.9
Sweden	1	116	0.81	107	4	114	1.33	164	Stockholm	59°21′	−2.9	6.6
W. Germany	—	—	—	—	2	117	1.44	147	Berlin	52°29′	−0.5	9.5
Denmark	—	—	—	—	11	112	1.17	187	Copenhagen	55°38′	0.1	8.5
USA	5	116	0.68	154	—	—	—	—	New York	40°46′	0.9	12.6
Netherlands	6	112	0.66	119	15	109	1.18	181	Utrecht	52°03′	1.7	9.4
Belgium	—	—	—	—	1	108	1.32	164	Brussels	50°48′	2.2	9.9
France	6	110	0.58	144	3	108	1.15	164	Paris	48°53′	3.1	10.9
U.K.	1	115	0.83	118	3	110	1.20	158	London	50°21′	4.2	10.5

Mean reproductive tiller weight is represented by dry weight in tall fescue but by fresh weight in medow fescue

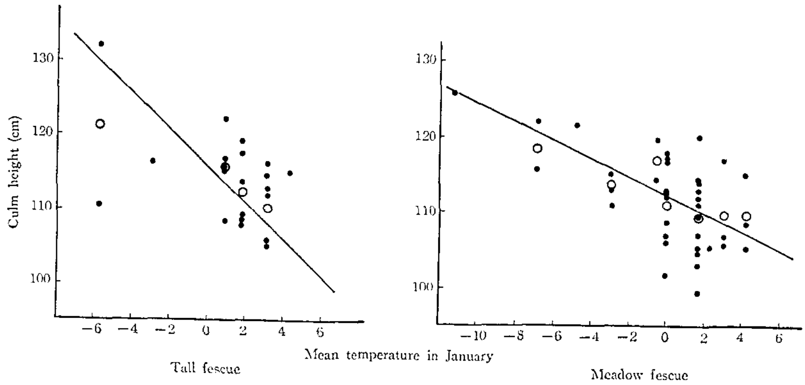


Fig. 4. Relations of culm height to mean temperature in January of countries of origin in cultivars of tall fescue and meadow fescue.
Open circle, mean of each country.

tries. Thus, it can be concluded that the trends in tiller size to climate were also observed in cultivars.

B. Variations in reproductive and vegetative growth

The extent of vegetative and reproductive growth is one of the most important characteristics for the cultivation of herbage grass species, because it has marked effects on herbage productivity and seed production. In this section, the main characteristics of vegetative and reproductive growth were examined under the different cutting treatment, and variations of them were compared between cultivars and natural populations.

Materials and Methods

Materials used were 21 cultivars in tall fescue and 18 cultivars (including two natural populations) in meadow fescue. Seeds of each cultivar were planted in paper pots and allowed to grow for about 60 days. After that, plants were transplanted to an experimental field in June 1979. A randomized block layout was used with two replications. Spacing was 50 cm apart in rows with inter-plant spacing of 25 cm, and one row consisted of 18 plants. Fertilizer was applied at the rate of 40 kg N, 60 kg P_2O_5 and 75 kg K_2O per hectare in the first year and 70 kg N, 60 kg P_2O_5 and 125 kg K_2O in the second year.

In the first year, the presence or absence of the ear emergence was recorded in all plants of each cultivar. In the second year, each row was split into three plots. Each of these three plots which consisted of six plants was used for the investigation of productivity at frequent and infrequent cutting treatments and seed productivity.

Frequent cutting treatment: Cuttings were made five times a year (21 May, 17 July, 21 August, 26 September and 18 October). At each cutting, plant DW was measured in five plants of each cultivar.

Infrequent cutting treatments: Cuttings were made three times (at the flowering time of each cultivar, 28 August and 8 October). At the flowering time of each cultivar, five plants were cut and then the number and DW of reproductive tillers and DW of vegetative tillers were recorded. And at the second and the third harvests, plant DW was measured.

Seed productivity: At the ripening time of each cultivar, five plants were cut and plant DW was measured in each population. After that seeds were threshed from ears and seed DW was recorded.

Results

Table 11 shows the correlation coefficients of the total DW at five- and three-cutting systems and regrowth ability (the ratio of total DW at five-times cutting to that at three-times cutting) with the yield components at flowering time. The similar correlation coefficients were obtained in both species. The total DW at three-times cutting was positively correlated with DW of reproductive tillers in tall fescue ($r=0.82^{**}$) and in meadow fescue

TABLE 11. Correlation coefficients of annual yields at three and five cutting treatment a year and regrowth ability with some morphological characters at flowering in tall fescue and meadow fescue

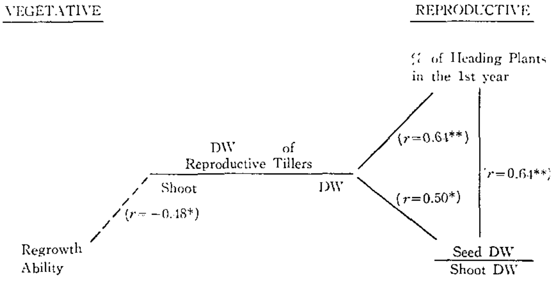
	Tall fescue			Meadow fescue		
	Annual yield		Regrowth ability	Annual yield		Regrowth ability
	3cut	5cut		3cut	5cut	
Shoot yield	.83**	.20	−.25	.87**	.20	−.51*
DW of reproductive tillers	.82**	−.05	−.45*	.84**	.04	−.64**
DW of vegetative tillers	.14	.38	.40	−.15	.44	.56
Reproductive tiller/shoot	.33	−.36	−.48*	.32	−.41	−.66**
No. of reproductive tillers	.47*	−.30	−.49*	.38	−.51*	−.71**
Mean weight of reproductive tiller	.22	.25	.10	.36	.60**	.21
First heading date	.22	.81**	.56*	.10	−.18	−.26

$$\text{regrowth ability} = \frac{\text{annual yield at 5 cut}}{\text{annual yield at 3 cut}}$$

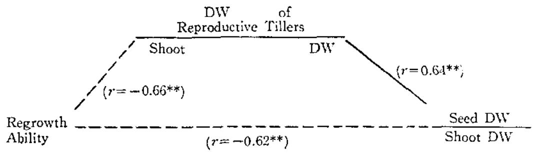
($r=0.84^{**}$). The total yields at five-times cutting, on the other hand, were positively correlated with DW of vegetative tillers, but negatively with the number of reproductive tillers in both species, although most of correlation coefficients were not significant. Regrowth ability correlated positively with DW of vegetative tillers but negatively with DW and the number of reproductive tillers and proportion of reproductive to vegetative tillers. Therefore, cultivars with larger reproductive system tended to show high productivity under infrequent cutting system relative to frequent cutting system, and thus low regrowth ability.

Furthermore, proportion of reproductive to vegetative tillers is also closely related to efficiency of seed production and heading behaviour. Proportion of reproductive tillers showed positive correlation with reproductive effort (seed DW/shoot DW) in tall fescue ($r=0.50^{*}$) and in meadow fescue ($r=0.64^{*}$). In addition, cultivars with higher proportion of reproductive tillers tended to form inflorescence freely in the first year in tall fescue.

The relationship between the attributes related to vegetative and reproductive growth in both species is summarized in Figure 5. Correlation coefficients were similar in both species. The relative proportion of reproductive to vegetative tillers plays an important role in determining the relative merits



Tall fescue



Meadow fescue

Fig. 5. Relationship between characteristics related to vegetative and reproductive growth in tall fescue (above) and meadow fescue (below).

between vegetative and reproductive growth. Reproductive tiller DW/shoot DW showed negative correlation with regrowth ability which is related to the degree of vegetative growth. But it correlated positively with seed DW/shoot DW and the percentage of heading plants in the first year, both of which show the activity of reproductive growth. Thus, it can be concluded that there is a negative correlation between vegetative and reproductive growth in terms of the relative proportion of reproductive and vegetative tillers.

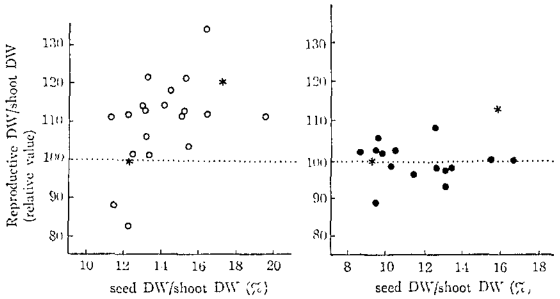


Fig. 6. Relationship between seed DW/shoot DW and relative values of reproductive tiller DW/shoot DW to "Hokuryo" in cultivars (left) and natural populations (right) of tall fescue.
○ cultivars ; ● natural populations ; * "Hokuryo" and "KY 31".

Figure 6 shows the relationship between relative proportion of reproductive tillers and reproductive effort in cultivars and natural populations of tall fescue. A comparison was made in reproductive tiller DW/shoot DW between cultivars and natural populations. There was a large variation among cultivars. However, cultivars tended to have a higher proportion of reproductive tillers than natural populations.

Discussion

The clinal variation of tiller size with winter cold was observed in cultivars of tall fescue and meadow fescue, and this was the same as found in natural populations of tall fescue. In timothy (*Phleum pratense*), SHIMADA and MAKI[58] reported that cultivars from Canada and USA showed longer and thicker culms with large head than those from Netherlands and U. K. which showed heavy tillering. And in orchardgrass (*Dactylis glomerata*), the cultivars from cold countries tended to have longer culm than those from warm countries (personal communication from Dr. IKEGAYA). Furthermore, KATAOKA and KANEKO[31] reported in natural populations of Barnyard millet, *Echnochloa crus-galli*, from different altitudes (300–810 m) that culm, inflorescence and leaf tended to be larger with increase in altitude. It is well known in animal that body size of vertebrate from cooler climates tends to be larger than those from warmer climates[34,43,55]. However, there is little information about the size trends with climates in plant species. Thus, further studies are required to confirm the climatic size trends in another plant species. The physiological implications of these climatic trends of tiller size will be discussed in the next chapter.

There was a negative relation between reproductive and vegetative growth. The greater proportion of reproductive tillers resulted in an efficient seed production, but it caused reduced herbage production under frequent cutting system. HYDER[29] and BROUGHAM[10] also pointed out that the relative proportion of reproductive and vegetative tillers was closely related to persistency and resistance to grazing. SOPER[62] also found in short-rotation ryegrass that the proportion of reproductive to vegetative tillers was of considerable importance in determining the persistency of the root and summer survival.

Cultivars and natural populations differed in relative proportion between vegetative and reporductive growth. Cultivars generally tended to show a higher proportion of reproductive tillers than natural populations, although a large variation existed between cultivars. TAKAHASHI[64] also reported in meadow fescue that cultivars tended to be inferior in regrowth ability and persistency to natural populations. It can be said that natural populations tend to place more emphasis on vegetative growth than cultivars.

The temperate herbage grasses now used originated less than ten-thousand years ago and evolved by the intervention of men and animals in Europe[8,56]. Thus, these grass species have been subjected to not only natural selection but also disturbance by men and grazing animals. As a result, various types of ecotype occurred through adaptation to their habitats. Particularly, grazing has a marked importance to the evolution of temperate grass species[27]. BROUGHAM[10] reported that difference in grazing intensity brought about the rapid changes in genotypic structure of ryegrass populations, and that intensive grazing favoured the perennial type, but lax grazing favoured the italian type. It is also reported that in well grazed permanent pastures, attributes of vegetative growth like high tillering capacity, prostrate growth form and high persistency were selected[8,9]. Since seedling establishment seldom occur in the permanent or well grazed pastures[53,69], reproductive growth and seed production seem to be of slight importance in maintaining survival in pastures. Instead, active vegetative growth and high perenniality may be favoured. Therefore, the higher proportion of vegetative tillers in natural populations may be due to adaptation to grazing.

The deliberate cultivation of a herbage grass by sowing seeds started only a few centuries ago. Furthermore, deliberate breeding began in this century[8]. BORRILL[8] pointed out the possibility that a cultivation system of herbage grass brought about an unintentional selection for high seed yield and thus a large reproductive system at the expense of leafiness and persistency. A selection for high forage yield under conservation is likely to result in a large reporductive system, because the first crop mostly consists of reproductive tillers. Thus, the trend of a high proportion of reproductive tillers in cultivars may reflect the emphasis on reproductive growth in the course of breeding history. Consequently, the balance between reproductive and vegetative growth is of particular importance for adaptation in natural environments as well as the performance in the agricultural conditions in temperate grasses.

III. Dry matter allocation and adaptive strategy

It was shown in the previous chapters that the plant type (few large tillers or many small tillers) and the relative proportion of reproductive and vegetative tillers at flowering time played important roles in adaptation to natural environments. However, it has not been clarified why these characteristics have adaptive significance. Thus, in this chapter, adaptive implications of the plant type and the relative proportion of reproductive and vegetative tillers were examined from the viewpoint of dry matter allocation. The attention were particularly directed to the allocation to root and storage organ, because in perennial grasses the root growth and reservation of non structural carbohydrate seem to be important factors related to the survival of them.

Materials and Methods

Two experiments were set out in pot cultures and in field conditions.

Experiment 1: Materials used were two cultivars (Kentucky 31 and Hokuryo) and eight natural populations, three from Lowland (Bn 501, Bn 505, Bn 670), one from Liguria (Bn 759), two from Highland (Bn 767, Bn 949) and two from Turkey (It 77428, It 77450). On 25 May 1983, twelve seeds were sown in a pot (20 cm top diameter and 60 cm deep) filled with sandy soil and seedlings were thinned to four plants per pot after emergence. The randomized block design was used with three replications. Fertilizer was applied at 4 g N, 6 g P_2O_5 and 4 g K_2O per pot and water was supplied sufficiently every day. During the experiment pots were covered with the cheese cloth so that sunlight would not increase the soil temperature within the pot. At the harvest (September 12–15), the shoot was cut at the soil level and separated into vegetative and reproductive tillers. Number and DW of both types of tillers in each pot were determined. After that soil was washed from roots and the DW of roots was measured.

Experiment 2: Materials used were eighteen genotypes which derived from two cultivars (Kentucky 31 and Hokuryo) and four natural populations (Bn 503, Lowland ; Bn 759, Liguria ; Bn 949, Highland ; It 77450, Turkey) Three genotypes were randomly chosen from each of populations. Each genotype was randomly divided into single tillers and planted individually in paper pots (5 cm diameter and 5 cm deep) filled with sandy loam, peat and vermiculite mixtures on May 20, 1982. Plants were allowed to grow for 20 days under the shaded conditions and then transplanted into an experimental field on June 9, 1982. A randomized block layout was used with four replications. Spacing was 50 cm apart in rows with inter-plant spacing of 25 cm, and one row consisted of 16 plants. Prior to the transplanting, 40 kg N, 60 kg P_2O_5 and 75 kg K_2O per hectare were applied.

Measurements were made on the second year (1983). The first, the second and the third samplings were made on April 11–14, April 27–30 and May 16–19, respectively. It took four days to complete each sampling because of one replication per one day. At each sampling time, plants were cut at the soil level and the number of tillers were counted. Plant fraction of 3 cm stem base was taken out and dried at 95°C for one hours and then at 80°C for 48 hours for the measurement of water soluble carbohydrate. The rest of plant materials were dried at 80°C for 48 hours and weighed. Plant fractions of stem base were grounded to 42-mesh screen. Carbohydrate were extracted from tissues by mechanically shaking 200 mg sample in 50 ml of distilled water for 1 hours at room temperature ca. 20°C. Carbohydrate values were determined by the anthrone method. Carbohydrates were expressed as percent fructose on a dry weight basis. At the third sampling time, root DW was measured. Cubic soil section of 25 × 25 × 25 cm around hill was dug up and soil was washed from roots. Roots were dried at 80°C for 48 hours and root DW was recorded.

At the flowering and ripening times of each genotype, plants were cut at the soil level and number, DW and WSC content of the vegetative and reproductive tillers were measured. Root DW was also recorded at the flowering time in the same manner as vegetative growth. At the ripening time seed DW was measured in each plant.

Results

Experiment 1: The natural populations from Lowland and Liguria, and the cultivar, Kentucky 31 formed many inflorescences even in the first year. On the other hand, those from Highland and Turkey, and cultivar Hokuryo showed less or no inflorescences and high root : shoot ratio.

Figure 7 shows the relations of root DW to DW of vegetative and reproductive tillers. There was a high positive correlation between root DW and total shoot DW (r=0.725**). Root DW also showed markedly high positive correlation with DW of vegetative tillers but not with DW of reproductive tillers. Moreover, negative relation appeared between root DW and DW of reproductive tillers except two very unproductive populations from Turkey. These results indicate that growth of the vegetative tillers bring about the proportional root growth, but the reproductive tillers does not accompany the increase in root growth.

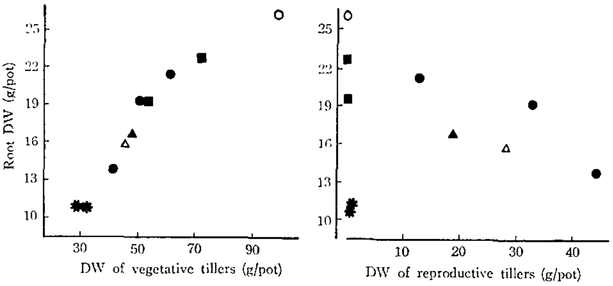


Fig. 7. Relations of root DW to DW of vegetative and reproductive tillers. Symbols as in Fig. 2.

Experiment 2: Figure 8 shows the relationships between number of tillers and mean tiller weight at three sampling times. Experimental field was covered with snow by the end of March and regrowth began at about the first week of April. Thus, plants at the first sampling time (April 14–17) had low DW. Mean tiller weight at this time was markedly lower than at the other stages. At the first sampling time, there was no clear correlation between number of tillers and mean tiller weight. However, at the second and third times, there appeared negative correlations between them. Thus, as time had passed, the difference in the plant type became clear.

Figure 9 shows the relations of WSC% at stem base to number of tillers and mean tiller weight at three sampling times. Two genotypes showed markedly high WSC% at the first and the second times. WSC%

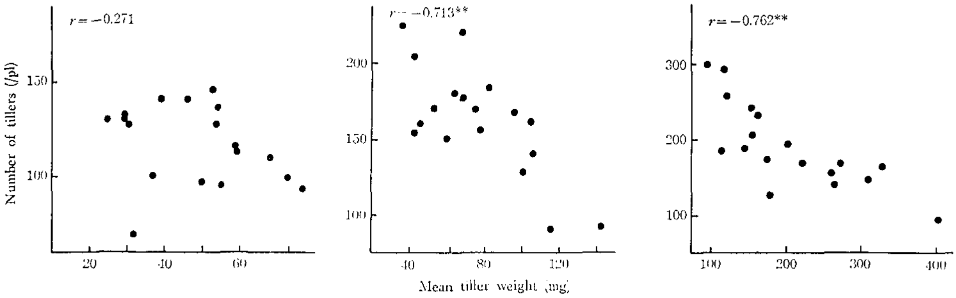


Fig. 8. Relationship between number of tillers and mean tiller weight at the first (left), the second (middle) and the third sampling time (right).

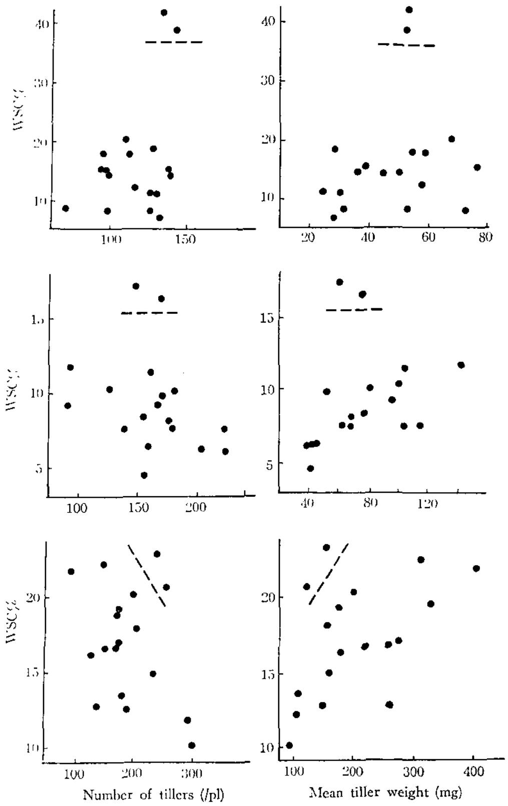


Fig. 9. Relations of water soluble carbohydrate content (WSC%) at stem base to number of tillers and mean tiller weight at the first (upper), the second (middle) and the third (below) sampling time.

decreased from the first to the second time but increased from the second to the third time. At the first sampling time, there was no clear relationship between WSC% and number of tillers, and mean tiller weight. However, when two genotypes with extremely high WSC% at the first stage were excluded, there appeared the negative relations between WSC% and number of tillers, but positive relations between WSC% and mean tiller weight at the second and the third times.

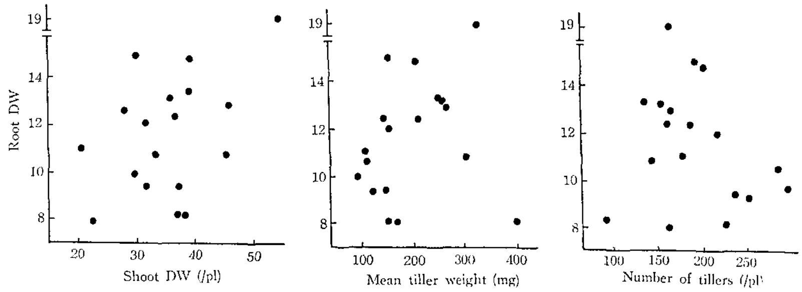


Fig. 10. Relations of root DW to the shoot DW, mean tiller weight and number of tillers.

Figure 10 shows the relations of root DW to mean tiller weight and number of tillers at the third sampling time. Genotypes with large tiller size tended to have larger root mass than those with small tiller size. However, genotypes with the largest tiller size showed small root biomass, because this genotype tended to form stolons and thus may allocate large assimilates to stolons instead of the root. On the other hand, genotypes with many tillers tended to have small root mass, although those with few tillers do not necessarily have large root masses. In this respect, genotypes with few large tillers tended to reserve more WSC% and to allocate more carbohydrate to root than those with many small tillers.

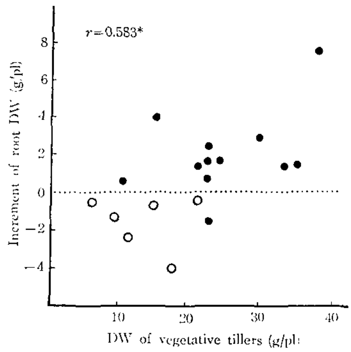


Fig. 11. Relationship between increment of root DW between the last sampling time at vegetative growth stage and flowering time, and DW of vegetative tillers at flowering time.
○ Cultivars : ● Natural populations.

There was a large difference in flowering time among genotypes (29 June to 15 July). However, there was no significant correlation between the earliness of flowering time and root DW at flowering ($r=0.246$) or increment of root DW between the third sampling time and flowering time ($r=0.305$). Figure 11 shows the relationship between increment of root DW during reproductive growth stage and DW of the vegetative tillers at flowering time. Increment of root DW was significantly correlated with the DW of the vegetative tillers ($r=0.583$*). But clear correlation was not found between root DW and DW of the reproductive tillers ($r=0.274$). All genotypes from both cultivars generally showed low DW of the vegetative tillers and the reduced root growth during the reproductive growth stage compared with those from natural populations.

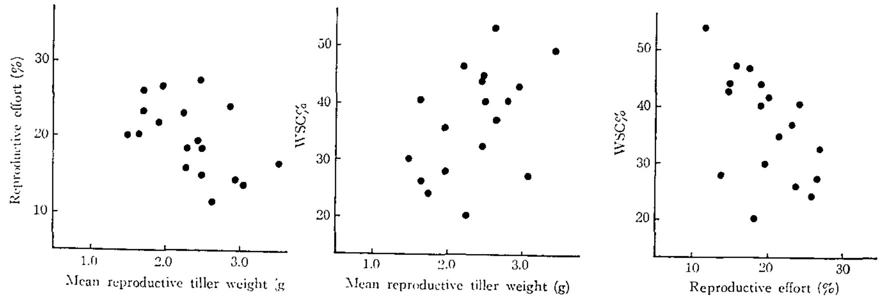


Fig. 12. Relationships among mean reproductive tiller weight, reproductive effort (seed DW/reproductive tiller DW) and water soluble carbohydrate content (WSC%) at the stem base of reproductive tillers at ripening time.

Figure 12 shows the relationship between reproductive effort (seed DW/reproductive tiller DW), mean reproductive tiller weight and WSC% of reproductive tillers. Reproductive effort was negatively correlated with mean reproductive tiller weight ($r=-0.471$*). On the other hand, WSC% was positively related to mean reproductive tiller weight ($r=0.438$) but negatively related to reproductive effort ($r=-0.534$*). Thus, genotypes with few large tillers tended to show smaller allocation to seed production but higher allocation to reservation of WSC during reproductive growth stage.

Discussion

In the present experiments, root DW showed a high positive correlation with DW of vegetative tillers, but not with DW of reproductive tillers. TROUGHTON[66,67,68)] pointed out that inflorescence formation caused a change in the relationship between root and shoot systems and brought about an increase in shoot growth relative to root growth. RYLE[51,52)] found in the experiment using ^{14}C that the transition from vegetative to reproductive growth caused marked changes in the pattern of distribution of labelled assimilates. The reproductive growth brought about increase in distribution of assimilates to the stem at the expense of distribution to the root, because of the active stem internode elongation during this stage. Therefore, too high a reproductive growth may have deteriorating effects on root growth. Cultivars tended to show larger shoot system relative to root system and a greater proportion of reproductive growth relative to vegetative growth than natural populations. This may be resulted from the artificial selection in the breeding program for high productivity under the fertile soils of the agricultural conditions. It was also reported in wheat35) that the cultivated species showed lower distribution of assimilates to root than their relative wild species.

Defoliation has also an adverse effect on the root growth, because the translocation of assimilates to the root is restrained by defoliation23). And as the frequency of defoliation is increased, root growth is progressively depressed2). Accordingly, a combination of active reproductive growth and frequent defoliation has deleterious effects on the root growth and may cause a reduction of persistency and resistance to grazing.

In this study, plants with few large tillers reserved higher concentration of WSC at the stem base than those with many small tillers during both vegetative and reproductive growth stage. According to the study by ZARROUGH *et al.*73), the population selected for high tillering rate showed lower WSC concentration at stem base than that for low tillering rate in tall fescue. Furthermore, ZARROUGH and NELSON72) reported that a genotype with few large tillers showed larger root mass than those with many small tillers.

The shoot produces the photosynthates. Part of these are used by the shoot itself, and the rest is translocated to the storing tissues and root. Therefore, the supply of carbohydrates is one of the main limiting factors of root growth. Plants with a rapid rate of tillering may require more carbohydrates for growth of young tillers than those with a slow rate of tillering, because newly formed tillers have to be supplied with carbohydrates from mature tillers untill they bear three to four leaves42,71). Thus, it seems that a negative relation between rate of tillering and supply of carbohydrate to the storing tissues and root system arise in terms of utilization of photosynthates, and plants with slow rate of tillering and large size of tiller can translocate more carbohydrate to the storing tissues and root system than those with high rate of tillering.

During the reproductive growth stage, plants with large reproductive tiller size tended to show higher WSC% but lower reproductive effort than those with small one. There was also significantly negative correlation

TABLE 12. Relationship between the plant type and dry matter allocation

Plant type		
Tiller size	Large	Small
Number of tillers	Few	Many
Dry matter allocation		
WSC% at stem base	High	Low
Root growth	High	Small
Reproductive effort	Low	High
Type	Saving	Generous
Distribution	Cold climate	Warm climate

between culm height and reproductive effort in the chapter I. Many studies[15] on cereals suggest that tall cultivars showed lower harvest index than dwarf ones. Thus, large tiller size results in low efficiency of seed production.

The relationship between the pattern of dry matter allocation and the plant type are summarized in Table 12. In general, average tiller size and the rate of tillering correlate negatively with each other, as long as the plant size does not differ markedly. Thus the both characters are alternative. The plants with few large tillers can reserve more carbohydrate at the stem base and translocate more to the root system because of the small expense of assimilates to the growth of young tillers and to seed production. On the other hand, the plants with many small tillers utilize assimilates for the growth of young tillers and high seed production at the expense of root growth and the reservation of non structural carbohydrate. Thus, the two plant types are characterized by the contrastive pattern of dry matter allocation, "saving" type which saves assimilates and "generous" type which uses up them.

The characteristics relating to reproduction are of great importance in the evolution of organism. In herbage species, seedling establishment is generally very rare in the grassland[53,59,69]. However, once establishment is achieved, the genotype generally has a high perenniality of more than several hundreds years[26]. Thus, selection seems to be directed toward high survival of the adult plant rather than fecundity in perennial herbage species. Adult survival may be determined by different factors between two types of environments. High stress tolerance may be favoured in the environments imposing on high density independent mortality factors like cold climates, but high competitive ability may be favoured in those imposing high density dependent ones like warm climates.

Plants with few large tillers tended to be distributed in cold climates, in which low temperature in winter, short growing season and low mineral nutrients seem to be the main limiting factors of the growth and survival of plants. The "saving" allocation pattern is likely to be favourable in cold climates, because a high concentration of carbohydrate brings about an increase in cold tolerance[32,60] and rapid regrowth in early spring[39], and large root mass is advantageous for withstanding infertile soil conditions and drought[11]. On the other hand, plants with many small tillers tended to be distributed in warm climates in which competitive pressure may be the important factor in limiting the growth and survival. The "generous" allocation pattern seems to be advantageous in warm climates, because high tillering rate frequently confers the high competitive ability in temperate grasses[22,30,44,45,70]. Thus, it is suggested that the pattern of dry matter allocation plays an particularly important role in the climatic differentiation of the plant type, although another factors such as dispersibility seem to be also involved.

IV. Summary

The variations of morphological and physiological characteristics in natural populations and cultivars of tall fescue were evaluated under the uniform field conditions, and the adaptive and agronomic implications of these characteristics were examined with special reference to dry matter allocation. The results obtained are as follows :

1. Natural populations of tall fescue from North Africa (Tunisia) showed particularly low winter hardiness and were subjected to severe winter damage. Natural populations from Europe were classified mainly by morphological characteristics at flowering time into three groups as follows : Lowland group (France, U. K. and European Alps below 1000 m), Liguria group (Liguria Apennine) and Highland group (European Alps above 1000 m). Variation of these morphological characteristics was closely associated with altitude and winter temperature of collection site of each population, and populations from cold climates showed larger reproductive tiller size than those from warm climates.

2. There were large variations in life history characteristics among the three groups. Generally, Highland populations showed smaller seed size, slower germination, higher root : shoot ratio, lower competitive ability, less free heading in the sowing year, later heading date in the second year, shorter duration of reproductive growth, lower reproductive effort and marked decrease in growth rate after reproduction than Lowland populations. Liguria

populations tended to show intermediate characteristics between the two groups. Thus, Highland populations seem to have been selected for high tolerance to severe winter and short growing season, but Lowland populations seem to have been for high competitive ability.

3. Variations of morphological characteristics at flowering time in cultivars of tall fescue and meadow fescue were examined in relation to climatic conditions of countries of origin. Cultivars from cold countries tended to have few larger reproductive tillers than those from warm conutries.

4. There was a negative relation between reproductive and vegetative growth in terms of the relative proportion of reproductive and vegetative tillers at flowering time. The greater proportion of reproductive tillers resulted in an efficient seed production but it caused the reduced herbage production under the frequent cutting system. Cultivars and natural populations differed in relative proportion of vegetative and reproductive growth, cultivars generally tended to show a relatively higher proportion of reproductive growth than natural populations.

5. The adaptive implications of the plant type (few large tillers or many small tillers) and relative proportion of reproductive and vegetative tillers at flowering were examined in relation to dry matter allocation to root system and storage part. There was a negative relation (trade-off) between rate of tillering and supply of carbohydrates to root system and storage part in terms of utilization of photosynthates, and plants with slow rate of tillering and large tiller size tended to translocate more carbohydrates to root system and storage part than those with high rate of tillering. The inflorescence formation caused the marked changes in the relationship between root and shoot systems. The growth of vegetative tillers brought about the proportional root growth, but that of reproductive tillers did little increase in root mass.

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