STUDIES ON ECOTYPIC VARIATIONS AMONG NATURAL POPULATIONS OF TIMOTHY (*PHLEUM PRATENSE* L.)

VII. Diallel analysis of seasonal growth pattern

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Introduction

In a series of our experiments, natural populations of timothy (*Phleum pratense* L.) showed different seasonal growth habits corresponding to the locality of habitat in Hokkaido, northern island of Japan[31,32]. Namely, the regrowth in early spring of the northeastern population started later and its growth suppression in late autumn occured earlier than those of the south-western one. Furthermore, the growth in mid-summer was less vigorous in the northeastern population.

Another study of growth pattern from early spring to mid-summer clarified that shape of growth curve was very similar between two populations, but each developmental stage along the curve was delayed in the northeastern population[33]. It was inferred that the late start of leaf growth in early spring caused such a time lag of developmental stages.

As a result of correlation analysis, it was revealed that the characteristic seasonal growth habit was related to climatic conditions at habitat. On the whole, the northeastern area has a shorter growing season and more severe winter than the southwestern one. It is well known in forage plants that growth potential at low temperature is inversely related to cold tolerance[2~4, 19,23]. Therefore, the growth habit of the northeastern population in early spring and late autumn seems to play an important role to resist the erratic

frost injury and to survive the severe winter by keeping high level of cold tolerance.

Thus, one of the main environmental factors responsible for the population differentiation of timothy in Hokkaido is climatic conditions and the north-eastern and southwestern populations are regarded as distinct climatic ecotypes.

On the other hand, genetic variation as well as environmental hetero-geneity is indispensable to population differentiation. So genetic studies are necessary to clarify the mechanism of ecotypic differentiation.

The purpose of this study is to investigate the genetic basis for the inter-population variation of seasonal growth pattern of timothy in Hokkaido using a diallel cross method.

Materials and Methods

The diallel cross was made among five populations, each of which was represented by two randomly taken plants, and ten parental plants were used
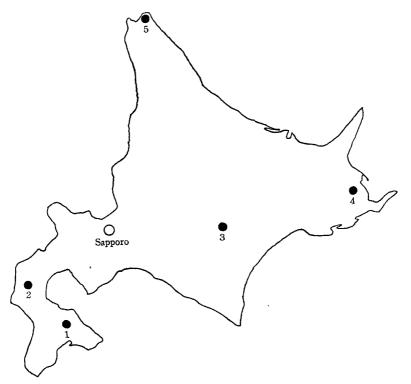

Fig. 1. Map of Hokkaido showing collection sites of five parental populations used in diallel cross.

in a total. They were raised from seed sample collected at the original habitat. The collection sites in Hokkaido are shown in Fig. 1. Populations of 1 and 2 had been originated in the southwestern area and those of 3, 4 and 5 in the northeastern one.

In 1978, each of ten plants seeded in the previous year was devided into ten ramets. Nine of these ramets were crossed with the other nine plants and the remaining one was selfed to check the selfing rate. The cross was made without emasculation; two ramets to be crossed were planted in a pot and, after heading, they were closed in a glassine paper. By this way, ten plants were crossed in all possible combinations including reciprocals, and 90 families were yielded excluding selfed family.

Selfing rate was checked on each parental plant using 500 florets. The seed set percent by selfing is given in Table 1. As the rates were extremely low, the contamination by selfed seeds in crossing was ignored.

TABLE 1. Seed set percent (%) by selfing of plant used in diallel cross.

Population	1	2	3	4	5
Plant					
1	0.0	0.0	0.2	0.0	1.8
2	0.0	0.0	0.2	7.2	0.4

Family seedlings were grown for two months in a glasshouse and they were transplanted into experimental field in Sapporo in June 1979 in a randomized block design with two replications. In each replication, five seedlings per family were grown in 0.5 m apart in a row spaced 1.0 m apart from the others.

In 1980, from the regrowth in early spring to the seed maturity in mid-summer, two vigorous tillers of each plant were cut off weekly at the soil surface. Dry weights of a tiller and its component organs (stem, leaf and ear) were measured. The measurements were made of tiller from May 14 to July 9, stem and leaf from May 14 to June 18, and ear from July 9 to August 6.

To clarify the seasonal growth pattern, relative growth rate (RGR) was calculated from the dry weight data for each week. Diallel analysis was conducted by a computer in Hokkaido University Computing Center.

Results

RGRs for 90 families during the above period are partly shown in Table 2. Results of diallel analysis for tiller, stem, leaf and ear are given in Tables 3, 4, 5 and 6, respectively. The diallel analysis was carried out on the basis of method by YATES[29] and HAYMAN[5]. In tables, terms a, b, c and d stand for additive, dominance, average reciprocal and residual reciprocal effects, respectively. The variation due to each of these effects was partitioned into those among and within populations.

TABLE 2. Relative growth rate (RGR, g/g/day) in the period from May 14 to May 21.

		Female parent									
Population		1		2		3		4		5	
Plant		1	2	1	2	1	2	1	2	1	2
Male parent 1	1		0.095	0.021	0.053	0.076	0.081	0.013	0.034	0.039	−0.016
			0.099	0.059	0.077	0.076	0.084	0.036	0.049	0.058	0.027
			0.091	−0.018	0.026	0.075	0.077	−0.011	0.017	0.020	−0.054
	2	0.012		0.073	0.020	0.097	0.014	0.022	0.068	0.017	0.030
		0.035		0.103	0.055	0.104	0.061	0.040	0.088	0.060	0.050
		−0.014		0.043	−0.020	0.091	−0.033	0.003	0.044	−0.026	0.018
2	1	0.025	0.090		0.022	0.018	0.053	0.055	0.071	0.050	0.021
		0.056	0.101		0.041	0.051	0.050	0.075	0.089	0.060	0.055
		−0.008	0.074		0.004	−0.012	0.057	0.032	0.054	0.039	−0.007
	2	0.101	0.100	0.086		0.079	0.040	0.102	0.082	0.097	0.016
		0.114	0.113	0.089		0.094	0.055	0.102	0.087	0.101	0.037
		0.086	0.086	0.083		0.061	0.026	0.101	0.076	0.092	−0.002
3	1	0.075	0.058	0.062	0.085		0.085	0.027	−0.002	0.030	0.085
		0.083	0.082	0.087	0.087		0.077	0.045	−0.001	0.051	0.082
		0.065	0.032	0.035	0.082		0.092	0.006	−0.003	0.011	0.091
	2	0.113	0.028	0.090	0.022	0.082		0.100	0.101	0.087	0.074
		0.122	0.065	0.096	0.040	0.087		0.102	0.087	0.092	0.082
		0.106	−0.011	0.085	0.004	0.077		0.097	0.115	0.082	0.067
4	1	0.092	0.020	0.110	0.010	0.090	0.024		0.119	0.049	0.008
		0.105	0.052	0.112	0.045	0.099	0.041		0.113	0.070	0.032
		0.074	−0.011	0.109	−0.024	0.078	0.007		0.125	0.031	−0.017
	2	0.012	0.007	0.029	0.104	0.018	0.021	0.046		0.059	0.041
		0.031	0.046	0.036	0.109	0.032	0.024	0.065		0.075	0.069
		−0.008	−0.030	0.021	0.097	0.005	0.021	0.024		0.042	0.015
5	1	0.009	0.086	0.097	0.050	0.018	−0.003	0.049	0.023		0.025
		0.049	0.079	0.110	0.063	0.036	0.025	0.059	0.060		0.039
		−0.030	0.095	0.083	0.036	0.000	−0.030	0.038	−0.012		0.012
	2	0.111	0.056	0.081	0.032	0.003	0.035	0.051	0.031	0.027	
		0.124	0.054	0.095	0.034	0.021	0.062	0.077	0.061	0.059	
		0.098	0.060	0.066	0.031	−0.010	0.010	0.023	0.006	−0.003	

Upper figure: RGR for weight of a tiller
Middle figure: RGR for stem weight per tiller
Lower figure: RGR for leaf weight per tiller

RGR for weight of a tiller

Diallel analysis for RGR of tiller (Table 3) showed that there was a significant difference among families in the periods from May 14 to May 21

TABLE 3. Diallel analyses for RGR of weight of a tiller.

Source of variation	df	Mean squares (× 1000)							
		Sampling date							
		May			June				July
		14 — 21	21 — 28	28 — 4	4 — 11	11 — 18	18 — 25	25 — 2	2 — 9
Family (F)	89	2.380**	0.210	0.159	0.169	0.160	0.304	0.159	0.149*
a	9	1.814*	0.230	0.298	0.246	0.195	0.292	0.361*	0.304*
Am. pop.	4	3.559*	0.184	0.255	0.158	0.191	0.268	0.574	0.397
Wi. pop.	5	0.419	0.267	0.332	0.317	0.198	0.311	0.191	0.230*
b	35	2.072*	0.213	0.137	0.244	0.100	0.310*	0.141	0.148*
Am. pop.	10	1.893	0.288	0.067	0.291	0.062	0.425	0.118	0.147
Wi. pop.	25	2.144	0.182	0.164	0.225	0.115	0.263	0.151	0.149
c	9	4.465*	0.170	0.125	0.154	0.206	0.275	0.111	0.111
Am. pop.	4	3.411	0.099	0.154	0.184	0.136	0.182	0.190	0.135
Wi. pop.	5	5.308	0.227	0.101	0.129	0.262	0.350	0.047	0.091
d	36	2.298**	0.213	0.155	0.082	0.199	0.310	0.137	0.121
Am. pop.	6	2.997	0.151	0.078	0.038	0.081	0.079	0.187	0.248*
Wi. pop.	30	2.159**	0.225	0.171	0.090	0.222	0.356*	0.127	0.096
Block (B)	1	0.322	0.708	0.012	0.648	1.694**	0.113	6.054**	0.198
F × B	89	0.944	0.284	0.145	0.166	0.172	0.264	0.141	0.098
a × B	9	0.461	0.324	0.277	0.253	0.185	0.767	0.192	0.084
Am. pop.× B	4	0.785	0.603	0.273	0.229	0.168	0.930	0.120	0.158
Wi. pop× B	5	0.201	0.101	0.281	0.273	0.198	0.637	0.249	0.024
b × B	35	1.037	0.300	0.147	0.191	0.196	0.165	0.128	0.081
Am. pop.× B	10	0.350	0.604	0.240	0.129	0.241	0.094	0.064	0.089
Wi. pop.× B	25	1.311	0.179	0.109	0.215	0.178	0.193	0.154	0.078
c × B	9	0.999	0.249	0.071	0.056	0.144	0.381	0.298	0.126
Am. pop.× B	4	0.153	0.274	0.111	0.057	0.112	0.031	0.213	0.124
Wi. pop.× B	5	1.677	0.230	0.039	0.055	0.169	0.662	0.367	0.128
d × B	36	0.961	0.268	0.129	0.148	0.153	0.207	0.102	0.111
Am. pop.× B	6	1.465	0.219	0.097	0.234	0.025	0.296	0.054	0.136
Wi. pop.× B	30	0.860	0.278	0.136	0.131	0.178	0.189	0.112	0.106

*, ** : Significant at 5% and 1% levels, respectively.
Am. pop.: Among populations   Wi. pop.: Within populations
a : Additive effect (additive genetic variation)
b : Dominance effect (non-additive genetic variation)
c : Average reciprocal effect (consistent variation between reciprocal families)
d : Residual reciprocal effect (inconsistent variation between reciprocal families)

and from July 2 to July 9. In the former period, additive, dominance, average reciprocal and residual reciprocal effects were all significant. But their variations among populations were not significant except for additive

TABLE 4. Diallel analyses for RGR of stem weight per tiller.

Source of variation	df	Mean squares (× 1000)				
		Sampling date				
		May			June	
		14 — 21	— 28	— 4	— 11	— 18
Family (F)	89	1.512**	0.283	0.161	0.205	0.216
a	9	1.235	0.373	0.149	0.189	0.269
Am. pop.	4	2.253*	0.675	0.118	0.149	0.311
Wi. pop.	5	0.421*	0.132	0.174	0.221	0.236
b	35	1.441**	0.291	0.181	0.308	0.134
Am. pop.	10	1.594	0.255	0.084	0.373	0.080
Wi. pop.	25	1.379*	0.306	0.220	0.282	0.156
c	9	3.016*	0.290	0.156	0.196	0.253
Am. pop.	4	1.891	0.253	0.097	0.231	0.199
Wi. pop.	5	3.917	0.320	0.204	0.168	0.295
d	36	1.275	0.252	0.145	0.110	0.273
Am. pop.	6	1.170	0.163	0.066	0.067	0.086
Wi. pop.	30	1.296	0.269	0.161	0.119	0.310
Block (B)	1	0.555	1.355*	4.941*	0.045	3.927**
F × B	89	0.671	0.341	0.176	0.178	0.209
a × B	9	0.507	0.400	0.246	0.293	0.232
Am. pop. × B	4	1.038	0.701	0.293	0.225	0.198
Wi. pop. × B	5	0.082	0.159	0.209	0.348	0.260
b × B	35	0.576	0.306	0.179	0.192	0.226
Am. pop. × B	10	0.294	0.528	0.212	0.124	0.287
Wi. pop. × B	25	0.689	0.218	0.165	0.219	0.201
c × B	9	0.622	0.301	0.103	0.066	0.178
Am. pop. × B	4	0.045	0.392	0.199	0.057	0.094
Wi. pop. × B	5	1.084	0.227	0.026	0.073	0.246
d × B	36	0.818	0.370	0.175	0.164	0.196
Am. pop. × B	6	1.055	0.397	0.106	0.326	0.043
Wi. pop. × B	30	0.770	0.365	0.188	0.131	0.226

*, **: Significant at 5% and 1% levels, respectively.
Am. pop.: Among populations   Wi. pop.: Within populations
a : Additive effect (additive genetic variation)
b : Dominance effect (non-additive genetic variation)
c : Average reciprocal effect (consistent variation between reciprocal families)
d : Residual reciprocal effect (inconsistent variation between reciprocal families)

effect. In the latter period, though additive and dominance effects were significant, these effects among populations had not significance. On the other hand, significance was detected in the residual reciprocal effect among populations.

TABLE 5. Diallel analyses for RGR of leaf weight per tiller.

Source of variation	df	Mean squares (× 1000)				
		Sampling date				
		May			June	
		14 — 21	— 28	— 4	— 11	— 18
Family (F)	89	3.848**	0.458	0.337	0.288*	0.142
a	9	3.086	0.915	0.987	1.074**	0.171
Am. pop.	4	6.349**	0.862	1.309	0.343	0.105
Wi. pop.	5	0.476	0.957	0.726	1.659**	0.224
b	35	3.407	0.464	0.263	0.282	0.106
Am. pop.	10	2.857	0.556	0.263	0.241	0.074
Wi. pop.	25	3.627	0.427	0.263	0.299	0.119
c	9	6.296*	0.228	0.194	0.166	0.165
Am. pop.	4	5.314	0.152	0.381*	0.206	0.152
Wi. pop.	5	7.082	0.290	0.045	0.134	0.176
d	36	3.854**	0.395	0.282	0.127	0.164
Am. pop.	6	5.700	0.217	0.170	0.130	0.103
Wi. pop.	30	3.485**	0.430	0.305	0.126	0.176
Block (B)	1	3.740	12.479**	2.464**	7.930**	0.184
F × B	89	1.664	0.459	0.247	0.190	0.152
a × B	9	1.014	0.732	0.525	0.189	0.114
Am. pop. × B	4	1.680	0.851	0.509	0.263	0.079
Wi. pop. × B	5	0.481	0.637	0.537	0.129	0.142
b × B	35	2.134	0.511	0.234	0.240	0.169
Am. pop. × B	10	0.690	0.912	0.414	0.181	0.226
Wi. pop. × B	25	2.712	0.351	0.162	0.264	0.147
c × B	9	1.539	0.424	0.175	0.100	0.136
Am. pop. × B	4	0.504	0.482	0.246	0.114	0.181
Wi. pop. × B	5	2.367	0.376	0.118	0.090	0.100
d × B	36	1.401	0.349	0.208	0.163	0.150
Am. pop. × B	6	2.124	0.217	0.124	0.136	0.028
Wi. pop. × B	30	1.256	0.376	0.225	0.168	0.174

*, **: Significant at 5% and 1% levels, respectively.
Am. pop.: Among populations   Wi. pop.: Within populations
a : Additive effect (additive genetic variation)
b : Dominance effect (non-additive genetic variation)
c : Average reciprocal effect (consistent variation between reciprocal families)
d : Residual reciprocal effect (inconsistent variation between reciprocal families)

RGR for stem weight per tiller

With respect to RGR for stem, families differed significantly only in the period from May 14 to May 21 (Table 4). Additive, dominance and average

TABLE 6. Diallel analyses for RGR of ear weight per tiller.

Source of variation	df	Mean squares (× 1000)			
		Sampling date			
		July			Aug.
		9 — 16	— 23	— 30	— 6
Family (F)	89	0.610**	0.375**	0.194	0.238
a	9	2.574**	0.593	0.512	0.821
Am. pop.	4	1.658	0.410	1.014*	0.467
Wi. pop.	5	3.307**	0.740	0.111	1.104
b	35	0.516	0.400	0.152	0.261
Am. pop.	10	0.713	0.513	0.175	0.136
Wi. pop.	25	0.437	0.354	0.143	0.311
c	9	0.281	0.564*	0.116	0.098
Am. pop.	4	0.170	0.402	0.055	0.050
Wi. pop.	5	0.369	0.694	0.165	0.137
d	36	0.293	0.250	0.175	0.105
Am. pop.	6	0.074	0.201	0.132	0.054
Wi. pop.	30	0.337	0.260	0.183	0.115
Block (B)	1	17.018**	0.044	3.629**	0.000
F × B	89	0.267	0.219	0.163	0.200
a × B	9	0.287	0.215	0.451	0.468
Am. pop.× B	4	0.555	0.283	0.598	0.582
Wi. pop.× B	5	0.073	0.161	0.333	0.377
b × B	35	0.313	0.265	0.121	0.213
Am. pop.× B	10	0.512	0.312	0.193	0.195
Wi. pop.× B	25	0.234	0.246	0.092	0.220
c × B	9	0.191	0.116	0.112	0.192
Am. pop.× B	4	0.299	0.067	0.053	0.083
Wi. pop.× B	5	0.104	0.155	0.160	0.279
d × B	36	0.237	0.200	0.146	0.122
Am. pop.× B	6	0.136	0.054	0.227	0.131
Wi. pop.× B	30	0.257	0.229	0.128	0.120

*, **: Significant at 5% and 1% levels, respectively.
Am. pop.: Among populations   Wi. pop.: Within populations
a : Additive effect (additive genetic variation)
b : Dominance effect (non-additive genetic variation)
c : Average reciprocal effect (consistent variation between reciprocal families)
d : Residual reciprocal effect (inconsistent variation between reciprocal families)

reciprocal effects were significant. For additive effect, variations among and within populations were both significant. In this case, mean values of families of which either parent was common were as follows; 0.072, 0.075, 0.068, 0.066 and 0.061 for common parental populations of 1, 2, 3, 4 and 5, respec-tively. Thus, families of northern population tended to have lower RGR than those of southern one.

RGR for leaf weight per tiller

The difference among families was significant in the period from May 14 to May 21 as well as for stem (Table 5). In this period, additive effect among populations, average and residual reciprocal effects had significance. There was also a significant difference among families from June 4 to June 11 and it was largely attributable to additive effect. Furthermore, average reciprocal effect among populations from May 28 to June 4 had significance. Mean values of reciprocal differences (female minus male) in the cross of which either parent was common were as follows; −0.002, −0.002, 0.009, 0.000 and −0.006 for numerical order of populations, respectively. Thus, reciprocal difference was notable in the cross with population 3 as a common parent.

RGR for ear weight per tiller

This character showed a significant difference among families in the two successive weeks from July 9 to July 23 (Table 6). Additive effect in a earlier week and average reciprocal effect in a later week had significance. In addition, additive effect among populations from July 23 to July 30 was significant. In this case, families of northern population 5 had the highest mean value (0.034) and those of southern population 1 had the lowest (0.025).

Discussion

Diallel analysis for RGR of weight of a tiller suggested that there was a large genetic variation in the growth rate in early spring, since families differed widely in the period from May 14 to May 21. This agrees well with previous studies[31,33] showing a evident differentiation among populations for the growing behaviour in early spring. In this period, only the additive effect was apparent. After that period, genetic factor was not apparent except for residual reciprocal effect from July 2 to July 9. So it is pointed out that differentiation of seasonal growth pattern in natural populations of timothy in Hokkaido is based on an additive gene action of polygenic system controlling the growth rate under low temperature conditions in early spring.

It appears certain that genetic variation is more or less present within

a population of allogamous plant. In fact, such variations have been already reported for various characters in perennial ryegrass[9,21] and meadow fescue[22] by diallel crosses. In the present study, additive genetic variation within populations as well as among populations was observed for the RGR of stem from May 14 to May 21. So population differentiation for seasonal growth pattern will evolve further, if natural selection works upon such a genetically heterogenous population.

In a previous paper[30], it was demonstrated that main genetic factor responsible for the variation of germination characteristics was also additive effect. So far, it has been reported in many plant species that inter-population variation is largely ascribable to additive effect and based on polygenic system[6~13,15~18,24~28]. Environmental factors such as temperature, moisture, day length and solar intensity change gradually and continuously over large areas, and form various environmental gradients. Therefore, adaptive characters which are influenced by their selection pressure will also show gradients in the phenotypic expression. On the other hand, polygenic system has a nature that individual effect of genes at a number of different loci is minute, but their similar and cumulative effect creates enormous number of genotypes leading to continuous genetic variation. These circumstances seem to imply that polygenic system enables the population within a species to fit more precisely to various environmental gradients over the species range. Furthermore, additive genetic variation is likely to be fixed rapidly by natural selection.

Dominance effect was not found in any periods of growing stage. The presence and direction of dominance of quantitative characters are concerned with the nature of past selection worked upon[14]. When a single optimum phenotype is favoured, selection towards it may be stabilizing where the optimum is a central phenotype near the mean of population, or it may be directional where the optimum is an extreme phenotype. With stabilizing selection towards a central optimum, selection on some individuals will be in one direction, but on others it will be in the other. In such cases, dominance will not be unidirectional, but ambidirectional, and in crossing test it may appear to be absent because of the cancelling effects of opposing dominances. Thus, our results showing no apparent dominance effect may be interpreted as either lack of opposing dominant gene actions or failure of detection of it because of the cancelling effect. At present, it remains unknown.

Average reciprocal effect was observed for the RGR of leaf from May 28 to June 4. The source of reciprocal difference falls into two categories.

One is the differential growth vigour and microenvironment of maternal plant and the other is the extranuclear or cytoplasmic inheritance of maternal factor. The former may have some influences upon seed and seedling characters through the amount and constitution of seed nutrients, but it seems improbable that it consistently affects the growth of aged plant. On the other hand, it has been revealed that cytoplasmic variation exists in the population of perennial ryegrass by a diallel analysis of F_2 generation [25] and selection within clones[1,20]. HAYWARD and BREESE[8] have pointed out that cytoplasmic effect and nuclear-cytoplasmic interaction also play an important role in the environmental adaptability of population. At present, we can not determined to what extent the reciprocal difference is ascribable to cytoplasmic effect. However, above findings in perennial ryegrass seem to suggest that cytoplasmic effect should not be ruled out in discussing the genetic system of ecotypic differentiation of timothy.

Acknowledgement

Summary

The present study was carried out to investigate the genetic basis of inter-population variation for the seasonal growth pattern of timothy using a diallel cross method.

Five populations collected from Hokkaido, each of them being represented by two plants, were crossed in all possible combinations including reciprocals. Families from the diallel cross were grown in experimental field and relative growth rate (RGR) of tiller was measured in each week from early spring to mid-summer.

Families differed in the RGR of tiller during the two periods from May 14 to May 21 and from July 2 to July 9. In the former period, additive, dominance, average reciprocal and residual reciprocal effects were all signi ficant But partitioning the variation due to each effect into those among and within populations indicated that the variation among populations was not apparent except for additive effect. In the latter period, though additive and dominance effects were significant, their variations among populations were not evident. This indicates that main genetic factor responsible for the population differentiation of seasonal growth pattern is additive effect of polygenic system controlling the growth rate in early spring.

For the RGR of stem from May 14 to May 21, additive genetic variation within populations as well as among populations was observed, suggesting the potentiality of further differentiation of seasonal growth pattern.

Moreover, average reciprocal effect among populations was found for the RGR of leaf from May 28 to June 4. Thus, it would be necessary to take a cytoplasmic effect into consideration in discussing the population differentiation of timothy.

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