異なる生育地のシロクローバにおける再生産戦略

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Reproductive Strategy in White Clover (*Trifolium repens* L.) of Different Habitats

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Synopsis

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Investigations at six different habitats and a transplanting experiment were conducted in order to clarify the environmental and genetic variation of the reproductive strategy in spontaneous and cultivated white clover. Reproductive effort of seed propagative organs at different habitats was ranged widely from 38% at riverside to 5% at lawn and pasture. Thus reproductive effort was closely related to the environmental conditions of each habitat, such as the types of vegetation and defoliation regime. In the transplanting experiment, the genetic difference on reproductive effort was significant among plant groups obtained from different habitats, and it varied from a maximum of 22% at at riverside to a minimum of 5% at meadow and lawn. The relationship between habitats and transplanting experiment on reproductive effort was extremely low as compared with other characters. Therefore white clover seems to adapt itself to different environments through the plastic reproductive strategy in addition to the genetic variation.

Key words : Allocation, Habitat, Plasticity, Reproductive strategy, *Trifolium repens* L..

Introduction

White clover (*Trifolium repens* L.) is an exotic species which has been cultivated in the grasslands of Japan. However, at present, some of its offsprings which escaped from the grasslands have spread widely over varying habitats as a weed. Such a high adaptability of this species is concerned with the genetic variation on growth characteristics which are classified agronomically as wild, common and ladino types. It also seems to be closely related to the flexibility on the allocation of photosynthetic product between seed and vegetative organs in response to the differences of the competition with other plant species[1,11,12], the nutritive and moisture conditions in soil[9,10], and the defoliation regimes by human and livestock[2,3].

MACARTHUR[8] outlined some generalized theorems of natural selection which stated that organisms in more open environments were selected for greater reproductive capacity (r-

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strategist), while organisms in close habitats were selected for greater ability to compete for resources, through the cost of low reproductive potential (k-strategist). Many researches were conducted on the adaptive nature of allocation in plant and most of them showed that the pattern of allocation among species was an inherent characteristic which was closely related to its habitats. Few reports are available on the plastic response in which populations of a perennial plant species at widely varying habitats are compared with regard to the pattern of energy trade-off between seed and vegetative reproductive methods. The previous report[6] showed that wild white clover possessed fairly high plasticity on the reproductive methods closely related to the degree of plant succession at habitats.

This study was conducted to clarify the environmental and genetic variation on the reprodutive effort of spontaneous and cultivated white clover which grew at different vegetation and defoliation regimes through the investigation of habitats and transplanting experiment.

Materials and methods

Experiment 1. Investigation of reproductive effort at habitats

The investigation of spontaneous and cultivated white clover of six different habitats around Obihiro University was carried out at its full blooming stage during middle of July, 1980. Five quadrats of 30 cm × 30 cm were set up at each habitat, and the total plant weight above ground, No. of heads, weight of heads and length of petiole per quadrat of white clover were measured. The reproductive effort[5] of seed propagative organs was evaluated as (weight of heads/total plant weight above ground) × 100 (%). At present white clover at riverside, roadside, wasteland and lawn seems to be offsprings which escaped from the cultivated grasslands many years ago, while those of pasture and meadow are certainly common and ladino types of cultivars.

The general conditions of six habitats investigated in this study were as follows ;

1) riverside……flooding area of Satsunai River in Obihiro where the soil was sandy and the lowest plant cover was available among six habitats.
2) roadside……side of non-paved road which was often subjected to tramples by human and vehicles.
3) wasteland …unutilized place previously used as a road, now with invasion of some kinds of herbs.
4) lawn ……lawn in the campus which was frequently mowed by machinery and was intensively trampled by human.
5) pasture ……grassland of the university ranch where dairy cattle were grazed.
6) meadow ……mixed sown grassland of orchardgrass, timothy and white clover which was mowed by machinery under three cuttings a year.

Experiment 2. Investigation in transplanting experiment

Five plants of white clover were collected from each habitat investigated in the experiment 1 during middle of May, 1981. Two runners with the length of 10 cm were cut from each plant and they were grown in the greenhouse for 25 days. Then they were transplanted in the experimental field with the spacing of 1 meter within and between rows. After transplanting, monthly observations of runner extension and growth form were carried out.

Number of heads and length of petiole were measured in late September. Then the plants were cut at the ground level and were separated into three parts as the leaves, runners and heads and their dry weight was recorded.

Results and discussion

1. Reproductive effort at habitats

Table 1 shows the variation of the characters investigated at six habitats. Total plant weight above ground was higher at pasture and meadow as compared with the other four habitats. Weight of heads was higher at riverside and roadside, while it was lower at lawn and pasture. According to these results, the reproductive effort estimated as the ratio of weight of heads to total plant weight above ground was high at riverside and roadside with values of 38% and 30% respectively, while it was low at lawn and pasture with values of less than 5%, and was intermediate at wasteland and meadow. The variation of number of heads showed a similar tendency to the reproductive effort.

It is known in general that the reproductive effort is higher to lead the r-strategist, under the conditions with more physical disturbances and more open environments[4,8]. In this experiment, the reproductive effort of white clover was extremely high at riverside and roadside where the open environments were subjected to some kind of physical disturbances without defoliasion, while it was very low at lawn and pasture with frequent defoliation by human or livestock. These differences indicate a feature of adaptive mechanism in white clover to variable growing conditions. It may be due to the efficient allocation of limiting product to seed propagative organs to increase the dispersal ability under the ecologically open habitats. On the other hand, product is allocated to vegetative reproductive organs for increasing the ability of its own maintenance under the intensive defoliation regimes. Furthermore, the pattern of allocation in white clover at different habitats in this study are corresponding to the three types of plant response to stress defined by GRIME[4]. These three types have following features ; (1) The stress-response of competitor maximizes the capture of resources for high competitive ability in productive and relatively undisturbed conditions. (2) Those of the ruderal ensure the production of seeds in severely disturbed environments. (3) Those of the stress-tolerator bring about reductions in both vegetative and reproductive

Table 1. The variation of total plant weight above ground, weight of heads, reproductive effort, No. of heads and length of petiole in white clover at six habitats.

Habitat	Total plant weight above ground (g)	Weight of heads(g)	Reproductive[1] effort(%)	No. of heads	Length of petiole(cm)
Riverside	63.3	24.1	38.0	64.6	8.3
Roadside	80.4	24.2	30.1	66.6	10.4
Wasteland	66.9	10.8	16.1	55.7	7.6
Lawn	56.7	1.6	2.9	12.4	6.8
Pasture	150.3	7.2	4.8	9.0	9.4
Meadow	246.2	19.2	7.8	25.0	17.0

Data obtained within a 30 cm×30 cm area.
[1] Reproductive effort was estimated as (weight of heads/total plant weight above ground) ×100 (%).

vigour for endurance under continuously unproductive environments. It can be considered that the plants of maedow and wasteland have competitive strategy, those of lawn and pasture have stress tolerant strategy and those of riverside and roadside have ruderal strategy.

In this experiment, white clover investigated at pasture and meadow are centainly cultivars, however at other four habitats it is perhaps offsprings escaped from the cultivated grasslands. Therefore it is assumed that the large differences of reproductive effort closely related to habitats might be due to the genetic variation, resulted from the natural selection of a long duration. Then it is also necessarry to detect the genetic variation of reproductive effort of the plant groups used in this study.

2. Reproductive effort in transplanting experiment

The runner extension and growth form of plants collected from different habitats were observed continuously after transplanting. The pattern of runner extension was different among plant groups as shown in Fig. 1. It was rapid in the plant groups of roadside and meadow, in contrast to those of riverside and lawn. The growth form also differed among groups, such as the plants of meadow and wasteland were erect types, the lawn and riverside were prostrate types, and the pasture and roadside were intermediate between them. Thus it was found in transplanting experiment that the genetic differences among groups were related to growing conditions of native habitats. Table 2 shows the variation among plant groups on total plant weight above ground, numfer of heads, reproductive effort of seed propagative organs and length of petiole in transplanting. The plants of meadow denoted greatest performances in all characters investigated, though those of lawn and riverside were the smallest on the contrary. Table 3 shows the analysis of variance on the above characters. There were significant genetic differences among all characters. When the degree of variation among characters was compared with the coefficient of variation, white clover possessed large differences genetically on the characters relating to the seed propagation, such as weight of heads, numfer of heads and reproductive effort. Fig. 2 shows the proportion of allocation to

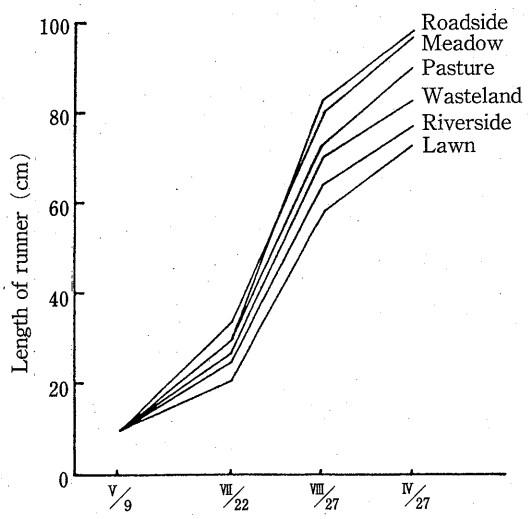

Fig. 1. The runner extension in white clver collected from six habitats.

the three organs, namely leaves, heads and runners. The proportion of leaves was about 50% with a small difference among plant groups, while the proprtion of heads and runners differed greatly among groups. The proportion of heads ranged from a minimum of 5% to a maximum of 22% of lawn and pasture respectively. There was a negative significant correlation between the proportion of heads and that of runners ($r=-0.825$) .

Table 2. The variation of total plant weight above ground, weight of heads, reproductive effort, No. of heads and length of petiole among plant groups collected from six habitats in transplanting experiment.

Habitat	Total plant weight above ground(%)	Weight of heads(g)	Reproductive effort(%)	No. of heads	Length of petiole(cm)
Riverside	58	9.1	14.5	82	9.5
Roadside	93	12.5	14.3	94	15.8
Wasteland	75	13.0	15.5	61	15.7
Lawn	49	2.9	5.0	19	12.0
Pasture	90	8.4	11.6	45	13.9
Meadow	125	27.3	22.1	125	22.2
Coeffient of variation(%)	33.5	67.5	63.7	52.9	29.0

Table 3. The analysis of variance on some characters in transplanting experiment.

Factor	D.f.	Mean square				
		Total plant weight	Weight of heads	Reproductive effort	No. of heads	Length of petiole
Plant groups	5	7350*	677**	306*	14075**	186.6**
Replication	1	7863	284	112	3724	2.8
Error	53	2612	122	112	3086	13.6

*=Significant at 5% level. **=Significant at 1% level.

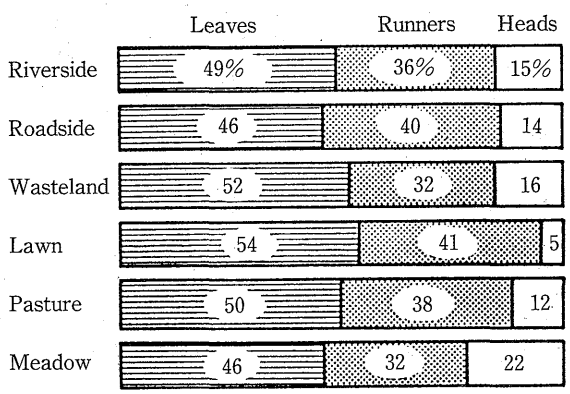

Fig. 2. The proportion of allocation to leaves, runners and heads of white clover collected from different habitats in transplanting experiment.

The differences of phenotypic plasticity among plant groups are shown in Fig. 3 with comparisons between habitats and transplanting experiment on some characters. The degree of phenotypic plasticity of plant groups differed distinctly among characters, and the differences were larger in weight of heads, numfer of heads and reproductive effort in relation to the seed propagation than total plant weight and length of petiole. The coefficient of correlations between two different environments were over 0.8 for both total plant weight and length of petiole, while it was 0.436 for numfer of heads and it was 0.273 for reproductive effort. These facts suggest that in white clover the phenotypic expression of the plant weight and the length of petiole was controlled intensively by genetic factors, while the reproductive strategy, such as head formation was much variable to environmental changes. Such plastic responses of the reproductive methods were reported by the previous investigation of white clover in relation to the plant succession[6], and also other plants in relation to the density, nutrition and moisture conditions of soil[7].

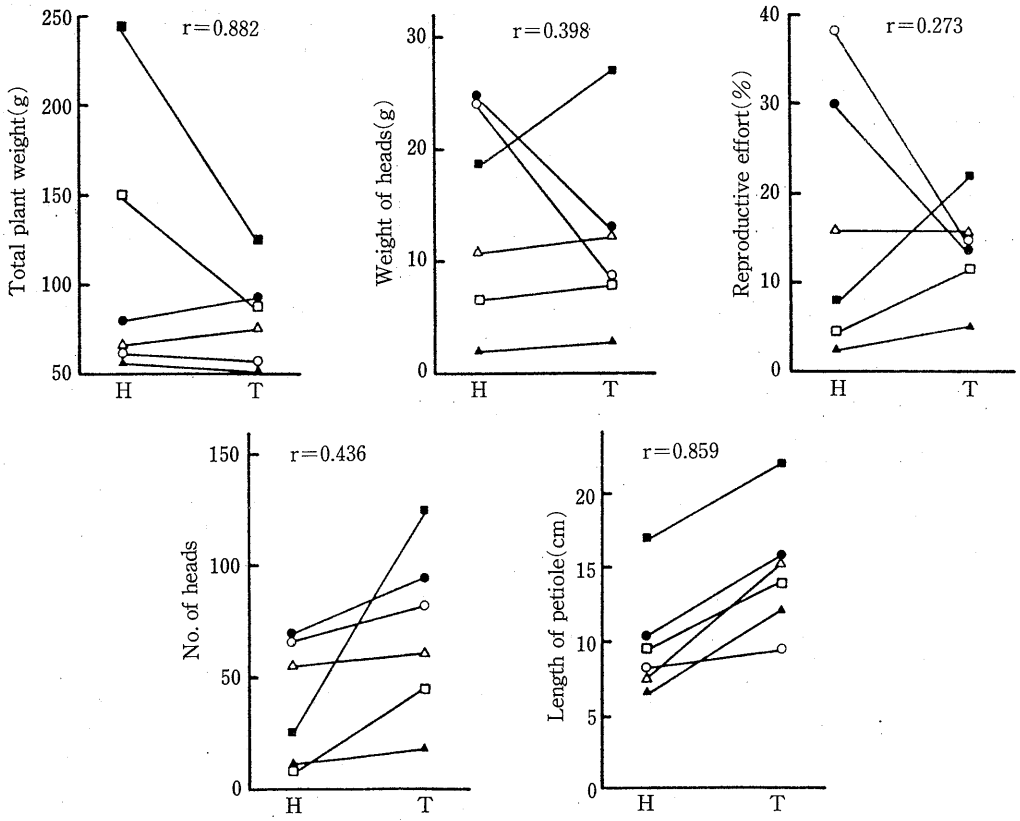

Fig. 3. The comparisons on total plant weight, weight of heads, reproductive effort, No. of heads and length of petiole between habitats and transplanting experiment.
H and T indicate the places investigated. H: habitat, T: transplanted field.
r indicates the coefficient of correlation of each character between habitat and transplanting experiment.
○——○: Riverside, ●——●: Roadside, △——△: Wasteland, ▲——▲: Lawn, □——□: Pasture, ■——■: Meadow.

It is concluded from these results that white clover might be adapted to different environments through the reproductive strategy due to high plasticity, in addition to genetic variation, on the allocation of photosynthetic product.

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異なる生育地のシロクローバにおける再生産戦略

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要 約

自生あるいは栽培されているシロクローバの再生産戦略について環境変異および遺伝変異を明らかにするために，6つの異なる生育地（川原，路傍，野原，芝地，放牧地，採草地）における調査と移植実験を行った。生育地における種子繁殖器官の再生産効率は川原での38%から芝地および放牧地での5%まで大きな変異がみられ，再生産効率はそれぞれの生育地の植生，刈取り方法，物理的撹乱などの環境条件と密接な関係があった。移植実験において，異なる生育地の植物間に再生産効率についての有意な遺伝変異が認められ，採草地のものが最大で芝地のものが最小であった。また，生育地の調査と移植実験の関係から，種子繁殖に関連する形質に特に大きな可塑性があることが認められた。したがってシロクローバは，再生産戦略に関する遺伝変異と大きな可塑性によって環境の変化に適応しているものと考えられた。

キーワード：可塑性，再生産戦略，分配，シロクローバ，生育地．

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