Intraspecific Variation in the Reproductive Allocation of Arrowhead (*Sagittaria trifolia* L.) at Different Altitudes

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Abstract: To clarify the variation pattern in reproductive allocation of *Sagittaria trifolia* L., 20 accessions collected from rice paddies located from Wakasa Bay to the southern extremity of Kii Peninsula were evaluated. These paddies were at altitudes of from 10 m to 610 m.

A remarkable cline in plant biomass was found along the environmental gradient dependent on altitude and topographical features of the original place of accession. The plant biomass tended to increase with the decrease in altitude. Moreover, an accession collected from a small terraced paddy on a steep slope in a narrow valley showed extremely small value in plant biomass.

Two kinds of propagules, achene and tuber, showed different variation patterns in reproductive allocation with relation to total biomass. Sexual reproductive allocation was little related to plant biomass, while a clear negative correlation was observed between allocation to tubers and total biomass.

It was suggested that the greater amount of light supply in low altitudes results in larger plant size which leads to stronger competitive ability, by reducing the allocation to vegetative reproduction; a reduced amount of light supply and a less competitive

situation with rice plants at higher altitudes, however, allows smaller plant size and greater allocation to tubers.

Trade-off between number of tubers per plant and individual tuber weight suggested that this species has higher competitive ability at low altitudes, but higher reproductive capacity at higher altitudes.

Key words : *Sagittaria trifolia* L., Reproductive allocation, Adaptation, Intraspecific variation.

Introduction

Sagittaria trifolia L. is one of the most troublesome perennial paddy weeds and is distributed throughout east Asia¹²⁾. This weed grows in diverse altitudes, from near sea level to places above 1,000m. The plant emerges either from a tuber or an achene in spring to early summer after puddling and leveling of rice paddy. It produces tubers and achenes, and the aerial part of the plant withers within a year. *S. trifolia* is known to show intraspecific variations in many characters, i. e., plant length, propagule production, response to nitrogen and sprouting behavior^{11,17,18,19)}.

A number of studies have been conducted on the reproductive strategies of plants focusing on the propagule output and pattern of energy or dry weight allocation^{1,2,3,5,7,9,13,14,15)}. Harper⁸⁾ stated that the allocation to reproductive organs in different taxa of flowering

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plants differed greatly. *S. trifolia* showed intraspecific variation in many characters, therefore, allocation to reproductive organs is thought to be diverse in this weed.

The objective of this research was to investigate the mode of differentiation in reproductive allocation of *S. trifolia* L. collected from paddy fields of broad ecological amplitudes near sea level to elevations above 600 m, and the adaptive strategies for the diversity in physical and biotic environments are discussed. Generally, it is difficult to distinguish whether the differences observed in diverse locations are genetic or phenotypic. Therefore, all plants were raised and examined under identical conditions.

Materials and Methods

One hundred twenty-five plants were collected from rice paddies at 20 different locations within a longitudinally narrow belt from Wakasa Bay to the southern extremity of the Kii Peninsula (Fig. 1). Based on preliminary observation, one typical accession from each population was selected and used. The original places were from 10 m to 610 m in altitude and divided into 5 groups according to their geographical and topographical differences: flat lands in the coastal region (F), hill-foot regions (H), small basins in mountainous regions (S), mountain slopes (M) and plains in the central Kinki district (P) (Table 1).

Twenty sprouted tubers per accession were planted on July 7 in 860 ml white polyvinyl-plastic cups filled with paddy soil, one tuber per cup at Aburahi Laboratories (34° 51' N, 136° 16' E, Alt. 260m; Koka-cho, Shiga Prefecture, Japan). All plants were basally fertilized with N 8, P 8, K 8 kg/10a. All ramets were grown under a flooded condition until harvested.

Four plants per accession were harvested

Fig. 1. Location and topographical site of the accessions collected.

- ▲ : Plain in the central Kinki district.
 - : Flat land in the coastal region.
 - : Hill-foot region.
 - △ : Small basin in a mountainous region.
 - : Mountain slope.
- Numbers correspond to those in Table 1.

on August 11, August 31, September 27, October 18 and early December. At the last harvesting, the aerial parts of the plant had completely withered. The below-ground parts were washed free of soil, and all organs were separated, dried in an 80°C oven for longer than 48 hr and weighed. Although ideally energy calorific contents should be measured as the net production⁹⁾, dry weight allocation was treated as the energy alloca-

Table 1. The origin of accessions used in this study

Accession	Locality			Habitat
	No.	Latitude	Longitude	Altitude
1		35° 30'	135° 46'	10m
2		26'	50'	90m
3		16'	49'	400m
4		12'	46'	350m
5		11'	39'	270m
6		10'	49'	610m
7		07'	49'	220m
8		05'	47'	160m
9		34° 56'	41'	60m
10		54'	43'	10m
11		53'	46'	10m
12		49'	48'	20m
13		46'	49'	10m
14		39'	46'	80m
15		14'	44'	500m
16		02'	47'	220m
17		33° 50'	47'	60m
18		41'	59'	10m
19		36'	55'	10m
20		28'	50'	70m

P : Plain in the central Kinki district,
F : Flat land in the coastal region,
H : Hill-foot region,
S : Small basin in a mountainous region,
M : Moutain slope

tion in this study, because Hickman and Pitelka¹⁰⁾ showed that the dry weight allocation pattern could approximate the energy allocation pattern.

Harper and Ogden⁹⁾ stated that if there is relatively little shedding of parts during growth to maturity of an annual plant, net production might be approximated by the biomass at maturity:

Estimate of net reproduction effort=
$$\frac{(\text{Total weight of propagules})}{(\text{Total biomass weight at maturity})}$$

S. trifolia transfers energy stocked in above-ground organs into achenes and tubers, however, by the time these were fully ripened, the above-ground organs had withered almost completely. The reproductive allocation of

this species, therefore, was estimated by the following equation.

(I) Achene
Reproductive allocation=
$$\frac{(\text{Total dry weight of achenes}) / (\text{Total biomass weight at maximum growth})}{(\text{II) Tuber}}$$

Reproductive allocation=
$$\frac{(\text{Dry weight of tubers at last harvesting}) / (\text{Total biomass weight at maximum growth})}$$

Results

Figure 2 shows the total plant biomass at maximum growth in relation to the altitude of original locations; the plant biomass decreased with increase in altitude. The biomass from lower altitudes, F, P and H showed higher value than those from higher altitudes, S and M, while the biomass of accession No. 4 collected from a mountain slope showed an especially low value.

The relationships between total plant biomass and reproductive allocation to the two different propagules, achenes and tubers, are shown in Figures 3 and 4, respectively; the value of reproductive allocation to achenes and tubers varied among the accessions from 0 to 16.5% and 9.0 to 35.4%,

Fig. 2. Intraspecific variation in total dry weight on the altitude of original collection site. ($Y = -0.003x + 1.290$, $p < 0.01$)
Symbols with numbers are same as in Fig. 1.

Fig. 3. Intraspecific variation in the relationship between total dry weight and reproductive allocation to achenes. ($r=0.254$, n. s.) Symbols with numbers are same as in Fig. 1.

Fig. 4. Intraspecific variation in the relationship between total dry weight and reproductive allocation to tubers. ($r=-0.732$, $p<0.01$) Symbols with numbers are same as in Fig. 1.

respectively. The reproductive allocation to achenes was little related to total biomass ($r=-0.254$, n. s.), while a clear negative correlation was observed between the allocation to tubers and total biomass ($r=-0.732$, $P<0.01$). The 2 smallest of the 20 accessions, Nos. 4 and 6 showed absolutely no allocation to achenes, while their allocation to tubers was very high. Accessions from the lower

Fig. 5. Intraspecific variation in the relationship between individual tuber weight and number of tubers per plant. ($r=-0.552$, $p<0.05$) Symbols with numbers are same as in Fig. 1.

altitudes, F, P and H, which attained larger total plant biomass showed lower allocations to tubers as compared with those from higher altitudes, S and M. The percent allocation to tubers of accession No. 4 was especially high.

Figure 5 shows the trade-off relationship between number of tubers per plant and mean dry weight of an individual tuber. Accessions of group F produced a small number of heavy tubers. Mean tuber weight tended to decrease with the increase of altitude, while, in contrast, the number of tubers per plant increased with altitude. Accession No. 4 of group M produced the lightest tubers.

Discussion

The twenty original locations of *Sagittaria trifolia* L. included a broad variety of geographical and topographical conditions (Fig. 1 and Table 1). Based on these different conditions, the locations were divided into 5 groups.

Generally, the day length at lower altitudes is longer than that at higher ones, so that the amount of light supply was expected to decrease with increase in altitude. The excep-

tional case in the 5 groups was group M. Accession No. 4 of group M was collected from a small terraced paddy on a steep slope of a narrow valley. Sunbeams were intercepted by an especially high skyline at this location, thus the light supply to the paddy was less than that at other comparable altitudes. Moreover, the paddy of group M was irrigated cold water from a mountain stream. Rice plants, the strongest competitor of this weed, grow more slowly in conditions where the light supply is less, and their maximum biomass increases with increased light.

A remarkable cline in plant biomass was discovered along the gradient of environments due to differences in altitude and configuration of original locations (Fig. 2). The cline of plant size in identical environment experiments was consistent with that observed in the original populations. It is strongly suggested that the gradient of light supply introduced the clinal variation in plant size of this weed.

The reproductive allocation to achene exhibited wide variation, and was little related to total biomass (Fig. 3). Under poorly growing conditions, this weed produced only tubers. In my previous study, the production ratio of achene to tuber in weight increased with increase of plant size¹⁶⁾. Therefore, in *S. trifolia* vegetative reproduction seems to precede sexual reproduction, the latter occurring only when extra resources exist.

The seedling of this weed is easily controlled by herbicides and has low competitive ability. Usually the plants emerge from tubers in paddy. Therefore, it is easily suspected that young plants from achenes is hardly contributable to recruitment of the local population. In spite of the great inferiority of achene in reproductive efficacy, most of the accessions produced fruitful achenes. I was not able, however, to find any reasonable

explanation for the variation in allocation to achene. This may indirectly suggest that achene production is additional in reproductive strategy of *S. trifolia*. It is assumed that the major roles of achene in this species may be dispersal and/or preservation of genetic diversity within a certain range.

Accessions with larger total biomass, which were collected from locations supplied with a larger amount of light, showed less allocation to tubers than those with smaller biomass, which were collected from locations with a smaller amount of light (Fig. 4). Lower energy allocation to tubers allows the plants to allocate more energy to other organs, resulting in an increase in competitive ability. Larger tuber size also allows them to be more competitive (Fig. 5).

A condition with a greater light supply is generally accompanied with stronger competitors. Competition with rice plants must increase with increase in light. In an elegant study of *Mimulus primuloides*, Douglas⁴⁾ suggested that physical and biotic (competitive) factors may partly bring about differentiation in dry weight allocation to reproduction. It is suggested that a greater light supply at low altitudes bring not only larger plant size but stronger competitive ability at the sacrifice of allocation to vegetative reproduction. Reduced light supply allows decreased plant size, and decreased competition with rice plants allows increased allocation to tubers at higher altitudes. A large number of small tubers in these habitats may expand the possibility of the increasing of populations under low competition. In short, the variation in vegetative reproduction of this weed appeared to be adaptive to both physical and biotic (competitive) environments of paddy.

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異なる高度における水田多年生雑草オモダカ (*Sagittaria trifolia* L.) の再生産効率の変異 について

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摘 要

本研究は若狭湾から紀伊半島南端までのほぼ経線沿いの近畿地方を中心とした地域から採取したオモダカにおける再生産効率の変異およびその生育地に対する適応性について調査検討したものである (Fig. 1 および Table 1)。実験材料は海拔高度10m から610 m にわたった20ヶ所の水田から採取した。

各系統の現存量と採取地の高度および地表の形態との間には明らかな関連性が認められた (Fig. 2)。一般に、高度が高いほど現存量の最高値は小さくなる傾向が認められた。また、日照が山陰で遮られる狭い谷間で水温の低い用水を使用する棚田由来系統の現存量は特に小さかった。高度および地表の形態は生育するオモダカに与えられる光量に大きく影響するものと思われ、受光量の差異により個体サイズのクラインが形成されているものと推察された。

オモダカの2種類の繁殖体、種子および塊茎の再生産効率と個体現存量の関係は全く異なっていた (Fig. 3 および 4)。種子の再生産効率と現存量の間には明瞭な関係は認められなかったが、塊茎は明らかな負の相関関係を示し、高度が低い地域由来の大型の個体は栄養繁殖への投資率が低いことが示された。

オモダカは低高度地域では、受光量が多いが、最大の競合者である水稻との競合に対して高いエネルギー投資が必要となるため、塊茎への再生産効率を低くしている。一方、比較的高い高度の地域では、受光量は少ないが、水稻の生育も低高度地域に比べ旺盛ではないので競合に対する高い投資を必要としないため、高い塊茎への再生産効率を確保している。従って、主たる個体群維持の手段である塊茎への再生産効率が生育地の物理的・生物的両条件に適応的であることが示唆された。また、塊茎の大きさと個数の関係においても、より高い競合力が必要とされる低高度地域では、比較的小数の大型塊茎を生産し、高い高度の地域では、比較的小型の多数の塊茎を生産することによって、個体群の維持を図っており、生育地の環境条件に適応的であることが示された (Fig. 5)。

キーワード：オモダカ，再生産効率，適応，種内変異

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