Gender Variation in Relation to
Resource Allocation in *Ambrosia artemisiifolia*

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*Ambrosia artemisiifolia*에 있어서
자원분배와 관련된 성비의 변이

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ABSTRACT

I examined the relationship between allocations to plant size components such as plant height, total leaf weight, and number of branches and to reproductive components such as the number and weight of male and female flowers in three populations of the monoecious, wind-pollinated *Ambrosia artemisiifolia*. In particular, the two types of gender of plants, phenotypic and functional gender, were related to resource allocation. Mean values of all plant size and reproductive components differed significantly among the three populations. Such inter-population differences did not exist for both photosynthetic and reproductive efforts. Plant size components were mostly positively correlated with reproductive components among plants. However, the relationships between photosynthetic effort and reproductive components were largely negative and inconsistent among populations. The phenotypic gender was much lower than 0.5 in all of the three populations. Pairwise correlations between functional gender and each allocation measurement such as plant size components, reproductive components, photosynthetic effort, and reproductive effort were not consistent across the three populations. These results suggest that the gender of *A. artemisiifolia* measured as flower production responds sensitively to environmental conditions which might differ within as well as among populations.

Key words: *Ambrosia artemisiifolia*, Correlations, Functional gender, Phenotypic gender, Resource allocation

INTRODUCTION

If a plant has a fixed amount of resources, then it must balance its resource allocation to its vegetative growth, maintenance, and reproduction. Resource allocation patterns vary in response to environmental conditions such as the amount of light, water, and

resources available. They also vary with the size of plants (Abul-Faitih *et al.* 1979) and with the life forms of plants (Primack 1979). For example, perennials which must maintain some vegetative structures for several to many years and do not necessarily have annual reproductive episodes are able to reduce reproductive effort in case. In contrast, annual plants must reproduce in a single season and may have little choice in controlling relative resource allocation to reproduction. However, if resource allocation is affected by selection (e.g., Bazzaz *et al.* 1987), allocation patterns may even differ among populations of annual plants. A change in the amount of resources a plant allocates to reproduction is of particular concern among plant ecologists because such a change is believed to be correlated with the reproductive fitness of plants.

Plant reproduction begins with production of flowers. Phenotypic gender of flowers is determined by the presence of structures such as anther and ovary. Most hermaphroditic species show some variation in floral structures such as anther numbers or petal size during a season or under experimental conditions, reflecting changes in resource allocation in response to environmental conditions (e.g., Stanton and Preston 1988, Kang and Primack 1991). The sex ratio of dioecious species or monoecious species is also affected by various environmental factors such as canopy position (Freeman *et al.* 1981), height of plants (Burd and Allen 1988), and neighbor effects (Lundholm and Aarssen 1994). In a group of studies relating phenotypic gender to diverse environmental conditions, plants under environmental stress tend to be small in size and function as males, while those in better environments than the former tend to be large and function as females (Charnov and Bull 1977, Willson 1983, Devlin 1988). However, in several wind-pollinated species such as *Zea mays, Ambrosia trifida*, and *A. artemisiifolia*, taller plants are largely males perhaps because of their advantage in effective pollen dispersal (Burd and Allen 1988, Ackerly and Jasienski 1990).

Phenotypic gender does not necessarily correlate with reproductive fitness of plants (Horowitz 1978, Sutherland 1986). For example, a hermaphroditic flower may appear to be equally male and female but in reality may contribute differently to the two sexual functions. Similarly, the numbers of male and female flowers on monoecious plants may not directly reflect the functional gender of plants, e.g., the relative reproductive success of either male or female parents, especially in populations with unequal sex ratios. Therefore, to understand the reproductive strategy of plants, the relationship between resource allocation to reproduction and both phenotypic and functional gender of plants in the population should be clarified. However, not many studies have been conducted regarding the relationship between resource allocation pattern and the gender of plants as male or female parents.

In this study, I address three, related questions. Firstly, I evaluate the difference in patterns of resource allocation among plants in three populations of *Ambrosia artemsiifolia*. Secondly, in this monoecious species, allocation to reproductive components is related to allocations to plant size components such as plant height, total leaf weight, and the num-

ber of branches. Thirdly, the variation in functional gender of plants in each population was examined in relation to the phenotypic gender and to the variation in resource allocation.

MATERIALS AND METHODS

Ragweed (*Ambrosia artemisiifolia*: Compositae) is a very common annual herb of cultivated ground and roadsides. Pinnately lobed leaves are both opposite and alternate. Flowering occurs during late summer - autumn. This species has greenish unisexual flowers which are self-compatible (Basset and Crompton 1975). Staminate flowers are on the racemes in 3~15 cm length, and pistillate flowers are present in small clusters in the axils of leaves. This plant is wind pollinated and a major cause of hay fever. The fact that it is a common weed that grows in variable environmental conditions makes it an ideal subject to study the phenotypic plasticity of plants. Since this species is annual, growth and reproductive measurements taken in the fall are believed to represent resource allocation for the life of the plant.

On Oct. 13, 1984, 20~25 plants were randomly sampled from three different sites. Both populations 1 and 2 were located in the Hammond Woods, MA, USA, and their habitats were open and exposed to direct sunlight. But these two sites differed slightly: population 1 was in an untended garden with trash scattered around in dry, loose, and sandy soil. *A. artemisiifolia* was the only species in that immediate vicinity and individual plants were fairly well dispersed. Population 2 was in a wet, rocky field that was densely inhabited by other genera such as *Bidens, Polygonum,* and *Abutilon.* Population 3 was the most different of the three populations. The ragweed plants were in the shade of a linden tree on a lawn in Brighton, MA. The lawn harbored low weeds and grasses. At the time of sampling, the soil was relatively dry.

For each plant collected, I measured its height, number of lateral branches, leaf dry weight, total dry weight, and number and dry weight of male and female flowers. All measurements were conducted after drying plant tissue in an 80℃ oven for at least 48 hr. In small plants, the male and female flowers were counted directly. In large plants the numbers were estimated by counting the flowers on a few randomly chosen branches on the plant. I did not measure the weight of roots because of the difficulty of getting a complete root sample, especially for small plants with a mass of delicate root hairs.

I calculated photosynthetic effort (leaf weight of the plant / total weight of the plant) and reproductive effort (total weight of male and female flowers / total weight of the plant) for each plant. The phenotypic gender (number of female flowers / number of male and female flowers) were obtained for each plant in each population. Functional gender of a plant (G_1) in each population was quantified following Lloyd (1980):

$$G_1 = d_1 \ / \ (d_1 + I_1E)$$

where d_l is the number of female flowers on the plant, I_l is the number of male flowers on the plant, and E is an equivalence factor (total number of female flowers in the population / total number of male flowers in the popultaion). The equivalence factor, in effect, makes the numbers of male and female flowers equivalent by reducing the total number of male flowers to the percent that actually may successfully pollinate a female flower and therefore contribute to the production of a fruit. The range of functional gender was from 0 (male flowers only) to 1 (female flowers only).

The ratio data such as reproductive effort were arcsine transformed and interval and count data were log 10 transformed to meet the assumption of normality.

RESULTS

Mean values of all the vegetative and reproductive components differed significantly among the three ragweed populations (Table 1). For example, mean plant height varied by a factor of 9 among the populations: plants in population 2 were the tallest, and those in population 3 the smallest. Population 1 was the intermediate in mean plant height. Similarly, tall plants in population 2 possessed both greater weight and number of plant size and reproductive components than smaller plants in populatoins 1 and 3. Mean total weight of plants in population 2 was 47 times greater than that in population 3, while the mean number of branches was 5 times greater in the former population than in the latter. Between these two populations, weight of flowers varied by a factor of 25 and 27 (male and female flowers, respectively) while number of flowers varied by a factor of 11 and 12 (male and female flowers, respectively). Intermediate sized plants in population 1 showed intermediate values for all of these three characteristics. Multiple range test showed that for plant height, total weight of plants, total leaf weight, and number and weight of female flowers, the three populations differed significantly from each other, in other words,

Table 1. Measurement of vegetative and reproductive characteristics of *Ambrosia artemisiifoaia* in three populations, Massachusetts, USA. Mean and standard deviation are given. Different alphabets in each column indicate a significant difference at $\alpha = 0.05$ level. Sample size is 25 (population 1), 20 (population 2), and 23 (population 3). ns = not significant

Characteristics	Population 1	Population 2	Population 3	P
Plant height (cm)	37.03 (14.21)a	81.28 (28.78)b	8.82 (2.72)c	⟨0.001
Total wt of plant (g)	2.49 (2.56)a	11.36 (16.06)b	0.24 (2.72)c	⟨0.001
Wt of leaves (g)	0.40 (0.35)a	1.66 (2.21)a	0.06 (0.10)a	ns
Wt of male flowers (g)	0.02 (0.02)a	0.25 (0.76)b	0.01 (0.01)a	⟨0.001
Wt of female flowers (g)	0.93 (1.20)a	2.96 (4.32)b	0.11 (0.20)c	⟨0.001
No of branches	9.96 (3.05)a	11.35 (5.91)a	2.41 (2.37)b	⟨0.001
No of female flowers	97.48 (110.18)a	233.20 (274.38)b	18.74 (32.62)c	⟨0.001
No of male flowers	486.68 (494.79)a	1138.05 (1628.62)a	106.26 (184.40)b	⟨0.001
Photosynthetic effort	0.18 (0.06)a	0.22 (0.16)a	0.23 (0.16)a	ns
Reproductive effort	0.41 (0.18)a	0.28 (0.18)a	0.42 (0.20)a	ns

in an order of population 2 〉 population 1 〉 population 3. On the other hand, mean numbers of branches and male flowers were significantly higher among plants in populations 1 and 2 than those in population 3. Weight of male flowers was significantly higher among plants in population 2 than in two other populations. Photosynthetic effort was slightly higher in populations 2 and 3 than in population 1. Reproductive effort was higher in populations with small plants (populations 1 and 3) rather than in population with tall plants (population 2). However, both of these ratios did not differ significantly among populations.

Plant size components were positively significantly related with reproductive components in most pairwise correlations (Table 2). Except for the number of female flowers in population 1, in each population, taller plants with more number of branches and more leaves tended to have more number of male as well as female flowers than smaller plants. The weight of flowers showed a weaker association with plant size components than number of flowers. For example, the weight of male flowers was independent of plant height and the number of branches in population 1, and the weight of female flowers was not associated with plant height and leaf weight in population 2. The relationships between photosynthetic effort and reproductive components were largely negative and inconsistent among populations. Among tall plants in population 2, higher photosynthetic effort was significantly associated with lower numbers of both male and female flowers and marginally significantly associated with lower weight of both types of flowers. Among intermediate sized plants in population 1, higher photosynthetic effort was significantly correlated with lower weight of female flowers, and consequently with weight of total flowers. In contrast, among small plants in population 3, a positive, though not significant, correlation was found between photosynthetic effort and number of male flowers.

The ratios of female flowers to male flowers were not close to 1:1 in all of the three populations (Table 3). These values indicated that the number of female flowers was only about one fifth to one third of that of male flowers. The coefficient of variation of phenotypic gender showed that the ratio of female to the total number of flowers was much more variable among plants in populations 2 and 3 than those in population 1. For example, in populations 2 and 3, there was a single, very small plant with all female flowers

Table 2. Pearson correlation coefficient between plant size and reproductive components. Pop=population. * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; † = $0.5 < P < 0.1$

		Plant height			Total weight of plant			Weight of leaves			Number of branches			Photosynthetic effort		
		Pop1	Pop2	Pop3	Pop1	Pop2	Pop3	Pop1	Pop2	Pop3	Pop1	Pop2	Pop3	Pop1	Pop2	Pop3
Total	No	0.44*	0.59**	0.50*	0.79***	0.69**	0.79***	0.71***	0.52*	0.79***	0.79***	0.83***	0.73***	-0.19	-0.58**	0.28
flowers	Wt	0.47*	0.17	0.63**	0.78***	0.54*	0.97***	0.63**	0.36	0.95***	0.50*	0.54*	0.78***	-0.50*	-0.41	0.01
Male	No	0.46*	0.63**	0.46*	0.78***	0.63**	0.69**	0.70***	0.45*	0.70***	0.70***	0.74***	0.64**	-0.17	-0.55*	0.34†
flowers	Wt	0.36	0.49*	0.49*	0.60**	0.65**	0.90***	0.55**	0.63**	0.93***	0.21	0.66**	0.62**	0.00	-0.40	0.05
Female	No	0.29	0.58**	0.57**	0.78***	0.67**	0.89***	0.70***	0.55*	0.82***	0.87***	0.85***	0.80***	-0.29	-0.66**	-0.06
fowers	Wt	0.52**	0.30	0.64**	0.79***	0.55*	0.97***	0.65**	0.39	0.96***	0.55**	0.62**	0.79***	-0.47*	-0.41	0.04

Table 3. Mean sex ratio (1 SD) and gender values by population. CV = Coefficient of variation

	Population 1	Population 2	Population 3
Sex ratio	0.22 (0.10)	0.31 (0.28)	0.24 (0.25)
CV	46	92	104
Phenotypic femaleness	0.17 (0.06)	0.25 (0.21)	0.21 (0.20)
CV	36	86	98
Functional femaleness	0.50 (0.10)	0.55 (0.19)	0.53 (0.17)
CV	20	34	33

(heights of 9.1 cm and 6.1 cm, respectively).

The range in functional gender varied among populations, especially in functional gender greater than 0.7 (Fig. 1). Unlike population 1 where maximum value of functional gender was 0.7, four plants each in populations 2 and 3 possessed functional gender > 0.7. In all three populations, plants with functional gender < 0.27 did not exist. Thus, the distribution of functional gender among plants appeared to be somewhat different across populations. The curve for population 1 increased rather sharply compared to that for both populations 2 and 3. That means, the change in functional gender between individual plants was more gradual in population 1 than in populations 2 and 3. All of the pairwise correlations between functional gender and plant size components were not significant. Functional gender was negatively correlated with photosynthetic effort only in population 3 ($r = -0.55$, P < 0.01). The correlation between functional gender and reproductive effort was positive in population 1 ($r = 0.50$, P < 0.05), but not in populations 2 and 3. Functional gender was negatively correlated with the number of flowers in populations 2 and 3 ($r = -0.59$, P < 0.01 and $r = -0.55$, P < 0.01, respectively), but not in population 1.
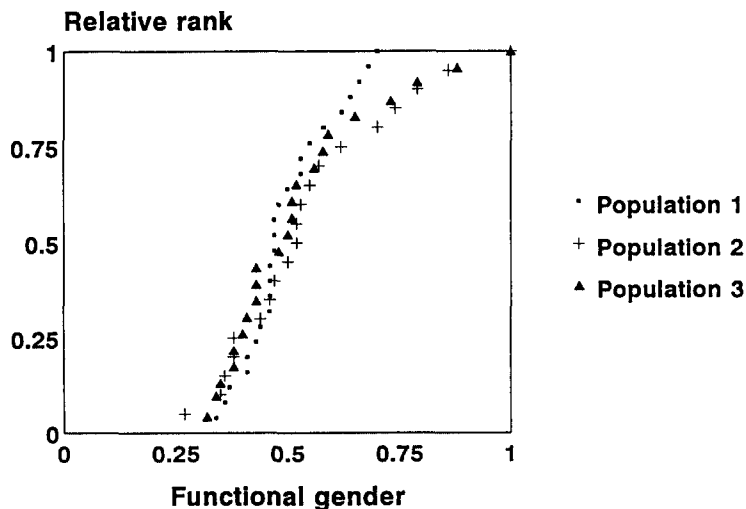
Fig. 1. The distribution of functional gender among plants in three populations of *A. artemisiifolia*.

After all, the relationships between functional gender and both plant size and reproductive components were not consistent across the three populations.

DISCUSSION

The three populations of *Ambrosia artemisiifolia* were quite distinct from each other for a number of characteristics measured in this study. These inter-population differences are likely to be related to the differing environmental conditions of the three populations. Populations 1 and 2 were in full sunlight while population 3 was continuously shaded by a large linden tree. The soil in population 2 was fairly moist while in populations 1 and 3 it was well drained and fairly dry. Density in population 1 also appeared to be relatively low compared to two other populations. Although I did not conduct quantitative experiments on physical or biological environmental differences between populations, the results of this study suggest that ragweed plants grow best in moist soil under full sunlight.

However, these inter-population differences in plant size and reproductive components did not exist in relative allocations to photosynthesis (photosynthetic effort) and to reproduction (reproductive effort). Although the larger plants were producing a greater number of branches and flowers as shown in other studies (McKone and Tonkyn 1986, Ackerly and Jasienski 1990), proportional resource allocations toward photosynthetic and reproductive components were similar across populations. These results disagree with those of Primack *et al.* (1981) who found that goldenrods in open disturbed habitats had greater reproductive efforts than plants at the edge of a forest or within the forest. They also contradict with those of Pitelka *et al.* (1980) who found that reproductive effort increased with plant size in *Aster*. Thus, for *A. artemisiifolia* of disturbed sites, size and number of individual reproductive and vegetative components could be very plastic in response to environmental conditions, yet variation in its overall relative allocation to photosynthesis or reproduction appears to be quite constrained.

Among plants in each population larger plants produce more number of both male and female inflorescences than smaller plants. However, photosynthetic effort was largely negatively correlated with the numbers and weight of flowers, suggesting a trade-off relationship between photosynthetic effort and allocation to reproduction. For example, higher relative allocation to photosynthetic tissue resulted in lower weight of female flowers in population 1 and in lower numbers of both male and female flowers in population 2. Thus, even among plants larger than a certain minimun size the effect of limited resources appeared to emerge through changes in the number or weight of certain sexual types of flowers depending upon the population. In contrast, plants with higher photosynthetic effort had more number of male flowers in population 3. It is certainly necessary for annual plants to maintain a certain level of photosynthetic effort to reproduce. Then, for extremely small plants such as those in population 3, it may be economical to produce relatively inexpensive male flowers (Freeman *et al.* 1981, Willson 1983, Develin

1988). The phenotypic gender in *A. artemisiifolia* was quite deviant from 0.5 in all three populations. It was similar to that in several other wind-pollinated monoecious species (Freeman *et al.* 1981), but was much lower than that in a *Lolium* species which is also wind-pollinated (Lemen 1980). In the latter species the sex ratio approached 0.50. The low phenotypic gender suggests that in this wind-pollinated herb occurring in somewhat disturbed sites three to five times greater production of male flowers than of female flowers may be an adaptive phenomenon to increase male reproductive success. If gender expression of monoecious species is, at least to a certain extent, subject to enviromental control, the gender ratio of monoecious species could show a range of variation among populations. However, the difference in mean phenotypic gender among populations of *A. artemisiifolia* was not great. The mean value of phenotypic gender was slightly higher among taller plants in population 2 (0.25), which was assumed to be a favorable site for the growth of *A. artemisiifolia*, than smaller ones in populations 1 and 3 (0.17 and 0.21, respectively). Thus, it is not clear whether such a small difference in mean gender between populations reflect an adaptive adjustment of gender in different populations.

Distribution of functional gender among plants was not exactly concordant across the three populations. However, compared to great inter-population differences in overall plant size and allocation patterns, the pattern of functional gender among plants was not quite constrasting among populations. In particular, the two populations, populations 2 and 3, presumably representing 'good' and 'bad' environment, respectively, showed quite similar patterns of gender variation among plants. In these two populations, several individual plants were functionally largely female and were relatively small in size (functional gender ⟩ 0.7). Such an extreme sexual behavior did not exist among plants in population 1. This inter-population difference in the pattern of functional gender is reflected in the magnitude of the coefficient of variation for gender: it was twice larger in populations 2 and 3 than in population 1. It is likely to be a result of competitive interaction among plants. Greater variation in size as well as reproductive output of several species has been related to greater competition (Solbrig and Solbrig 1984, Weiner 1988). In other words, the apparently low density in population 1 which might result in relatively weak competition could be responsible for the rather small coefficient of variation in gender at this site.

Although in *Zea mays* (Burd and Allen 1988), *Ambrosia trifida* (Abul-Faitih *et al.* 1979), and *A. artemisiifolia* (Ackerly and Jasienski 1990) taller plants function largely as males, functional gender in three populations of *A. artemisiifolia* in MA, USA, was not affected by plant size. Instead, various other factors depending upon population appeared to exert influence over the femaleness. McKone and Tonkyn (1986) also found that gender in *A. artemisiifolia* was not consistently related with environmetal treatments such as soil moisture and herbivory level. In populations 2 and 3, plants with relatively small number of flowers were likely to be more females than males because production of more flowers resulted in proportionately more number of male flowers than female flowers. This pattern was particularly conspicuous among small plants in population 3 where the number of male

flowers was positively associated with photosynthetic effort. Only in population 1 where interspecific competition or neighbor effects did not apparently exist, plants allocated more resources to reproduction behaved as more females than males. This inconsistent relationship between resource allocation to reproductive components and functional gender in *A. artemisiifolia* suggests that in plants with no minimum size for reproduction (Weiner 1988) like *A. artemisiifolia*, gender of plants measured as flower production may respond sensitively to various environmental conditions which differ among as well as within populations. The key environmental condition may include plant density (e.g., Whitehead 1983, Ackerly and Jasienski 1990), light environment (Jurik 1991) or neighbor effects (Lundholm and Aarssen 1994). In order to understand the intra-population variation in gender, it seems necessary to explore not only the resource allocation pattern but also the importance of environmental effects such as plant density, species composition, and, most importantly, light intensity and quality as recent studies have revealed.

적 요

식물의 키, 총 잎의 무게, 가지의 수와 같은 식물체 크기특성과 암꽃, 수꽃의 수와 무게와 같은 번식특성간의 관계를 암수딴꽃, 풍매화인 돼지풀(*Ambrosia artemisiifolia*)의 세 개체군에서 조사하였다. 특히 표현형적 성비와 기능적 성비와 같은 두가지 성비의 계량치를 자원분배와 관련지었다. 모든 식물체 크기와 번식특성의 평균값은 개체군간 유의하게 달랐다. 광합성투자비율과 번식투자비율에 대해서는 이러한 개체군간 차이가 존재하지 않았다. 식물체 크기특성과 번식특성은 개체간 거의 정의 상관이 있었다. 그러나 광합성투자비율과 번식특성간의 관계는 대부분 부의 상관이 있었고 개체군간 일관되지 않았다. 모든 개체군에서 표현형적 성비는 0.5보다 크게 낮았다. 기능적 성비와 식물의 크기특성, 번식특성, 광합성투자비율, 번식투자비율과 같은 각 자원분배 측정치와의 상관관계는 세 개체군에서 일정하지 않았다. 이 결과는 꽃의 생산으로 측정된 돼지풀의 성은 개체군간뿐 아니라 개체군내에서의 환경변이에 대해 예민하게 반응함을 시사한다.

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