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Comparative studies on phenotypic plasticity of two herbs, *Changium smyrnioides* and *Anthriscus sylvestris*[*]

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Abstract: The endangered medicinal herb, *Changium smyrnioides* can only be found in deciduous forest gaps within the middle to northern subtropical broad-leaved evergreen forest zone of China. The considerable plasticity of its shoot and root structure helps it to capture light more effectively in winter and early spring, and to adapt to the soil moisture conditions in its narrow habitat. Another medicinal plant, *Anthriscus sylvestris*, is of similar economic importance but commonly distributed widely. In contrast to *C. smyrnioides*, it has low structural plasticity. It is also specialized to adapt to the moist and sunny environment, where habitat, such as the banks of creeks and rivers, is abundant.

Key words: *Changium smyrnioides*, *Anthriscus sylvestris*, Endangered species, Plasticity, Subtropical zone, Winter species
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INTRODUCTION

Changium smyrnioides Wolff, a monotypic species of family Umbellaceae, occurs only in a narrow zone in the middle to eastern part of the Changjiang (Yangtze) River Basin, China. As a highly valued medicinal herb, the fleshy roots of this species are widely picked, and as its habitats are being disturbed increasingly by land use, it has become an endangered species (Qiu and Fu, 2001). *Anthriscus sylvestris* (L.) Hoffm belongs to the same family; has similar morphology and life form as *C. smyrnioides*; and can be found from the North Temperate Zone of China and Europe to the north edge of the tropical zone. In our study area, Hangzhou (120°10'E, 30°15'N), Zhejiang, China, it commonly occurs in areas overlapping the natural habitats of *C. smyrnioides*. *A. sylvestris* is also a medicinal herb and is commonly picked, but human disturbance does not pose a threat to its survival. What causes the difference between the two species in this respect?

Both species are winter species in the humid subtropical zone. However, the winter species are less common than warmer seasons species. Plants living in stressed environments are often characterized by low rates of nutrient absorption, effective nutrient retention, and slow growth rate in order to maintain a balance between resource demand and availability (Grime, 1979). However, winter plants usually have special structural and functional adaptation to tolerate the low temperature and for better capture of the relatively abundant solar irradiation. *C. smyrnioides* occurs in the undergrowth of scattered deciduous trees in the evergreen broad-leaved forest in China. It is therefore important for

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it to make proper use of the relatively abundant sunlight within a short period after deciduous trees defoliate in late autumn and before they re-foliate in spring. *A. sylvestris* occupies habitats similar to those of *C. smyrnioides*, but normally grows along the edges of the forest and the banks of creeks.

Phenotypic plasticity of plant structure is an important character in adaptation, and is one of the solutions in adaptation to the heterogeneous environments (Via *et al.*, 1995), enabling a plant to allocate resources optimally to different organs so as to avoid or reduce the impact of competition from neighboring plants (Brewer, 1999). Many studies have examined phenotypic plasticity as an individual mode of plant adaptation to the environment (Bradshaw and Hardwick, 1989; Via *et al.*, 1995).

Despite extensive research on plant plasticity, little is known about the plasticity of plant structures in response to the main factors in winter. Our field investigations suggested that the adaptation of the two species to winter environment and the endangerment of *C. smyrnioides* might be caused by its structure plasticity in response to light and soil water availability. Here we present a comparative study of the two plants' individual plasticity with the aim to examine their aboveground parts' phenotypic plasticity regard to the acquisition of light, and root plasticity in response to water available of wild winter species in the subtropical zone in the east coast of Asia. The results would help to explain the endangerment mechanism of *C. smyrnioides* and contribute to our understanding of the plasticity of some plants that are little studied.

MATERIAL AND METHODES

Field study was conducted at the South Peak, Wongjia Peak, Nantianzhu and Geling mountain range near Hangzhou city (120°10'E, 30°15'N), Zhejiang Province, China. *C. smyrnioides* mainly distributed under forest and side roads near the forest. There are about 5 major commensal trees (Chang *et al.*, 2002) in the community in which *C. smyrnioides* lives. *A. sylvestris* distributed at the edge of the forest, which had similar dominant trees, and major commensal herbs with *C. smyrnioides*, apart from the shrubs, which were relatively dense.

Field observation on the life histories of *C. smyrnioides* and *A. sylvestris* carried out from May 2000 to June 2001 by investigating 8 sample quadrats for each species, 4 quadrats (1 m×1 m) were set in the habitat with moist soil (mean water content θ=50.79%±8.46%, dry soil base), and another 4 quadrats were set in hill slope with dryer soil (θ=27.48%±4.81%) for both species. Growth measurements carried out monthly, or half-monthly within the period of rapid growth. After growth measurements, the underground parts were dug out completely. Samples were brought back to laboratory immediately and the shoot of every individual was divided into segments by clipping every 20 cm from the base to the top, keeping petiole and leaf angles as natural as possible (Mansi and Saeki, 1953). Leaves and flowers were separated from stems and branches. The lengths of leaf blade and petiole were determined. Leaf area was determined by a leaf area meter (Li-cor-3000, Lincoln, NE, USA). The root volume was measured by measuring water volume equilibrium. The biomass of every component was determined after oven drying at 80 °C for at least 72 h.

According to Hunt (1978), the leaf mass ratio (LMR, leaf mass per unit of total mass), aboveground leaf area ratio (LAR), aboveground/underground ratio (A/U) and the allometric relationship ($Y=bX^K$, Y: dependent variable, X: independent variable, b: constant, K: coefficient) were determined for each leaf sample; leaf area, leaf mass and stem mass of individuals were calculated by accumulating the leaf area and total mass of sample in each layer. The biomass of each species and each layer were accumulated; and the space distribution of *C. smyrnioides*, *A. sylvestris* and other plants in the community were determined from date on segments.

RESULTS

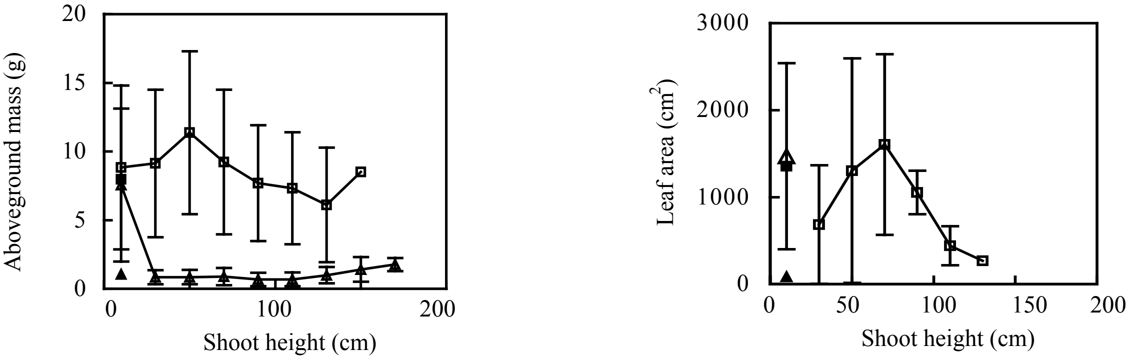
Aboveground structure of two species

Both *C. smyrnioides* and *A. sylvestris* began dormancy on June. However, *C. smyrnioides* regenerated in December, while *A. sylvestris* regenerated much earlier, in September. From autumn to early spring (March) of the next year, the shoots of both plants only consisted of leaves, which spread out and competed with other plants for space at 20 to 25 cm above soil level (some individuals attained 25 cm). From April to May (flowering) and June (fruiting), the average shoot height of *C. smyrnioides* was 106 cm (150 to 185 cm for taller samples), while most of the shoot biomass (89%) occurred in the 0 to 20 cm layer, less than 11% in the 20 to 170 cm upper layers, as the cauline leaf of *C. smyrnioides* retrogressed severely on the stem (Fig.1). The biomass of *C. smyrnioides* was only 16% that of the herbaceous layer community.

A. sylvestris also started growing in height from April onward. In May, the average stem height was 98 cm; some individuals could gain an apical height of 150 to 165 cm. In contrast to *C. smyrnioides*, its leaves had different distribution in the vertical direction (Fig.1). The leaf area gradually increased from 30 cm above soil, then started to decline above 70 cm. Similarly, the total aboveground biomass increased gradually from 10 cm above soil, the maximum value was at 50 cm, then started to decline. The biomass of *A. sylvestris* accounted for 47% of the total herbaceous community.

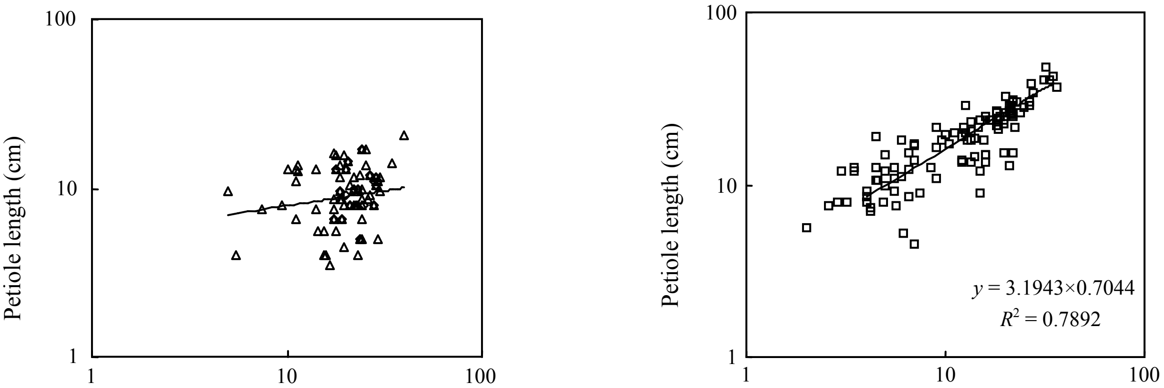
Petiole changes of two species

The leaf length and the petiole length of *C. smyrnioides* had no significant correlation ($P>0.05$) in the whole growing season (Fig.2). Similarly, the petiole length of *A. sylvestris* had smaller change while leaf length increasing in winter. From early



(a) (b)

Fig.1 Relationships between aboveground mass, leaf area and aboveground height of *Changium smyrnioides* (a) (triangle) and *Anthriscus sylvestris* (b) (square) in early summer (open) and winter (solid)



(a) (b)

Fig.2 Allometric relationships among petiole length and leaf length of *Changium smyrnioides* (a) and *Anthriscus sylvestris* (b)

summer, the petiole length of *A. sylvestris* increased with the increase of leaf length, the correlation being statistically significant ($P<0.01$). The allometric coefficient (K) of the petiole length and leaf length was lower than 1 ($P<0.001$), which means the increment of the petiole length was lower than that of leaf length.

Root structure of two species

There were several types of fleshy storage roots of *C. smyrnioides*, the main one being the fusiform fleshy root, and others being the long and thin fleshy taproots (like carrots, refer to Fig.1), and massive or forked roots. The taproots have almost no root crowns. The fusiform root mostly bears a long root crown of 15 to 20 cm or even longer than 30 cm, which can penetrate quite deeply, normally 40 to 50 cm, and in some samples more than 70 cm. In contrast to *C. smyrnioides*, *A. sylvestris* showed a shallow root system, only 2 to 20 cm below the soil surface. Some roots were decumbent on the ground and exposed above the soil. The average root volume of *C. smyrnioides* (26.2 cm^3) was 1.5 times that of *A. sylvestris* (10.2 cm^3).

For both species, the correlation coefficient between root volume and length was smaller than that between volume and root width, indicating that the increment of root volume was mainly contributed by root width, and that the plasticity of root length in both species was greater than that of root volume. The relationships between root volume and root biomass, however, had power correlations. Compared to *A. sylvestris*, *C. smyrnioides* was apt to increase root biomass rather than volume.

Table 1 Coefficients of the allometric relationships between the root traits ($Y=bX^K$) of *Changium smyrnioides* and *Anthriscus sylvestris*

Y-X	*Changium smyrnioides*			*Anthriscus sylvestris*		
	b	K	r^2	b	K	r^2
B-V	0.31	1.03	0.887^{**}	0.35	0.85	0.949^{**}
L-V	9.73	0.29	0.754^{*}	4.79	0.28	0.717^{*}
W-V	0.67	0.34	0.84^{*}	0.88	0.35	0.828^{*}

B: Biomass; V: Volume; L: Length; W: Width; b: Constant; K: Coefficient; *: significance at $P<0.05$ and **: $P<0.01$; n = 15 to 60

Biomass allocation and allometry among plant parts

The allometry between shoot height and mass in *C. smyrnioides* showed that the increasing of height was greater than that of mass, while in *A. sylvestris* the condition was vice versa (Table 2). The allometry between the mass and height of stem showed that both species tended to increase stem mass more than height; that the slope (K) in the formula of both species was >2, and that *A. sylvestris* (K=3.4) was much greater than that of *C. smyrnioides* (K=2.3).

With the increase of aboveground mass and height, the ratios of biomass allocated to the leaves gradually reduced in both plants (Table 2). However, the LAR and LMR of *C. smyrnioides* were generally greater than those of *A. sylvestris* (Table 3).

C. smyrnioides allocated less biomass to its aboveground parts than *A. sylvestris* (Table 3). The degree of correlation between height and root mass in *C. smyrnioides* was higher than that in *A. sylvestris*, but the relationship between aboveground and root biomass in the two plants were on the contrary. No significant correlation ($P>0.05$) was found between leaf and root mass of *C. smyrnioides* while significant correlation ($P<0.01$) was found in *A. sylvestris*.

Table 2 Coefficients of the allometric relationships between the shoot traits ($Y=bX^K$) of *Changium smyrnioides* and *Anthriscus sylvestris*

Y-X	*Changium smyrnioides*			*Anthriscus sylvestris*		
	b	K	r^2	b	K	r^2
S_hM-SH	0.14	0.71	0.706^{*}	0.00	3.09	0.758^{*}
S_tM-SH	0.00	2.26	0.954^{**}	0.00	3.46	0.815^{*}
RM-SH	0.60	0.56	0.647^{*}	0.01	1.34	ns
LM-SH	0.37	0.40	ns	0.00	2.43	ns
LMR-SH	2.58	−0.31	0.638^{*}	13.30	−0.82	0.618^{*}
LM-AM	0.85	0.83	0.933^{**}	0.40	0.89	0.91^{**}
RM-AM	3.29	0.71	0.619^{*}	0.91	0.87	0.819^{*}
RM-LM	5.02	0.21	ns	3.54	0.62	0.704^{*}

S_hM: Shoot Mass; SH: Shoot Height; S_tM: Stem Mass; RM: Root Mass; LM: Leaf Mass; LMR: Leaf Mass Ratio; AM: Aboveground Mass; b: Constant; K: Coefficient; *: significance at $P<0.05$ and **: $P<0.01$; ns: not significant; n = 15 to 60

Table 3 Leaf mass ratio (LMR), aboveground leaf area ratio (LAR) and aboveground/underground ratio (A/U) of *Changium smyrnioides* and *Anthriscus sylvestris*

Species		LAR	A/U	LMR
C. smyrnioides	Mean±*s.d.*	166.04±141.38	0.39±0.19	0.79±0.19
	n	32	25	32
A. sylvestris	Mean±*s.d.*	150.80±89.26	1.64±1.45	0.57±0.33
	n	55	44	55
F values		0.523	<0.001	<0.01

DISCUSSION

Plasticity of aboveground parts

Light capture is not only determined by the height and total leaf area of a plant but also by the geometric arrangement of its leaf area (Anten and Hirose, 1999). Because vertical components of radiation predominate over horizontal ones, incident photon flux density (PFD) will be higher on horizontally than on vertically inclined leaves (Mansi and Saeki, 1953). *C. smyrnioides*, as mentioned before, has only horizontally orientated leaves and this contributes to their ability to intercept light efficiently (Mansi and Saeki, 1953). Such ability is especially important for *C. smyrnioides*, as it has a relatively narrow light resource niche, from December to next March, when the deciduous trees have defoliated and there are few herbaceous plants to compete for solar irradiation. After March, many herbaceous plants grow vigorously in the understory, depriving *C. smyrnioides* of the light it requires; suggesting that *C. smyrnioides* is a shade-tolerant plant, as it is generally assumed that shade-tolerant species should produce their leaves in a single layer, while sun-adapted plants have leaves along the axial direction of the stem (Givnish, 1995; Anten and Hirose, 1999). *A. sylvestris* is a sun-loving species; its leaves are close to the stem, even in the winter when the stem is relatively very short. This can be considered as a waiting strategy for spring when the stem starts vertical growth, thereby keeping most leaves above the herbaceous layer to receive more sunlight.

Plasticity of petiole

Plants that arrange their leaf area in a planar array with minimal leaf overlap, rather than having more evenly distributed leaves along the axial direction of the shoot, will have an advantage in light capture and minimize self-shading (Horn, 1971). Petioles play an important role in adjusting leaf position. The petiole of *C. smyrnioides* has considerable phenotypic plasticity in the early growth period. The petiole length of *C. smyrnioides* does not correlate to leaf length, but is affected by the soil surface traits (the litter layer) in the budding period and later photosynthetic period. No matter how thick the litter layer (0 to 15 cm) is, the petiole of *C. smyrnioides* can push the basal leaves out of the litter and up to 20 cm above the soil surface for sufficient lighting. Moreover, in winter, the petiole can wrest a good position for capturing light, allowing leaves to change their angle to fit the light direction.

A. sylvestris, likes *C. smyrnioides*, does not have active vertical growth in autumn and winter. As mentioned before, its leaves grow in a cluster on top of a short stem. In spring, the plant starts vertical growth, and the leaf length increases with petiole length in order to extend the leaves on different levels for capturing light.

LMR and LAR

The allometric relationships between leaf area and leaf mass, as well as leaf mass and aboveground mass, differed considerably between species. For a given mass, the LMR and LAR in *C. smyrnioides* were higher than those in *A. sylvestris*, indicating that *C. smyrnioides* has less biomass than *A. sylvestris* to construct leaf area. Moreover, the difference between the species increased with the individuals' size. Several authors implied that LMR may decrease as plant height and light availability per unit leaf area increase (Anten and Hirose, 1999);

and that the plant with higher LAR could capture more light per unit of biomass (Hirose and Werger, 1995). The light availability of *C. smyrnioides*'s habitat is lower than that of *A. sylvestris*, so *C. smyrnioides* should do its best to raise the capture ability per unit biomass for light.

Plasticity of root structure and its adaptation mechanisms

The root crown of *C. smyrnioides* has strong plasticity in length, from 0 to 30 cm, in response to the soil water condition. A long root crown indicates that the root penetrates deeply into the soil. Plasticity for this trait may influence the ecological tolerance of individuals, and the field distribution of the species (Bell and Sultan, 1999). *C. smyrnioides* can therefore adapt to dry habitats and obtain moisture from deep soil layers or in wet places near creeks or in mountain lowlands where water is relatively abundant. In contrast, there is no root crown in *A. sylvestris*; hence it has a shallow root system, with part of the root growing above the ground surface. Based on these traits, *A. sylvestris* is only distributed within mountain catchments, or near the banks of creeks or rivers.

Allocation of mass aboveground and underground (the A/U ratio) differs considerably between species. For a given total mass, the mass of *C. smyrnioides* shoots was lower than that of *A. sylvestris*, indicating that *C. smyrnioides* allocates more mass to roots. Such an allocation can be seen as a drought-tolerant strategy.

In addition to water acquisition, plasticity of root crown has another function; i.e., it can prevent individuals of *C. smyrnioides* from being covered up by soil and so survive in steep slopes of a hill. Under such conditions, the root crown can grow upwards until the apical point of the individual emerges from the soil.

C. smyrnioides mechanism of being endangered

The phenotypic plasticity in *C. smyrnioides* is effective in the light capture by shoot and water acquisition by root in winter. Individuals finished vegetative growth after re-foliation of deciduous trees, so as to avoid shading and compete with other plants, similar to the results of Busso *et al.*(2001). Such a growth pattern of *C. smyrnioides* could be seen as a competition-avoiding strategy through temporal niche partition.

Generally speaking, the benefit of plasticity is the ability to produce a better phenotype environment match across more environments (Levins, 1968). However, the large plasticity in *C. smyrnioides* only fits certain environments, which were limited under the deciduous forest in humid subtropical zone in winter. Whereas, *A. sylvestris* only has limited plasticity in structure of both aboveground and underground parts; so that it can only distribute in a moist environment with plenty of light.

In *C. smyrnioides*, the phenotypic plasticity for structure was considerable and appeared in many aspects, including the leaf blade, petiole, leaf arrangement, root crown length and root depth, to fit the environment efficiently. However, such a costly phenotypic plasticity only fits a single narrow niche, i.e. the habitat of the deciduous forest, suggesting the species has been highly specialized to its natural environment.

As *C. smyrnioides* is highly specialized, it is almost restricted to the mid-north of the humid subtropical zone: in the temperate zone the temperature in winter is too low and in the south of the subtropical zone the deciduous trees cannot complete with evergreen trees. Even in the humid subtropical zone, deciduous forest distribution is also restricted and dispersed; i.e. the habitat has naturally heterogeneity. Without human disturbance (digging for medicine and deforestation), *C. smyrnioides* can maintain proper population size with no difficulty. However, if the habitat is disturbed seriously, the regeneration of its population is difficult, and it becomes an endangered plant.

As for *A. sylvestris*, it has low plasticity for structural response, so the expense is relatively low. Although its niche (with moist soil and plenty of light) is also narrow, its habitat, such as the banks of creeks and rivers, is abundant. Water flow also helps it disperse. This species is not limited to a subtropical zone, meaning its life history has plasticity in response to different temperatures.

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