

## Patterns of resource allocation in different habitats of *Kalimeris intergrifolia* in Northeast China

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### Abstract

Understanding parameters that drive plant resource allocation for reproduction in potentially economically and environmentally important species, such as *Kalimeris intergrifolia*, is essential to maximize production rates. Hence, this study evaluates the characteristics in reproductive resource allocation of two *K. intergrifolia* communities at a saline-alkali open meadow and at a semi-enclosed secondary broad-leaved forest fringe, in the Songnen plains region of northeast China. Ramets from each habitat type were sampled at three intervals during the ripening stage (June–October). Relative resource distribution was quantified by measuring the dry weight of the above-ground ramet components, including the stem, leaf, corymb and seeds. The results indicated high variability in the distribution of resource allocation for both types, with larger phenotypic plasticity being recorded for the forest fringe than the open meadow. However, the allocation of resources into reproductive organs was higher in the open meadow than in the forest fringe, demonstrating that the open community was advantageous to the reproduction. Furthermore, our results indicate that biomass accumulation determines plant reproductive functioning. However, as resource allocation for reproduction increases, the biomass of above-ground ramet components decreases. Allometry exists in the *K. intergrifolia* populations when plants are in the ripening stage. Therefore, the future studies will focus on the mechanism of allometry. In conclusion, our study indicates that habitat parameters influence the general quantity of resources utilized for reproduction in this species, suggesting that open habitats should be preferentially targeted for optimal commercial application.

**Additional key words:** biomass allocation; plant community; plant reproduction; Songnen Plain.

### Resumen

#### Patrones de asignación de recursos en diferentes hábitats de *Kalimeris intergrifolia* en el nordeste de China

Para maximizar las tasas de producción, es esencial comprender los parámetros necesarios para asignar recursos para la reproducción de las plantas en especies potencialmente importantes desde el punto de vista económico y ambiental, como *Kalimeris intergrifolia*. Se evaluaron las características de la asignación de recursos reproductivos de dos comunidades de *K. intergrifolia*, en una pradera abierta salino-alcálica y en la orla de un bosque secundario planifolio semi-cerrado, en las llanuras Songnen del nordeste de China. Se tomaron muestras de *ramets* a tres intervalos durante la etapa de maduración (junio–octubre) y se midió el peso seco de los diferentes componentes aéreos del *ramet*, incluyendo tallos, hojas, corimbos y semillas. Los resultados indicaron una alta variabilidad en la distribución de la asignación de recursos para ambos tipos, con una mayor plasticidad fenotípica en el margen del bosque que en la pradera abierta. Sin embargo, la asignación de recursos en los órganos reproductores fue mayor en el campo abierto que en la orla del bosque, lo que demuestra que la comunidad abierta fue ventajosa para la reproducción. Además, nuestros resultados indican que la acumulación de biomasa determina el funcionamiento reproductivo de la planta. Sin embargo, al aumentar la asignación de recursos para la reproducción, la biomasa de los diferentes componentes aéreos del *ramet* disminuye. Existe una alometría en las poblaciones de *K. intergrifolia* cuando las plantas están en la fase de maduración, por lo que hace falta estudiar el mecanismo de la alometría. Nuestro estudio indica que los parámetros del hábitat influyen en la cantidad de recursos utilizados para la reproducción de esta especie, lo que sugiere que para una aplicación comercial óptima deben utilizarse preferiblemente los hábitats abiertos.

**Palabras clave adicionales:** asignación de biomasa; comunidades de plantas; llanura de Songnen; reproducción de plantas.

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Abbreviations used: AC (forest fringe); RA-I (reproductive allocation I); RA-II (reproductive allocation II); ZD (meadow).

## Introduction

The inherent plasticity of plant characteristics, such as the production and allocation of substances and organ development, are fundamental in modeling life history strategies. In general, the total amount of resources available for any organism is limited and allocation to reproduction appears to be straightforward and mathematically tractable (Gadgil and Bossert, 1970; Cohen, 1971; Casper and Charnov, 1982). In practice, the levels of resources allocated to sexual and asexual reproduction may be altered under a variety of common environmental circumstances (Westley, 1993). As a consequence, the amount of resources may influence trade-offs among different functions such as growth, propagation, and defense (De Wree and Klinger, 1988; Cheplick, 1995). Therefore, the model of resource allocation reflects the characteristics of plant life history (Bostock and Benton, 1979). An adaptive strategy is often associated with a particular pattern of allocation that maximizes fitness in a given environment (Solbrig, 1994). The development of different parts of a plant is highly coordinated, which enables them to capture and use resources efficiently (Sachs, 2006). On occasion, sexual reproduction is an advantageous strategy facilitating adaptation to a certain habitat when both sexual and asexual reproduction is possible in plants (Li *et al.*, 2005). Biomass allocation to growth, reproduction, and defence has been used to identify adaptive strategies in plants (Taylor *et al.*, 1990). Virtually all adaptive strategy theories based on allocation patterns in plants define strategies in terms of biomass allocation (Bonser and Aarssen, 1996). Therefore, biomass allocation is one of the central concepts in modern ecology (Weiner, 2004).

*Kalimeris integrifolia* (Compositae) is a perennial and salt tolerant herb, which primarily inhabits the Songnen Plains of northeast of China, where salt concentration varies from 0.18% to 0.90% (Yang *et al.*, 2003; Zhang and Feng, 2009). *K. integrifolia* is found in a range of habitats, including natural meadows, grasslands, secondary broad-leaved forest fringes, roadsides, and abandoned agricultural fields (Yang *et al.*, 2003). This species often utilizes a specific ecological niche, in which it is the dominant or subdominant species, leading to a mosaic distribution (Ba *et al.*, 2002). *K. integrifolia* is valuable in agricultural pastures as highly nutritional and palatable fodder for domestic livestock (Yang *et al.*, 2003). Furthermore, existing research has indicated the potential of *K. in-*

*tegrifolia* for ecological repair, due to its ability to absorb and accumulate cadmium (Wei and Zhou, 2008; Wei *et al.*, 2009; 2011).

Studies to understand the ecological characteristics of *K. integrifolia* are therefore important based on its potential economic and environmental uses. Research has already indicated that the growth rate of this species increases with frequency of mowing (Ba *et al.*, 2005). Other research has recorded that, in the Songnen plains, seasonal changes in *K. integrifolia* communities directly influence the quantity of host-specific symbiotic mycorrhizal fungi (Bai, 2007, p. 4). In addition, the development, age structure and growth strategies of different age classes of ramets in *K. integrifolia* populations have been subject to investigation (Yang and Li, 2003; Yang *et al.*, 2003). However, there is limited quantitative information about the influence of general habitat characteristics on the patterns of resource allocation, especially into reproductive relative to vegetative functions. Hence, the goal of this study is to evaluate differences in allocation of resources in two *K. integrifolia* communities - a saline-alkaline open meadow and a semi-enclosed secondary broad-leaved forest fringe in the Songnen plains region of northeast China. The relative distribution of resources in these two communities was quantified by measuring dry weights of the plants' above-ground components, including stems, leaves, corymbs (inflorescence) and seeds.

## Material and methods

### Study species and site

*Kalimeris integrifolia* (Compositae) is a perennial plant characterized by both sexual reproduction and asexual propagation. The plant has an erect tuft and whole border leaf, while petioles are absent. A total of 28-76 capitulum form the corymb. This species blooms from June to October, and the seeds mature from July to November.

This study was conducted in Heilongjiang Province, which is geographically located in the midlands of the Songnen Plain in northeast China. The region has a temperate semi-arid monsoon climate. The annual rainfall ranges between 350 and 500 mm, of which 70% primarily falls from June to September (Li and Yang, 2004). The mean daily air temperature exceeds 10°C on 120-140 days yr<sup>-1</sup>, with an annual mean temperature of 5.0°C, approximately, and absolute maximum of

30°C and absolute minimum of -35°C (China Meteorological Administration, 2005).

Two sampling sites were selected based on the distribution of *K. integrifolia*. The natural characters of the study sites have been shown in Table 1. The distance between the two study sites is about 85 km. Three zones were delimited within each of the two plots and indicated by permanent tags as follows: (1) the low edge of the plot; (2) 10 m inland from the plot edge; (3) 20 m inland from the plot edge.

### Study methods and data analysis

The study was carried out between June and October in 2009. It was performed according to the method described by Li *et al.* (2007) with some modifications. When seeds had matured at each of the study sites, 50 ramets (entire plants cut at the basal stem, excluding roots) of *K. integrifolia* were cut at random on 3 occasions (18<sup>th</sup> July, 18<sup>th</sup> August, 18<sup>th</sup> December) from three zones in each of the two plots indicated above. Hence, 450 ramets were collected in the meadow, as well as in the forest fringe study areas. In the laboratory, 90 intact ramets out of 450 ramets from each sample site were selected. Each ramet was separately oven-dried at a temperature of 80°C in electric drying oven (ZFD-5140), until a virtually constant weight was obtained. The weight of stems, leaves, corymbs, and seeds were measured using a weighing balance to the nearest 1 mg. For each ramet, the number of filled seeds and unfilled seeds were collected and counted.

The weight of stems, leaves, and corymbs of each ramet were recorded, respectively. Allocation to vegetative above-ground organs was calculated as the proportion of stem or leaf weights relative to total weight. The coefficient of variation (CV, *i.e.* the ratio of the standard deviation to the mean) was used to evaluate the relative variation in the quantitative characters. Allocation into reproduction was evaluated by two relative measures,

reproductive allocation I (RA-I) and reproductive allocation II (RA-II), where RA-I was the relative amount (in %) of the corymb weight in total weight, and RA-II the proportion of the seed weight and total weight. The seed set was the percentage of filled seed in a total sample of seeds.

All functional relationships either between weights of plant organs or among calculated allocation measures were analyzed using linear function ( $y = a + bx$ ), power function ( $y = ab^x$ ), and exponential function ( $y = ae^{bx}$ ). An optimal relationship was selected as a descriptive model. In the present study, the values of  $R^2$  in the function mainly indicate the accurate of evaluation between two variables. The descriptive statistics with respect to the quantitative characteristics of the reproductive ramets of *K. integrifolia* were analyzed using SPSS 13.0 software. All regressions were analyzed using Origin 7.5. Overall statistical significance were established at the  $p < 0.01$  level.

## Results

### Quantitative characteristics of reproductive ramets

The florescence in the forest fringe plot initiated 6 days earlier than in the meadow plot (from June to October). Seventy percent of seeds matured in the middle of September. The two plots presented certain differences such as topography, pH, and salt concentration, etc (Table 1). As shown in Table 2, the corymb weight was subject to the greatest variability (76.12%) in the forest fringe plot, while the stem weight was subject to the greatest variability (51.15%) in the meadow plot. The coefficient of variation in the forest fringe plot had a range of 11.72-76.12%, while in the meadow plot it had a range of 17.29-51.15%, indicating a greater level of variation in the forest fringe plot than in the meadow plot. Mean values of seed set, corymb biomass, RA-I

**Table 1.** Characteristics of the study sites

Sampling sites	Location	Geographical coordinates	Topography	Soil type	NaCl concentration (%)	pH
Meadow plot	Natural meadow	125°93' E 46°04' N	Plain	Saline-alkaline soil	0.29	8.36
Forest fringe plot	Fringe of a secondary broad-leaved forest ( <i>Populus simonii</i> )	127°97' E 44°54' N	Hillside	Albissols	0.18	6.81

\* Source: Adapted from Cui *et al.* (2008) and Zhang and Feng (2009).

and RA-II in the meadow plot were higher than those in the forest fringe plot, indicating that the reproductive allocation of *K. intergrifolia* was also different in different habitats. These results show that the meadow plot populations had a reproductive advantage over the forest fringe plot populations in this species.

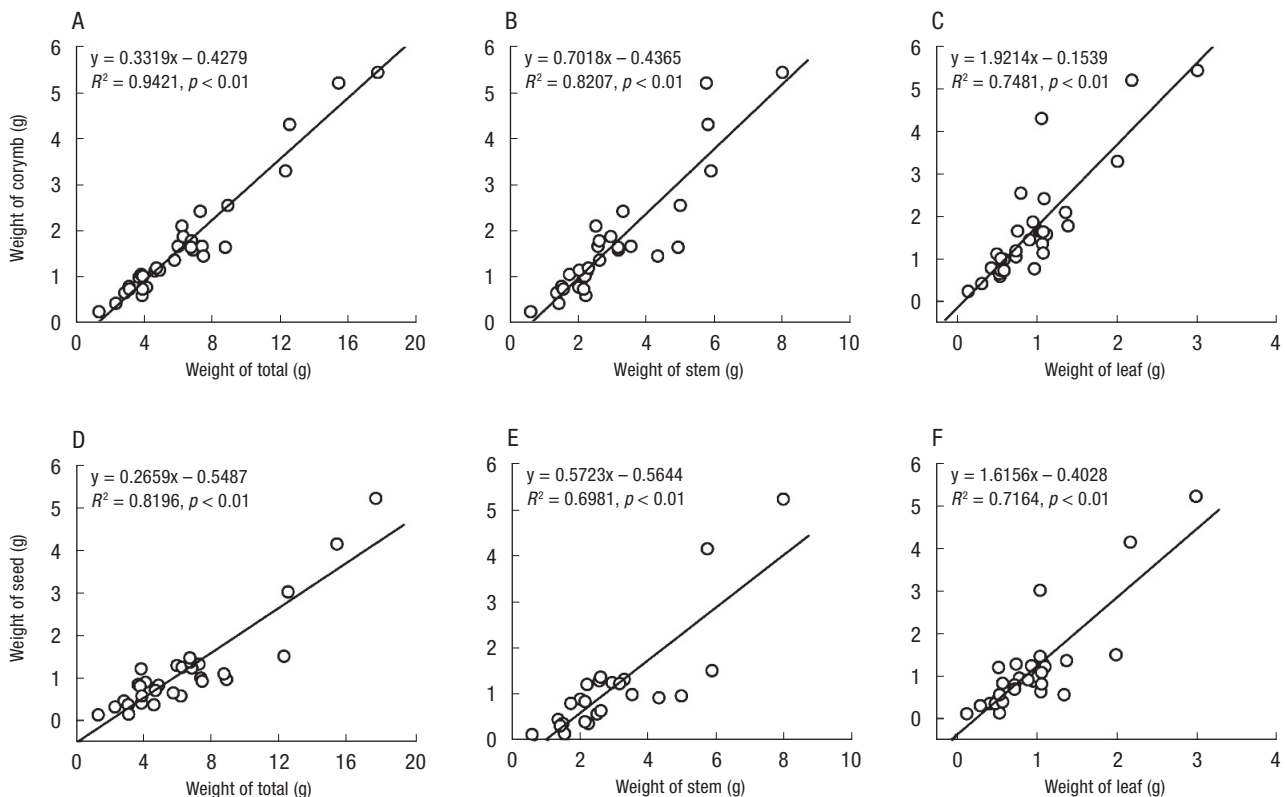
### Module reproductive biomass versus ramet component biomass

In the forest fringe plot, the biomass of both the corymb and seeds were found to be positively correlated with the total, stem and leaf weights ( $p < 0.01$ ; Fig. 1). Similar results were obtained for the meadow plot (Fig. 2). For both plots, the reproductive modules biomass exhibited an upward trend, with an increase in ramet component biomass. However, the proportion of co-variation between corymb weight and total weight was higher in the forest fringe plot ( $R^2 = 94.21\%$ ; Fig. 1A) than in the meadow plot ( $R^2 = 86.51\%$ ; Fig. 2A). Similar results were obtained either between corymb and stem biomass (Figs. 1B, 2B) or between corymb and leaf

biomass (Figs. 1C, 2C). The co-variation in the proportion of seeds and total weight biomass was higher in the forest fringe plot (81.96%; Fig. 1D) than the meadow plot (78.38%; Fig. 2D). Similar results were obtained either between seeds and stem biomass (Figs. 1E, 2E) or between seeds and leaf biomass (Figs. 1F, 2F). The values of  $R^2$  in the forest fringe plot were higher than in the meadow plot. These results indicate that evaluation of the forest fringe plot was more accurate than that of the meadow plot, when the reproductive biomass of the module was forecasted based on the corymb and seeds in the *K. intergrifolia* populations.

### Reproductive allocations versus ramet component allocations

In the forest fringe plot, a negative correlation was found between RA-I, RA-II and biomass allocation to stems and leaves ( $p < 0.01$ ; Fig. 3). Similar results were obtained for the meadow plot (Fig. 4). The results indicated that an increase in reproductive allocation occurred at the cost of decrease in weights of



**Figure 1.** Linear functional relationships between biomasses of reproductive and vegetative modules (A, D: total weight; B, E: stem weight; C, F: weight of leaves) in *K. intergrifolia* from the forest fringe plot (n = 90).

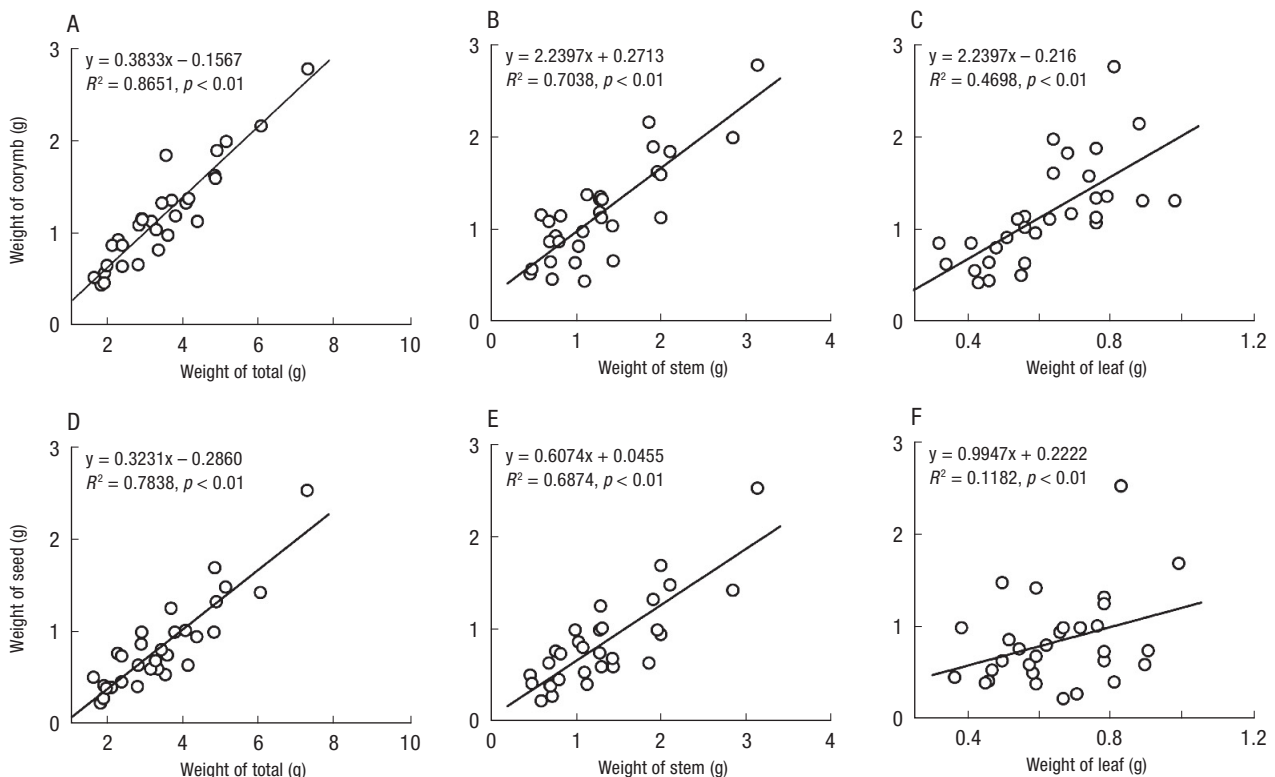
**Table 2.** Quantitative characteristics of *K. intergrifolia* in two different habitat types (Meadow = ZD; Forest fringe = AC)

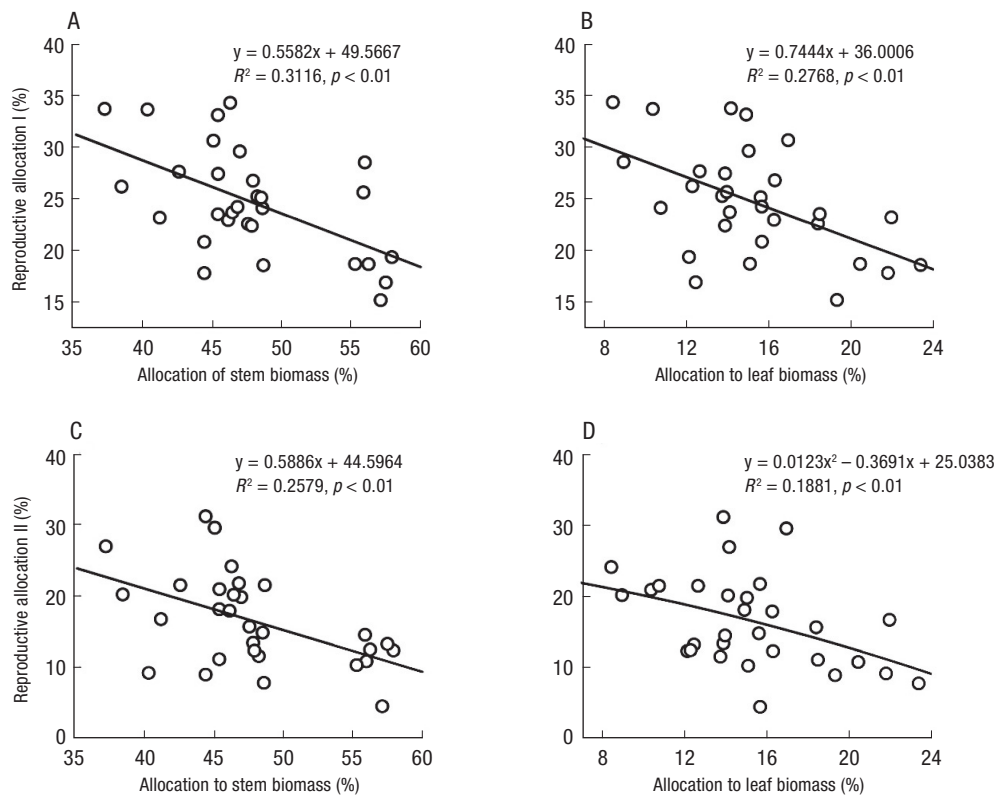
Quantitative character	Min		Max		Mean		SD		CV (%)	
	AC	ZD	AC	ZD	AC	ZD	AC	ZD	AC	ZD
Number of seeds (No)	695	2,247	13,439	7,176	4,628.73	4,319.70	3,056.82	1,149.37	66.04	26.61
Seed set (%)	40.58	48.65	90.60	92.37	70.64	72.09	14.00	12.47	19.82	17.29
Corymb weight (g)	0.24	0.43	5.44	2.78	1.17	1.18	1.30	0.55	76.12	46.94
Stem weight (g)	0.60	0.46	8.01	3.14	3.06	1.31	1.68	0.67	54.96	51.15
Leaf weight (g)	0.14	0.32	3.01	0.98	0.97	0.62	0.59	0.17	60.41	27.42
Ramet weight (g)	1.35	1.67	17.76	7.34	6.45	3.48	3.81	1.34	59.07	38.51
Allocation to stem biomass (%)	37.32	23.78	57.87	46.72	47.87	36.45	5.61	6.37	11.72	17.48
Allocation to leaf biomass (%)	8.43	8.88	23.37	35.05	15.23	19.80	3.70	7.72	24.28	38.99
RA-I (%)	15.17	22.89	34.29	41.40	24.66	32.67	5.23	5.65	21.21	17.29
RA-II (%)	4.44	11.83	31.11	34.56	16.39	23.25	6.51	6.78	39.72	29.16

vegetative plant modules. The values of  $R^2$  between RA-I and RA-II versus stems and leaves biomass in the forest fringe plot (Fig. 3A-3D) were higher than in the meadow plot (Figs. 4A, 4D). The results indicate that evaluation of the forest fringe plot was more accurate than that of the meadow plot, when reproductive module biomass was forecasted with respect to the corymb and seeds.

## Discussion

Published literature predicts that for plant species inhabiting open expanses or low-quality environments, sexual reproduction is an advantageous mode to propagate offspring for enhanced genetic diversity, particularly as seeds have a suite of characteristics for spreading, diffusion, and anti-interference

**Figure 2.** Linear functional relationships between biomasses of reproductive and vegetative modules (A, D: total weight; B, E: stem weight; C, F: weight of leaves) in *K. intergrifolia* from the meadow plot (n=90).

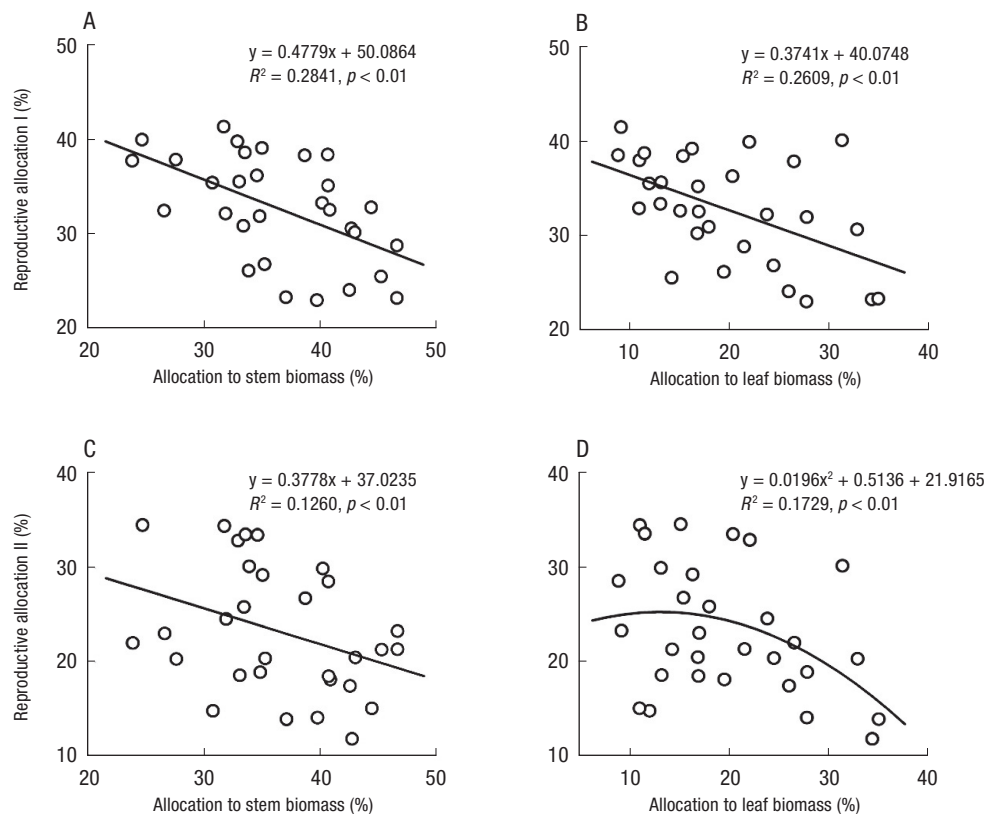


**Figure 3.** Functional relationships between allocations of reproductive and vegetative modules (A, C: allocation to stem biomass; B, D: allocation to leaf biomass) in *K. intergrifolia* from the forest fringe plot (n=90).

(Eriksson, 1997). For example, a study by McMahon and Ungar (1978) showed that when *Atriplex triangularis* grew in saline conditions, the quantity of dried matter allocated to the reproductive organs was higher than that of non-saline conditions. The findings of the current study support existing research, whereby the open meadow plot, which was situated on saline soils (Table 1), was demonstrated to allocate more resources than the forest fringe plot to the seed set (Table 2), which in turn would potentially enhance seed productivity, improve population competition and enlarge living space. Basically, the seed set values (RA-I and RA-II) of the *K. intergrifolia* population in the meadow plot were higher than in the forest fringe plot. Hence, individual fecundity was an advantageous strategy to adapt to the saline environment. The CV and the range of observation values were used to measure the phenotype plasticity and genetic variability, etc. (Li *et al.*, 2007). The present study indicates that shading in the forest fringe plot increased habitat variability and hence

phenotype plasticity, when compared to the open meadow plot.

A positive linear correlation was exhibited between reproductive growth and the above-ground growth in the *K. intergrifolia* populations (Figs. 1, 2). These results are congruent with the work of Weiner (1988), where more resources were allocated to reproduction as plant ramet biomass increased. In other words, the plant must acquire enough biomass before it can achieve reproductive functioning. Therefore, ramet total biomass must first increase to obtain more reproductive modules in practical production. The relationship between reproductive allocation and ramet component biomass also indicate a positive linear correlation in the current study (Figs. 3, 4) showing that reproduction was based on the cumulative biomass of above-ground parts of the *K. intergrifolia* populations in the two different habitats. Therefore, to obtain more reproductive modules in production practice, increasing ramet component biomass must be considered simultaneously. Based on the corymb and seeds, the evaluation in the forest fringe



**Figure 4.** Functional relationships between allocations of reproductive and vegetative modules (A, C: allocation to stem biomass; B, D: allocation to leaf biomass) in *K. intergrifolia* from the meadow plot (n=90).

plot was more accurate than in the meadow plot when the biomass of reproductive modules and reproductive allocation were predicted. Consequently, larger variability in reproductive module biomass and reproductive allocation were obtained for the meadow plot, which resulted in a lower level of evaluative accuracy.

In plants, the feature of life history strategy was that increased allocation to one function (*e.g.* reproduction) must tradeoff with a decreased allocation to another function (*e.g.* growth) (Bonser and Aarssen, 1996). There was a negative correlation in resource allocation between plant vegetative and ripening stages when resources are limited (Lalond and Roitberg, 1994). Similarly, a negative correlation was exhibited for each reproductive module biomass and reproductive allocation with respect to ramet component biomass for *K. intergrifolia* populations occupying the two different habitats. The results indicate that the increased reproductive allocation occurred at the cost of a decrease in the biomass of other components. In the allometry model, a non-linear relationship was observed between

RA-II values and biomass allocation of the leaf (Figs. 3D, 4D), which demonstrate another phenotypic plasticity model indicated by the *K. intergrifolia* populations. Allometry was closely correlated with the genetic factor when a plant is in the vegetative and ripening stages (Langlade *et al.*, 2005; Stojković *et al.*, 2009). Therefore, further studies should focus on the mechanism of allometry when plants are in the ripening stage.

Plants can adjust their trade-off patterns to fit the environment adaptation (Wu *et al.*, 2010). In this research, the trade-off strategies between reproduction and growth are clearly reflected by comparison in the reproductive characteristics of *K. intergrifolia* populations when located in an open natural meadow versus the forest fringe of a secondary broad-leaved forest. Adjustments to resource allocation were constantly being made, to acquire enough resources for growth/maintenance and reproductive output. Ultimately, adequate allocation of resources to reproduction ensures that a species is able to reproduce in different habitats with different resource availabilities.

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