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合歡山地區台灣高山田鼠啃食作用對玉山箭竹生長之影響

Effects of Taiwan Vole (*Microtus kikuchii*) Herbivory on Yushan
cane (*Yushania niitakayamensis*) Growth in Hehuan Alpine
Meadows

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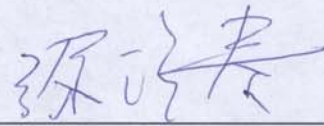
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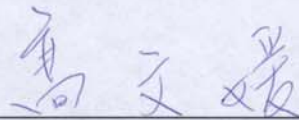
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摘要

草食動物雖常被認為對植物的更新、生長、存活有負向的影響，但可能也有正向的影響。草食動物在攝取植物不同部位時，會對植物的適存度有不同影響。在合歡山草原地區，主要的優勢植種為玉山箭竹(*Yushania niitakayamensis*)，主要的優勢小型哺乳動物為台灣高山田鼠(*Microtus kikuchii*)，過去的研究顯示玉山箭竹為高山田鼠主要偏好的植種。本研究希望了解高山田鼠與玉山箭竹之間的關係，因此進行檢驗了以下的假說：(1)台灣高山田鼠對於玉山箭竹的不同部位有取食偏好差異；(2)取食偏好與不同部位的營養成份相關，高偏好的部位含有較高的蛋白質及較低的纖維；(3)台灣高山田鼠對玉山箭竹的取食會增加箭竹冠層光的穿透量及地面掉落物，進而對玉山箭竹的生長有正向的影響。本研究分為實驗室內的取食偏好實驗和箭竹營養成分分析實驗，以及使用野外圍欄移除田鼠實驗和操弄覆蓋度、掉落物實驗兩大部分。實驗結果顯示，高山田鼠對於玉山箭竹各部位有顯著的取食偏好差異，且具有季節上的差異，五月時的取食偏好等級為筍>葉>地下莖=地上莖，在一月及十月時的取食偏好等級為葉>筍=地下莖=地上莖。高山田鼠對各部位的取食偏好與箭竹的酸洗纖維、粗蛋白質及灰份等營養成分含量顯著相關。高山田鼠的啃食活動會降低箭竹覆蓋度及增加掉落物，進行野外降低箭竹覆蓋度及移除掉落物的實驗顯示兩者對箭竹發筍均有顯著的影響。而圍欄實驗的結果亦顯示，移除田鼠會降低圍欄內箭竹筍與莖的比例。因此可得知台灣高山田鼠雖然取食玉山箭竹，但對箭竹的生長具有正向的影響。

關鍵字：台灣高山田鼠、玉山箭竹、動植物交互作用

Abstract

Although herbivores are often considered having negatively influence on the recruitment, growth, and survival rate of plants, they could benefit plants as well. The herbivorous consumption of different plant parts could have differential effect on fitness of the consumed plants. Yushan canes (*Yushania nitakayamensis*) is the dominant plant species, and Taiwan vole (*Microtus kikuchii*) is the dominant small mammal in alpine meadows at the Hehuan Mt.. The former species is the primary and preferred food of the latter species. In this thesis, investigation was set up to elucidate the relationship between the two species. Hypothesis of the study are (1) Taiwan voles have feeding preference on different parts of Yushan canes; (2) feeding preference can be explained by nutrient contents of different parts: highly preferred parts have higher protein and lower fiber contents than less preferred parts; (3) consumption by Taiwan voles has positive effects on the growth of Yushan canes by increasing light penetration into the canopy and aboveground litter. Feeding preference experiments and nutrient content analyses were performed in the laboratory, and field exclosures and field manipulation of canopy and litter were used to test the hypotheses. The results indicated that the ranks of feeding preference by Taiwan voles were shoot > leaf > culm = rhizome in May, and leaf > shoot = culm = rhizome in January and October. The preference was explained by nutrient contents, particularly the amounts of acid detergent fiber (ADF), crude protein (CP), and ash of Yushan cane parts. The exclusion of voles led to decreased shoot-culm ratios. Both the reduction of canopy cover and litter removal had significant effects on the emergence of new shoots after 1 year of field manipulation, indicating that Taiwan voles could facilitate shoot emergence of Yushan canes through increasing light availability and ground litter. I conclude that although Taiwan voles consume Yushan canes, they could benefit Yushan canes as well.

Key words: Taiwan Vole, Yushan Cane, Interaction

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Introduction

Plant-animal interaction is one of the central issues in community ecology. It has been well documented that insects affect the growths of plant populations by actions such as pollination, dispersing seeds, transmitting diseases, and herbivory (Hummel et al. 2009; Rosumek et al. 2009; Wagner 1997). Similarly, mammals could affect the growths of plant populations by above actions as well as altering soil nutrients and microbial communities (Borghi and Giannoni 1997; Darabant et al. 2007; Feeley and Terborgh 2005; Gomez-Garcia et al. 2004; Gomez-Garcia et al. 1999; Gough et al. 2008; Ritchie et al. 1998; Stuart-Hill and Mentis 1982; Zavada and Mentis 1992). Therefore, animals could not only negatively influence the recruitment, growth, and survival rate of plants, they benefit plants as well (Huntly 1991).

Herbivory by mammals is often considered having negative effects on plants. For example, in the Qinling Mountains of China, basal diameters of new shoots and clonal regeneration of culms of arrow bamboos, *Fargesia qinlingensis*, were significantly less in giant panda herbivory plots compared to control plots (Wang et al. 2007a; Wang et al. 2007b). In response to the foraging of herbivores, plants evolved counter strategies (Stuart-Hill and Mentis 1982). Some produced deterrents which provide mechanical or chemical protection (Alonso-Diaz et al. 2008). The physical property (Hudson et al. 2008), secondary metabolites (Alonso-Diaz et al. 2008), as well as nutrient contents (Bergeron and Jodoin 1987; Derting and Hornung 2003; Morrison and Hik 2008; Parsons et al. 2006; Willig and Lacher 1991) of plants could determine how much a plant is consumed by herbivores, which usually prefer individuals or parts with high proteins (Bergeron and Jodoin 1987; Deguchi et al. 2001), low fibers (Deguchi et al. 2001), and low secondary metabolites (Alonso-Diaz et al. 2008; Gomez-Garcia et al. 2004; Gomez-Garcia et al. 1999). Some plants tolerated foraging by reallocating the

biomass between roots and shoots, or increasing productivity (Ritchie et al. 1998). Some responses could in fact increase the fitness of plants. For example, in the Spanish Pyrenees, the density, asexual reproduction, and seedling abundance of a geophyte, *Merendera montana*, were higher in vole-active plots than vole-excluded plots. The burrowing activities of voles would increase the spreading of seeds, seedling, and asexual buds (Borghì and Giannoni 1997; Gomez-Garcia et al. 2004; Gomez-Garcia et al. 1999). Thus, herbivores seemed to have positive effects on the plant in those cases.

Yushan cane (*Yushania niitakayamensis* (Hayata) Keng f.) is a perennial monocarpic species classified as *Bambusoideae*. The phenology of Yushan cane has been documented by several researchers (Table 1). For example, Chen (1997) conducted a field survey at the Hehuan Mountain, and found Yushan cane produced new shoots from April to June, grew leaves from July to September, and some leaves withered from October to March. The sexual reproduction of Yushan cane is likely mass synchronous flowering and seeding, like most other bamboo species. Liao (2004) reported a mass flowering event in Snow Mountain during August~November 2001. There has been no periodicity of flowering recorded thus far, however. The Yushan cane uses rhizome ramets for asexual reproduction, which has been classified as metamorph II, running rhizome with sympodial culms (Lin 1976).

Generally, the aboveground growth of bamboos can be divided into two stages: the first-year shoots which are unbranched, covered in sheaths and the >1-year culms which are branched, lignified, without sheaths attached at the nodes (Tripathi and Singh 1994; Widmer 1998). Temperature and humidity are the two main factors that limit the production of shoots. An increase in temperature and humidity of soil would lead to early shooting (Wang and Kao 1986). Bamboo shoot farmers in Taiwan maintained bamboo fields by keeping high humidity of soil, plowing soil frequently, removing old

rhizomes, and fertilizing. Harvesting emerging shoots in proper ways would lead to a secondary shooting in the same year (Liu et al. 2009).

Chen (1983) showed that the allocation of biomass of different Yushan cane parts varied with phenology. He separated the Yushan cane into four parts: rhizome, culm (main stem with side branches removed), side branch (leaves removed), and leaf. The relative weight of rhizomes (% total weight per unit area) was at the highest point (~38%) a month (early February) before shooting (i.e., new shoots emergence) started in March, declined rapidly until shooting ended (~20%) in mid May, remained constant until late July (~20%) when it started to increase gradually. The relative weight of culms remained fairly constant (~45%) throughout the year, except a peak in late July (~61%). The peak coincided with the end of active growing season of new shoots, thus indicated the increase in culm weights came from the growth of new shoots. The relative weight of side branches was bimodal, with peaks (~20%) occurred in early February and late July, respectively. The relative weight of leaves remained constant (~10%) throughout the year. The seasonal pattern of biomass distribution observed by Chen (1983) suggested that Yushan canes started transfer energy to shooting in early spring (early February). New shoots started to emerge in March, stopped in May, yet continue to grow tall without branching until late July~August. The increase of side branches and new leaves on old culms started in May, peaked in June or later, and declined. New shoots started to grow side branches and leaves in August until pass late October.

The nitrogen concentration of different Yushan cane parts also changed with phenology (Chang 1981). The nitrogen concentrations of leaves were 2~6 times those of culms and rhizomes throughout the year. Higher nitrogen concentration occurred in August~October and March~May for leaves and rhizomes/culms, respectively. Yushan

cane was the most palatability food for Taiwan voles in the Hehuan Mountain (Ho 2009). With seasonal variation in nutrient contents, Yushan canes could be consumed by voles on different parts in different seasons which could have different effect on Yushan canes. For example, Chen (1997) suggested that depredation on emerging shoots by rodents could reduce the number of nodes, thus the overall height of Yushan canes.

Research questions

The question asked in the current research is: How does the herbivory by voles affect the growth of Yushan canes? The consumption of culms and leaves could decrease photosynthetic efficiency, and retard Yushan cane growth. Yet, it may increase light penetration through canopies and the amount of aboveground litter on the ground level, which might improve conditions in terms of soil temperature and humidity hence facilitate Yushan cane growth. The interactions of different positive and negative aspects of vole consumptions could vary with seasons since the consumption of different parts is likely affected by seasonal variation in nutrient contents of different parts. Based on above ideas, the concept map for the current study is shown in figure I..

This study hypothesize that

- (1) Taiwan voles have feeding preference on different parts of Yushan canes.
- (2) Feeding preference can be explained by nutrient contents of different parts: highly preferred parts have higher protein and lower fiber contents than less preferred parts.
- (3) Consumption by Taiwan voles has positive effects on the growth of Yushan canes by increasing light penetration and aboveground litter.

Materials & Methods

Study area

The field study was conducted in an alpine meadow (24°08'36.4"N, 121°17'17.4"E, 3007~3070 m in altitude) at the Hehuan Mountains of the Taroko National Park. The annual mean air temperature is 7.0 °C and rainfall 366 mm (Ho 2009). The Yushan cane (*Yushania niitakayamensis* (Hayata) Keng f.) was the dominant plant species in the meadow. The Taiwan vole (*Microtus kikuchii*), whose primary and preferred food was Yushan cane, was the dominant small mammal in the meadow (Ho 2009; Lin and Lin 1989).

Laboratory experiments and analyses

Two feeding experiments were used in the laboratory to determine the preference of different Yushan cane parts by Taiwan voles. The experiments, described in detail below, were conducted in the High-Altitude Station of the Institute for the Endemic Species Research, about 5 km from the mountain meadow where field experiments were performed. Nutrient analyses were conducted in a laboratory (the laboratory of Dr. Jih-Tay Hsu's) in the Department of Animal Science and Technology, National Taiwan University. All voles and plant samples used in the laboratory experiments and chemical analyses were collected from a meadow near the field site at the entrance to the Mt. Cilai, about 500 m from the mountain meadow where field experiments were performed.

Based on the phenology of Yushan canes at the Hehuan Mountains (Chen 1997), the laboratory experiments were performed in three seasons: January (during non-growing season, November~February), May (during shooting season, March~June), and September (during leaf-growing season, July~October) for two years, Jan-2008 ~ Oct-2009. Because of typhoons, the September experiments were postponed till October.

The Taiwan voles used in the experiments were captured before each experimental trial using Ugglan Special live traps ($25 \times 7.8 \times 6.5 \text{ cm}^3$), baited with roll oats mixed with peanut butter. A ball of crumpled newspaper was supplied to provide shelter. The captured voles were housed individually in plastic cages ($50 \times 25 \times 20 \text{ cm}^3$) with 10 cm thick wood shaving, and supplied with water, oats, and sweet potatoes for at least six hours to allow voles adapt to the laboratory environments. Only adult animals were used, with body weights $> 30 \text{ g}$ (Wu 2007), in the experiments.

Feeding preference experiments

Two types of feeding preference experiments were conducted: bite trials and cafeteria trials, in sequence. The bite trials tested the preference of voles for aboveground Yushan canes: shoots or culms with leaves. The shoots had no leaves in May, but had a few leaves on the tips in October and January. How canes were consumed by voles was also observed to document the consumption behaviors. The cafeteria trials tested the preference of voles for different Yushan cane parts, including rhizome, culm, leaf, and shoot.

In 2008, I used nine voles in January, seven in May, four in June, and ten in October. In 2009, I used three voles in January, March, and May each, and two in July, and October each.

Bite trials

The bite trials were set up to mimic the way voles would encounter Yushan canes in the wild. During each trial, for each replicate, ten >1 -year live culms and ten first-year shoots were arranged in a 5×4 checkerboard pattern by inserting the bases of cut culms or shoots into a $10 \times 5 \times 5 \text{ cm}^3$ (LxWxH) wet flower-arrangement foam. The foam was then placed in a $30 \times 20 \times 15 \text{ cm}^3$ (LxWxH) plastic cage fenced in with 1-cm

mesh, 60-cm high mesh wires. A Taiwan vole was introduced into the cage at 8 pm, provided with 15g of sweet potato and oat, each (control food). At the 4th (midnight) and 12th (8 am) hours, the numbers of culms and shoots bitten by voles were counted. It was defined that a culm or shoot was bitten by voles if over one-third of circumference was gnawed. The bite trials were performed in 2008 only.

Cafeteria trials

During each trial, for each replicate, 10 g of Yushan cane rhizome, culm, leaf, and shoot each, and 15 g of sweet potato and oat each were arranged in a 50 × 25 × 20 cm³ (LxWxH) cage. Each Yushan cane part was wrapped in wet paper towels in a 7.8 × 7.8 × 1 cm³ (LxWxH) plastic dish to reduce water loss. A Taiwan vole was introduced into the cage at midnight. After 12 hours (at noon the next day), the vole was removed, and the left-over was collected and weighed. To estimate weight loss of plant parts due to dehydration, an experimental control was created during the same period of time by placing the same amount of food with similar set up in a separate cage without voles (Ho 2009). The weights of left-over Yushan cane parts were then adjusted for weight loss due to dehydration. The cafeteria trials were performed in both 2008 and 2009.

Manly's Alpha (Krebs 1999) was calculated to quantify the preference of each vole for each plant sample (*i*) in a 12-hr trial.

$$\text{Manly's Alpha } (\alpha_i) = \ln(p_i) / \sum \ln(p_i)$$

$$p_i = T_C / T_0$$

$$T_C = T_L \times (C_0 / C_L)$$

p_i : proportion of plant sample left unconsumed

T_C : weight of plant sample left unconsumed after 12 hrs. adjusted for water loss

T_0 : weight of plant sample offered to vole

T_L: weight of plant sample left unconsumed

C_O: weight of control plant sample in the beginning of trials

C_L: weight of control plant sample after 12 hrs.

Nutrient content analyses

In 2008 and 2009, Yushan cane parts were collected from the field when the cafeteria trials were conducted to analyze their nutrient contents. All collected samples were weighed immediately, and kept in plastic bags to prevent water loss. They were temporarily stored in a 4 °C refrigerator before they were freeze dried, ground, and stored in -20 °C within a week. Five components of nutrient contents, including water, ash, neutral detergent fiber (NDF), acid detergent fiber (ADF), and crude protein (CP) of each Yushan cane part were measured using standard methods: water (AOAC 2000), ash (AOAC 2000), NDF (Vansoest et al. 1991), ADF (Goering and van Soest 1970), and CP (AOAC 2000). Detail descriptions of methods are given in the Appendix. The amount of hemicellulose were also calculated by subtracting ADF from NDF.

Field experiments

Two field experiments were performed: enclosure experiment and canopy-litter manipulation experiment, to determine the effects of Taiwan vole consumption on the growth of Yushan canes. The experiments, described in detail below, were conducted in the mountain meadow nearby the Songsyue Lodge. The enclosure experiment tested the overall effects of Taiwan vole exclusion on the growth of Yushan cane, and the canopy-litter manipulation experiment simulated the effects of increased litter and decreased canopy caused by vole consumption on the growth of Yushan canes.

Exclosure experiment

A pair of $2 \times 2 \text{ m}^2$ vole exclosures were set up at six sites on the mountain meadow in Dec-2007. Each pair contained a vole-proof exclosure, and a leaky exclosure serving as a control treatment. Each exclosure was constructed by 1-cm mesh meshwire extended 80-90 cm aboveground and 30-40 cm deep belowground holding in place with PVC pipes staked to the ground. A 25 cm wide transparent plastic film was fixed to the top edges of the meshwire on the vole-proof exclosure to prevent voles from entering by climbing. The leaky exclosure served as a control treatment had large openings on the ground level that allowed voles enter freely. Small mammal traps placed inside vole-proof exclosures during periodic trapping indicated there was no vole. Every four month from May-2008 to Oct-2009, I randomly selected four $20 \times 50 \text{ cm}^2$ long transects within each exclosure to census the number of culms and shoots of Yushan canes.

Canopy-litter manipulation

To simulate the foraging of voles on Yushan cane growth, 12 plots with 100% Yushan cane cover were selected in the meadow randomly. In each plot, a trio of different treatments was set up. The treatments, each $50 \times 50 \text{ cm}^2$ in size, were: (1) canopy reduction in which I removed several culms and attached leaves to reduce ~50% foliage cover; (2) litter removal in which I removed the majority (>90 %) of leaf litter; (3) control in which no culm, leaf or litter were removed. The three treatments in each plot were within 2 meters of each other. Every four month from May-2008 to Oct-2009, the treatments were maintained, and two $25 \times 25 \text{ cm}^2$ areas in each treatment in each plot were randomly selected to count the number of culms and shoots of Yushan canes. The amount of litter produced by Yushan canes every four months from litter removal plots (N=12) was oven-dried in 60°C for 48 hrs and weighed.

Field shoot survey

In order to understand the consumption of Yushan cane shoots by herbivores in the field, I marked 99 1st-year shoots in a 5×5 m² area in the meadow in June 2008. Every six months for the next 18 months, I recorded the heights and conditions of marked shoots to see if they were consumed by herbivores.

Statistical analyses

For the bite trials, the numbers of >1-year culms and first-year shoots that were bitten by voles were counted. Results from May and June trials were combined to represent the shooting season. Results from different individuals in a season were pooled together. The differential consumption were examined by using a 2 x 3 (part x season) contingency table, followed by a Chi-square test in each month as post hoc comparisons. The bite trials were performed in 2008 only.

For the cafeteria trials, Manly's α was calculated for each Yushan cane part for each vole tested. The feeding preference of different parts were examined by using two-ways (part x season) fixed-factor ANOVAs, followed by Scheffe's tests as post hoc comparisons. Results from different individuals in a season served as replicates. The cafeteria trials were performed in 2008 and 2009, yet only results from 2008 in this analysis were used because extremely small sample sizes in 2009. Results from May and June trials were combined to represent the shooting season.

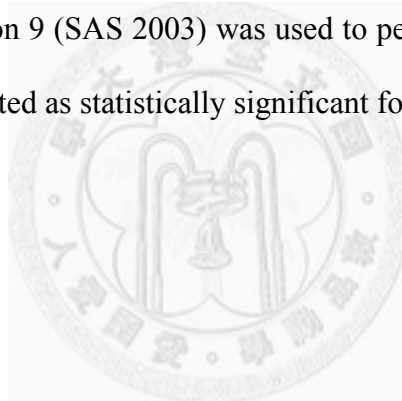
To determine the nutrient contents that explained the feeding preference (Manly's α), the average of Manly's α of different individuals in a season were calculated to find a feeding preference value for a given month. Individual nutrient contents were first analyzed separately with simple linear regressions to show the effects of each nutrient content. Then the stepwise selection technique was used in a multiple-regression model

to identify key nutrients in explaining the preference. The results from both 2008 (Jan., May, Jun., & Oct.) and 2009 (Jan., Mar. May, Jul., & Oct.) in these analyses were used.

In both exclosure and canopy-litter manipulation experiments, the ratio of >1-year culms to first-year shoots in different seasons were calculated, and the differences between treatments were examined by using logistic regressions (Allison 2005).

The amount of leaf litter produced every four months in the canopy-litter manipulation experiment were analyzed using an ANOVA with blocking to test the differences among the 12 plots (blocks) and 3 seasons, followed by Scheffe's tests as post hoc comparisons (Shen 2005).

None of the data sets violated the assumptions, such as normality, of statistical tests performed. SAS version 9 (SAS 2003) was used to perform all statistical analyses. A p-value < 0.05 was accepted as statistically significant for differences.



Results

Laboratory experiments and analyses

Feeding preference experiments

Bite trials

The numbers of >1-year culms and first-year shoots of Yushan canes gnawed by Taiwan voles were counted in January, May, and October 2008. Chi-square tests on 2 x 3 (part x season) contingency tables were significant for both the 4hrs. ($\chi^2_{(6)}=32.65, p < 0.001$, Fig. 2A) and 12hrs. ($\chi^2_{(6)}=21.53, p < 0.001$, Fig. 2B) tests, thus indicated that the parts were gnawed differently in different seasons. Separate chi-square tests showed Taiwan voles significantly preferred first-year shoots over >1-year culms during the first 4hrs in May ($\chi^2_{(1)}=59.51, p < 0.001$) and October ($\chi^2_{(1)}=21.78, p < 0.001$), and over the whole 12hrs periods in May ($\chi^2_{(1)}=67.50, p < 0.001$) and October ($\chi^2_{(1)}=37.24, p < 0.001$). No difference was detected in January during first 4hrs ($\chi^2_{(1)}=1.56, p =0.21$) and over whole 12hrs period ($\chi^2_{(1)}=2.06, p =0.15$).

During the bite trials, when voles consumed the branches and leaves of >1-year culms, they would climb or fell the culms, clip the leaves off the side branches at the leaf petioles, and ate from the petiole ends of leaves. They often did not consume the whole leaves, and discard the leaf tips, thus produced litter on cage floors. Furthermore, the voles showed seasonal differences in their foraging behaviors on first-year shoots. In May, the shoot growing season, the voles would fell the shoots at proximately 3~5 cms from the ground, gnaw off the exterior (barks), and eat the interior of shoots. In October and January, the leaf-growing and non-growing seasons, respectively, the voles would

feed on the leaves on the culms and tips of first-year shoots. They either climbed or felled the stems to do so.

Cafeteria trials

The same voles used in bite trials were used to examine their feeding preference of different parts (rhizome, culm, leaf, and shoot) of Yushan canes. Because there was no significant difference between male and female voles in feeding preference (Three-way ANOVA, part x season x sex, sex effect, $F_{1,107} = 0.62$, $p = 0.43$), data were pooled between sexes and analyzed with a two-way ANOVA (part x season). The preference for Yushan cane parts differed among seasons (Two-way ANOVA, part x season interaction, $F_{6,108} = 24.25$, $p < 0.001$). Feeding preference in May was significantly different from that in January or October. In descending preference, the ranks were shoot > leaf > culm = rhizome in May, and leaf > shoot = culm = rhizome in January and October. The overall ranks were leaf > shoot > culm = rhizome (Table 2).

Nutrient content analyses

The nutrient contents of different Yushan cane parts (rhizome, culm, leaf, and shoot) were analyzed in all seasons and years when cafeteria trials were performed. All nutrient contents measured, including ash, NDF, ADF, hemicellulose, and CP, were expressed as percentage of dry matter weight (% DM), except water which was expressed as percentage of fresh weight (% FW). Results were presented in Table 3 and Figures 3~8. Each nutrient contents measured was significantly related to the feeding preference of different parts of Yushan cane, when they were analyzed separately with simple linear regressions (Table 4). CP ($r^2=0.73$, $p < 0.001$), ash ($r^2=0.60$, $p < 0.001$), hemicellulose ($r^2=0.42$, $p < 0.001$), and water ($r^2=0.18$, $p < 0.01$) were positively, while

ADF ($r^2=0.75$, $p < 0.001$) and NDF ($r^2=0.67$, $p < 0.001$) were negatively related to feeding preference.

Followed up on the simple linear regressions, a multiple regression with stepwise selection was used to identify key nutrient contents that explain feeding preference. Since NDF was the combination of hemicellulose and ADF, NDF wasn't included into the multiple regression model. The result indicated ADF, CP, and ash were the key nutrient contents. The final regression model gave: Preference = $0.60149 - 0.011$ ADF + 0.017 CP - 0.017 ash (Table 5, $r^2=0.79$, $p < 0.001$).

Field experiments

Exclosure experiment

Although the exclosures were established in Dec-2007, and the survey for the numbers of shoots and culms started in Jan-2008, new shoots did not emerge until Mar-2008, it would be inappropriate to use the measurement in Jan-2008 as baselines. I used the measurement in May-2008 as baselines instead. The numbers of shoots and culms varied over time (Fig. 9A). In Jan-2008, the numbers of shoots is 48.3 ± 8.3 (MEAN \pm 1SD) per m² in exclosures and 62.9 ± 20.3 (MEAN \pm 1SD) per m² in control treatments. The numbers of culm is 593.3 ± 143.5 (MEAN \pm 1SD) per m² in exclosures and 675 ± 149.6 (MEAN \pm 1SD) per m² in control treatments. In May-2008, the numbers of shoots is 35 ± 8.6 (MEAN \pm 1SD) per m² in exclosures and 25.4 ± 14.3 (MEAN \pm 1SD) per m² in control treatments. The numbers of culm is 418.8 ± 95.6 (MEAN \pm 1SD) per m² in exclosures and 427.1 ± 96.3 (MEAN \pm 1SD) per m² in control treatments. In Sep-2008, the numbers of shoots is 28.3 ± 3.3 (MEAN \pm 1SD) per m² in exclosures and 32.1 ± 2.1 (MEAN \pm 1SD) per m² in control treatments. The numbers of culm is 417.9 ± 55.3

(MEAN±1SD) per m² in exclosures and 432.1±148.5 (MEAN±1SD) per m² in control treatments. In Jan-2009, the numbers of shoots is 40.4±4 (MEAN±1SD) per m² in exclosures and 47.5±2 (MEAN±1SD) per m² in control treatments. The numbers of culm is 380±106.1 (MEAN±1SD) per m² in exclosures and 404.2±77.9 (MEAN±1SD) per m² in control treatments. In May-2009, the numbers of shoots is 30.8±3.7 (MEAN±1SD) per m² in exclosures and 50.8±1.3 (MEAN±1SD) per m² in control treatments. The numbers of culm is 425.4±67.5 (MEAN±1SD) per m² in exclosures and 357.5±59.2 (MEAN±1SD) per m² in control treatments. In Sep-2009, the numbers of shoots is 31.3±6.1 (MEAN±1SD) per m² in exclosures and 48.8±2 (MEAN±1SD) per m² in control treatments. The numbers of culm is 353.3±117.5 (MEAN±1SD) per m² in exclosures and 306.7±101 (MEAN±1SD) per m² in control treatments. The shoot-culm ratios remained relatively constant in vole-proof exclosures, while the ratios significantly increased over time in control (Fig. 9B), using either May-2009 (Logistic Regression, treatment x time interaction, $\chi^2 = 18.24$, $p < 0.001$) or Oct-2009 (Logistic Regression, treatment x time interaction, $\chi^2 = 16.29$, $p < 0.001$) as the end point. Detail test results were given in Table 6.

Canopy-litter manipulation

Reducing canopy cover had a significant effect, the shoot-culm ratio of Yushan cane increased over time (Fig. 10), using the ratio in May-2008 as baseline. The ratio became higher than that of control, using either May-2009 (Logistic Regression, treatment x time interaction, $\chi^2 = 22.67$, $p < 0.001$) or Oct-2009 ($\chi^2 = 7.11$, $p < 0.01$) as the end point. Removal of litter also had a significant effect, the shoot-culm ratio of Yushan cane remained low over time (Fig. 10), using the ratio in May-2008 as baseline. The ratio of shoot-culm in the treatment became lower than that of control (Logistic

Regression, treatment x time interaction, $\chi^2 = 3.81$, $p = 0.05$), using Oct-2009 as the end point. Detail test results were given in Table 7.

The amount of litter produced per four month differed in time and plot (block-ANOVA, time effect, $F_{4,44}=30.11$, $p < 0.001$, plot effect, $F_{11,44}=5.59$, $p < 0.001$, Fig. 11). Post hoc tests (Scheffe's tests) indicated the ranks in the amount of litter produced per month were Sep-2008~Jan-2009 = Sep-2009~Jan-2010 > Jun-2008~Sep-2008 = May-2009~Sep-2009 > Jan-2009~May-2009. Plot D had a greater amount of litter than the other 11 plots. Abundant Yushan cane clippings and vole feces indicated that plot D had high vole activity.

Field shoot survey

The 99 first-year shoots marked in Jun-2008 had an average height of 28 ± 11 cm (MEAN \pm 1SD). Over seven months, only 4 shoots showed evidence of being gnawed by voles, and the height of shoots became 38 ± 11 cm in Jan-2009. After a year, only 8 shoots had evidence of vole herbivory, and the heights of shoots became 39 ± 11 cm in Jun-2009.

Discussion

The voles did show significant feeding preference for different parts of Yushan cane in different seasons. The ranks of preference were shoot > leaf > rhizome = culm in May (shooting season), and leaf > shoot = rhizome = culm in January (non-growing season) and October (leaf-growing season), as revealed by the cafeteria experiments (Table 2), and supported by bite trials (Table 1). The differential preference was likely influenced by the seasonal changes in nutrient contents of different Yushan cane parts (Table 3, Fig. 3~8). First of all, simple linear regressions showed the amount of each nutrient contents measured was significantly correlated with feeding preference (Table 4). A multiple regression with stepwise selection further indicated the best predictive nutrient contents for the feeding preference was ADF, CP, and ash, in decreasing importance (Table 5). The ADF alone explained 75% of variations in feeding preference, while adding CP only improved the explanatory power to 78%, and adding ash further improved the explanatory power to 79%.

In fact, the differential preference matched very well the seasonal changes in ADF and CP. Nutrient content analyses showed that the amounts of ADF were culm > rhizome > leaf > shoot in May (shooting season), and culm = shoot > rhizome > leaf in January (non-growing season) and October (leaf-growing season). The amounts of CP were leaf = shoot > rhizome = culm in May, and leaf > shoot = rhizome = culm in January and October. That was, leaves of Yushan canes had the lowest ADF and highest CP among all parts almost year round except shooting season. Coincidentally, voles preferred to forage on leaves almost year round except shooting season. During the shooting season, when the first-year shoots with the lowest ADF and highest CP among all parts newly emerged from underground, voles showed significant preference for shoots, and leaves became voles' second preferred food.

Several previous studies also showed that food with low ADF was considered high quality for voles (Bergeron and Jodoin 1987; Goldberg et al. 1980). For example, Goldberg et al. (1980) found voles would not prefer some food with high nutritious contents due to its high fiber contents. The feeding behaviors of Taiwan voles further supported the key role of fibers. During the bite trials in May, the shooting season, the voles would fell the shoots at base close to the ground, gnaw off the exterior, and eat the interior of shoots. In October and January, the voles would only feed on the leaves on the culms and tips of first-year shoots. When feeding on leaves, they would clip the leaves off the branches at the leaf petioles, ate from the petiole ends, and discard the leaf tips. Leaf tips of Yushan canes were brownish dry, compared to other parts of leaves, and suggested lower palatability. These behaviors suggested voles were avoiding parts with high fiber contents as much as they could. In this discussion, I used ADF as a synonym of fibers.

The preference of Taiwan voles was less affected by CP. Previous studies had shown that food with high percentage of CP was considered high-quality (Bergeron and Jodoin 1987) and a criterion of food selection (Goldberg et al. 1980; Harju and Hakkarainen 1997) for voles. The amount of ash came in third as the determinant of feeding preference by voles. Ash was the combination of inorganic compounds in food (AOAC 2000) that could be critical for voles (Dubay et al. 2008). Other chemical contents measured or calculated, including hemicellulous and water did not affect the preference of voles much, although Ho (2009), after performing palatability trials of 13 common meadow plants over a year, found that hemicellulous was an important nutrient content influencing palatability of plants to Taiwan voles. Ho (2009) also found that the amounts of secondary compounds of alpine plants were very low, and did not have effects on palatability. The bamboo shoots could have high total cyanide contents,

which is a lethal substance for animals (Haque and Bradbury 2002). (Jao 2000) reported that the shoots of *Dendrocalamus latiflours*, *Bambusa edulis*, and *B. oldhamii* contained hydrogen cyanide, while it was not detected in the shoots of *Phyllostachys pubescens*, *Phyllostachys makinoi*, and *Pseudosasa usawai*. Although I did not measure secondary compounds in different parts of Yushan cane, they could have affected the feeding preference of voles.

While it's nearly impossible to directly observe the consumption behaviors of voles in the field, the feeding experiments suggested that Taiwan voles strongly preferred Yushan cane leaves almost year round, except in the shooting season when the first-year shoots would be heavily depredated. Taiwan voles are small mammals with high metabolic rates, and do not hibernate. They could reach high densities in some years, thus could potentially greatly depress photosynthetic structure, i.e., leaves, as well as asexual reproduction, i.e., new shoots, of Yushan canes. Based on the extent of defoliation observed during the bite trials, Taiwan voles could defoliate Yushan canes substantially in the field. Particularly, the availability of high quality Yushan cane parts should be quite high year round. Yushan cane leaves were all green in the leaf and shoot growing seasons. In the non-growing season, only the outer layers of canopies that exposed to wind would wither, while the substratum of foliage remained green (Chen 1997). The fresh clipping piles of leaves and twigs could be found year round in the meadow. Such a magnitude of herbivory by Taiwan voles could reduce Yushan cane fitness substantially.

Although at the first glance Taiwan voles seemed to benefit from Yushan canes at the cost of the latter, the relationship between the two species was more complicated than that. The defoliation of Yushan canes reduced the canopy cover and increased the amount of leaf litter on the ground. The former would increase light penetration to the

ground, and the latter would maintain higher temperature and humidity on the ground than otherwise. Those changes in microclimate could facilitate the emergence of new shoots (Liu et al. 2009; Wang and Kao 1986), thus asexual reproduction of Yushan canes. In deed, both reducing canopy cover and maintaining ground litter had a significant effect on the shoot-culm ratios of Yushan canes. Although the former had a greater effect than the latter, the shoot-culm ratios increased over time under both treatments (Fig. 10). Together, they could increase shoot-culm ratios by 100% over a 22 months period, as shown by the vole exclusion experiment (Fig. 9). In addition to the effects of canopy and litter, herbivory could sometimes stimulate compensatory growth of plants. For example, several studies showed that the debarking of willow stems by voles and lemmings could result in the mortality of damaged stems, while stimulate the emergence of large numbers of new shoots at tree bases (Elmqvist et al. 1987; Predavec and Danell 2001). The Yushan canes might be showing a compensatory growth after Taiwan voles' foraging. Nevertheless, the overall effects of Taiwan voles on Yushan canes seemed to be positive.

Although Taiwan voles loved newly emerging shoots in the laboratory feeding trials, the voles might not consume new shoots in the field frequently, as supported by my survey of 99 shoots. Only 8 out of 99 first-year shoots in a 25 meter square area had evidence of vole herbivory after a year. The result was surprising given voles' love for new shoots in the laboratory, and the high vole density at the survey area (Ho 2009). However, it was likely that voles avoided consuming new shoots in the field to increase the growth of Yushan canes to provide sufficient high quality food year round. Because the presence of Taiwan voles increased overall shoot-culm ratios of Yushan canes, the latter seemed to benefit from the former.

In conclusion, Taiwan voles did have differential feeding preference on the parts of Yushan canes in different season. Leaves were preferred year round except in shooting seasons when newly emerged shoots were preferred. Feeding preference can be explained by nutrient contents of different parts: highly preferred parts have lower fiber (ADF) and higher protein (CP) contents than less preferred parts. Consumption by Taiwan voles increased the shoot-culm ratios and could have overall positive effects on the growth of Yushan canes. This study suggested that the two species have a mutualistic relationship. Nevertheless, future studies examining their mutual influence on fitness are required to confirm such a claim



Reference

- Allison PD (2005) Logistic regression using SAS : theory and application. Wiley, New York, NY, USA
- Alonso-Diaz MA, Torres-Acosta UJ, Sandoval-Castro CA, Hoste H, Aguilar-Caballer AJ, Capetillo-Leal CM (2008) Is goats' preference of forage trees affected by their tannin or fiber content when offered in cafeteria experiments? *Animal Feed Science and Technology* 141:36-48
- AOAC (2000) Official method of analysis, 18 edn. Associations of Official Analytical Chemists, Arlington, VA, USA
- Bergeron JM, Jodoin L (1987) Defining high-quality food resources of herbivores - the case for Meadow Voles (*Microtus pennsylvanicus*). *Oecologia* 71:510-517
- Borghi CE, Giannoni SM (1997) Dispersal of geophytes by mole-voles in the Spanish Pyrenees. *Journal of Mammalogy* 78:550-555
- Chang MH (1981) Ecology and control of Yushan cane. In: Master thesis, Department of Forestry. National Taiwan University, Taipei, Taiwan
- Chen CF (1983) Resource allocation of *Yushania niitakayamensis*. In: Master thesis, Department of Forestry. National Taiwan University, Taipei, Taiwan
- Chen YF (1997) Taiwan vegetation vol.3 : subalpine coniferous forest and alpine meadow. Avanguard Press, Taipei, Taiwan
- Darabant A, Rai PB, Tenzin K, Roder W, Gratzner G (2007) Cattle grazing facilitates tree regeneration in a conifer forest with palatable bamboo understory. *Forest Ecology and Management* 252:73-83

- Deguchi Y, Sato S, Sugawara K (2001) Relationship between some chemical components of herbage, dietary preference and fresh herbage intake rate by the Japanese serow. *Applied Animal Behaviour Science* 73:69-79
- Derting TL, Hornung CA (2003) Energy demand, diet quality, and central processing organs in wild white-footed mice (*Peromyscus leucopus*). *Journal of Mammalogy* 84:1381-1398
- Dubay SA, Hayward GD, del Rio CM (2008) Nutritional value and diet preference of arboreal lichens and hypogeous fungi for small mammals in the Rocky Mountains. *Canadian Journal of Zoology* 86:851-862
- Elmqvist T, Ericson L, Danell K, Salomonson A (1987) Flowering, Shoot Production, and Vole Bark Herbivory in a Boreal Willow. *Ecology* 68:1623-1629
- Feeley KJ, Terborgh JW (2005) The effects of herbivore density on soil nutrients and tree growth in tropical forest fragments. *Ecology* 86:116-124
- Goering HK, van Soest PJ (1970) Forage fiber analyses. Agriculture handbook No.379. United States Department of Agriculture, Washington D.C., USA
- Goldberg M, Tabroff NR, Tamarin RH (1980) Nutrient variation in beach grass in relation to beach vole feeding. *Ecology* 61:1029-1033
- Gomez-Garcia D, Azorin J, Giannoni SM, Borghi CE (2004) How does *Merendera montana* (L.) Lange (Liliaceae) benefit from being consumed by mole-voles? *Plant Ecology* 172:173-181
- Gomez-Garcia D, Giannoni SM, Reine R, Borghi CE (1999) Movement of seeds by the burrowing activity of mole-voles on disturbed soil mounds in the Spanish pyrenees. *Arctic Antarctic and Alpine Research* 31:407-411

- Gough L, Shrestha K, Johnson DR, Moon B (2008) Long-term mammalian herbivory and nutrient addition alter lichen community structure in Alaskan dry heath tundra. *Arctic Antarctic and Alpine Research* 40:65-73
- Haque MR, Bradbury JH (2002) Total cyanide determination of plants and foods using the picrate and acid hydrolysis methods. *Food Chemistry* 77:107-114
- Harju A, Hakkarainen O (1997) Effect of protein and birch-bark powder on selection of food by root voles (*Microtus oeconomus*). *Journal of Mammalogy* 78:563-568
- Ho HC (2009) The interaction between Taiwan vole (*Microtus kikuchii*) and alpine meadow herbs at the Hehuan area: effect of nutrition and abundance of dominant herbs. In: Master thesis, Institute of Ecology and Evolution Biology. National Taiwan University, Taipei, Taiwan
- Hudson JMG, Morrison SF, Hik DS (2008) Effects of leaf size on forage selection by collared pikas, *Ochotona collaris*. *Arctic Antarctic and Alpine Research* 40:481-486
- Hummel GM, Schurr U, Baldwin IT, Walter A (2009) Herbivore-induced jasmonic acid bursts in leaves of *Nicotiana attenuata* mediate short-term reductions in root growth. *Plant Cell and Environment* 32:134-143
- Huntly N (1991) Herbivores and the dynamics of communities and ecosystems. *Annual Review of Ecology and Systematics* 22:477-503
- Jao ML (2000) Studies on analysis of hydrogen cyanide in the bamboo shoots. In: Master thesis, Department of Horticulture. National Taiwan University, Taipei, Taiwan
- Krebs CJ (1999) *Ecological methodology*, 2nd edn. Addison-Wesley Educational Publishers, Inc.

- Liao MC (2004) Studies on reproduction biology of *Yushania niitakayamensis* (Hay.) Keng f.
In: Master thesis, Department of Forestry. National Chung Hsing University,
Taichung, Taiwan
- Lin CY, Lin LK (1989) The survey of alpine meadow ecosystem in Taroko National Park.
Taroko National Park, HuaLien, Taiwan
- Lin WC (1976) The classification of subfamily Bambusoideae in Taiwan (continued).
Bulletin of the Taiwan Forestry Research Institute 271:1-75
- Liu KC, Yen SH, Yeh CY, Li LS, Chang TR (2009) The SOP of *Bambusa oldhamii* Munro
production and management. Agriculture and Food Agency, Council of Agriculture,
Executive Yuan, Taipei, Taiwan
- Morrison SF, Hik DS (2008) Discrimination of intra- and inter-specific forage quality by
collared pikas (*Ochotona collaris*). Canadian Journal of Zoology-*Revue Canadienne*
De Zoologie 86:456-461
- Parsons MH, Lamont BB, Davies SJJF, Kovacs BR (2006) How energy and coavailable foods
affect forage selection by the western grey kangaroo. *Animal Behaviour* 71:765-772
- Predavec M, Danell K (2001) The role of lemming herbivory in the sex ratio and shoot
demography of willow populations. *Oikos* 92:459-466
- Ritchie ME, Tilman D, Knops JMH (1998) Herbivore effects on plant and nitrogen dynamics
in oak savanna. *Ecology* 79:165-177
- Rosumek FB et al. (2009) Ants on plants: a meta-analysis of the role of ants as plant biotic
defenses. *Oecologia* 160:537-549
- SAS (2003) SAS 9 for Windows. In. Statistical Analysis Systems Institute Inc., Cary, NC,
USA
- Shen ML (2005) Experimental designs. Jeou Chou Book Co,Ltd., Taipei, Taiwan

- Stuart-Hill GC, Mentis MT (1982) Coevolution of African grasses and large herbivores. *African Journal of Range and Forage Science* 17:122-128
- Tripathi SK, Singh KP (1994) Productivity and nutrient cycling in recently harvested and mature bamboo savannas in the dry tropics. *Journal of Applied Ecology* 31:109-124
- Vansoest PJ, Robertson JB, Lewis BA (1991) Methods for Dietary Fiber, Neutral Detergent Fiber, and Nonstarch Polysaccharides in Relation to Animal Nutrition. *Journal of Dairy Science* 74:3583-3597
- Wagner D (1997) The influence of ant nests on Acacia seed production, herbivory and soil nutrients. *Journal of Ecology* 85:83-93
- Wang TD, Kao YB (1986) The growth and development of bamboo. *Modern silviculture* 2:27-65
- Wang W, Franklin SB, Certain MC (2007a) Seed germination and seedling growth in the arrow bamboo *Fargesia qinlingensis*. *Ecological Research* 22:467-474
- Wang W, Franklin SB, Ouellette JR (2007b) Clonal regeneration of an arrow bamboo, *Fargesia qinlingensis*, following giant panda herbivory. *Plant Ecology* 192:97-106
- Widmer Y (1998) Pattern and performance of understory bamboos (*Chusquea* spp.) under different canopy closures in old-growth oak forests in Costa Rica. *Biotropica* 30:400-415
- Willig MR, Lacher TE (1991) Food Selection of a Tropical Mammalian Folivore in Relation to Leaf-Nutrient Content. *Journal of Mammalogy* 72:314-321
- Wu JS (2007) Mating system of Taiwan vole (*Microtus kikuchii*): evidence from field data and microsatellite DNA. In: Master thesis, Department of Life Science. Tung Hai University, Taichung, Taiwan

Zavada MS, Mentis MT (1992) Plant-animal interaction - the effect of permian megaherbivores on the glossopterid flora. *American Midland Naturalist* 127:1-12



Tables

Table 1. The phenology of Yushan canes (*Yushania niitakayamensis*) observed in this study compared to those reported in previous studies, including Chang's observations at WangHsiang area (望鄉), DaSyue Mt. (大雪山), KuanWu area (觀霧) (Chang 1981), Chan's observation at Chu-Tung area (竹東) (Chan 1983), Chan's observation at Mt. He-Huan (合歡山) (Chan 1997), and Liao's observation at Snow Mt. (雪山).

	Month											
	1	2	3	4	5	6	7	8	9	10	11	12
Chang (1981)	Leaves wither			New shoots emerge			Growth peak		Leaves wither			
Chen (1983)	Growth terminate		New shoots emerge			Growth peak		Growth terminate				
Chen (1997)	Leaves wither			New shoots emerge			Growth peak			Leaves wither		
Liao (2004)	Leaves wither			New shoots emerge			Leaves growth & Flowering				Leaves wither	
This study	Little growth & Leaves wither			New shoots emerge			New shoots grow taller			Growth slow down & leaves wither		
				Old culms grow branches & leaves			Old culms grow branches & leaves					

Table 2. The feeding preference of Yushan cane parts, expressed as Manly's α (MEAN \pm 1SE), in different seasons. Different lower case letters for different parts within each season denote significant differences based on pair-wise post hoc comparisons using Scheffe's tests. A post hoc test is also performed on pooled data with seasons or parts combined. Different upper case letters denote significant differences.

	Rhizome ^C	Culm ^C	Leaf ^A	Shoot ^B
January ^A	0.0365 \pm 0.0100 ^b	0.0064 \pm 0.0047 ^b	0.3948 \pm 0.0775 ^a	0.0248 \pm 0.0143 ^b
May ^B	0.0072 \pm 0.0065 ^c	0.0080 \pm 0.0033 ^c	0.2655 \pm 0.0328 ^b	0.4996 \pm 0.0593 ^a
October ^A	0.0446 \pm 0.0132 ^b	0.0037 \pm 0.0022 ^b	0.4084 \pm 0.0465 ^a	0.0100 \pm 0.0046 ^b



Table 3. The nutrient contents of different Yushan cane parts and the index of preference (Manly's α) for different parts by Taiwan voles in 2008 and 2009.

Month	Yushan Cane Part	Preference (Manly's α)	Ash (% DM)	NDF (% DM)	ADF (% DM)	Hemicellulose (% DM)	CP (% DM)	Water (% FW)
Jan-2008	Culm	0.0064	1.57	85.95	63.86	22.08	1.95	39.11
	Leaf	0.3948	9.23	72.50	37.71	34.79	12.09	47.71
	Rhizome	0.0365	2.68	74.09	49.70	24.39	4.72	53.28
	Shoot	0.0248	2.37	83.00	59.03	23.97	6.06	51.43
May-2008	Culm	0.0082	1.57	83.29	63.29	20.01	1.57	39.64
	Leaf	0.2102	10.07	72.35	37.13	35.22	17.52	56.29
	Rhizome	0.0114	2.18	75.00	47.76	27.24	2.99	63.64
	Shoot	0.5948	7.14	64.84	31.20	33.64	18.75	90.07
Jun-2008	Culm	0.0076	1.66	90.50	63.12	27.38	1.64	42.70
	Leaf	0.3622	8.75	70.32	34.35	35.97	19.47	61.69
	Rhizome	0.0000	3.53	82.83	54.52	28.31	4.57	65.27
	Shoot	0.3329	6.98	61.95	32.26	29.69	17.62	92.13
Oct-2008	Culm	0.0037	1.56	86.24	60.48	25.76	5.07	39.37
	Leaf	0.4084	8.48	71.76	36.56	35.20	17.06	54.31
	Rhizome	0.0446	2.82	78.26	48.63	29.63	3.16	64.36
	Shoot	0.0100	2.94	88.74	54.89	33.84	7.00	64.96
Jan-2009	Culm	0.0008	1.50	81.60	55.64	25.96	1.74	33.63
	Leaf	0.3658	8.53	66.13	36.09	30.05	11.95	42.14
	Rhizome	0.1981	3.73	70.01	44.41	25.59	3.35	58.37
	Shoot	0.0000	2.24	84.75	59.06	25.68	2.29	48.25
Mar-2009	Culm	0.0017	2.29	84.84	57.89	26.94	2.20	43.99
	Leaf	0.1483	11.14	70.59	37.00	33.59	13.52	36.81
	Rhizome	0.0601	2.96	75.78	49.02	26.77	2.45	56.88
	Shoot	0.0251	1.58	81.86	56.62	25.23	1.70	34.17

Table 3. (Continued)

Month	Yushan Cane Part	Preference (Manly's α)	Ash (% DM)	NDF (% DM)	ADF (% DM)	Hemicellulose (% DM)	CP (% DM)	Water (% FW)
May-2009	Culm	0.0464	0.84	84.99	57.72	27.27	1.56	36.35
	Leaf	0.2815	9.75	69.80	35.52	34.28	15.14	45.48
	Rhizome	0.0206	3.36	79.34	52.33	27.01	2.63	61.96
	Shoot	0.5309	7.17	67.01	32.62	34.39	13.65	87.67
Jul-2009	Culm	0.0000	2.05	85.93	59.58	26.35	1.51	38.34
	Leaf	0.4344	8.43	69.23	36.22	33.01	14.03	53.11
	Rhizome	0.0031	2.32	76.85	50.18	26.67	2.68	60.25
	Shoot	0.1025	6.29	78.14	42.29	35.85	8.67	83.11
Oct-2009	Culm	0.0014	1.84	84.32	61.35	22.98	1.91	39.25
	Leaf	0.1942	9.88	72.94	40.39	32.56	14.03	53.83
	Rhizome	0.0106	2.83	78.49	50.98	27.51	2.76	61.93
	Shoot	0.0079	1.79	87.02	53.60	33.41	3.73	60.03

Table 4. The relationship between vole feeding preference of Yushan cane parts and their nutrient contents based on simple linear regressions. N = 36 for all analyses. The levels of significance were denoted as ** $p < 0.01$, *** $p < 0.001$.

Nutrient Variable	β	Adjusted R^2	$F_{1,34}$
Ash	0.0426	0.5959	52.62***
NDF	-0.0194	0.6749	73.67***
ADF	-0.0147	0.7548	108.74***
Hemicellulose	0.0266	0.4230	26.66***
CP	0.0247	0.7342	97.68***
Water	0.0052	0.1853	8.86**



Table 5. The relationship between vole feeding preference of selected Yushan cane parts and their nutrient contents based on a stepwise multiple regression, N = 36. The levels of significance were denoted as ** $p < 0.01$, *** $p < 0.001$.

Nutrient Variable	Parameter Estimate		Regression Model	
	β	t -value	Adjusted- R^2	$F_{3,32}$
ADF	-0.011	-3.41**		
CP	0.017	2.87**	0.7929	45.66***
Ash	-0.017	-1.53		



Table 6. Statistical results of logistic regressions comparing the shoot-culm ratios between the vole-exclusion treatment and control. The numbers in the cells give Chi-square values. The parentheses give p -values.

Month	Plot	Treatment	Time	Treatment x Time
May-2008 vs. May-2009	15.73 (0.0077)	2.07 (0.1503)	8.82 (0.0030)	18.24 (<0.001)
May-2008 vs. Oct-2009	2.93 (0.7110)	0.87 (0.3510)	21.20 (<0.001)	16.29 (<0.001)



Table 7. Statistical results of logistic regressions comparing the shoot-culm ratios between the canopy-litter treatment and control. The numbers in the cells give Chi-square values. The parentheses give p -values.

Month	Reduce canopy vs. Control				Decrease Litter vs. Control			
	Plot	Treatment	Year	Treatment x Year	Plot	Treatment	Year	Treatment x Year
May-2008 vs. May-2009	11.77 (0.3810)	9.66 (0.002)	13.23 (<0.001)	22.67 (<0.001)	13.82 (0.2433)	0.64 (0.4248)	0.88 (0.3475)	0.0006 (0.9803)
May-2008 vs. Oct-2009	15.02 (0.1818)	45.77 (<0.001)	0.86 (0.3529)	7.11 (0.0077)	16.49 (0.1239)	2.93 (0.0868)	7.88 (0.0050)	3.81 (0.0510)



Figures

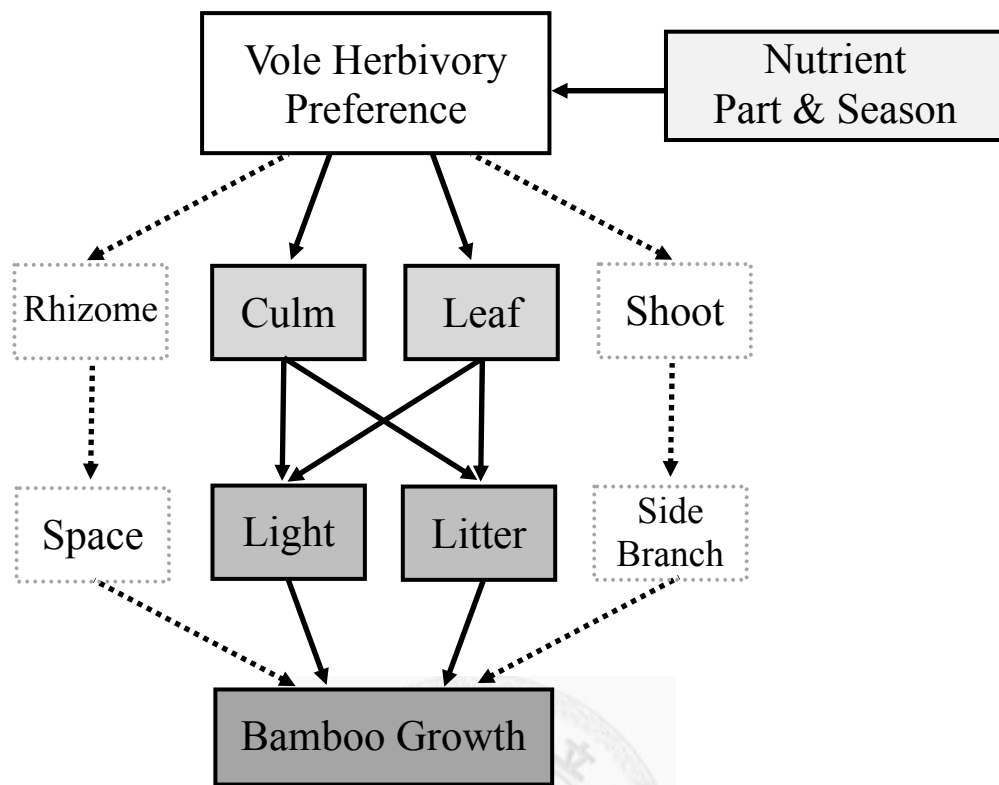


Fig. 1. The concept map for the current study. Variations in nutrient contents of different Yushan cane parts in different seasons affect the consumption by voles. In turn, the differential consumption of parts could vary the availability of underground space, penetrating light from canopy, the amount of ground litter accumulated, and side branches produced, which influence the growth of Yushan canes.

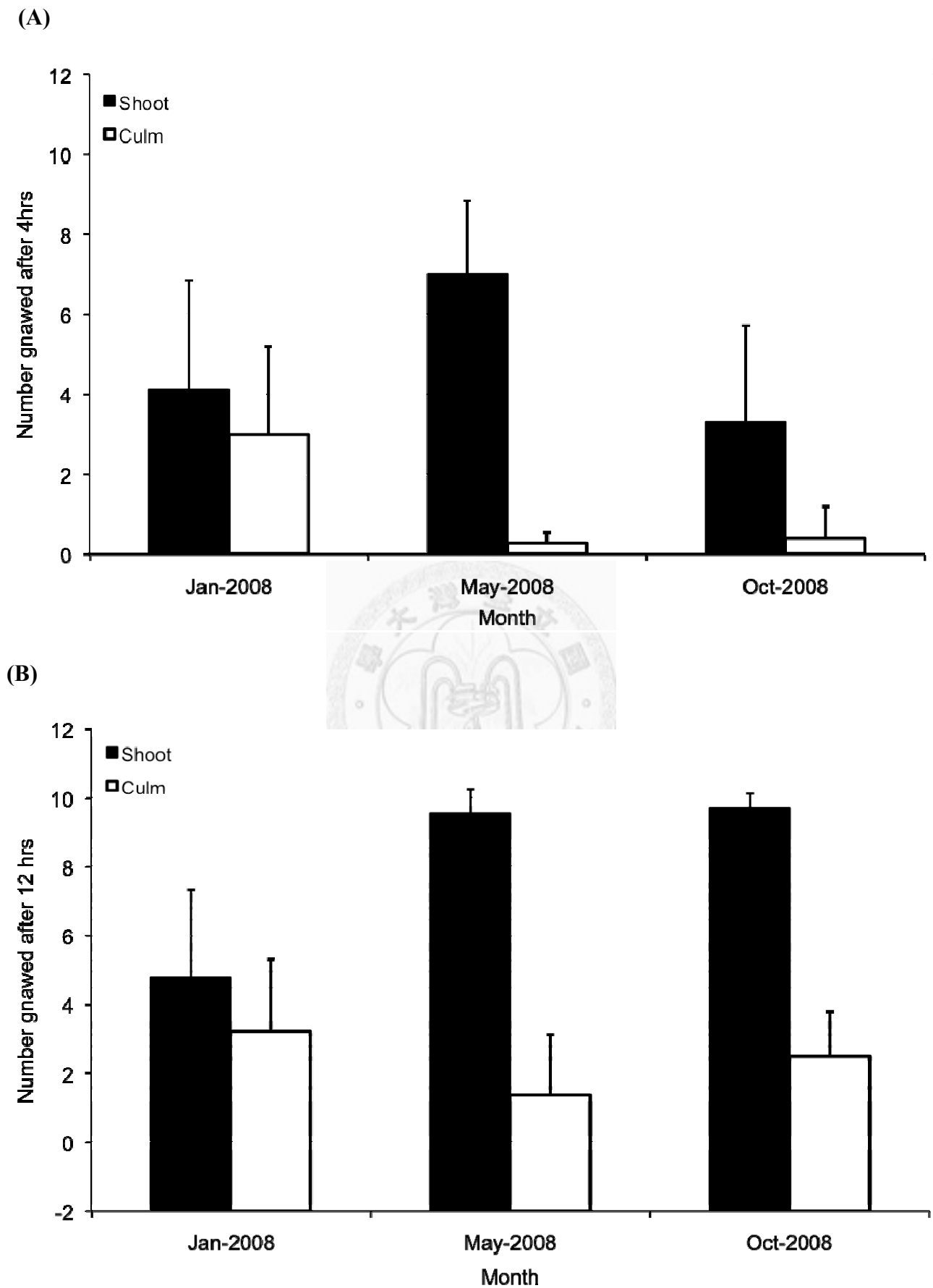


Fig. 2. The numbers (MEAN \pm 95% CI) of >1-year culms and first-year shoots gnawed by Taiwan voles (A) during the first 4 hrs., and (B) over the whole 12 hrs. of bite trials in three seasons.

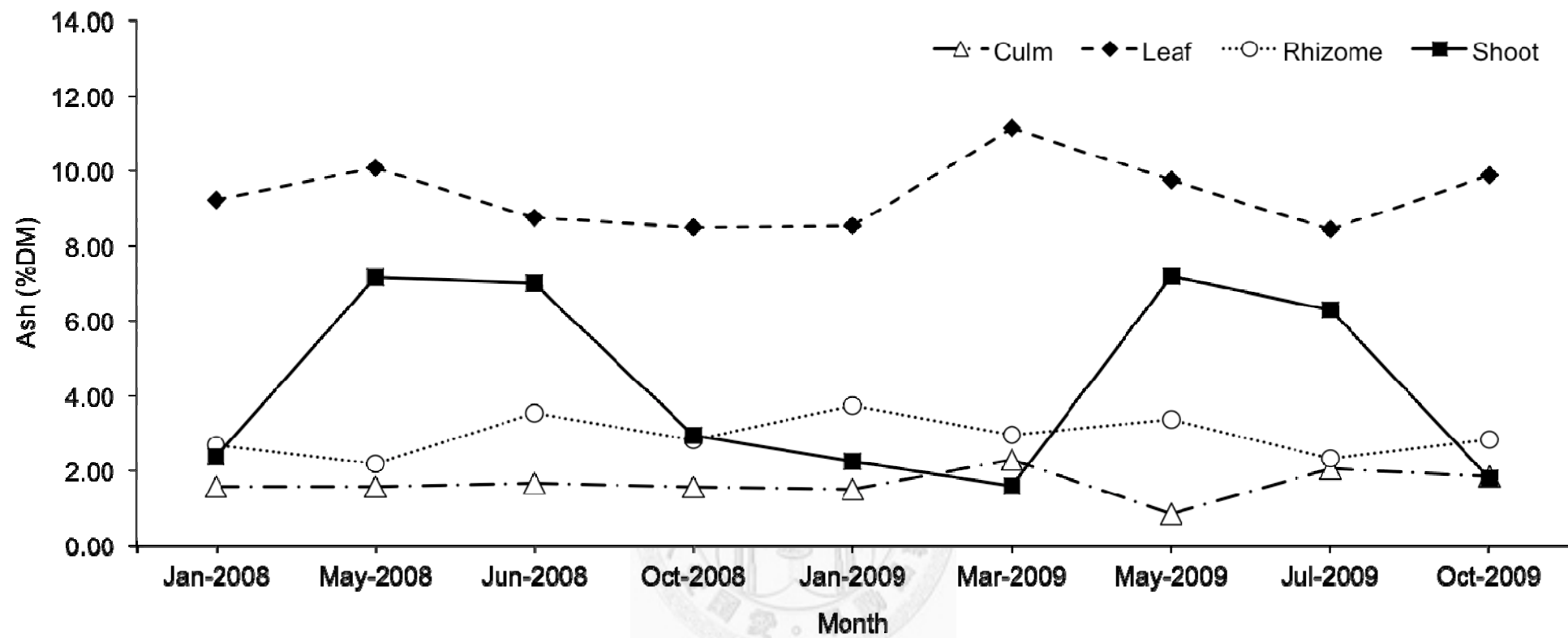


Fig. 3. The amount of ash (in % dry matter weight) in different Yushan cane parts in different seasons and years.

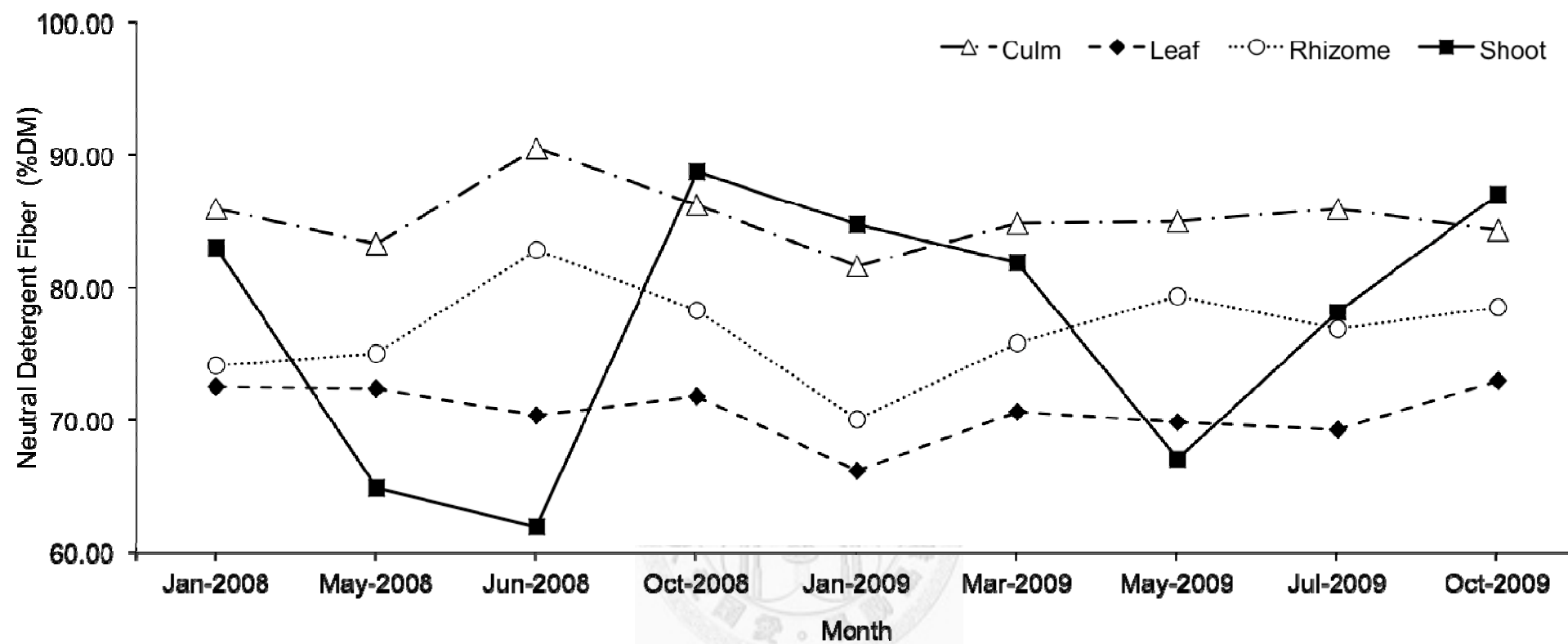


Fig. 4. The amount of neutral detergent fiber (in % dry matter weight) in different Yushan cane parts in different seasons and years.

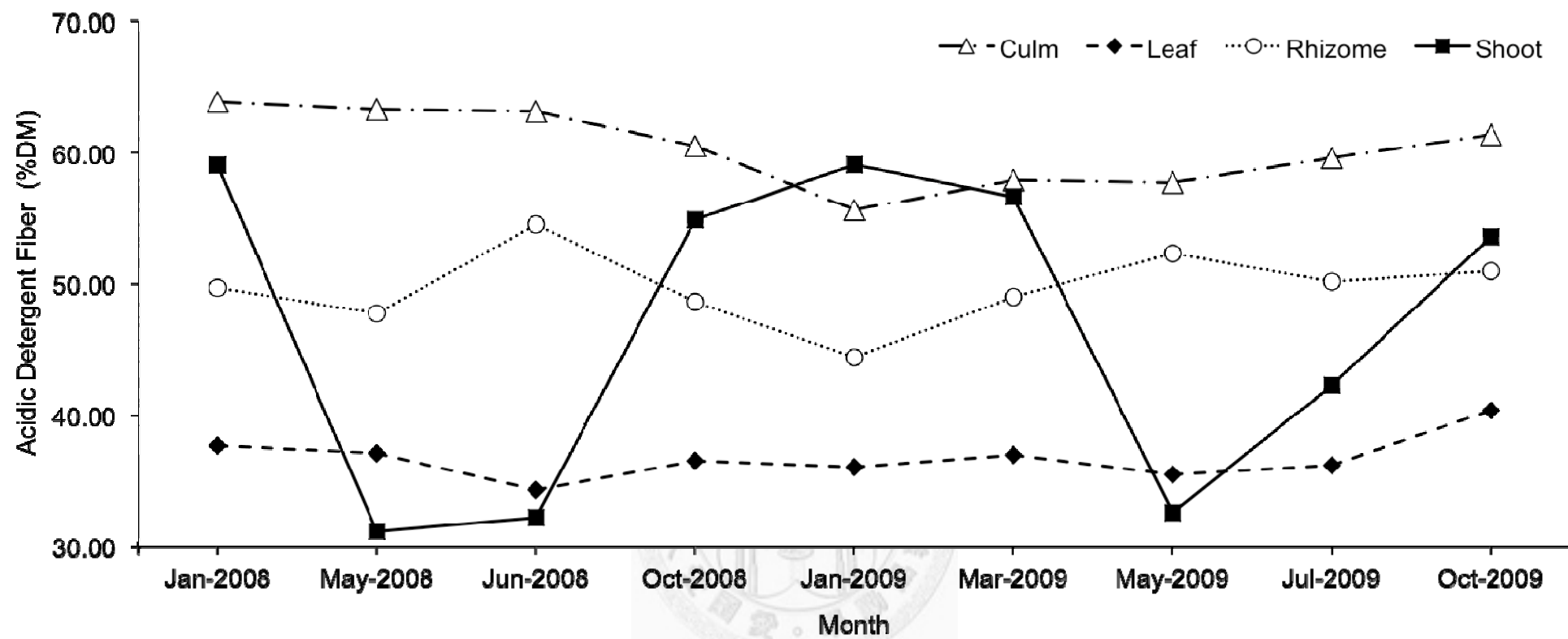


Fig. 5. The amount of acidic detergent fiber (in % dry matter weight) in different Yushan cane parts in different seasons and years.

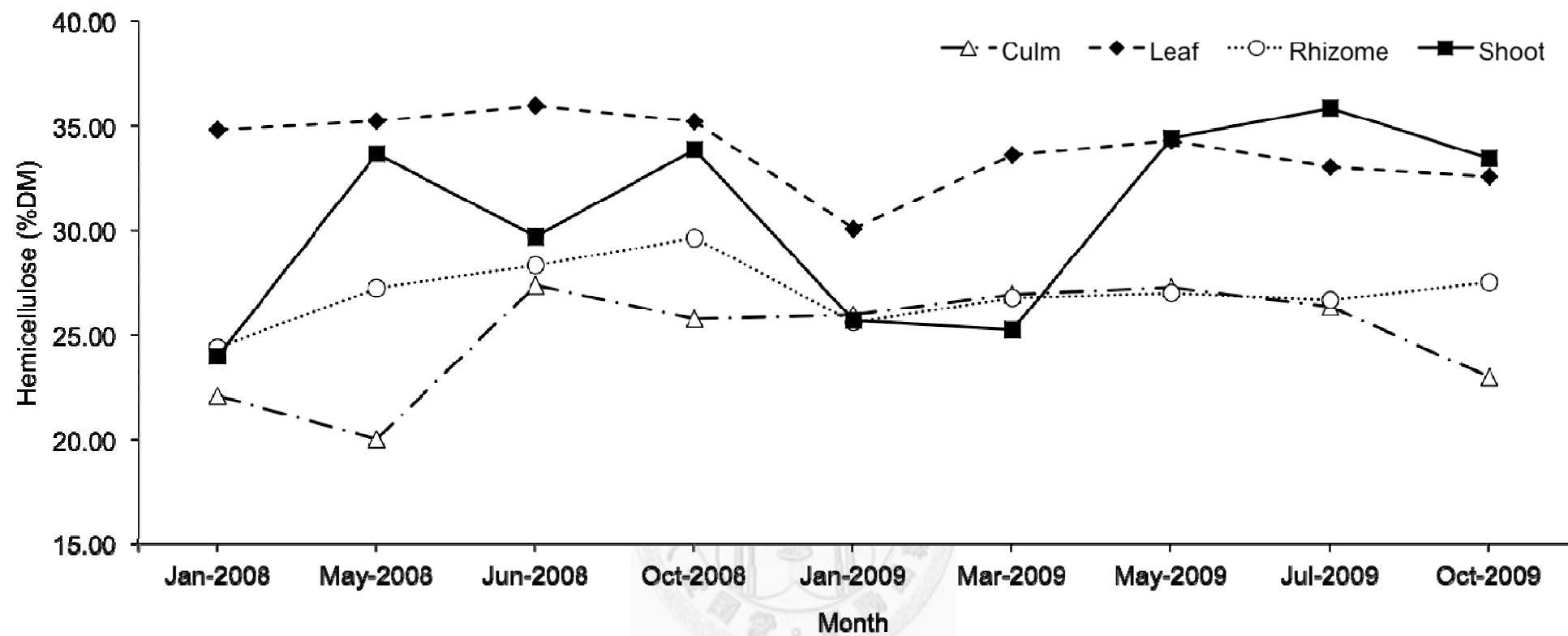


Fig. 6. The amount of hemicellulose (in % dry matter weight) in different Yushan cane parts in different seasons and years.

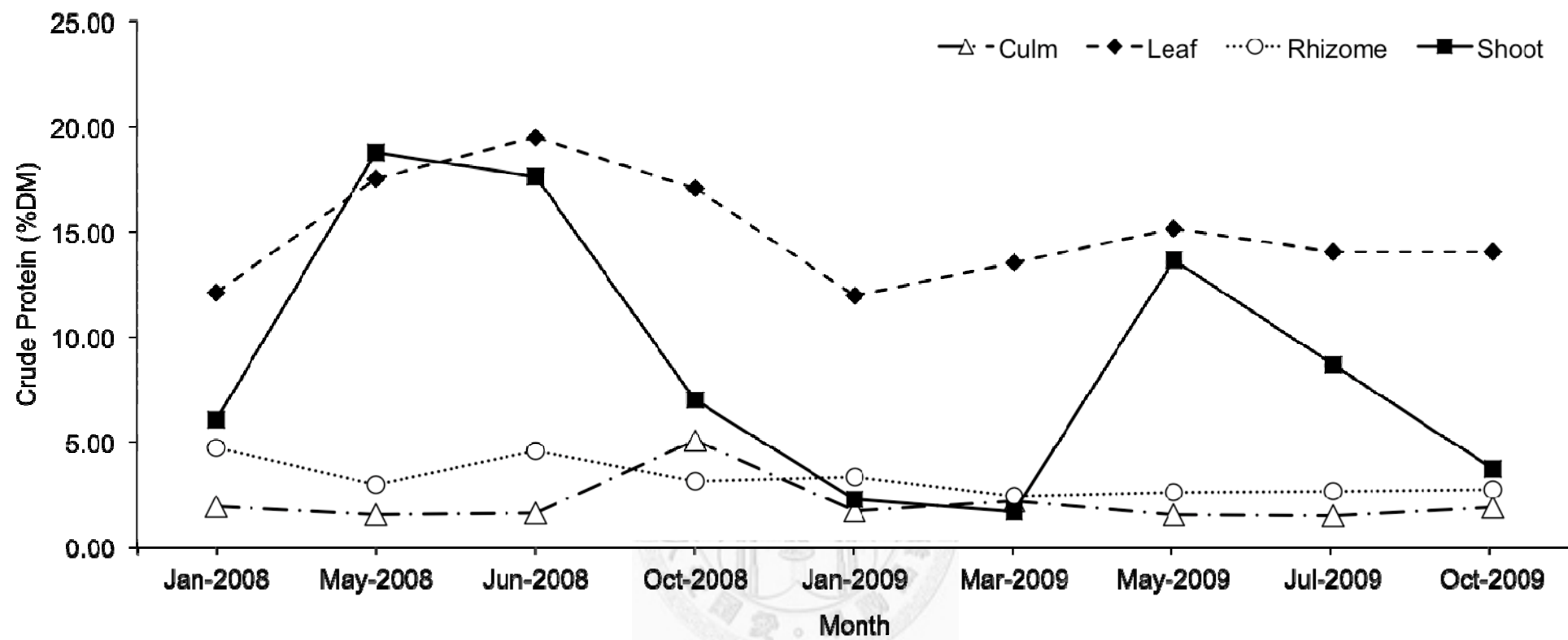


Fig. 7. The amount of crude protein (in % dry matter weight) in different Yushan cane parts in different seasons and years.

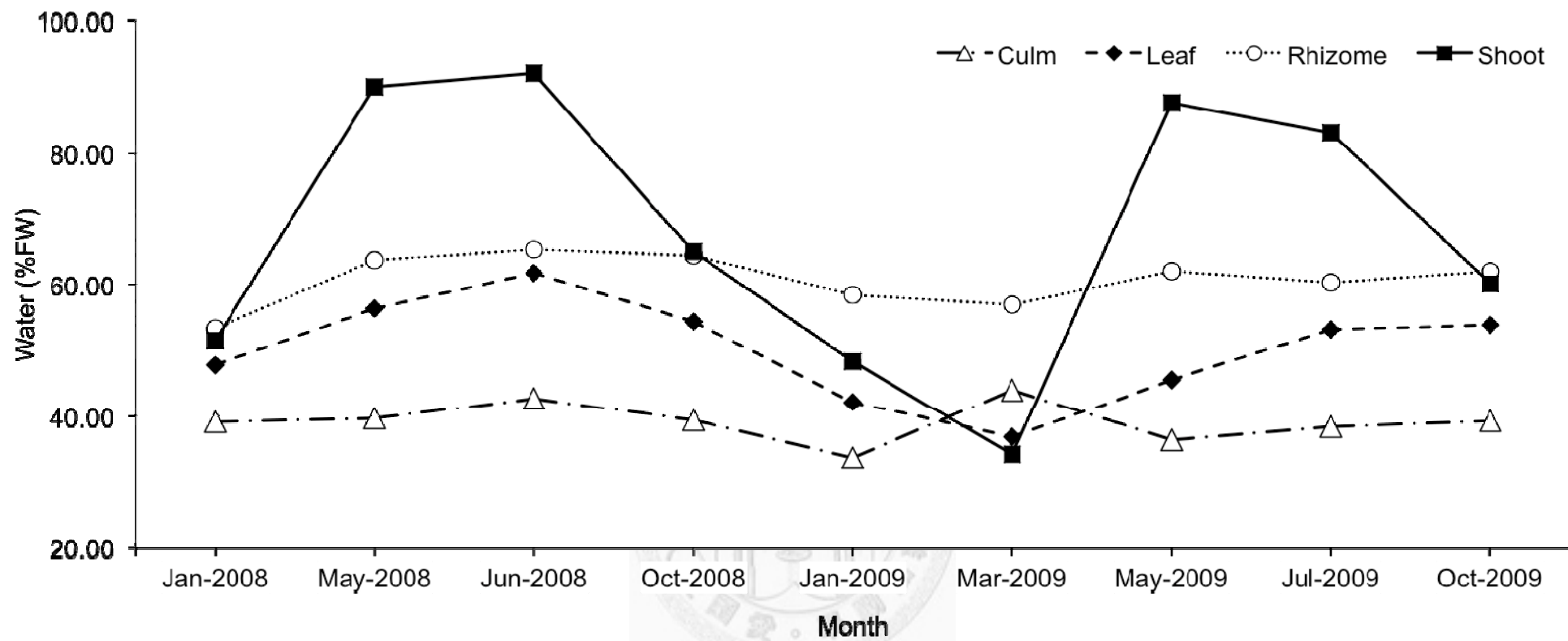


Fig. 8. The amount of water (in % fresh weight) in different Yushan cane parts in different seasons and years.

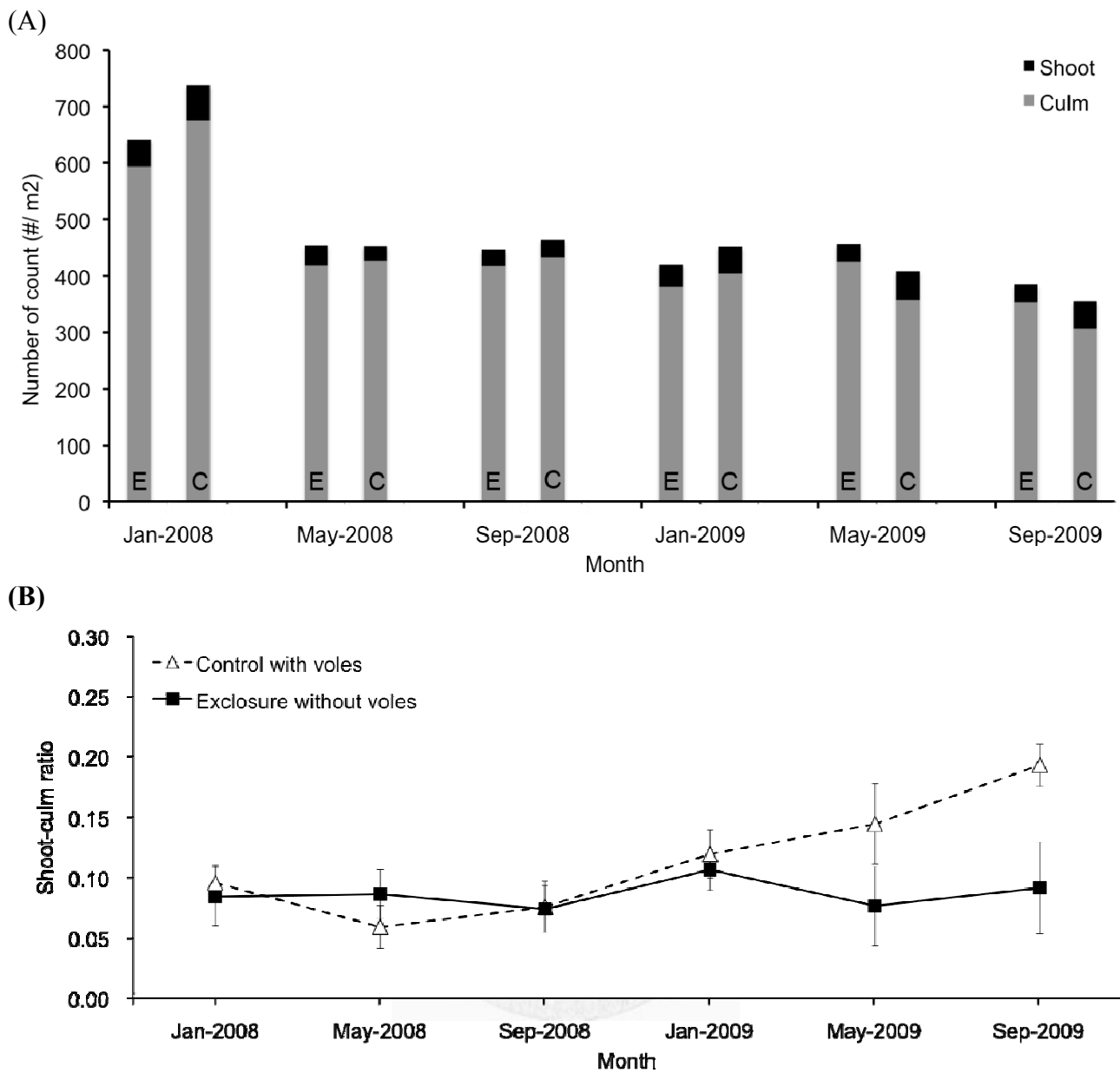


Fig. 9. (A) the number of shoots and culms, and (B) the shoot-culm ratios (MEAN \pm 95% CI) of E: vole-exclusion and C: control treatments in different seasons and years.

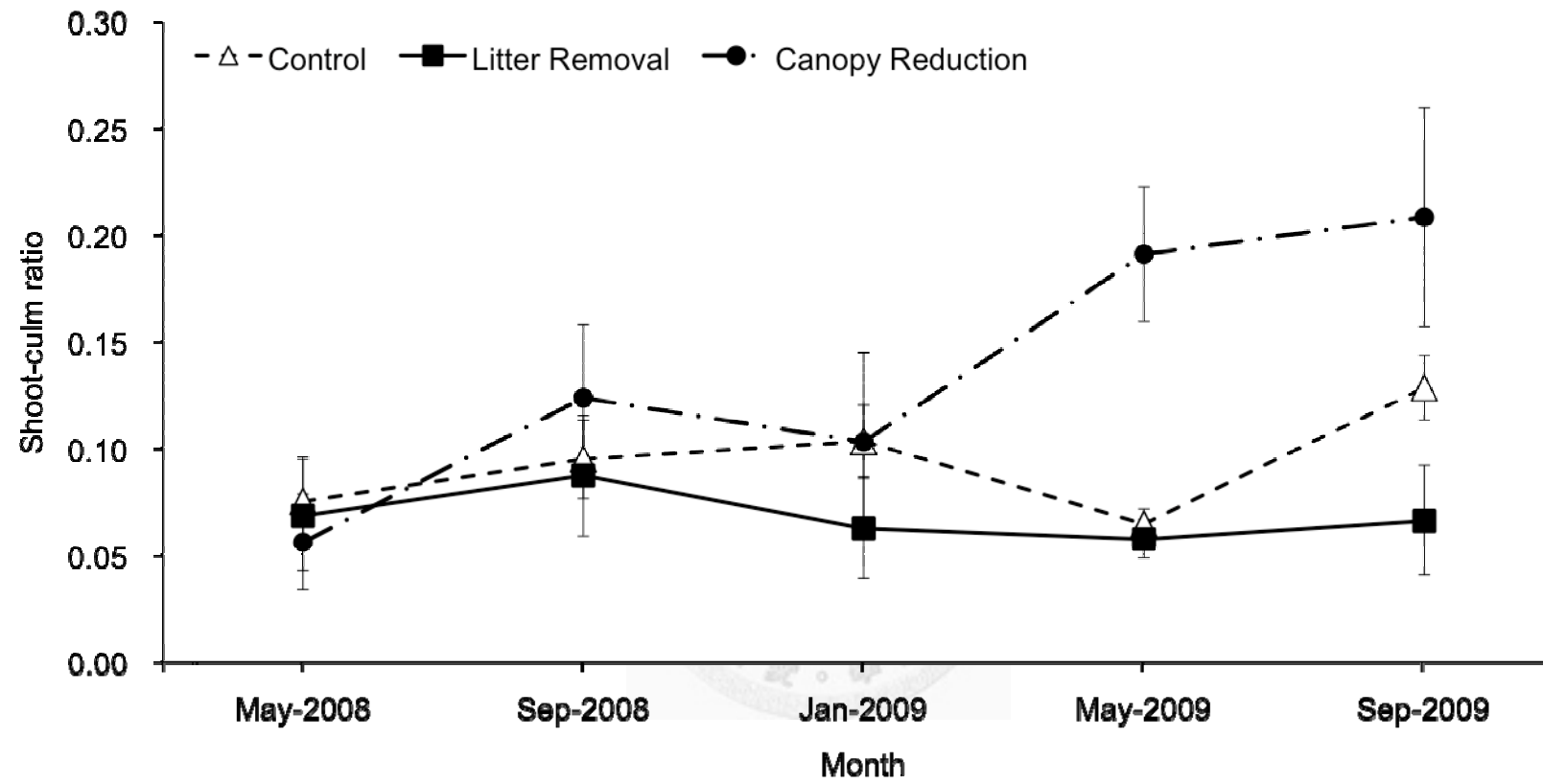


Fig. 10. The shoot-culm ratios (MEAN \pm 95% CI) of canopy reduction, litter removal, and control treatments in different seasons and years.

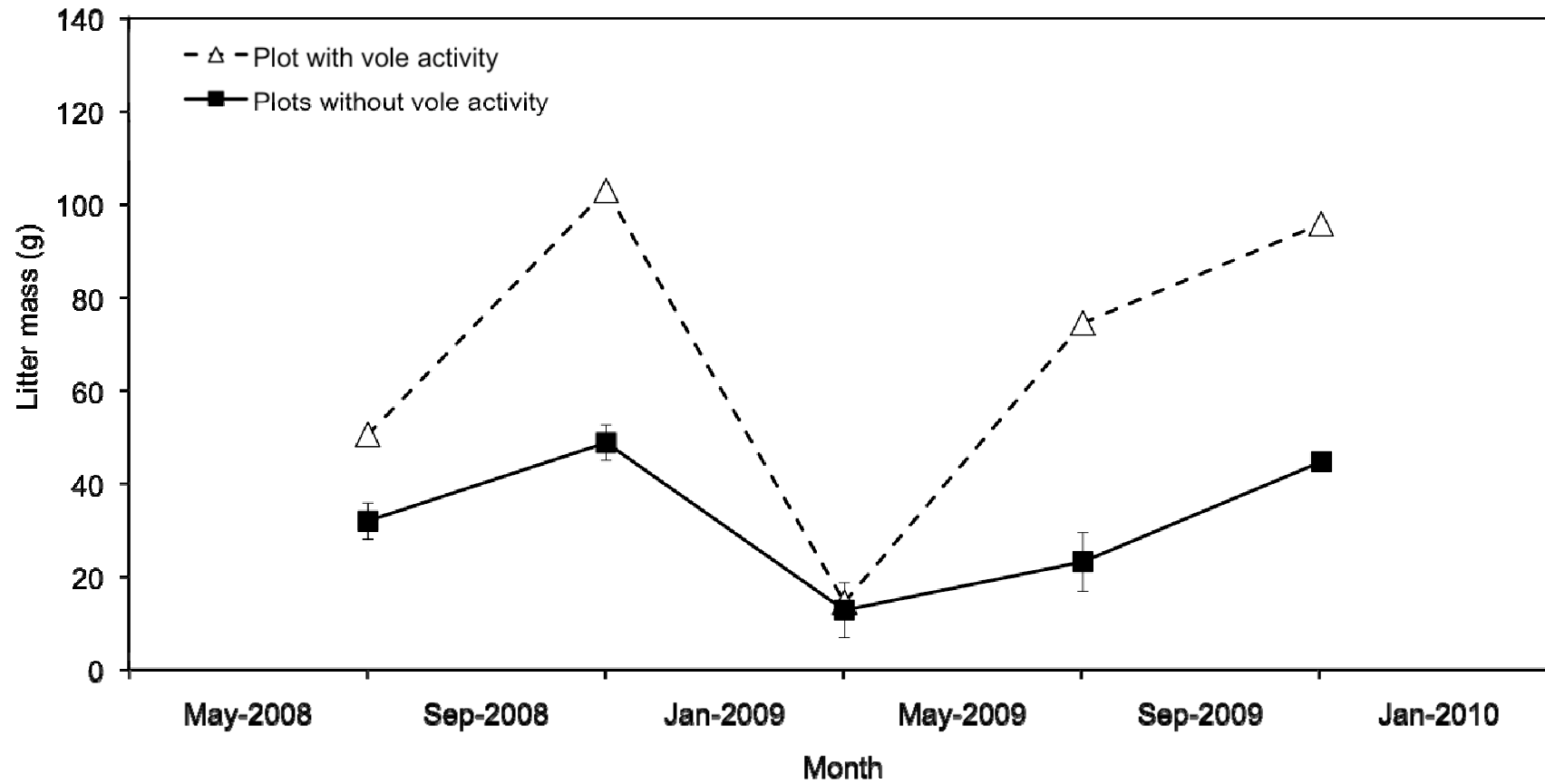


Fig. 11. The amount of Yushan cane litter produced (mean \pm 95% CI) per 50 x 50 cm² area per time period in different years.

Appendix

(一) 水份(water)分析方法 (AOAC 2000)

磨碎後樣品精秤 1g 置於乾淨坩鍋，以 105°C 烘乾，後置於乾燥皿中，帶冷卻至室溫後秤重，即可得水份。

(二) 灰份(ash)分析方法 (AOAC 2000)

坩鍋洗淨後，以 600°C 灰化，避免先前樣品殘留。磨碎後樣品精秤 1g 置於乾淨坩鍋，以坩鍋蓋覆蓋後送入灰化爐，以 600°C 灰化 6 小時，使殘餘物不再有灰塊，呈現白色或灰白色。待溫度降至 150°C，取出坩鍋置於乾燥皿中冷卻至室溫後秤重，即可得灰份。

(三) 中洗纖維(neutral detergent fiber, NDF)分析方法 (Vansoest et al. 1991)

取 30g sodium lauryl sulfate、18.6g EDTA、6.81g sodium borate decahydrate、4.56g anhydrous Na_2HPO_4 、10 mL 2-ethoxyethanol 溶於去離子水至 1 L，即得中洗溶液。以精秤方式取樣品 0.5g 置於無緣燒杯，加入 50 mL 中洗溶液、0.5g Na_2SO_3 、以及 2 mL Decalin，置於平板加熱器加熱，並加裝冷卻水回流裝置，沸騰 30 分鐘後在加入 50 mL 中洗溶液，並加入 100 μL heat stable α -amylase，再持續加熱沸騰 30 分鐘。之後移至玻璃過濾坩鍋進行抽氣過濾，並以沸騰去離子水多次沖洗，最後以丙酮潤洗。裝載有殘餘物之玻璃坩鍋置於 105°C 烘乾 8 小時，移入乾燥皿冷卻至室溫後秤重，即可得中洗纖維重。

(四) 酸洗纖維(acid detergent fiber, ADF)分析方法 (Goering and van Soest 1970)

取 20g cetyl trimethylammonium bromide (CTBA) 加入 1 L 的 1 N H_2SO_4 中，待其完全溶解，即為酸洗溶液。以精秤方式取樣品 0.5g 置於無緣燒杯，並加入 100 mL 酸洗溶液，置於平板加熱器加熱 60 分鐘，並加裝冷卻水回流裝置，之後移至玻璃過濾坩鍋進行抽氣過濾，並以沸騰去離子水多次沖洗，最後以丙酮潤洗。裝載有殘餘物之玻璃坩鍋置於 105°C 烘乾 8 小時，移入乾燥皿冷卻至室溫後秤重，即可得酸洗纖維重。

(五) 粗蛋白質(crude protein)分析方法 (AOAC 2000)

秤取標準品 $(\text{NH}_4)_2\text{Fe}(\text{SO}_4)_2 \cdot 6\text{H}_2\text{O}$ 及樣品 0.3g，分別將空白組、標準品及樣品以 10 mL 98% 濃硫酸以及一枚含硒催化劑裝置於粗蛋白消化管及加熱分解器，並連接廢氣淨化裝置，加熱 1 小時至樣品反應呈現透明為止。將反應完成後的消化管裝置於凱氏氮蒸餾機器，加入去離子水 60 mL 及 50% NaOH 溶液 40 mL，設定蒸餾 5 分鐘，之後以內含有混合 methyl red 及 bromocresol green 指示劑之 25 mL 4% 硼酸溶液接收游離 NH_3 ，並以 0.1 N H_2SO_4 滴定，計算出粗蛋白質率。