

## Effects of spatial distribution on plant associational defense against herbivory

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### Abstract

Several studies have shown that consumption of a focal plant by herbivores depends not only on its own defense traits but also on the characteristics of the neighboring plants. A number of studies have reported on plant associational defense in relation to neighboring plant palatability but the effect of the spatial distribution of the focal plant within patches of different neighboring plants has received less attention. We conducted a manipulative experiment to determine whether and how spatial distribution of focal plants affects the associational defense between plant species. In our experimental setup sheep encountered two patches varying in spatial distribution of the focal plant within patches (dispersed or clumped) and patch quality, good patch and bad patch, where the focal plant, *Lathyrus quinquenervius*, was neighbored to high- (*Chloris virgata*) or low-palatable (*Kalimeris integrifolia*) species, respectively. Results showed that, when focal plants were dispersed within both patches, the risk of attack was significantly lower for focal plants in the patches with low- than high-palatable neighbors, indicating associational defense. Alternatively, when focal plants were clumped within both patches, they were consumed in bad-patch as much as in good-patch plots, which indicates the absence of associational defense. However, if the focal plants have different spatial distributions in the two patches (dispersed in good-patch and clumped in bad-patch or vice versa), sheep foraging success for focal plants was greatly reduced in dispersed spatial pattern irrespective of the palatability of neighboring plants. Therefore, we concluded that spatial distribution is as important as traits of neighboring plants in predicting vulnerability of the focal plant to grazing by generalist herbivores. The outcome of plant associational defense for different types of neighborhood strongly depends on the magnitude of herbivore foraging selectivity between and within patches, which further depended on the contrasts between plant species or between patches.

### Zusammenfassung

Verschiedene Studien haben gezeigt, dass die Konsumption einer bestimmten Pflanzenart durch Herbivore nicht nur von ihrer eigenen Abwehr abhängt, sondern auch von den Eigenschaften der benachbarten Arten. Eine Reihe von Studien hat über die nachbarschaftliche Abwehr von Pflanzen in Bezug auf die Genießbarkeit der benachbarten Pflanzen berichtet, aber der Effekt der räumlichen Verteilung der fokalen Art auf Flächen mit unterschiedlichen Nachbararten hat weniger Aufmerksamkeit erfahren. Wir führten ein manipulatives Experiment durch, um zu bestimmen ob und wie die räumliche Verteilung der fokalen Pflanze die nachbarschaftliche Abwehr unter Pflanzenarten beeinflusst. In unserem Experiment trafen Schafe auf jeweils zwei Versuchsbeete mit unterschiedlicher räumlicher Verteilung der fokalen Art (zerstreut oder geklumpt) und/oder

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unterschiedlicher Flächenqualität, “gutes Beet” und “schlechtes Beet”, wobei die fokale Art, *Lathyrus quinquerivius*, mit einer guten Futterpflanze (*Chloris virgata*) bzw. einer schlechten Futterpflanze (*Kalimeris integrifolia*) vergemeinschaftet war. Die Ergebnisse zeigten, dass wenn die fokale Art in beiden Versuchsbeeten zerstreut verteilt war, das Risiko gefressen zu werden für fokale Pflanzen, die mit dem gut genießbaren Nachbarn zusammenstanden, signifikant geringer war als für solche mit dem wenig genießbaren Nachbarn, was auf Gemeinschaftsabwehr hindeutet. Wenn andererseits die fokalen Pflanzen auf beiden Versuchsbeeten geklumpt standen, wurden sie auf “schlechten Beeten” ebenso stark befreßen wie auf “guten Beeten”, was auf das Fehlen von nachbarschaftlicher Abwehr hinweist. Wenn indessen die fokalen Pflanzen unterschiedliche räumliche Verteilung auf den beiden Beeten haben (zerstreut auf dem “guten Beet” und geklumpt auf dem “schlechten Beet”, oder umgekehrt), war die Nahrungssuche der Schafe bei zerstreuter Verteilung unabhängig von der Genießbarkeit der Nachbarart deutlich weniger erfolgreich. Daher schließen wir, dass die räumliche Anordnung ebenso wichtig ist wie die Eigenschaften der Nachbarpflanzen, wenn die Gefährdung einer fokalen Pflanze durch generalistische Herbivore vorhergesagt werden soll. Das Resultat nachbarschaftlicher Abwehr für unterschiedliche Typen von Nachbarschaft hing stark von der Selektivität der Herbivoren innerhalb und zwischen den Versuchsbeeten ab, was desweiteren von den Unterschieden zwischen den Pflanzen bzw. zwischen den Versuchsbeeten beeinflusst wurde.

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**Keywords:** Associational plant defense; Spatial distribution; Selectivity; Herbivory; Neighboring plant contrast

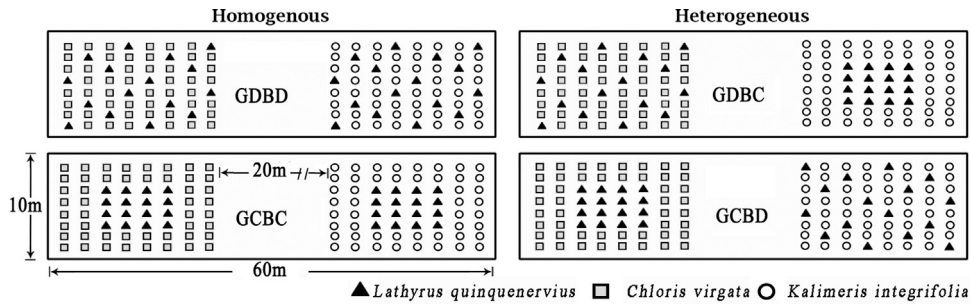
## Introduction

Herbivores are important agents of change in ecosystems (Hobbs 1996). Plants use different defense mechanisms (chemical and mechanical) to decrease damage from herbivores (Cooper & Owen-Smith 1986; Provenza & Balph 1990). Neighboring plants can either decrease (associational defense) or increase (associational susceptibility) the vulnerability of a focal plant beyond its innate ability to avoid herbivory (Atsatt & O’Dowd 1976; Pfister & Hay 1988; Callaway, Kikodze, Chiboshvili, & Khetsuriani 2005). This in turn depends on the scale at which herbivores make foraging decisions.

Herbivores make foraging decisions at several hierarchical scales. Plant communities are chosen at the landscape scale, patches at the plant-community scale, and individual plants (or plant parts) at the bite scale within a patch (Senft et al. 1987; Bailey et al. 1996). At patch level, herbivores can make selection decisions between patches and within a patch, and this has important consequences for vulnerability of individual plants and, subsequently, for the outcome of associational relationships. According to the associational defense hypothesis (syn. associational resistance, associational plant refuge or plant defense guild; Tahvanainen & Root 1972; Atsatt & O’Dowd 1976; Pfister & Hay 1988; Hjalten, Dannell, & Lundberg 1993; Hambäck, Agren, & Ericson 2000) the focal plant gains protection in low- rather than high-quality patches. This is because herbivores avoid low quality patches in favor of high quality patches. This, in turn, will increase focal plant vulnerability in high quality patches leading to associational susceptibility (Parker & Root 1981; Thomas 1986; White & Whitham 2000). According to the concept of neighboring contrast defense (Bergvall, Rautio, Kesti, Tuomi, & Leimar 2006; Rautio, Kesti, Bergvall, Tuomi, & Leimar 2008) in a situation where there is no patch choice or herbivores are not discriminating between patches, the focal plant gains protection in the high-quality patch. This

is because herbivores avoid the focal plant in favor of a more preferred or palatable neighbor. On the other hand, the focal plant is more vulnerable in low-quality patches as herbivores selectively consume it, leading to neighboring contrast susceptibility.

The neighboring associational relationship is a complex plant-to-plant interaction in which the outcome of the interaction affects and is affected by the herbivores. The herbivore’s decision to stay or leave a patch is made in response to different patch characteristics (Senft et al. 1987; Bergvall et al. 2006). Palatability of plants is considered the determining factor of plant associational defense (Callaway et al. 2005; Bergvall et al. 2006). Hjalten et al. (1993) using voles (*Microtus agrestis*) and hares (*Lepus timidus*) showed that consumption of moderately preferred white birch (*Betula pubescens*) decreased when presented with less palatability gray alder (*Alnus incana*), indicating associational defense. However, when white birch was presented with preferred rowan (*Sorbus acuparia*), the intake increased showing associational susceptibility. Such an associational relationship can in turn be affected by the level of defense or degree of contrast between neighboring plants. Bergvall and Leimar (2005) showed significant difference in the consumption of low-defended food by fallow deer (*Dama dama*) at different levels of tanning concentrations. That is, intake of low-defended food was significantly higher in twofold than in fivefold tanning concentration difference. Further, there is increasing evidence that the spatial distribution pattern affects foraging decisions of herbivores and, subsequently, the neighboring plant association (Hambäck et al. 2000; Hewitson, Dumont, & Gordon 2005; Bergvall, Rautio, Sirn, Tuomi, & Leimar 2008; Wang et al. 2010a). Such spatial distribution patterns affect searching success for preferred species, which subsequently influences foraging costs of the herbivore (Dumont, Maillard, & Petit 2000; Parsons & Dumont 2003). Results showed that foraging success by herbivores for preferred species was greater in a clumped than a dispersed distribution



**Fig. 1.** Spatial arrangement of the treatments, focal plant (*Lathyrus quinquenervius*) neighbored to highly palatable (*Chloris virgata*) in good-patch and to low palatable (*Kalimeris integrifolia*) in bad-patch. Four treatments: GDBD, GCBC, GCBD and GDBC – good (G) and bad (B) patches with dispersed (D) or clumped (C) distribution pattern.

pattern (Clarke, Welch, & Gordon 1995; Dumont, Maillard, & Petit 2000; Parsons & Dumont 2003). On the other hand, a random dispersion of an unpalatable plant population can greatly reduce intake of the palatable species (Wang et al. 2010b).

Here, we investigated the effect of the spatial pattern of a focal plant on plant associational defense in relation to palatability of neighboring plants. Unlike previous investigations, which presented food in the form of pellets or hays, our experimental setup attempted to simulate a natural situation by offering plants grown in pots and at the same time these pots were used to create a well-defined spatial pattern. We used three native plant species: *Lathyrus quinquenervius* as the focal plant, *Chloris virgata* the highly palatable neighbor and *Kalimeris integrifolia* as the low-palatable neighbor. Focal plant was neighbored to *C. virgata* and *K. integrifolia* to create good and bad patches respectively either with dispersed or clumped distribution pattern. We specifically addressed the following questions: (1) Does the focal plant gain protection when it is associated with a highly palatable or a less palatable neighbor? (2) How will spatial distribution (clumped or dispersed) of the focal plant among different neighbor plants affect its associational defense? (3) What are the mechanisms by which spatial pattern affects plant associational defense?

## Materials and methods

### Study species

The experiment was conducted at the Grassland Ecological Research Station of Northeast Normal University, Jilin Province, PR China. A total of 12, two-year-old, female Northeast fine-wool sheep (body weight  $34.2 \pm 0.81$  kg, mean  $\pm$  SE) were used.

Three native plant species from three functional groups with different palatability to sheep were used. *L. quinquenervius*, a legume, was our focal plant, and *C. virgata*, a grass, and *K. integrifolia*, a forb, were the two neighboring plants with high and low palatability to sheep, respectively. The relative palatability of the three species to sheep was calculated as the biomass consumed of each species related to the

total biomass consumed (Wang et al. 2010a; Huang, Wang, Wang, Li, & Alves 2012). Relative preference (r.p.) for *C. virgata*, *L. quinquenervius* and *K. integrifolia*, was 0.45, 0.36 and 0.19, respectively. Plants were collected from adjacent grassland and transplanted into separate pots (20 cm diameter  $\times$  15 cm high) in early June. All plants were cut to about the same height, approximately 10 cm above ground and covered about the same surface area of the pot (see Appendix A). Plants were watered twice a week and allowed to regenerate.

## Treatment and experimental design

Four treatments with different distribution patterns were created. Each treatment comprised of two patch qualities, good-patch and bad-patch, with either clumped or dispersed spatial pattern. In the good patch, the focal plant, *L. quinquenervius* was neighboring the highly palatable species, *C. virgata*, while in the bad-patch arrangement, the focal plant was neighboring the lowly palatable species, *K. integrifolia*. In the dispersed spatial pattern, focal plants were systematically randomized within the patch, while in the clumped spatial pattern, the focal plant was aggregated in the center of the patch and surrounded by the neighboring plant (Fig. 1). The two patches within the treatments were either homogeneous (both good and bad patches having dispersed (GDBD) or clumped (GCBC) distribution patterns) or heterogeneous (good-patch clumped and bad-patch dispersed (GCBD) or vice versa (GDBC)) (Fig. 1). In the experimental setup, the two patches were positioned at the two ends of a 60 m  $\times$  10 m experimental enclosure. Each patch consisted of 36 pots (16 focal and 20 neighbor plants). The distance between the two patches was 20 m. Within a patch, each pot was placed 2 m vertically and 1 m horizontally apart from neighboring pots.

## Field preparation and experimental procedure

Experiments were conducted in July/August 2011. The 60 m  $\times$  10 m experimental area was fenced and all vegetation was removed before the trial. A patch was defined as rectangular 8 m  $\times$  16 m area with 36 pots. The sheep were trained to walk and forage in the field in groups before the

start of the experiment. The 12 sheep were randomly divided into four groups of three sheep. The trials were conducted during 0400–0800 h, the normal grazing time for sheep. During trials, one group of three sheep was released from holding pens into the experimental area through a middle gate located between the two patches. A group was allowed to feed for 15 min and then moved back to holding pens. The four groups of three sheep were tested only once a day. Each treatment was repeated four times. After each trial, all pots were replaced. To preclude effects of spatial memory on diet selection, the position of the two patches was exchanged between trials. Changes in height of all plant species before and after grazing were recorded. Moreover, each plant species from a sample of 20 pots were cut above surface and the height of each plant (and branches) were measured. Finally the plant species were dried in an oven at 70 °C for 48 h and is used to get dry mass vs. height regression equation.

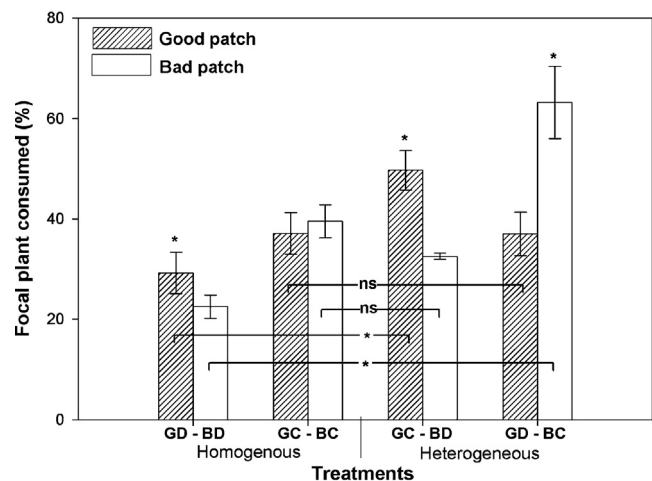
## Data analysis

Dry mass intake was calculated based on change in plant height (before and after grazing) using the regression equation of height vs. dry mass. Intake of sheep was calculated as the percentage of the dry mass consumed. The group of three sheep was the unit of replication. Behavioral data of individual sheep were averaged for each group.

To analyze the effects of both spatial pattern and patch quality on focal associational defense, a comparison in the intake of the focal plant was compared between good and bad patches. The effect of spatial distribution pattern between treatments was analyzed by comparing patches of the same quality neighbored to the same patch. For example GD and GC were compared by comparing GD (in GDBC) to GC (in GCBC), since both are neighbored to BC in these treatments. Further, the effect of spatial pattern was analyzed by comparing whole-plot consumption of the focal plant between treatments. Overall sheep selectivity within and between patches, as indicated by the difference between the composition of the diet and that of the available plants (Laca & Demment 1996), was examined. The overall selectivity index (OSI), was determined by the following equation (Wang et al. 2010a; Huang et al. 2012):

$$OSI = \frac{\sum_{i=1}^n (q_i - p_i)^2}{\max_{1 < i < n} \{1 - 2q_i + \sum_{i=1}^n q_i^2\}}$$

where ' $p_i$ ' is the proportion of the  $i$ th food (or patch) in the consumed diet, ' $q_i$ ' is the proportion of the  $i$ th food (or patch) in the given diet, and ' $n$ ' is number of species (or patches) offered. OSI=0 when the same proportions of each food (or patch) offered are consumed (i.e., completely unselective), and OSI=1 when only one food type is consumed (i.e., completely selective). Foraging selectivity within-patches was calculated based on sheep consumption of different plant species within a patch. Total food consumption of the



**Fig. 2.** Comparison of focal plant intake (% consumed,  $\pm 1$  SE,  $n=4$ ) between patches as affected by patch quality (G: good-patch or B: bad-patch) and spatial arrangements (C: clumped or D: dispersed). Values with asterisks are significantly different ( $p < 0.05$ ).

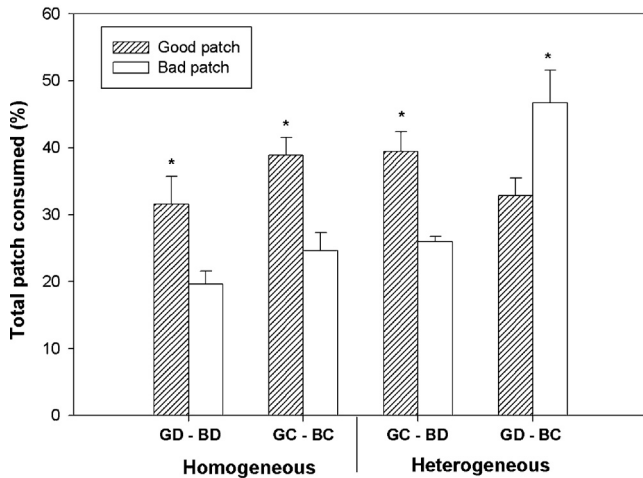
different patches was used to calculate foraging selectivity between patches.

All the above comparisons were made using two-way ANOVA, followed by Duncan's test for post hoc comparison where the significance level was set to  $p=0.05$ . The statistical analyses were conducted using SAS 6.12 statistical package (SAS Institute Inc. 1989). Assumptions of normality and heteroscedasticity were tested prior to analysis.

## Results

In the homogenous treatment (GDBD), intake of the focal plant was significantly lower ( $p < 0.05$ ) in bad-patch than in good-patch. Similarly, when the distribution pattern of the focal plant in good patches was changed to clumped in the heterogeneous treatment (G CBD) intake was still lower in bad-patch than in good-patch. However when the distribution pattern of the focal plant in bad-patch was changed from dispersed (GDBD) to clumped (GDBC) the intake was greater in bad-patch than in good-patch. In the homogeneous treatment with both patches clumped (GCBC), sheep consumption of the focal plant in bad-patch was as high as in good-patch (Fig. 2). However, when spatial pattern of either patch was changed to dispersed in heterogeneous treatments (GDBC and GCBD), focal plant intake was significantly lower for dispersed than clumped patterns regardless of patch quality ( $p < 0.05$ ).

Comparing intake of the focal plant between patches with different spatial patterns but of the same quality, showed that the focal plants were better defended in the dispersed than in the clumped distribution pattern both in good and bad patches when the neighboring patches were dispersed ( $p < 0.05$ , Fig. 2). That is, between GD (in GDBD) and GC (in GCBD) or BD (in GDBD) and BC (in GDBC).

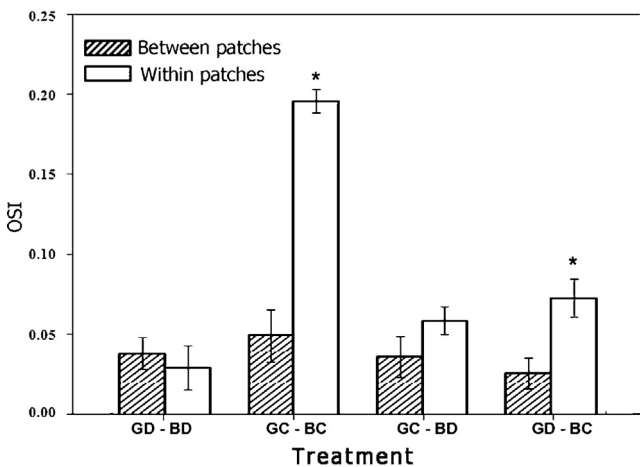


**Fig. 3.** Comparison of total patch (focal plus neighboring plants) consumption (% consumed, +1 SE,  $n=4$ ) between patches within treatments as affected by patch quality (G: good-patch or B: bad-patch) and spatial arrangements (C: clumped or D: dispersed). Values with asterisks are significantly different ( $p < 0.05$ ).

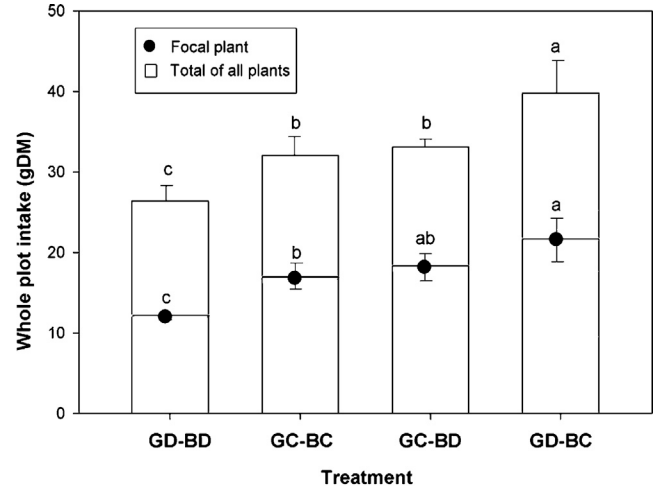
However, when the neighboring patches were clumped, intake of focal plants, regardless of patch distribution pattern, was not significantly different.

In all treatments except GDBC, total patch intake (focal plus neighboring plants) was greater in good-patch than in bad-patch (Fig. 3). In GDBC however, the intake was the reverse. Comparing OSI between and within patches, our results showed that within patches OSI was greater than between patches in treatments GCBC and GDBC, but not significantly different in GDBD and GCBD (Fig. 4).

Comparing total plot intake among treatments showed no significant difference between GCBC and GCBD. GDBD had the highest and GDBC the lowest total intake of all treatments ( $p < 0.05$ ; Fig. 5). Similarly, whole plot focal plant



**Fig. 4.** Sheep foraging selectivity, comparing overall selectivity index (OSI) between- and within-patches (mean  $\pm$  SE) for four groups of three sheep. Values with asterisks are significantly different ( $p < 0.05$ ).



**Fig. 5.** Whole plot consumption of focal plant and total of all plants (gDM +1 SE,  $n=4$ ) by sheep as affected by spatial distribution pattern. Values with different letters within each category in each treatment are significantly different ( $p < 0.05$ ).

intake in GDBD was significantly lower than all other treatments ( $p < 0.05$ ) and was highest in treatments GDBC but not significantly different to GCBD.

### Discussion

Our results suggest that sheep selectivity and the ultimate associational relationship between focal plant and its neighboring plant was the net outcome of the contrast within and between patches in terms of distribution pattern and patch quality. Differences between patches within a community can affect foraging selectivity, thereby affecting associational relationships between neighboring plants (de Vries Wallis & Daleboudt 1994; de Vries Wallis, Laca, & Demment 1999). In accordance to that, greatest associational defense for the focal plant was achieved when there was less contrast between as well as within patches in terms of spatial distribution pattern. Moreover, the spatial distribution of focal plants affected associational defense by changing the extent of sheep foraging at different spatial scales (between and within patches).

In homogenous treatments where both patches were dispersed (GDBD), intake of the focal plant as well as total patch intake was lower in bad-patch (BD) than in good-patch (GD), corresponding to associational defense in bad-patch. However, when the spatial pattern of bad-patch (BD) was changed to clumped in treatment GDBC, within-patch selectivity was greater than between-patch selectivity, which caused higher intake in bad-patch than in good-patch, leading to neighboring contrast susceptibility (Bergvall et al. 2006). Differences between patches (de Vries Wallis et al. 1999) and the magnitude of the differences (Bergvall & Leimar 2005) determine the foraging selectivity of herbivores within a community. Comparing relative preference (r.p.) for the focal plant, *Lathyrus quinquevicius* (r.p. = 0.36), to *K. integrifolia*

( $r.p. = 0.19$ ) in bad patches and to *C. virgata* ( $r.p. = 0.45$ ) in good-patches, shows that the magnitude of contrast is greater within bad patches than within good patches. Therefore, in BC, greater contrast in the clumped distribution pattern coupled with the greater contrast in relative preference for the focal plant has probably increased the intake of the focal plant. However, the dispersed distribution pattern in BD has possibly reduced sheep ability to selectively feed on the focal plant, which has led to associational defense. This is in agreement with a previous experiment, where random distribution of the less preferred species reduced intake of the preferred species (Wang et al. 2010a).

In treatment GCBC, the focal plant was centrally aggregated in both patches and therefore more easily encountered than its neighboring plants. Although, total patch intake was lower in bad-patch than in good-patch, the focal plant was equally vulnerable in bad- (BC) and good- (GC) patch. When one of the two clumped patches in GCBC was changed to the dispersed pattern (GCBD and GDBC), the effect of spatial pattern was more evident than patch quality. That is, irrespective of patch quality, our focal plant was better defended in dispersed patches than in clumped patches, and total patch intake as well as lower for dispersed conditions.

The dispersed pattern probably decreased the sheep's ability to locate preferred plant species, thereby decreasing consumption (Duncan & Young 2002). In accordance to that, in GCBD, intake in BD was lower than in GC leading to associational defense of the focal plant in the bad patch. On the other hand, foraging success of preferred species was greater in clumped than dispersed arrangements (Clarke et al. 1995; Parsons & Dumont 2003). Clumped distribution patterns probably reduce the cost of searching for the preferred plant and thereby enhance animal foraging efficiency (Laca 1998; Dumont et al. 2000). Accordingly, BC (in GDBC) has greater contrast in terms of relative preference ( $r.p.$ ) for the focal plant as well as in terms of the distribution pattern (clumped). This has possibly led to the greater within-patch than between-patch selectivity. This subsequently led to greater intake of the focal plant in BC than in GD, which resulted in neighboring contrast susceptibility in the focal plant under bad-patch conditions.

Foraging decisions at one scale can affect foraging decisions at another scale (Bailey et al. 1996). In accordance to that, comparing between patches of the same quality but of different distribution patterns, our results showed that, intake of focal plant was influenced by its distant neighboring patch distribution pattern. That is, the focal plant was better defended in dispersed distribution pattern when the neighboring patch was dispersed (Fig. 2). However, when the neighboring patch was clumped, consumption of the focal plant did not differ significantly between clumped and dispersed distribution patterns.

Comparing among treatments, our results showed greater vulnerability of the focal plant in treatments with patches differing in spatial patterns. In homogenous treatments (i.e., GDBD and GCBC), the two patches in each treatment have

the same spatial pattern. The clumped distribution patterns in GCBC differ more strongly than the dispersed patterns in GDBD, which makes GDBD the least contrasted or the most complex spatial distribution pattern. Moreover, the magnitude of contrast is greater within bad patches than within good patches, therefore bad-patch with a clumped distribution pattern (BC) is expected to have the highest contrast. Further, both heterogeneous treatments (GCBD and GDBC) have better contrast in terms of distribution pattern than homogenous treatments, however, greater contrast in BC makes GDBC the most contrasted or least complex spatial pattern. This has possibly caused the greater intake of focal plant in GDBC. This could be related to limited learning ability of grazers in a more complex foraging environment (Duncan & Young 2002; Ginane, Duncan, Young, Elston, & Gordon 2005). Moreover, there was significant difference in the intake of focal plants as well as whole plot consumption between the extremes GDBD (low contrast) and GDBC (high contrast). However, the intermediates (GCBC and GCBD) were not quite significantly different from the two extremes (GDBD and GDBC) as they could be regarded as intermediates where the level of contrast was not strong enough to make statistical significance.

All in all, the magnitude of contrast in terms of preference and spatial distribution patterns at different scales has affected the magnitude of sheep selectivity which in turn determines focal plant associational relationship. Our findings showed that spatial distribution is as important as traits of neighboring plants in predicting vulnerability of the focal plant to grazing by generalist herbivores. Moreover, the degree of contrast in terms of preference and patch characteristics affected the extent of sheep feeding selectivity at different scales (between or within patches), which eventually determined the associational relationship. Therefore, in determining neighboring plant associational relationship, all the controlling factors and the magnitude of each factor need to be considered. Further, under natural environmental conditions it will be very difficult to predict the associational defense effects between plants due to the complexity of herbivore foraging selectivity and plant spatial relationships.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.baae.2013.09.007>.

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