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THE RELATIONSHIPS BETWEEN ABOVEGROUND BIOMASS AND VORONOI AREA OF COEXISTING SPECIES IN AN OLD-FIELD COMMUNITY

ABSTRACT: Voronoi area of coexisting species in a community has an important role in determining their performances as it is related with the available resources around individuals. Biomass formed within certain Voronoi area probably can be a mark of species that characterised resource competition ability of coexisting species in natural community. In this article, we tried to probe the subject in the following three aspects: 1) what is the apparent relationship between individuals’ aboveground biomass and their available Voronoi area for species in natural community? 2) what is the possible theoretic relationship between them? 3) additionally, whether there are any possible indices that can be elicited from species’ occupied Voronoi area to reflect species’ competitive ability.

Using individual-based investigation of aboveground biomass and their corresponding positions, Voronoi area of all individuals of coexisting species in an old field community were computed. The growth of an individual could be regard as a process to compete for resources that is limited by the available area or volume encompassed by the neighborhood individuals. We extended logistic growth model to describe the relationship between Voronoi area and aboveground biomass of coexisting species by relating limiting rhizospheral resource with the Voronoi area around an individual. Theoretically, the individual’s aboveground biomass is also controlled by factor-ceiling effects of Voronoi area. So the extended model was fitted with boundary analysis method. And also, their linear relationship was fitted. Under the prediction that competitive ability is one of the main driving factors of community succession, two parameters as the Voronoi area of coexisting species and the Voronoi area per unit of aboveground biomass were used to check whether they can designate species’ competitive abilities and competitive hierarchies. This was presented by fitting the two parameters with the successional niche positions that was represented by the ordination values along abandonment ages of old field communities in the local area.

The results showed that: 1) For most species, the linear regression demonstrated that Voronoi area of an individual that occupied larger Voronoi area tended to have greater aboveground biomass. The nonlinear regression of showed that the relationship might depend upon species’ growth characteristics, like shade tolerance and root proliferation. Generally, the relationship could be better fitted by the extended logistic growth model using boundary analysis method than by the linear regression, except for some shade-preferring or clone species. If factor-ceiling effects were considered, at the highest, about 48% of the variation of aboveground biomass could be interpreted by Voronoi area. For some other species with light preference or clone proliferation, the determination coefficient was around zero. 2) Species’ averaged Voronoi area had significant and positive Kendall’s tau-b and Spearman correlations with
successional niches, and species’ per-unit aboveground biomass positions of Voronoi area has significantly negative rank correlation with successional niche positions. These indicate that both of them can reflect species’ competitive ability and hierarchy to some extent.

KEY WORDS: Voronoi area, plant performance, aboveground biomass, boundary analysis, extended logistic model, competitive ability, competitive hierarchy, successional niche position

1. INTRODUCTION

In plant communities, an individual grows and reproduces following its special eco-physical traits by acquiring resources. If any kind of the resources, such as light, soil nutrients and moisture, are lacking or limiting, plant growth or reproduction will be inhibited. In most natural communities, inhibition of growth or reproduction caused by shading, limited soil nutrients or moisture, is ubiquitous. In herbaceous communities, as shading inhibition hardly exists or is negligible compared to inhibition caused by the lack of soil nutrients or moisture, individual biomass or seeds production is considered mainly related to the available soil nutrients in a certain area, especially for those insoluble and immobile soil nutrients, such as iron, calcium, and silicon. In a low density community, the ability to acquire immobile essential nutrients for an individual is mainly associated with its root range. If local community density is high enough to make the rhizospheres of neighborhood individuals contacted or crossed, plants have their own main nutrient providing area, though plants can extend their roots into the rhizospheres of surrounding plants to absorb nutrients. In such case, the available nutrient providing area may be diminished, as neighborhood individuals will deprive the target individual of the resources. When the limited soil nutrients are easily soluble and mobile, such as moisture and available nitrogen, plants still have their main nutrient providing area when the nutrients are absorbed as quickly as they are supplied, even if their roots are not contacted or crossed. In the above two cases, performances of individuals will be confined by their nutrient providing areas encircled by neighbors.

The Voronoi tessellation method, also called Dirichlet or Thiessen tessellation (Dugan 2005), or non-overlapping domain method (Benjamin and Hardwick 1986, Kenkel et al. 1989), has been used widely to estimate plant performance (Mithen et al. 1984, John et al. 1985, Firbank 1987), and to analyse spatial pattern (Fransen et al. 1998) and dynamics of vegetation (Mercier and Baujard 1997). In plant population, the fitness of a target individual can be expressed as a function of distance, angle, number and size of neighborhoods close to the targets (Mackie-Dawson et al. 1995). The former three parameters virtually define the Voronoi area, so Voronoi tessellation method can also be used to analyse competition (Berger and Hildenbrandt 2000, O’Brien et al. 2007, Bergera et al. 2008). Mithen et al. (1984) reported that individual biomass can be expressed as a power function of Voronoi area in Lapsana communis population. Several authors, working under carefully controlled conditions with even-aged populations, used Voronoi area as a descriptive tool of plants’ spatial distribution pattern and performances (Mithen et al. 1984, Matlack and Harper 1986, Aguilera and Lauenroth 1993). However, in natural community the relationships between these variables are easily entangled by spatial resource heterogeneity, variability of individual growth duration caused by seedling emergence time and the variability of competitive ability of coexisting species. Thus, it is difficult to describe these relationships by simple functions. There is lack of individual-based investigation that relates the Voronoi area and plant performance in multi-species natural communities.

In natural community, species have different competitive ability. In a community with fully exhibited inter-specific competition (for example, an old-field community after long lasting succession), species abundance hierarchy reflects their competitive hierarchy. Species with the strongest competitive ability usually has the highest abundance (Roush and Radosевич 1985, Miller and Werner 1987, Keddy and Shipley 1989). Competition has been also considered as an important driving mechanism of vegetation succession. According to the maximum growth rate theory (Grime 1979), species
with the highest resources acquisition ability, may finally dominate later stages of succession by outcompeting species which dominate at early stages of succession. We assumed that the relative competitive ability of species has good correlation with successional niche positions, which can be represented by the Detrended Canonical Correlation Analysis (DCCA) scores along the successional stages in local area. Competitive ability is related to the resources acquisition ability, like the resource absorption and utilisation rates. We assumed that species with strong competitive ability may tend to occupy larger area and at the same area, species with strong competitive ability may grow better than those with relative weak competitive ability.

In this article, we assumed that: 1) the performance of an individual should have an increasing tendency when its Voronoi area increases. 2) The performance of an individual could be expressed as a logistic function of the Voronoi area, which is proportional to the amount of available resources. Individual aboveground biomass is not only determined by its Voronoi area, but also is influenced by its traits, such as life stage, growth duration or emergence time. These factors have an envelope or a factor-ceiling effect (Scheiner and Gurevitch 2001) on the relationship between plant performance and Voronoi area. So we examined the extended logistic formula by boundary analysis to estimate the upper boundary of the curve of individuals’ aboveground biomass against their occupied Voronoi area (Thomson et al. 1996). 3) For co-existing species in natural community, two parameters as averaged Voronoi area or Voronoi area per unit of biomass may be two useful predictors of their relative competitive ability. It is reported that relative competitive ability of species is responsible for community succession, species in later successional stage rank before the ones in early successional stage in competitive ability and hierarchy. So, the correlations between successional niche positions as independent variable and the two parameters as dependent variables were plotted to test whether the above two indexes can describe species competitive ability and hierarchy.

2. MATERIAL AND METHODS

2.1. Field data

The study site is located in Gaoqiao town of Shaanxi Province, China, belonging to typical hilly region of the Loess Plateau 36°39’N; 109°11’E, altitude ranging from 1,050 to 1,380 m. The region has the continental climate, with warm, rainy summers and cold, dry winters. The annual precipitation regime is characterised by a unimodal distribution pattern, with a peak occurring from June to September. This contributes to about 70% of the annual precipitation. The dry season is from November to May. During the past 35 years the mean annual temperature has ranged from 7.7 to 10.6°C and precipitation has ranged from 490.5 to 663.3 mm. The annual average frost-free period is around 157 days. The annual land use system in this area is short fallow agriculture with two ploughs in the spring. The experimental site is located on a plateau. The soil is loess. It is degraded due to soil erosion and 50 years cultivation without fertilisation. Therefore, the nutrient level is relatively low (Table 1). This area is devoid of any dominant native vegetation because it has been opened up and cultivated for food supply in the past. Now, the dominating herb species in the loess hilly area are Lespedeza davurica, Bothriochloa ischaemum, and Artemisia giraldii, which all appear in the late2.2. Individual-based investigation

In April 2003, an Artemisia sacrorum + Artemisia giraldii community with flat soil surface was selected to measure positions of individuals and their aboveground biomass. A 10×10 m² plot was closed by wire netting to protect against human and herbivore distur-

<table>
<thead>
<tr>
<th>Layers (cm)</th>
<th>Organic matter (%)</th>
<th>Total nitrogen (%)</th>
<th>Total phosphorus (%)</th>
<th>Total potassium (%)</th>
<th>Nitrate nitrogen (mg kg⁻¹)</th>
<th>Ammonium nitrogen (mg kg⁻¹)</th>
<th>Available Potassium (mg kg⁻¹)</th>
<th>Available Phosphorus (mg kg⁻¹)</th>
<th>Calcium carbonate (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0–20</td>
<td>0.44</td>
<td>0.027</td>
<td>0.042</td>
<td>1.63</td>
<td>2.79</td>
<td>10.24</td>
<td>63.3</td>
<td>2.35</td>
<td>18.15</td>
</tr>
<tr>
<td>20–40</td>
<td>0.32</td>
<td>0.023</td>
<td>0.044</td>
<td>1.73</td>
<td>2.57</td>
<td>11.12</td>
<td>55.6</td>
<td>1.4</td>
<td>14.96</td>
</tr>
</tbody>
</table>
In September 2004, at the end of the growing season, measurements were carried out. The centre zone of the plot was subdivided into 8 row and 8 columns, totally 64 numbered grids of 80×80 cm (Fig. 1). Measurements were conducted in the order of grid number. Plant locations were represented by points (the centre of stem or bunch was measured). Investigation method was illustrated in Fig. 1, in which distances i and j (from points A and B, respectively) were measured with a ruler, and coordinate x and y were computed by Pythagorean Theorem, to represent the position of individual at that grid (Fig. 1). After all grids were investigated, data of plant locations in each grid was arranged and combined according to grid number.

2.2. Data analysis

Data including the positions of all individuals of every species were dealt with R package (functions of voronoi.mosaic, voronoi.area and plot.dichlet were used). Voronoi polygons were constructed by the perpendicular bisectors of lines drawn between an individual and all nearby plants. The polygon around a plant included all points in the plane which are closer to that plant than to any others. Individuals’ Voronoi polygons were partly illustrated in Fig. 2. Table 2 listed two parameters about Voronoi area, one is averaged Voronoi area occupied by species (simply called as Voronoi area), and Voronoi area per unit of aboveground biomass of species in the A. sacroru+ A. giraldii community. The degree of inequality in the Voronoi areas and the aboveground biomass of individuals were measured using Gini coefficient (Mithen et al. 1984). Gini coefficients varied between 0 and 1, a small value showing relative equality and a high one – inequality. The Gini coefficient was calculated by R package.

In a local natural community, co-existing species have their special statistical performances and occupied Voronoi area, and these species also have their numerical successional niches (including successional stage, breadth) (Pacala and Rees 1998, Du et al. 2006). In order to illustrate the association between the above two parameters and successional niches or stages (equivalent to the positions of species in the ordination plot of old field communities), that is the change tendency of the two parameters of different species along secondary succession. We plotted Voronoi area and Voronoi area per unit of aboveground biomass of each species against the successional nich positions that was represented by the DCCA coordinate values along abandonment ages (Du et al. 2008) (Fig. 4). The correlation between them was tested using Kendall’s tau-b and Spearman method.

We used aboveground biomass of individuals of different species as a dependent variable, and their corresponding Voronoi area as an independent variable. The apparent linear trended line was fitted (Fig. 3). Besides, as in-

Fig. 1. Illustration of position and description of an individual and the individual-based investigation.
Aboveground biomass and Voronoi area of coexisting species

individuals’ growth is enveloped by factor-ceiling effect, the extended logistic equation was fitted using boundary analysis method to find the upper border of the relationship between individuals’ aboveground biomass and their occupied Voronoi area. The positive residuals after the first cycle analysis were used to fit the upper boundary (Fig. 3). All statistical analyses were conducted on the data without edge effect, that is, data of individuals that are close to the investigation borderline were not used. The fittings were conducted with origin software 7.5.

3. RESULTS

3.1. Voronoi area of co-existing species and Voronoi area per unit of aboveground biomass in the natural community

Voronoi area occupied by individuals of different species varied from 0.0262 ± 0.0155 to 0.0426 ± 0.0246 m² (Mean ± SD). The Gini coefficients of Voronoi area of species varied from 0.31 to 0.41, and of the values of aboveground biomass varied from 0.46 to 0.77. The inequality of Voronoi area was smaller than that of aboveground biomass (Table 2). The Voronoi area per unit of aboveground biomass ranged from 0.029 ± 0.063 to 0.275 ± 0.356 cm² g⁻¹. It means that, on average, one square meter of Voronoi area could minimally produce 3.64 gram of fresh aboveground biomass of Heteropappus altaicus, maximally – 34.48 gram of Artemisia giraldii.

3.2. Apparent relationship between Voronoi area and aboveground biomass

The apparent relationship between Voronoi area and aboveground biomass of different species was fitted using linear regression. Except Artemisia giraldii and Ixeris chinesis, aboveground biomasses of most species

Table 2. Statistical data for Voronoi area and aboveground biomass of important species in the old field community.

<table>
<thead>
<tr>
<th>Plants</th>
<th>Voronoi area occupied by individuals</th>
<th>Gini’s coefficients of individual’s Voronoi area</th>
<th>Gini’s coefficients of individuals’ aboveground biomass</th>
<th>Per-gram-aboveground biomass of Voronoi area (mean±SD) (m² g⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N  Mean±SD (m²)  Min  Median  Max</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Heteropappus altaicus</td>
<td>92  0.0353±0.0222  0.00671  0.02764  0.14421</td>
<td>0.32</td>
<td>0.59</td>
<td>0.275±0.356</td>
</tr>
<tr>
<td>Stipa bungeana</td>
<td>109 0.0365±0.0243  0.00178  0.03356  0.12023</td>
<td>0.36</td>
<td>0.69</td>
<td>0.233±0.276</td>
</tr>
<tr>
<td>lespedeza davurica</td>
<td>184 0.0397±0.0272  0.00295  0.03274  0.14218</td>
<td>0.38</td>
<td>0.51</td>
<td>0.068±0.24</td>
</tr>
<tr>
<td>Deyeuxia langsdorffii</td>
<td>46  0.0395±0.03    0.00414  0.03062  0.15144</td>
<td>0.39</td>
<td>0.45</td>
<td>0.089±0.178</td>
</tr>
<tr>
<td>Potentilla bifurca</td>
<td>65  0.0276±0.0175  0.00181  0.02537  0.07264</td>
<td>0.36</td>
<td>0.62</td>
<td>0.190±0.318</td>
</tr>
<tr>
<td>Artemisia giraldii</td>
<td>83  0.0426±0.0246  0.00974  0.03574  0.121</td>
<td>0.32</td>
<td>0.69</td>
<td>0.029±0.063</td>
</tr>
<tr>
<td>Ixeris chinensis</td>
<td>20  0.0262±0.0155  0.00692  0.02338  0.0719</td>
<td>0.32</td>
<td>0.46</td>
<td>0.681±0.678</td>
</tr>
<tr>
<td>Artemisia sacrorum</td>
<td>172 0.0418±0.0241  0.00542  0.03765  0.13231</td>
<td>0.31</td>
<td>0.77</td>
<td>0.040±0.1</td>
</tr>
<tr>
<td>Potentilla chinensis</td>
<td>39  0.0386±0.0294  0.00094  0.02934  0.12228</td>
<td>0.41</td>
<td>0.71</td>
<td>0.135±0.22</td>
</tr>
<tr>
<td>Poa sphondylodes</td>
<td>126 0.0357±0.0234  0.00364  0.03119  0.10843</td>
<td>0.36</td>
<td>0.59</td>
<td>0.127±0.202</td>
</tr>
<tr>
<td>Artemisia scoparia</td>
<td>397 0.0275±0.02   0.00136  0.02249  0.11518</td>
<td>0.39</td>
<td>0.42</td>
<td>0.240±0.332</td>
</tr>
</tbody>
</table>
tended to be greater with a greater Voronoi area (Fig. 3). The aboveground biomasses of *Poa spondylodes* and *Artemisia scoparia* individuals showed significant positive correlation with corresponding Voronoi area.

3.3. Logistic model to infer the relationship between aboveground biomass and Voronoi area, and boundary analysis method

The greatest height of plants in the community was about 50 cm. There was no obvious overlapping of crowns between plants except some small accessory sciophilous plants, like *Ixeris chinensis*. So, firstly, we assumed that shoot competition could be neglected, and growth of individuals was inhibited only by underground competition. Secondly, we assumed that plant mainly competed for one of the most limited soil elements that are distributed homogeneously, that is to say, the amount of available soil resources per volume is the same.

Given that a resource is limited and imobile, individual growth is controlled by the amount of resource available to the individual that is proportional to its Voronoi area and absorption rate and assimilation efficiency of this resource by the individual. We can infer additionally that individual growth rate is proportional to the present biomass of the individual and to the difference between maximal possible biomass and its actual biomass divided by maximal possible biomass.

The absorption rate of an individual could be defined as individual’s absorption amount of the most limited nutrients in a short time, written as:

\[
a = \frac{dR}{dt}
\]

(1)

where: \(a\) = absorption rate of limited nutrient; \(R\) is the absorbed quantity of limited resource.

Then the logistic equation is:

\[
\frac{dB}{dt} = arB\left(\frac{B_M - B}{B_M}\right)
\]

(2)

where: \(B\) = biomass of an individual; \(r\) = ration of biomass formation and absorption of a limited nutrient, equivalent to the limited nutrient usage efficiency; \(B_M\) = the maximum biomass formed when there are no nutrient limitation controlled by the intrinsic growth traits of concerned species.

<p>| Table 3. Results of boundary analysis using the extended logistic growth equation. |
|---------------------------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|</p>
<table>
<thead>
<tr>
<th>Fitting methods</th>
<th>Parameters</th>
<th><em>Heteropappus alpinus</em></th>
<th><em>Stipa bungeana</em></th>
<th><em>Lespedeza davurica</em></th>
<th><em>Deyeuxia langsdorffii</em></th>
<th><em>Potentilla bifurca</em></th>
<th><em>Artemisia giraldii</em></th>
<th><em>Artemisia chinesis</em></th>
<th><em>Artemisia sacrorum</em></th>
<th><em>Potentilla chinensis</em></th>
<th><em>Poa spondylodes</em></th>
<th><em>Artemisia scoparia</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Extend logistic model</td>
<td>(B_M)</td>
<td>1.24</td>
<td>2.21</td>
<td>16.43</td>
<td>2.31</td>
<td>1.87</td>
<td>73.25</td>
<td>0.16</td>
<td>129.00</td>
<td>8.34</td>
<td>2.53</td>
<td>0.36</td>
</tr>
<tr>
<td></td>
<td>(\alpha)</td>
<td>1.67E+02</td>
<td>5.23E+11</td>
<td>4.18E+10</td>
<td>8.35E-01</td>
<td>3.87E+158</td>
<td>1.92E+22</td>
<td>4.88</td>
<td>6.10E+148</td>
<td>6.5E+148</td>
<td>3.46E+74</td>
<td>8.04E+148</td>
</tr>
<tr>
<td></td>
<td>(\beta)</td>
<td>0.029</td>
<td>0.17</td>
<td>0.50</td>
<td>0.015</td>
<td>84.44</td>
<td>0.23</td>
<td>5.29</td>
<td>2.99</td>
<td>36.12</td>
<td>1.59</td>
<td>25.28</td>
</tr>
<tr>
<td></td>
<td>(F)</td>
<td>10.87”</td>
<td>32.81”</td>
<td>16.64”</td>
<td>0.32</td>
<td>5.02E-31</td>
<td>37.96”</td>
<td>0.15</td>
<td>12.65”</td>
<td>0.15</td>
<td>17.72”</td>
<td>0.20</td>
</tr>
<tr>
<td></td>
<td>(N)</td>
<td>32</td>
<td>42</td>
<td>71</td>
<td>14</td>
<td>19</td>
<td>28</td>
<td>7</td>
<td>50</td>
<td>44</td>
<td>7</td>
<td>153</td>
</tr>
<tr>
<td>Determination coefficient</td>
<td>0.26</td>
<td>0.45</td>
<td>0.19</td>
<td>0.026</td>
<td>0.08</td>
<td>0.029</td>
<td>0.21</td>
<td>0.03</td>
<td>0.28</td>
<td>0.13</td>
<td>0.28</td>
<td>0.0013</td>
</tr>
<tr>
<td>Linear</td>
<td>Slope</td>
<td>2.05E-4</td>
<td>5.69E-4</td>
<td>0.0016</td>
<td>7.78E-5</td>
<td>3.23E-4</td>
<td>-0.010</td>
<td>1.71E-4</td>
<td>0.032</td>
<td>-1.69</td>
<td>0.0011</td>
<td>2.85E-4</td>
</tr>
<tr>
<td></td>
<td>Intercept</td>
<td>0.35</td>
<td>0.59</td>
<td>7.58</td>
<td>1.03</td>
<td>0.62</td>
<td>27.62</td>
<td>0.12</td>
<td>22.61</td>
<td>2.44</td>
<td>0.51</td>
<td>0.13</td>
</tr>
<tr>
<td></td>
<td>Determination coefficient</td>
<td>0.0065</td>
<td>0.017</td>
<td>0.0028</td>
<td>0.00057</td>
<td>0.0038</td>
<td>0.0049</td>
<td>0.0088</td>
<td>0.011</td>
<td>0.00018</td>
<td>0.036”</td>
<td>0.069”</td>
</tr>
</tbody>
</table>

Note: \(N\) = Numbers of the positive residuals after the first cycle of boundary analysis; parameters \(B_M\), \(\alpha\) and \(\beta\) have the same meanings as equation 7; *\(P<0.05\), ** \(P<0.01\).
Aboveground biomass and Voronoi area of coexisting species

We have:

\[
\frac{dB}{dR} = \frac{dB}{adt} = rB \left( \frac{B_M - B}{B_M} \right) \tag{3}
\]

Integrate the equation (2) with respect to biomass from small biomass \( B \) at initial time to larger biomass \( B \) at later time. The above equation (3) has the following integrated solution:

\[
B = \frac{B_M}{e^{-C}e^{-rdn} + 1} \tag{4}
\]

where: \( C = \) constant; \( R \) is defined as the absorption amount of an individual, could also be regard as the decrease amount of the most limited soil nutrients.

We can assume that the available resource \( R \) is proportional to the Voronoi area \( V \) multiplied by root depth \( d \) and the resource concentration \( n \). Equation (3) can be transformed to the following equation (5) when Voronoi area is referred as an independent variable:

\[
R = dnV \tag{5}
\]

Let \( e^{-C} = \alpha, rdn = \beta \), then:

\[
B = \frac{B_M}{e^{-\alpha}e^{-\beta} + 1} \tag{7}
\]

Though equation (7) was reasonably based on a given individual, we could apply regression to a group of individuals. Boundary analysis was used to identify the upper boundary of the point distribution of aboveground biomass vs. Voronoi area rather than the centre of the point distribution, as there are factors other than Voronoi area that also act as limiting factors to aboveground biomass. The regression results of equation (7) show that the aboveground biomass of most species, except *Deyeuxia langsdorffii*, *Potentilla bifurca*, *Potentilla chinensis* and *Artemisia scoparia*, can be significantly depicted by the extended model using boundary analysis (Fig 3. and Table 3).
3.4. Changes of individuals’ Voronoi area and the Voronoi area averaged on aboveground biomass of different species along secondary succession

Averaged Voronoi area of the species has significantly positive correlation with the ordination values that represent the successional niche positions (Fig. 4, R = 0.763, P = 0.0063). This shows that species which occurred or dominated at later successional stage tend to have larger Voronoi area. Correlation coefficient between Voronoi area per unit of aboveground biomass and the successional niche positions is −0.534 (P = 0.090). Voronoi area per unit biomass tends to decrease along the secondary succession. The rankings of species’ averaged Voronoi area and Voronoi area per unit of aboveground biomass have significant positive and negative correlations with the rankings of the successional niche positions (Spearman correlations are 0.609 and −0.627, P = 0.047 and 0.039, respectively).

4. DISCUSSION

4.1. The relationship between plant performance and Voronoi area is non linear

Plants occupy different areas under varied local density of population or community. For most species, the individuals tend to have larger biomass when they have larger Voronoi area, but for those species with aggregated distribution result from such traits as shade toleration or clone propagation, the new seed established individuals in empty space may be small. Species with the traits, like *A. giraldii*, *I. chinensis* and *P. chinensis* in our case, may lead to negative slope trend lines (Fig. 3). Biomass of a plant is the performance of its intrinsic genetic traits influenced extrinsically by the resource availability and neighbourhood interaction (mainly resource competition) termed as phenotype plasticity. In monospecific population with small genotype variability, it can be considered that plant performances are mainly determined by seedling emergence and resource competition. In a competition experiment with monospecific population (*Agrostemma githago* L. and *Triticum aestivum* L.), Firbank (Firbank 1987) reported that seedling emergence and resource competition, when simulated in a linear fashion, can only account for about 50% of the variance of shoot weight, which suggest that influences of the two factors are nonlinear. Our case also testified that the nonlinear technique of the extended logistic growth formula has higher goodness of fitting than the linear simulation. If we take into account diversity of natural community, spatial heterogeneity of soil, the asymmetric competitive ability of the species (Weiner *et al.* 1997), and the differing depletion of limited resources at seedling and adult stage (John *et al.* 1985), the nonlinear regression may be more appropriate to predict the plant performance Voronoi area.

![Fig. 4. Correlations between species’ average Voronoi area (A) and Voronoi area per unit of aboveground biomass (B) and their successional niche positions. The successional niche positions of species were the values along the first axes of DCCA ordination of old field communities in local area (Du *et al.* 2008).](image-url)
4.2. Limitations of the use of the extended logistic growth formula to predict the plant performance by their occupied Voronoi area

Although largely a higher proportion of the biomass variation can be interpreted by Voronoi area using the extended logistic growth formula than using the linear fashion simulation, it was yet clear from the results of our investigation in a natural community that Voronoi area couldn’t account for a very high proportion of the variation in individual aboveground biomass. This may be caused by following reasons:

1. Soil heterogeneity might decrease the proportion of plant performance variation explained by variation of Voronoi area. Plants tend to clump in favourable microhabitats. The soil heterogeneity with different spatial scales, durations and contrast can cause different limiting effects on growth and plant performance (Wijesinghe and Hutchings 1997).

2. The assumption of linear relationship between growth rate of aboveground biomass and nutrient absorbing ability (see equation 2) may be inconsistent with the real nutrient usage process (see equation 2). Firstly, as nutrients uptake of species is used not only to form biomass, some fraction of them will also be lost in the form of abscission or root exudates. The proportion of nutrients used to form biomass varies between species, and perhaps also varies with size of plants (Hikosaka and Hirose 2001). Secondly, as the ration of shoot/root is not constant for plants with different size or growth stage, probably it is better for the model regression to use whole biomass as dependent variable than only aboveground biomass.

3. Some phenomena in natural community may be potentially incompatible with the implicit assumptions hidden in the formula derivation, which may reduce the goodness of its fitting to experimental data. One assumption is that individuals confront alone with resource competition. For sexual offspring, they exploit space and resources in an independent way. The assumption is true, because they can’t obtain resources from parents or other ramets. But this is not true in the case of clone plants and the biomass formation of clone plants perhaps can’t be well described by the logistic formula. In our case, Deyeuxia langsdorffii, Potentilla bifurca and Ixeris chinensis belong to clone plants, all of them can propagate by rhizome. Another assumption is that species we investigated are not shade tolerant species. The actual case is that Ixeris chinensis is such species growing better under other species shade, though probably it is competed intensively from the shade-providing species whose Voronoi area may be underestimated. The third one is that the investigated species have no nutrient and space niche separation (including vertical orientation of root systems). They should compete for the same kind of soil resources at the same layer, and they should not compete for light. The last assumption is that the investigated space should be fully colonized. Existing empty space may lead to overestimation of the occupied area. Especially Voronoi area of individuals around the empty space may be wrong. Finally, the logistic formula was based on assumption about single limited resource. If there are several limited resources, the biomass formation of individuals is the combined result of limitation from these resources. In such case, the logistic formula should not be applicable.

4.3. Are there any parameters referred from Voronoi area and plant performance that can indicate species relative competitive ability or competitive hierarchy?

In order to obtain an insight whether there are some parameters able to predict the competitive ability or hierarchy of co-existing species in natural community, two parameters - averaged Voronoi area of species, and Voronoi area per unit of aboveground biomass – were examined. The significant rank correlations between averaged Voronoi area of species, average Voronoi area per unit of aboveground biomass and successional niche positions implies that the two parameters could both describe the competitive hierarchy. Species with top rank of Voronoi area and low rank of Voronoi area per unit of abovegro-
round biomass tend to rank high in competitive hierarchy. And the significant correlation between species’ averaged Voronoi area and their ordination values implied that Voronoi area of coexisting species in natural community could predict species’ relative competitive ability to some extent.

Besides, parameter $b$ in the formula (7) may also be useful to predict species relative competitive ability, if the growth rate is responsible for this ability. In the formula (7) parameter $b$ is equal to product of root depth, nutrient concentration and the ration of biomass formation and absorption of the limited nutrient. Given that the first two parameters are the same for all species, according to the maximum growth rate theory (Grime 1979), strong competitive species are those having quick growth and high absorption rate of the nutrient. Parameter $b$ should correlate with successional niche positions or the DCCA ordination values in our case. However, we found no significant correlation. For species with significant regression of the logistic model using boundary analysis (Table 3), the Kendall's tau-b and Spearman correlation coefficients between $b$ and ordination values were 0.6 ($P = 0.691$) and 0.657 ($P = 0.156$), respectively. Such results implied that in our investigation site (belong to medium-yield habitat in the loess hilly region), processes described by theory other than the maximum growth rate theory, e.g., the minimum resource requirement theory (Tilman 1982), are responsible for species competitive ability and vegetation succession. We deduced that, in relative high-yield habitat where nutrients are barely limited, competitive ability is related with the resources acquisition, like the resource absorption and assimilation rates. In relative low-yield habitat, species competitive ability is mainly associated with the ability of tolerance to the low resources level, which is mainly related to the mean resident time of limited nutrients. Under medium-yield habitat, both the two processes of absorption and tolerance to the resource limitation may determine co-existing species’ competitive ability.

The inequality of Voronoi area is strongly influenced by the spatial distribution-defining processes, such as seeds' dispersion, seedling establishment and density-dependent mortality resulting from competitive interactions (Antonovics and Levin 1980, Hutchings and Discombe 1986, Hutchings 1997). Annual or biennial plants with random dispersion, quick growth and weak competitive ability traits, like Artemisia scoparia in our case, will potentially have a larger inequality of Voronoi area. On the other hand species with a strong competitive ability (like Artemisia giralldii and Artemisia sacrorum in our case) tend to generate a regular spatial pattern and have small inequality of Voronoi area but large variability of size.

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5. REFERENCES


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