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CHANGES IN SPECIES RICHNESS
AND COMMUNITY PRODUCTIVITY DURING SUCCESSION ON THE LOESS PLATEAU (CHINA)

ABSTRACT: We investigated changes in species richness, community biomass, and productivity during secondary forest succession in Ziwuling area of the Loess Plateau of China. Species richness (number of taxa) increased as the succession proceeds, and peaked at the climax forest community, but the richness growth gradually slowed down as the succession advanced. Community biomass rapidly increased from the herbaceous stage to the shrub stage and declined slightly in the climax forest stage. The maximum community biomass occurred in the pioneer forest stage. Community productivity followed an unimodal curve in the succession, and the maximum productivity occurred in the shrub community at the middle succession stage, and the communities maintained a low and stable productivity at the later succession stages. The herb and shrub species together determined community diversity during succession, while the tree species contributed less to diversity in the communities. The herb and shrub layers had a relatively low biomass, but contributed almost half of the productivity of the forest communities. The relationships between species richness, community biomass and productivity were unimodal during succession, but only the relationship between species richness and community biomass was significant.

KEY WORDS: species richness, community biomass, community productivity, secondary succession, Loess Plateau

1. INTRODUCTION

Community succession is a central topic in ecological research. Succession patterns are predictable and broadly applied in the restoration of degraded ecosystems (Dobson et al. 1997, Van der Putten et al. 2000, Wang 2006). During succession, community structure and function change, with changes in species diversity, species compositions, community biomass, primary production, respiration, and nutrient retention (Molles 1999).

Species richness or diversity is an essential characteristic of communities, and plays an important role in ecological research (Howard and Lee 2003, Zhang et al. 2005). Several studies have shown that species diversity is dynamic in early succession and is a cause as well as effect of succession (Van der Putten et al. 2000, Wang 2006). The dominance of some weedy species can suppress later-successional colonizers, but introducing later-successional plant species can weaken the suppression and accelerate suc-
cessation (Martinez-Ruiz et al. 2007, Li et al. 2008).

Community biomass and productivity are regarded as important indicators of ecosystem function since they are the vectors of ecosystem energy flow and matter cycling (Hughes and Roughgarden 2000). Changes in biomass and productivity over time reflect succession processes. Borrmann and Likens (1979) summarized the general model for biomass accumulation during the secondary forest succession: biomass and productivity gradually increase until productivity peaked at the middle succession stage, and then the biomass continued to increase at the late succession stage while the productivity decreased dramatically. The biomass production of a forest ecosystem is much more complicated than any current model can simulate as it varies with time and space.

The relationship between species diversity or richness and community productivity or biomass has been discussed extensively over the past two decades (Rosenzweig 1992, Abrams 1995, Waide et al. 1999, Mittelbach et al. 2001, Guo 2003, 2007, Gillman and Wright 2006). The unimodal relationship in which species diversity peaks on intermediate productivity or biomass has received most support (Rosenzweig 1992, Waide et al. 1999, Mittelbach et al. 2001, Guo 2003, 2007). These results have been based on data collected on various spatial scales at one certain time, while little attention has been paid to the relationships between community diversity and biomass or productivity at one location over time (Guo 2003, Bischoff et al. 2005). Furthermore, most studies have been conducted on grassland ecosystems, ignoring the difference between community biomass and productivity. Forests have scarcely been mentioned in the biodiversity debate due to the difficulty of conducting experiments in ecosystems with slow dynamics. Since forest community biomass is not highly correlated with productivity, the relationships between species diversity and biomass or productivity may be very different.

Here we address the following questions: (1) How do species richness (number of taxa) and community biomass and productivity vary during secondary forest succession? (2) How do the growth forms of plants vary during secondary forest succession? (3) What are the relationships between species richness, community biomass and productivity in secondary forest succession? To answer these questions, we chose a secondary forest succession sequence in the Loess Plateau of China to study temporal variation in species richness, community biomass, productivity and plant growth forms in terms of successional gradients.

2. MATERIAL AND METHODS

The study was conducted on Lianjiabian forest farm located at the northern Ziwuling area, Heshui County, Gansu, China. The study area has landforms typical of loess hilly topography and a mid-temperate continental monsoon climate. Longitude ranges within 108°10’ and 109°18’E, latitude between 35°03’ and 36°37’N, and an altitude within 1211–1453 m (Jia et al. 2005). The whole Ziwuling area (107°30’–109°40’E, 33°50’–36°50’N) stands in the central-southwest part of the Loess Plateau, bordering on Shaanxi and Gansu Province and covering a total area of 23000 km². The Ziwuling area is one of the few places in the Loess Plateau with relatively natural secondary forests. The region has an altitude within 1100–1756 m above sea level and a relative height difference within 200–400 m. The average annual precipitation is 587.6 mm, and average annual air temperature is 7.4ºC and its annual accumulated temperature ≥10°C is 2 671.0°C (Zou et al. 2002). The soil in the region is calcareous “cinnamon soil” or forest Haplic Greyzem soil, which evolved from primary or secondary loess of 50–100 m in depth (Zou et al. 2002, Jia et al. 2005). The natural biomes are deciduous broadleaf forests and the climatic climax vegetation is a Quercus liaotungensis Koidz forest (Zhu 1991). Populus davidiana Dode and Betula platyphylla Suk communities dominate pioneer forests; and Sophora davidii (Franch.) Skeels, Hippophae rhamnoi
des (Linn.), Rosa xanthina Lindl and Spiraea pubescens Turcz are the main shrub species; and Bothriochloa ischaemun (Linn.) Keng, Carex lanceolata Boott, Potentilla chinensis (Ser) and Stipa bungeana Trin are the main herb species.
The secondary forests regenerated naturally on abandoned lands after many local inhabitants emigrated from the Ziwuling area during a national conflict in 1842–1866. Chen (1954) investigated the vegetation recovery in Ziwuling area in 1950s and found that *P. davidiana* made up 70% of the vegetation cover after an about 100-years. Zou et al. (2002) investigated the vegetation succession in Ziwuling area for three times (1962, 1982 and 2000). He found that the *P. davidiana* forests were replaced by the *Q. liaotungensis* forests after an about 50-years. Thus, the recovery period for *Q. liaotungensis* forests was about 150 years. In 1940–1960s, famine, war and disasters led some people to immigrate and reclaim land in the region. Due to human emigration and immigration, some arable land was again abandoned in different areas, so different successional stages can be observed on degraded sloping land. Based on previous research, we chose seven communities that were at different succession stages in the Ziwuling area. The communities’ ages were determined by two methods. For the shrub and herbaceous communities with less than 60 years recovery, we verified the length of time by visiting local elders and referring to land contracts between farmers and the government. For the forest community which recovered over 60 years, we determined the time by boring tree rings and checking related written sources.

We conducted our survey from July 15 to August 5 in 2005. The sample areas were determined according to the size of the communities involved. For each forest community, four 20 m × 20 m tree plots were delineated and then five shrub patches and five herb patches were chosen in each tree plot. For shrub and herbaceous communities, five plots were chosen. In addition, a plot of herbaceous vegetation was chosen in each shrub plot. The areas of the shrub plots were 5 m × 5 m and those of the herb plots were 2 m × 2 m. The species and individuals of each plot were counted and recorded. The height, DBH (diameter breast height) and coverage of each tree and the ground diameter of the shrub and herb species were also measured. The most distant samples are not more than 5 km apart and the largest relative elevation difference between two samples is less than 120 m. Most of the samples have a slope gradient below 20 degrees and face northward (Table 1).

In order to measure the community biomass and productivity, we divided the communities into tree layer (h > 3 m), shrub layer (0.5 m ≤ h ≤ 3 m) and herb layer (h < 0.5 m). The aboveground biomass of the tree layer was measured by destructive sampling. Firstly, we have chosen the dominant tree species of the forest communities and measured the DBH of all individuals and then determined the target trees of each plot. Secondly, the target trees were cut and divided into trunks, branches and leaves, and weighed, then, some fresh samples were taken, dried and weighed in lab to measure the dry biomass. Finally, the community biomass of the tree layer was calculated from density. The aboveground parts of the shrub and herb layer were harvested to determine their biomasses. The harvested area was 2 m × 2 m for the shrub layer and 1 m × 1 m for the herb layer. The biomass measurement of the shrub and herb layers involved five replications, and four replications for tree layer.

Having the biomass of each layer measured, the community biomass was calculated as the sum of the values for three layers. The productivity of each layer was calculated by dividing the biomass by age of each layer. The leaf age of trees was considered as one year old when calculated forest productivity. The age of the tree layer was obtained by stump ring counting, and the age of the shrub layer was estimated by the dominant shrub species with an average of five years, and the age of the herb layer was assumed to be one year. The community productivity was the sum of the productivity values of each layer. Since *S. davidii* and *H. rhamnoides* shrub communities had obvious trunk and branches, their community biomasses and productivities were measured in the same way as tree layer.

The species richness (number of taxa) and the aboveground biomass and productivity were used to represent community biomass and productivity as in previous studies (Howard and Lee 2003, Zhang et al. 2005, Guo 2003, 2007). We calculated the quadratic regressions to analyze the relationship between species diversity, community biomass and productivity. All graphs and analyses were performed using SigmaPlot 10.0 Software (Systat Inc., San Jose, CA).
3. RESULTS

As the succession proceeded, the species richness increased, reaching a maximum in *Q. liaotungensis* climax forest at the latest succession stage (Fig. 1A). The species richness increased from 28 in the herbaceous community at the early succession stage to 61 in the climax forest community at the late succession stage.

Taking the whole successional sequence into account, there was an increase of 14 species in the shrub communities compared with the herbaceous communities, 11 species in the pioneer forest communities compared with the shrub communities, and 8 species in the climax compared with the pioneer forest communities. The rate of increase in species richness declined during succession.

Community biomass tended to increase sharply in the early succession stages, then increased slowly at middle succession stages and declined slightly at the late succession stages (Fig. 1B). The maximum community biomass occurred in the pioneer forest community. The community biomass rapidly accumulated at the early succession stages, increasing about 20 times from the herbaceous communities to the shrub communities. However, its increase dramatically slowed down so that the community biomass only increased by 2.3% from the shrub communities to the pioneer forest communities. And the community biomass of the climax forest decreased by 15% compared with the pioneer forest communities. The community biomass generally remained stable after the shrub community.

Community productivity followed an unimodal pattern during succession, with the maximum productivity appearing in the shrub community (Fig. 1C). Community productivity increased dramatically at the early succession stages, and increased about 2.4 times from the herbaceous communities to the shrub communities. After that, community productivity decreased 60% from shrub communities to pioneer forest communities and further being reduced 16% in the climax forest community. The community maintained a low and stable productivity at the late succession stages.

Species richness in the herb layer, shrub layer and tree layer showed different patterns during the succession. Herb species dominated in the herbaceous and shrub communities at the early succession stages and they decreased in the forest communities at the late succession stages (Fig. 1A). The number of shrub species gradually increased, peaking at the climax forest community. The increase of species richness in shrub layer was accompanied by a decrease in the number of the herb species. Tree species richness was relatively low and declined during the succession, and there were only two tree species in the climax forest community.

<table>
<thead>
<tr>
<th>Number</th>
<th>Succession stage</th>
<th>Altitude (m)</th>
<th>Aspect (°)</th>
<th>Slope (°)</th>
<th>Coverage (%)</th>
<th>Dominant species in different layer</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Grassland 1</td>
<td>1357</td>
<td>NE75</td>
<td>3–6</td>
<td>62</td>
<td>H: <em>Lespedeza bicolorr</em></td>
</tr>
<tr>
<td>2</td>
<td>Grassland 2</td>
<td>1330</td>
<td>NE55</td>
<td>14–16</td>
<td>95</td>
<td>H: <em>B. ischaemum</em></td>
</tr>
<tr>
<td>3</td>
<td>Shrub 1</td>
<td>1346</td>
<td>NW67</td>
<td>20–22</td>
<td>45</td>
<td>S: <em>S. davidii</em>; H: <em>C. lanceolata</em></td>
</tr>
<tr>
<td>4</td>
<td>Shrub 2</td>
<td>1343</td>
<td>NE65</td>
<td>12–15</td>
<td>65</td>
<td>S: <em>H. rhamnoides</em>; H: <em>C. lanceolata</em></td>
</tr>
<tr>
<td>5</td>
<td>Forest 1</td>
<td>1448</td>
<td>NE45</td>
<td>13–16</td>
<td>65</td>
<td>T: <em>P. davidiana</em>; S: <em>S. schneideriana</em>; H: <em>C. lanceolata</em></td>
</tr>
<tr>
<td>6</td>
<td>Forest 2</td>
<td>1432</td>
<td>NE42</td>
<td>10–12</td>
<td>53</td>
<td>T: <em>B. platyphylla</em>; S: <em>Viburnum mongolicum</em>; H: <em>C. lanceolata</em></td>
</tr>
<tr>
<td>7</td>
<td>Forest 3</td>
<td>1433</td>
<td>NW30</td>
<td>22–25</td>
<td>60</td>
<td>T: <em>Q. liaotungensis</em>; S: <em>Rosa hugonis</em>; H: <em>C. lanceolata</em></td>
</tr>
</tbody>
</table>

Table 1. Plot features in different succession stages in Ziwuling area on the Loess Plateau. Grassland 1 and 2 are the grass succession stage, Shrub 1 and 2 are the shrub succession stage, Forest 1 and 2 are the pioneer forest stage, Forest 3 is the climax forest stage. Number in the parentheses after succession stage are the abandonment time in years. H: herb, S: shrub, T: tree.
Diversity and productivity during forest succession

The biomass of the herb and shrub layers generally decreased during succession and the maximum biomass of herb and shrub layers was observed in the herbaceous community (stage 2) and shrub community (stage 4; Fig. 2B). In forest communities at the late succession stages, the biomass of the tree layer was much greater than the shrub and herb layers, and the maximum tree biomass occurred in the pioneer forest stage (stage 6).

The productivity of the different layers showed a similar trend to their biomass: the productivity in the herb and shrub layers declined during succession with maximum productivity in herbaceous and shrub communities (stage 2 and stage 3). The productivity of tree layer varied little over time (Fig. 2C).

A significant unimodal relationship was found between species richness and community biomass during succession (Fig. 3A). The peak values of community biomass appeared at the intermediate species richness that corresponds to the middle succession stages.

The relationship between species richness and community productivity was also unimodal over the course of succession, but the pattern was not clear (Fig. 3B). The peak of community productivity occurred earlier than that of biomass.

There was also no significant relationship between community biomass and productivity in the course of succession (Fig. 3C). However, an unimodal relationship between community biomass and productivity performed better than a monotonic function.

4. DISCUSSION

The study showed that the species richness, community biomass and productivity varied in different ways during succession on the Loess Plateau (Fig. 1). Howard and Lee (2003) summarized four patterns of species richness over succession time: increasing, decreasing, peak in the middle, and no trend. Our study indicated that the species richness increased rapidly in the early succession stages.
stages and fluctuated slightly in the later succession stages. The trends in species richness are generally consistent with the increasing diversity hypothesis (Bazzaz 1975, Deyn et al. 2003, Zhang et al. 2005). Seed dispersal and resource competition are possible explanations. In our study, there were 28 herb species at the early stage, which indicated a relatively rich soil seed bank, but there were few woody plant seeds in the early abandoned lands. Bai et al. (2007) reported that 26 herb species and only 2 shrub species were found to exist in soil seed bank on early abandoned lands in Loess Hilly Region of China. The herb species were the pioneers that established and colonized on abandoned lands at early succession stages because they have high fecundity, long-distance dispersal, rapid growth and high resource use capacities. *L. bicolor* and *B. ischaemum* are the dominant species at the early herb stages. *L. bicolor* is a leguminous plant with wide niche and *B. ischaemum* is a C4 plant with high water use efficiency. These herb species increased soil nutrients and moisture, improved the microenvironment, and provided the settlement conditions for late invaded species.

The competitive exclusion hypothesis leads to the hypothesis that the highest species diversity occurs at mid-succession stage when most species have already dispersed and established while the less shade tolerant species have not yet been eliminated. Our results were not completely consistent with this hypothesis, since the highest species richness occurring at late succession stage. This may be due to climate and environmental conditions in the study area. Wang (1991) suggested that the annual rainfall of 550–700 mm and the annual air temperature of 9–12°C were the environmental indexes of the warm temperate forest zone on the Loess Plateau. In our study area, the average annual precipitation of 587.6 mm fits within this range, but the average annual air temperature of 7.4°C is outside these limits. Thus, only a few tree species can survive in this area even in late succession stages (Fig. 2A). As succession continued, the community’s structural complexity increased, vertical and horizontal micro-environmental
heterogeneity are enhanced and more environment resources can be exploited. Also, the tree canopy was not completely closed; this is conducive to the coexistence of shade-tolerant and shade-intolerant species in the forest communities. These factors may explain why maximum species diversity occurs in late succession stages.

Biomass is the result of the long-term cumulative production of the plant community. Productivity is more a function of current conditions. Community biomass is not consistent related to productivity for the woody species. Bormann and Likens (1979) proposed a biomass accumulation model of the natural recovery forest ecosystem. They divided the forest biomass accumulation into four phases: (1) 10–20 year reorganization phase during which the ecosystem loses its biomass and nutrients, (2) aggradations phase of more than a century during which the ecosystem accumulates biomass and reaches its peak, (3) transition phase during which the biomass of the ecosystem declines somewhat from its peak, and (4) steady state phase during which the biomass of the ecosystem fluctuates around a mean level. Although we did not observe a reorganization phase and it is difficult to distinguish the transition and steady state phases in our study (Fig. 1B), the results generally follow the model. Forest succession is a complex and long-term process; there cannot be a completely consistent single model for real forest ecosystem.

In our study, community productivity increased in the early stages of succession and then declined in the later stages. This pattern is consistent with previous studies (Gower et al. 1996, Aarssen et al. 2003, Guo 2007). Gower and colleagues (1996) hypothesized that the decrease of leaf photosynthetic rate of the community would be a potential cause for the decline in aboveground net primary production of the forest community in late succession. Our previous study also found a unimodal pattern in leaf photosynthetic rates of the dominant species that was consistent with the variation of community productivity during succession (An and Shangguan 2007). The low leaf photosynthetic rates of the late succession species likely played an important role in the decrease in community productivity. Moreover, light became a limit as the canopy is shading the forest communities at

![Figure 3](image-url)

**Fig. 3.** Relationships between species richness (number of taxa) and biomass (A), between species richness and productivity (B), and between biomass and productivity (C) along the successional gradient.
the late succession stages and that could also reduce community productivity.

The understory shrubs and herbs represented less than 10% of the whole community biomass (Fig. 2B). These components seem unlikely to contribute much in terms of their mass, but their biomass turned over much more rapidly than did that of the trees with which they coexist, and the aboveground net primary productivity of shrubs and herbs was almost equal to that of the trees (Fig. 2C). As a result, the understory produced a substantial proportion of the annual litter fall that returned to the soil thereby contributing to the total annual nutrient cycling of the ecosystem. Shrub and herb species contributed greatly to plant richness (Fig. 2A). The abundant shrub and herb species probably had an important effect on the tree seedlings. Legumes probably enhance the survival and growth of tree seedlings by increasing soil nitrogen levels and shrub canopy can improve seedling performance by buffering against high radiation and temperatures. This supports the idea that understory vegetation is a major driver of forest succession by affecting tree seedling regeneration and soil processes (Gomez-Aparicio et al. 2004, Nilsson and Wardle 2005).

Richness, biomass, and productivity are interrelated and exert reciprocal influences on one another (Guo 2007). In early succession, habitats have low biomasses and suffer less competitive pressures, so there are still resources and space available for new species from the regional species pools or the soil seed bank to colonize. During this phase, community richness, biomass and productivity increase together (Fig. 3A, B, C). As succession proceeds, surviving individuals grow larger and the canopy closes so competition intensifies. Some species are eliminated through competition, and the species richness declines (Fig. 3A). Weis et al. (2007) reported that species diversity had positive effects on biomass in early succession and negative effects in late succession. However, any biomass fluctuations or drops in late succession may create opportunities for understory species to emerge, thus increasing species richness (Guo 2003). In our study, neither the species richness nor community biomass declined much in the late succession stages but fluctuated slightly (Fig. 1A, B). Fluctuations in species richness and community biomass were not synchronous in late succession (e.g. stages 5, 6 and 7, Fig. 1A, B). High community biomass implies intense competition leading to a negative effect on species richness, while fluctuations in biomass create opportunities for increase species richness. We presume that the relatively low community productivity would be the premise of above conclusion for it released the competitive pressure in community that made the coexistence of high species diversity and high community biomass in the late succession stages.

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