

Morphological plasticity of clonal plant *Phyllostachys praecox* f. *prevernalis* (Poaceae) in response to nitrogen availability

Chun-Lei Yue^{1*}, Kui-Hong Wang¹ & Yin-Mei Zhu²

¹ Zhejiang Forestry Academy, Hangzhou, 310023, China (*author for correspondence, e-mail: yue_chunlei@yahoo.com.cn)

² College of Environment and Resource, Zhejiang University, Hangzhou, 310029, China

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We studied the morphological plasticity of clones in *Phyllostachys praecox* f. *prevernalis* (Poaceae) in response to nitrogen availability in a field experiment. With increasing nitrogen availability, number of ramets per clone increased significantly, whereas the spacer became clearly shorter. Rhizome branching angle and internode length was not responsive to nitrogen availability. Although rhizome length of ramet decreased with increasing nitrogen availability, total rhizome length of clone had no significant variation. In higher nitrogen availability, the total biomass of clone increased significantly. The distribution of more ramets in relatively high nitrogen availability can enable *Phyllostachys praecox* f. *prevernalis* to fully exploit patchy nitrogen. With decreasing nitrogen availability, the clone invested higher percentage allocation of biomass into the underground growth, to enhance acquisition efficiency for nitrogen in soil.

Key words: clonal growth, morphology, nitrogen availability, *Phyllostachys praecox* f. *prevernalis*

Introduction

Clonal growth is characterized by the ability of plants to naturally produce offspring shoot and root units (ramets), which are genetically identical to the parent, and which are potentially independent (Cook 1985, Pitelka & Ashmun 1985, Hutchings & Bradbury 1986). The interconnected ramets are displaced in the different sites, which may lead to the formation of fairly large and long-lived clonal systems.

Heterogeneity is recognized as a fundamental aspect of ecosystem, and observations indicate

that natural environments are spatially and temporally heterogeneous at scales, which are relevant to plants (Jackson & Caldwell 1993, Robertson & Gross 1994, Hutchings & Wijesinghe 1997). Light, nitrogen, water and carbon dioxide, for example, are heterogeneously distributed. In heterogeneous environments, clonal plants show morphological plasticity in response to the quality of the local habitat, and this plasticity may enhance acquisition efficiency for essential resources (Hutchings & de Kroon 1994). There is evidence that morphological plasticity of a species defines the foraging response to different

soil fertilities (Cain 1984, de Kroon & Hutchings 1995).

The morphology of clonal species can be partly described using few parameters such as spacer length, branching intensity and branching angle. These parameters are plastic to some degree, resulting in the development of different morphologies under different conditions of resource supplies (de Kroon & Hutchings 1995). Some species displace more feeding sites (ramets) in microenvironments with abundant resources, by shortening spacer length and increasing branching intensity (Slade & Hutchings 1987a, 1987b, Evans 1992, Dong 1993). Different clonal plant species show varying capacities to morphologically respond to their environment. Thus, field studies on clonal growth in the different level of resource availability may enhance the understanding of the foraging behavior and evolution of clonal plants.

The bamboo *Phyllostachys praecox* f. *prevernalis* (Poaceae) is a clonal species, distributed in the eastern subtropical zone of China (Fang 1998). Its young shoots are famous as a new kind of natural health food. In recent years, research of this species focused on cultivation and introduction techniques (Feng *et al.* 1996, He *et al.* 2001). Its clonal growth form and biomass allocation pattern has been studied under conditions of different light supply (Yue *et al.* 2004). The main aim of the present study was to document its morphological plasticity under the conditions of different nitrogen availability, and to understand its ecological strategy for different nitrogen supplies. In addition, this study offered evidence for making more general statements concerning clonal growth of bamboo.

Material and methods

Biological characteristics of *Phyllostachys praecox* f. *prevernalis*

Phyllostachys praecox f. *prevernalis* is indigenous to China, mainly distributed in Zhejiang province, frequently in plains and low mountains. It produces excellent edible bamboo shoot, and has been widely introduced to the south of China. *Phyllostachys praecox* f. *prevernalis* pro-

duces monopodial rhizomes. The reproduction is generally accomplished asexually by the production of rhizome from the parent plant, and sexual reproduction is far less common.

Study site

The study site is located in the experiment base of Zhejiang Forestry Academy (30°16'N, 120°12'E; 50 m above sea level), which has a mean annual temperature of 16.2 °C, a mean annual accumulated temperature of 5119.4 °C and a mean annual precipitation of 1320 mm. The frost-free period averages 246 days, and extends from March to November. The soil is classified as red earth, in which organic matter, total nitrogen and total phosphorus content are 1.62%, 0.129% and 0.096%, respectively. The field was ploughed and raked to a level surface, prior to the commencement of experiments

Experiment design

The experiment commenced in early August 1999. Twelve 6-m × 6-m plots were established in the experimental field. As parent plants, two-year-old individuals of *Phyllostachys praecox* f. *prevernalis*, growing in the same habitat, were excavated from soil and randomly planted in plots. Plants were uniform-sized with an average height of 2.6 m and an averaged basal diameter of 2.3 cm. Each plot contained nine plants, and distance between plants was 1.5 m. Plots were fertilized with urea at a dose of 0, 20, 40 and 60 g m⁻², respectively, forming four nitrogen availability levels: control, low, middle and high. Fertilization was repeated every three months throughout the course of the experiment. Each treatment had three replicates.

Sampling and data analysis

In early August 2001, all clones in each plot were carefully excavated from the soil, and the roots and rhizomes were washed free of all soil. The following parameters were measured: number of ramets per clone, total rhizome length of clone,

rhizome length of a ramet (total length of rhizomes within a ramet), spacer length (the distance between consecutive ramets), internode length of rhizome (the distance between consecutive nodes on a rhizome), branching angle of rhizome, total biomass of clone, above- and below-ground biomass. Biomass was dried at 80 °C for 24 hours. All data were tested for significant effects of the nitrogen treatments on clonal growth using a one-way ANOVA with mean values. Relationship between measured variables and nitrogen availability was determined by linear regression analysis.

Results

Morphological response of ramet

The treatments had clear impacts on the morphology of a ramet (Table 1). With increasing nitrogen availability, height and basal diameter of a ramet increased, and the differences in height and basal

diameter between treatments were significant. With increasing nitrogen supply, rhizome length of a ramet significantly decreased. In the highest nitrogen availability, rhizome length of a ramet was decreased by ca. 50% as compared with that in control. No significant differences in rhizome diameter and internode length between the treatments were detected.

Architectural change of clone

There was no ramet mortality in any treatment throughout the experiment, but the number of ramets per clone differed greatly between the treatments (Table 2). With increasing nitrogen availability, the number of ramets per clone increased. In the highest nitrogen availability, the number of ramets per clone was about twice as high as that in the control, indicating that relatively high nitrogen availability was beneficial to the occurrence of a ramet. Total rhizome length of a clone was not significantly affected

Table 1. Height and diameter of ramet, rhizome length of ramet, rhizome diameter of ramet and internode length of rhizome in different treatments. Values are means \pm SE, ** = $P < 0.01$, * = $P < 0.05$, n.s. = non-significant.

| Morphological traits of ramet | Nitrogen content | | | | Significance level |
|----------------------------------|------------------|---------------|---------------|---------------|--------------------|
| | Control | Low | Medium | High | |
| Height of ramet (m) | 3.1 \pm 0.4 | 3.4 \pm 0.3 | 3.7 \pm 0.5 | 4.1 \pm 0.4 | * |
| Diameter of ramet (cm) | 2.6 \pm 0.3 | 3.1 \pm 0.2 | 3.4 \pm 0.3 | 3.7 \pm 0.5 | * |
| Rhizome length of ramet (m) | 2.6 \pm 0.4 | 2.0 \pm 0.3 | 1.4 \pm 0.2 | 1.2 \pm 0.2 | ** |
| Rhizome diameter of ramet (cm) | 2.1 \pm 0.2 | 2.2 \pm 0.2 | 2.2 \pm 0.3 | 2.4 \pm 0.4 | n.s. |
| Internode length of rhizome (cm) | 3.9 \pm 0.4 | 3.8 \pm 0.3 | 3.4 \pm 0.6 | 3.4 \pm 0.5 | n.s. |

Table 2. Ramet number of clone, total rhizome length of clone, length of spacer, diameter of rhizome, branching angle of rhizome, biomass of clone in different treatments. Values are means \pm SE, ** = $P < 0.01$, * = $P < 0.05$, n.s. = non-significance.

| Clone | Nitrogen content | | | | Significance level |
|---|------------------|------------------|------------------|------------------|--------------------|
| | Control | Low | Medium | High | |
| Ramet number of clone | 4.1 \pm 0.6 | 5.2 \pm 0.5 | 7.0 \pm 0.4 | 8.1 \pm 0.9 | ** |
| Total rhizome length of clone (m) | 10.6 \pm 1.6 | 10.0 \pm 1.2 | 9.7 \pm 0.9 | 10.3 \pm 1.1 | n.s. |
| Length of spacer (cm) | 42.9 \pm 6.1 | 30.1 \pm 4.3 | 26.0 \pm 3.1 | 19.9 \pm 4.4 | ** |
| Branching angle of rhizome | 44.6° \pm 4.8° | 45.4° \pm 6.5° | 45.1° \pm 5.1° | 44.8° \pm 3.7° | n.s. |
| Total biomass of clone (kg) | 2.24 \pm 0.17 | 2.75 \pm 0.35 | 3.11 \pm 0.32 | 3.59 \pm 0.42 | ** |
| Below-ground biomass/ above-ground biomass | 0.908 | 0.783 | 0.56 | 0.45 | ** |

by nitrogen availability, whilst spacer length significantly declined with increasing nitrogen availability (Table 2). No significant differences in rhizome diameter and internode length between the treatments were detected (Table 2). The rhizome branching angle remained almost unchanged under the condition of different nitrogen availability (Table 2).

Clonal biomass and its allocation

With an increase in nitrogen availability, the total biomass of a clone increased (Table 2). The differences in the total biomass between the treatments were highly significant. Underground biomass/aboveground biomass ratio of a clone increased significantly in lower nitrogen availability, indicating that clones invested relatively more biomass in the growth of underground parts.

Discussion

In heterogeneous habitats, morphological plasticity of the rhizome, spacer length and the branching angle of the rhizome have important ecological consequences for resource acquisition. In clonal plants, the response of spacer length to environment varies. With the increasing nitrogen availability, spacer length may increase, or may change little in different species (Grime & Crick 1986). For rhizomatous species, in most cases the responses of spacer length to nutrient availability were small and statistically insignificant (de Kroon & Hutchings 1995). In this study, with increasing nitrogen availability, spacer length of *Phyllostachys praecox* f. *prevernalis* clones decreased significantly and the number of ramets per clone increased. The results are similar to those for *Brachypodium pinnatum* (de Kroon & Hutchings 1995). In nature, the distribution of nitrogen in horizontal space is usually heterogeneous and this pattern of morphological response can enable *Phyllostachys praecox* f. *prevernalis* to fully exploit patchy nitrogen. Rhizome branching angle is another important aspect of clonal growth form, which might be expected to display plasticity in a patchy environment.

A more acute branching angle can result in a more linear structure than an obtuse branching angle, and therefore more acute branching angles might be predicted in adverse conditions (Slade & Hutchings 1987a). However, in *Phyllostachys praecox* f. *prevernalis* there were no significant differences in rhizome branching angle in response to different nitrogen availability. Perhaps its rhizome branching angle is under genetic control.

Under the condition of different nitrogen availability, the allocation pattern of biomass in *Phyllostachys praecox* f. *prevernalis* clones displayed clear changes. In low nitrogen availability, increased growth of underground parts was observed in clones of *Phyllostachys praecox* f. *prevernalis*, which would help to increase acquisition efficiency in low nitrogen conditions.

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