Responses to Water Stress and a Functional-structural Growth Model of Plant Species Growing in Semi-arid Desertified Areas of Northeast Asia

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Abstract

The most effective way to combat desertification and restore ecosystems in arid/semi-arid regions is through vegetation rehabilitation. In this study, an accumulation of basic eco-physiological information on plant species was integrated with a functional-structural growth model for selecting the best plant species or species combinations and predicting/assessing the rehabilitation.

We examined the growth responses to water stress of 16 plant species growing in arid/semi-arid grasslands in China and Mongolia using environment-controlled growth cabinets. The dry weight growth decreased with increasing water stress in all species, while the degree of depression of the relative growth rate differed among species even of the same life forms such as shrubs, grasses or forbs, and was almost entirely due to the reduction in the net assimilation rate. Some species showed a decrease in their specific leaf area and some showed an increase in their root/shoot ratio, both of which indicated adaptation to fields where water deficiencies occur frequently.

We developed an individual-based 3-D plant structure model of several plant species using the Lindenmayer system (L-system) and an object-oriented modeling framework for constructing a “functional-structural plant growth model” based on morphological/eco-physiological characteristics. Plant morphological parameters above/underground were collected in environment-controlled experiments. Stereoscopic individual-based whole plant growth could be simulated, and by comparing plant structures simulated by the program with those of cultivated real plants, the performance of the model could be confirmed to have a potential to simulate 3-D morphological growth of plant species. This model could also simulate the dry weight growth and eco-physiological responses to water stress.

Key words: desertification, eco-physiology, forb, grass, Lindenmayer system (L-system), morphology, object-oriented modeling framework, shrub, 3-D simulation

1. Introduction

Desertification is one of the most serious ecological and environmental problems in arid and semi-arid regions of Northeast Asia (Zhu et al., 1988; Zha & Gao, 1997; Yang & Lu 2002; Zhou et al., 2004; Yang et al. 2005), influencing sustainable development and the environmental quality of local areas (Liu et al., 1996; Jiang et al., 2003; Wang et al., 2004). The most effective way to combat desertification and restore the ecosystems in these areas is through vegetation rehabilitation (Zhu et al., 1988; Zha & Gao, 1997; Guo, 1998; Koizumi et al., 2000; Li et al., 2004; Maki, 2008).

Seed germination, seedling establishment and vegetative/reproductive growth characteristics of the main plant species in desertified grasslands are essential biological indices for evaluating the effectiveness of measures to combat desertification using vegetation. In recent years, responses have been studied of some plant species to environmental stresses such as water deficiency (Gao & Zhou, 1993; Gutterman, 1993; Tobe et al., 2000, 2005; De Villalobos & Peláez, 2001; Zheng et al., 2003, 2005, 2008). However, there is little knowledge on the response of main plant species to water stress in arid/semi-arid regions of Northeast Asia, which should be basic information for practices to combat desertification, such as selection of suitable species for rehabilitation of desertified areas.

In addition, the planning of rehabilitation with vegetation in arid/semi-arid regions is difficult, because no satisfactory simulation models for predicting and assessing the growth of the main species selected in these regions are available.
regions have been developed thus far. Numerous researchers have foreseen the increasing importance of modeling and simulation as components of plant biology/ecology (e.g., Room, 1996; Minorsky, 2003). For desertification rehabilitation, therefore, it will be necessary to develop individual plant growth models of main species growing in desertified and restored environmental conditions.

In the present paper, we aim to demonstrate the eco-physiological characteristics of many plant species through environment-controlled growth experiments and to develop an individual-based “functional-structural growth model” for several main species.

2. Responses to Water stress of Plant Species Growing in Semi-arid Desertified Areas of Northeast Asia

2.1 Plant species selected for clarifying growth characteristics.

As mentioned above, there has been a lack of knowledge on species characteristics regarding water stress in desertified areas of Northeast Asia. First, we collected seeds of many plant species from arid/semi-arid regions in China and Mongolia (Fig. 1), and investigated the effect of water stress on the growth of the following 16 plant species: shrub species of *Artemisia frigida*, *Artemisia halodendron*, *Artemisia ordosica*, *Caragana korshinskii* and *Caragana microphylla*; grass species of *Achnatherum splendens*, *Agropyron cristatum*, *Cleistogenes squarrosa*, *Clinelymus dahuricus*, *Leymus chinensis* and *Stipa krylovii*; and forb species of *Chenopodium album*, *Medicago sativa*, *Melilotus suaveolens*, *Peganum nigellastrum* and *Salsola collina*.

2.2 Experimental procedure

We used several environment-controlled growth cabinets at the National Institute for Environmental Studies (NIES), Japan (Fig. 2). The seeds, collected in semi-arid regions of Northeast Asia, were brought to Japan and germinated in a mixed medium with 70% sand (well-washed river/sea sands) and 30% artificial soil (Engei-baido: Kureha Chemical Industry Co. Ltd., Japan). After breeding for one to two weeks in an environment-controlled greenhouse (25°C, 70% RH), the seedlings were transplanted into pots (7 cm in diameter, 11 cm in height) containing the same medium (0.35 liter) as that used for germination. The potted plants were grown in the same greenhouse and watered as needed with tap water.

Two to three weeks after transplanting, each species was transferred to an artificially lit growth cabinet (Fig. 2). Under conditions of 25/15°C (light/dark) air temperature, 50/60% (light/dark) relative air humidity and 1,000 µmol m⁻²s⁻¹ in photon flux density during light periods (14/10 hrs of light/dark periods), the plants were treated with different amounts of water, i.e., 30, 60, 90 and 120 mm per month. Each water potential in the soil became stable after about one week, and the averaged water potential during the experiments was –25.2, –9.7, –3.4, and –2.7 kPa, respectively.

These treatments continued for four weeks and then the plants were harvested. Plants were separated into leaves, stems and roots. Leaf areas were measured using an LI-3100 area meter (LI-COR, Inc., Lincoln, NE, USA). All plant tissues were oven-dried at 80°C for more than three days and weighed separately. The relative growth rate (RGR) and the net assimilation rate (NAR) of each plant species was estimated using the following equations:

\[
RGR = \frac{1}{W} \frac{dW}{dt} = (\ln W_2 - \ln W_1) / (t_2 - t_1)
\]

\[
NAR = \frac{1}{F} \frac{dW}{dt} = \frac{(W_2 - W_1)(\ln F_2 - \ln F_1))}{(t_2 - t_1)(F_2 - F_1)}
\]
where $W_i$ and $F_i$ are the dry weight of whole plant and leaf area at time $t_i$ ($t_i$: initial, $t_f$: final), respectively. The leaf area ratio (LAR) was calculated from leaf area divided by whole plant biomass, while the specific leaf area (SLA) was calculated from leaf area divided by leaf dry weight. The leaf weight ratio (LWR) was calculated from leaf weight divided by whole plant biomass, and the root/shoot (R/S) ratio was calculated from root (under-ground biomass) divided by leaf and stem (above-ground biomass).

All growth parameters among treatments were compared by Tukey’s multiple range test (5% level). The software used for the statistical analysis was “Excel Statistical Analysis 2006 (Social Survey Research Information Co., Ltd., Japan).”

### 2.3 Growth responses to water stress

Photographs of six main species (shrubs: Artemisia halodendron and Caragana microphylla, grasses: Cleistogenes squarrosa and Stipa krylovii, and forbs: Peganum nigellastrum and Chenopodium album) out of the 16 plant species and the dry weights of their leaves, stems, roots and whole plants after four weeks of treatment are shown in Figs. 3 and 4, respectively. The dry weight growth decreased with increasing water stress in all the 16 species examined.

As compared with the average summer precipitation (about 90 mm/month) in the Horqin sandy land (a typical semi-arid sandy grassland in Inner Mongolia, China), a 30% increase in precipitation enhanced the growth of four of the shrub species, $A$. halodendron, $A$. ordosica, $C$. korshinskii and $C$. microphylla, whereas it reduced the growth of $A$. frigida. The six grass species, $A$. splendens, $A$. cristatum, $C$. squarrosa, $C$. dahuricus, $L$. chinensis and $S$. krylovii, showed an increased growth tendency with increasing precipitation. In particular, $L$. chinensis and $S$. krylovii showed an obvious increase at 120 mm/month relative to 90 mm/month. At 120 mm/month, the growth of four of the forb species, $C$. album, $M$. sativa, $P$. nigellastrum and $S$. collina, indicated an increasing tendency, while $M$. suaveolens showed a growth reduction.

On the other hand, when precipitation was decreased, i.e., water stress was intensified, the growth of all plant species reduced, though the degree of depression differed among species. For example, when precipitation was...
decreased to one third (30 mm/month), the dry weight reduction was less than 30% in C. microphylla, whereas the dry weight decreased by 85% or more in A. frigida and A. orodosica. Among the grass species, L. chinensis and S. krylovii showed reduction rates of 75% or more, which is remarkable compared to the other four grass species. Among the forb species, the growth of P. nigellastrum decreased remarkably, by about 80%, while the degree of reduction of M. sativa was only 25%.

2.4 Growth analysis for evaluating the eco-physiological responses to water stress

The relative growth rate (RGR), specific leaf area (SLA) and root/shoot ratio (R/S ratio) of the 16 plant species are shown in Fig. 5. Each value under -3.4 kPa in water potential (90 mm/month) is assumed to be 100%. The RGR decreased with increasing water stress in all plant species in the experiment, though the degree of depression in RGR differed among species even of the same life forms, i.e., shrubs, grasses or forbs. In particular, the RGRs of A. orodosica, C. dahuricus, L. chinensis, S. krylovii, C. album and M. suaveolens were reduced markedly with an increase in water stress, while those of others decreased slightly. These RGR reduction responses were mainly due to the decrease in NAR under water-stressed conditions, as was observed by Zheng et al. (2008).

RGR can be expressed as a product of NAR (physiological index) and LAR (structural index). Furthermore, LAR can be expressed as a product of LWR (partitioning index) and SLA (morphological index). Among the grass species, A. splendens, C. squarrosea, C. dahuricus, L. chinensis, S. krylovii and among the forb species, C. album were remarkably influenced in structural/ morphological characteristics under water stressed-conditions. In these species, an increase in water stress caused SLA to decrease remarkably, which suggested a tendency to produce thicker leaves under water-deficient conditions. These SLA responses suggested an attempt to reduce the amount of transpiration under water-stressed conditions, which might be an adaptive strategy in semi-arid desertified regions (Zheng et al., 2008).

C. album, M. sativa, P. nigellastrum, S. collina among the forb species and A. orodosica among the shrub species distributed more biomass to the roots under water-deficient treatments, as observed in the increase in the R/S ratio under water-stressed conditions. This assimilate allocation to roots generally increases when plants are subjected to water stress (Waring & Schlesinger, 1985; Wilson, 1988). Zheng et al. (2008) also reported that several species growing in arid/semi-arid regions decreased shoot biomass more than root biomass under water-deficient conditions. Similar results have been reported by other researchers (Sharp & Davies, 1979; Nicolas et al., 1985; Xiong et al., 2000). Therefore, this response might also be an adaptive characteristic of plants for survival in arid/semi-arid regions where water deficiencies occur frequently.

3. “Functional-structural Growth Model” for Predicting/assessing Plant Growth

3.1 Models of plant growth and development

Individual-based models have received attention in recent years (Ito et al., 2004; Iwasa, 2004). Kurth (1994) reported on recent developments in plant modeling methodologies, in which individual-based models could be divided into two categories (Perttunen et al., 1998). One type of model is the process model, which deals with physiological processes and gives a detailed account of metabolism and plant growth in terms of mass variables. The other type is the morphological model, which describes plants’ structures and development in space. In addition, many models synthesized from these two approaches have been developed (i.e., Yan, 2004; Barczi, 2007).

Not only eco-physiological characteristics but also stereoscopic structures of plants are closely related to the strategies of species’ existence and growth. However, plant structures have been simplified or abstracted in many present ecosystem simulations used in forecasting and assessing environmental problems (Ito et al., 2004;
Yan et al., 2004; Barczi et al., 2008; De Reffye et al., 2008). Therefore, it is difficult to simulate complicated interactions between individual plants and their surrounding environments with precision. Plant growth in arid/semi-arid areas is greatly influenced by disturbance factors such as wind velocities related to sand movement (accumulation and dispersion), soil moisture distributed spatio-temporally non-uniformly, and so on (Koizumi et al., 2000; Maki, 2008).

Therefore, it is crucial to have an understanding of the stereoscopic (3-D) structures of above/underground parts of individual plants which are closely related to these disturbance factors in order to predict/assess vegetation rehabilitation in desertified regions. It will be necessary to develop a “functional-structural growth model” of typical semi-arid plant species, capable of simulating the influence of environmental factors on plants from both eco-physiological and morphological aspects and the interactions between plants and environments.

3.2 Lindenmayer system (L-system) and object-oriented modeling framework

The “Lindenmayer system (L-system)” proposed by Lindenmayer (1968) is one such morphological model. The L-system, which describes the initial state and growth rules of plant structures using certain sets of codes, is an algorithm suitable for explaining morphological aspects of plant growth. (Prusinkiewicz & Lindenmayer, 2004). For modeling the complex structures of higher plants, several extended versions of the L-system have been developed (e.g., Mech & Prusinkiewicz, 1996; Prusinkiewicz, 1998, 2004). We selected the “Open-L-system” as our basic system and modified the existing codes for our objectives (Fig. 6). In order to construct a plant growth model which could simulate morphological/eco-physiological plant responses to environmental factors such as water deficiency so as to enhance desertification rehabilitation planning, we needed to develop a “functional-structural growth model” based on the morphological/eco-physiological characteristics of several plant species, which could describe above/underground 3-D plant structures using the L-system.

We designed an “object-oriented modeling framework” as was necessary for developing a functional-structural growth model. The most important definition in the framework was that the growth of each plant structural object (e.g., leaves, roots) was determined by surrounding environmental factor values (e.g., light intensity, temperature, soil moisture).

3.3 Collecting morphological parameters and modeling plant growth

We analyzed branching patterns and basic structural units of plant shoots and roots using several species of real plants cultivated in environment-controlled greenhouses and/or growth cabinets at NIES. We collected above/underground plant parameters such as stem length, number of leaves, root length, angle of rooting direction, etc. Collecting precise morphological parameters during the plant growth/development of several main species growing in semi-arid desertified areas of Northeast Asia by conducting environment-controlled growth experiments could improve simulation models based on the L-system in order to elaborate/develop a functional-structural plant growth model.

To clarify the relationship between water stress and above/underground growth, we analyzed distributions of vertical root surface, root development angle and shoot structures of *A. halodendron* and *C. squarrosa* as plant materials under different soil water conditions. Under dry conditions, lateral root development, main shoot elongation and branching shoot number of *C. squarrosa* were markedly restricted, and lateral root elongation and main root elongation of *A. halodendron* were also restrained as compared with under wet conditions, while the root angle trend was approximately similar regardless of water conditions in both species.

These obtained data were translated into the L-system data format and then used as input for simulation. L-system data templates for different shoot styles (Fig. 7), typical taproot-lateral root and fibrous root systems (Fig. 8) were designed for *A. halodendron* and *C. squarrosa*, respectively.

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**Fig. 6** Principle of the Lindenmayer system (L-system) and L-system codes.
3.4 Integration of object models for 3-D plant growth simulation

The performance of the model was analyzed by comparing plant structures simulated by the present program with those of cultivated real plants, and the present model was confirmed to have a potential to simulate 3-D above/underground growth of semi-arid plant species (Figs. 7 and 8). By integrating above/underground object models, an individual-based “3-D plant structure model” which could simulate plant growth, including temporal plant structural change, was developed (Fig. 9).

The developed model could (1) show the change in the position and direction of apices in 3-D space resulting from the growth of the basal portion of the plants and (2) simulate budding and branching. This L-system modeling tool could simulate largely different above/underground structures in different plant species fairly well in a similar manner with different input data. As for simulation output, the program could compute the vertical distribution of the relative proportion of root surface area, as well as that of shoot surface area. It should be noted that the model just simulates the geometry of plant structures, and it has limitations in simulating some structural characteristics formed as a result of responses to environmental pressures on growth processes.

In order to simulate plant growth more realistically, a controlling function for shoot branching should be added to the basic structural model, and important information on functional parameters (e.g., RGR, NAR, SLA, R:S ratio, etc.) based on dry weight growth must be linked in order to develop a useful “functional-structural growth model.” Preliminary studies linking these eco-physiological characteristics to the model were conducted with *A. halodendron* under water-stressed and normal conditions, and almost satisfactory results have been obtained from not only morphological but also eco-physiological aspects, by comparing the original data mentioned in Section 2 with the simulation output. Definition of the surrounding space and environment to simulate the interaction between plant growth and environmental factors might also be considered in the development of a refined model capable of expressing such information/data obtained from field surveys and experiments in order to integrate an ecosystem restoration prediction model in the future.
Responses of the 16 plant species (five species of shrub, six of grass, and five of forb) growing in semi-arid regions to water supply changes were clarified using several environment-controlled growth cabinets. Water deficiency reduced the growth of these species, while different species showed different eco-physiological responses to water stress, even among the same life forms such as shrubs, grasses or forbs. The results also indicated several adaptive mechanisms to water stress in species growing in semi-arid regions.

Individual-based 3-D plant structure models of several plant species were developed using the Lindenmayer system (L-system) and an object-oriented modeling framework for constructing a “functional-structural growth model” based on morphological and eco-physiological characteristics. Stereoscopic individual-based whole plant growth could be simulated, and the performance of the model was confirmed to have a potential to simulate plant growth, from both morphological and eco-physiological responses to water deficiency.

For better rehabilitation planning, including the selection of suitable plant species, what is needed is database arrangements of both eco-physiological and morphological characteristics of each plant species and environmental factors in each desertified area, together with development of a more precise “functional-structural growth model” for predicting/assessing the future growth of the introduced plant species in rehabilitated regions. Simultaneously, monitoring of vegetation and environments through the rehabilitation process in the fields where previously severely desertified is also important for the sake of enabling verification/inspection of the rehabilitation method/approach, including model development.

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