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Growth responses of *Picea mongolica* seedlings to defoliation rate

ZOU Chun-jing[1,2], HAN Shi-jie[2], QI Shu-yan[3], XU Wen-duo[2], LI Dao-tang[1]

(1. College of Life Science & Biotechnology, Shanghai Jiaotong University, Shanghai 200030, China. E-mail: zou19680504@163.com; 2. Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang 110016, China; 3. Normal College, Shenyang University, Shenyang 110016, China)

Abstract: *Picea mongolica* W. D. Xu. is an endemic species in China. The spruce forest is only found in semi-arid habitat in Inner Mongolia Autonomous Region of China. Based on the simulative defoliation experiment, it was proved that *Picea mongolica* seedlings had the compensatory and overcompensatory effects under the certain defoliation rate. The results of variance analysis on growth indexes showed that in PM Ⅰ (natural regeneration seedlings under *Picea mongolica* forest), the differences of H_1 (height in June 23) and H_2 (height in September 3) were extremely significant, and the difference of D(diameter at the breast height) were not significant. In PM Ⅱ (artificial regeneration seedlings under *Betula platyphylla* Suk. forest), the difference of H_1 was significant, the difference of H_2 was not significant, and the difference of D was extremely significant. The regression equations were established and the compensatory and overcompensatory points were obtained. In PM Ⅰ, the compensatory points of H_1, H_2, and D were 0.7628, 0.7436, 0.5725, and the overcompensatory points were 0.6056, 0.5802 and 0.2909 respectively. In PM Ⅱ, the compensatory points of H_1, H_2, and D are 0.5012, 0.3421, 0.2488, and the overcompensatory points are 0.4137, 0.2633 and 0.0747 respectively. These results suggested that the induction of compensatory growth mechanisms in spruce seedlings required a threshold level of defoliation, and the insects in *Picea mongolica* forest could be controlled in a certain degree.

Keywords: *Picea mongolica* W. D. Xu.; compensate; overcompensate; growth; defoliation rate

Introduction

Many ecologists have shown their research interests in plant's ability to compensate for damage(Maschinski, 1989; Houle, 1996). Plants have a flexible system of growth. They usually produce more leaves, this apparently serving as an insurance against possible losses of photosynthetic organs (Ericsson, 1980). When leaves are removed, resources that would be allocated to them are subsequently reallocated to adjacent remaining leaves, thus enhancing photosynthetic productivity(Kozlowski, 1971). This compensation allows damaged plants to regain their fitness through extra growth (Rosenthal, 1994; Strauss, 1999). Many tree species that grow under tropical and temperate climates display rhythmic elongation under controlled environments (Foggo, 1996; Coley, 1985). Growth periods alternate with periods of rest even though there are no changes in environmental conditions, indicating that the shoot growth pattern is genetically determined. Correlations, and particularly correlative inhibitions between plant parts, are among the factors that control onset and course of growth and dormancy (Sutherland, 1984). Correlative inhibition may originate in two ways: long distance correlative inhibition exerted by other parts of the plant, or short distance inhibition exerted either by the bud basal tissue or by intrinsic properties of the bud itself. From this point of view, hormonal relationships of dormancy play a prominent role in the course of growth. For example, the observation that leaves supply abscisic acid to the apex(Orchard, 1980; Lee, 1982) may account for the renewed growth of the terminal bud after removal of mature leaves. Moreover, low productive habitats, like deserts, constrain the ability of plants to regrow after damage (Rosenthal, 1994; Strauss, 1999; Gedge, 1994).

Complete or partial defoliation evokes many morphological and physiological responses in plants including production of new assimilatory tissue, and enhanced production of carbohydrates(Ericsson, 1980; McNaughton, 1983). Most of these responses have been interpreted as mechanisms for compensatory growth (McNaughton, 1983; Foggo, 1996; Price, 1991). Plants can, in many cases, compensate for biomass losses by defoliation, and their capacity to grow after damage depends on resource availability (Hamilton, 1998). Response to defoliation is influenced by genotype(Nugent, 1995; Lang, 1985), by the nutritional status of the plant (Chapin, 1979; Mattson, 1980; McNaughton, 1985; Ovaska, 1993), as well as by the timing of defoliation(Ericsson, 1980; Olson, 1989). The interaction between defoliation and vegetative and physiological activities, especially in trees, has been investigated extensively in recent years (Heichel, 1984; Reich, 1993; Ovaska, 1993; Lovett, 1993; Thornton, 1997).

Picea mongolica W. D. Xu. is endemic and endangered species in China, and only found in Baiyinaobao National Natural Reserve, Inner Mongolia Autonomous Region (Xu, 1998a). The ecosystem locates at the transitional zone from Large Xinganling Mountains to Hunshandake Sandy Land, which is typical semi-arid region in China. *Picea mongolica*, a valuable coniferous species which is increasingly used for afforestation in the north of

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China, displayed a rhythmic growth pattern under controlled constant conditions (Xu, 1998b). The duration of the growth flush was from June to August. Growth cessation occurs from September. There were over 8000 hm^2 *Picea mongolica* forest before. At present, there are only less than 2000 hm^2 due to natural factors and human activities. Moreover, there happened serious diseases and insects. There are many defoliating insects, such as *Cephalicia abietis* L., *Acantholyda peiyingaobaoa* Hsiao, *Gilpinia baiyinaobaoa* Hsiao, and also many pests eating trunk, such as *Ips duplicatus* Sahalberg, *Ips typographus* Sahalberg. As to pests eating cone, there are *Pseudotomoides strobilallus* Linnaeus (Xiao, 1998; Han, 1998). The defoliating insects were taken as the biological control objective, because it is preliminary pests. In recent years, a lot of manpower, material resources, and financial capacity are used in the Reserve to control insect pests. However, the effect is not so good as imagination.

The objective of this study is to test the effect of the defoliation rate on the compensatory growth ability of *Picea mongolica* in a semi-arid habitat of China.

1 Materials and methods

1.1 Study site

The study was conducted in Baiyinaobao Natural Reserve (43°30′—43°36′N, 117°06′—117°16′E) in the east of Inner Mongolia Autonomous Region, China. The area is covered by sand, and the thickness of the sand is 10—100 m. The climate here is a typical temperate continent steppe climate. The annual average temperature is -1.4 ℃. The annual average precipitation is 448.9 mm and the potential evaporation is 1526 mm.

The community was dominated by *Picea mongolica* with scattered individuals of *Betula platyphylla*, and *Populus davidiana* Dode. The mean age of the stand was 110 years. The mean height of trees, weighted by basal area, was 17 m. The zonal soils of the area are mainly black soil and brown soil on dunes, which are podzolic, and there also are meadow soil, marsh soil and salt soil on riverbanks, and meadows. The groundwater table is at a depth of 5—8 m. The mean thickness of the humus layer was ca. 50 mm.

1.2 Field survey

According to phytocoenology of *Picea mongolica* forest, two sites were selected in the center of the reserve. The first is natural regeneration seedlings under *Picea mongolica* forest (PM I), and the second is artificial regeneration seedlings under *Betula platyphylla* forest (PM II). 30 seedlings of about 10 year-old were selected in each site. The method is artificial simulative defoliation experiment. The conditions of study sites are shown in Table 1.

1.3 Defoliation treatments

In spring, before needle extending phase of *Picea mongolica* (June 3), the seedlings were grouped into six groups, and each group includes five individuals (total 60 individuals). Six defoliation rate levels, 0%, 20%, 40%, 60%, 80%, and 100% were adopted. We determined basic data of height and base diameter, and determined growth of height (ΔH) and base diameter (ΔD) in needle extending prosperous phase (June 23) and growth stop phase (last phase, September 3) respectively. We took relative growth rate as the compensatory and overcompensatory effects indexes.

Table 1 General conditions of the study sites

Sites	*SD*	*D*	*CD*	*RLI*, %	*H*	*BD*	*A*
PM I	5	N	0.3	87.00	28.76	0.723	10
PM II	7	NE	0.9	41.00	31.43	0.561	10

Notes: *SD*. slope degree; *D*. direction of slopes; *CD*. canopy close degree; *RLI*. relative light intensity; H height(cm); BD base diameter(cm); A. age

1.4 Measurements and statistics

Measurements continued for one growing season. We adopted relative growth rate, variance analysis, and regression analysis to research the compensatory and overcompensatory effects of *Picea mongolica* seedlings to defoliation rate. One way ANOVA, with defoliation as the main treatment, followed by Fisher PLSD tests, were used to compare the effects of defoliation on final characteristics of seedlings.

2 Results

2.1 Growth response of *Picea mongolica* seedlings to defoliation rate

The response of growth indexes to defoliation rate is not only depended on defoliation rate, but also on different environmental conditions (Fig. 1).

Growth indexes of *Picea mongolica* seedlings change with defoliation rate, and they have tendency of increasing in the beginning. However, growth indexes decrease when defoliation rate is more than 60%. In PM I, the effects are bigger, and the persistent time is longer (Fig. 1 I). In PM II, the effects are smaller, and the persistent time is shorter (Fig. 1 II). *Picea mongolica* is a shadow-enduring tree species, and its seedlings need shading condition. But seedlings (more than 7 years old) need a certain light intensity. In PM I, the canopy close degree of the forest is about 0.3, and the relative light intensity under forest is 87%. In PM I, defoliation improve tangent area of needle and light, and enhance the photosynthetic rate, which improve the growth rate. Therefore, *Picea mongolica* seedlings growth, particular height growth can increase even when defoliating rate is about 60%. In PM II, the canopy close degree is 0.9, and the relative light intensity under forest is only 41%. Under this condition, light intensity is just enough for seedlings photosynthesis, and seedlings growth will be limited once the defoliating rate is more than 40%. Furthermore, the response of base diameter is weaker. The reason perhaps is that base growth follows height growth, and height growth spends plenty of matter and energy. When defoliation rate is small, base diameter increases due to the compensatory effect, however, there is restrain effect once defoliation rate is big, especially in PM II.

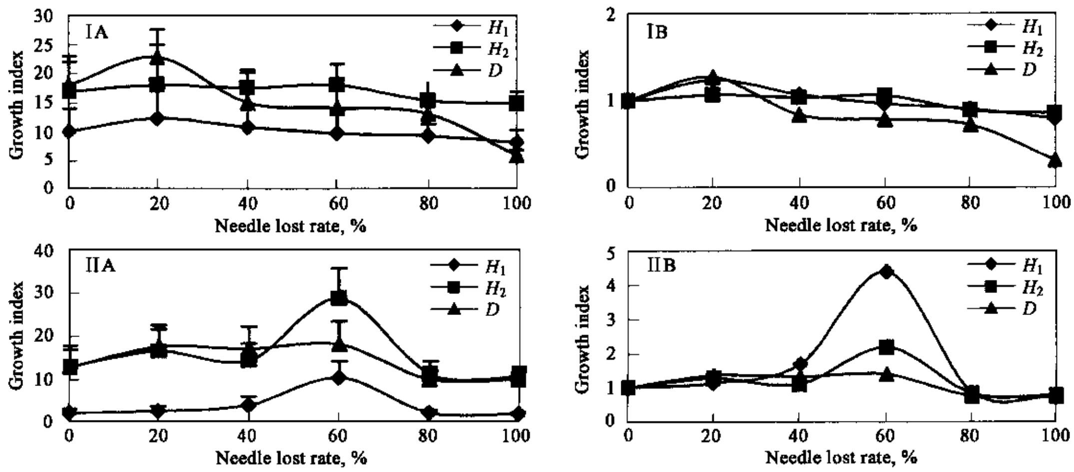

Fig.1 The response curve of *Picea mongolica* growth indexes
H_1: height in June 23; H_2: height in September 3; D: diameter at breast height

2.2 Variance analysis on growth indexes of *Picea mongolica* seedlings

We adopted 6 groups and 5 reduplicate data to carry out variance analysis on growth indexes of *Picea mongolica* seedlings. The results (Table 2) indicated further that the compensatory and overcompensatory effects of *Picea mongolica* seedlings under different defoliation rate. In PM I, the differences of H_1 and H_2 are extremely significant, and the difference of D is not significant. In PM II, the difference of H_1 is significant, the difference of H_2 is not significant, and the difference of D is extremely significant.

Table 2 Variance analysis of growth index

SE		*DF*	*SSD*	*MSD*	*F*-value	*P*
H_1(I)	IRG	5	364.003	72.801		
	IAG	24	274.244	11.468	6.348	<0.01
	Sum	29	639.247			
H_2(I)	IRG	5	1014.791	202.958		
	IAG	24	616.177	25.674	7.905	<0.01
	Sum	29	1630.968			
D (I)	IRG	5	451.368	90.274		
	IAG	24	1584.782	66.033	1.367	<0.10
	Sum	29	2036.150			
H_1(II)	IRG	5	136.123	27.225		
	IAG	24	249.078	10.378	2.623	<0.05
	Sum	29	385.201			
H_2(II)	IRG	5	209.577	41.915		
	IAG	24	531.292	22.137	1.893	<0.10
	Sum	29	740.869			
D (II)	IRG	5	950.299	190.060		
	IAG	24	1142.141	47.589	3.994	<0.01
	Sum	29	2092.440			

Notes: H_1. height in June 23; H_2. height in September 3; D. diameter at breast height; *SE*. source of error; *IRG*. inter-group; *IAG*. intra-group; *DF*. freedom degree; *SSD*. surplus square difference; *MSD*. mean square difference

In order to calculate the compensatory and overcompensatory points of *Picea mongolica* seedlings to defoliation rate, the mathematical models should be established.

2.3 Models of the growth response of *Picea mongolica* seedlings to defoliation rate

The defoliation rate X (0-1) was considered as independent variable, and the growth indexes, such as H, D as dependent variable. The mono thrice functions were adopted, and the multinomial regression models were as follows:

$$H_1(\text{I}) = 1.7493 + 5.0744x + 23.5356x^2 - 30.5208x^3$$
$$(SSe = 39.2849,\ r = 0.8665),$$
$$H_2(\text{I}) = 13.2672 + 11.4920x + 25.3442x^2 - 40.5093x^3$$
$$(SSe = 119.0211,\ r = 0.9658),$$
$$D(\text{I}) = 12.6317 + 48.0858x - 106.6287x^2 + 54.9310x^3$$
$$(SSe = 15.3362,\ r = 0.9940),$$
$$H_1(\text{II}) = 10.2983 + 12.7205x - 32.7382x^2 + 15.5903x^3$$
$$(SSe = 2.2966,\ r = 0.9979),$$
$$H_2(\text{II}) = 17.4523 + 0.0120x + 4.7153x^2 - 11.8518x^3$$
$$(SSe = 1.1477,\ r = 0.9996),$$
$$D(\text{II}) = 20.0065 + 4.9603x - 35.0042x^2 + 15.9492x^3$$
$$(SSe = 27.0742,\ r = 0.9906).$$

As far as relative coefficient (r) is concerned, all of r values are more than 0.8665. As to surplus mean square difference (SSe), there is only one abnormal value SSe = 119.0211, but it is only 7% of total SSe. Therefore, thrice multinomial models are feasible. According to these mathematical models, the compensatory and overcompensatory points of *Picea mongolica* seedlings to the defoliation rate could be calculated.

2.4 The compensatory and overcompensatory points of *Picea mongolica* seedlings

We carried out growth indexes of *Picea mongolica* seedlings as normalization, and then gained the response curve (Fig.1 B).

Sketchy estimate of the compensatory and overcompensatory points are as follows: x value in $y = 1$ is the compensatory point, x value in y maximum is the overcompensatory point. The estimate results are as follows: in PM I, the compensatory points of height growth in prosperous phase and last phase, base diameter growth are 0.73, 0.72, and 0.75 respectively, and their overcompensatory points are 0.60, 0.60 and 0.40 respectively(Fig.1 IB); in PM II, their compensatory points are 0.45, 0.30, and 0.28 respectively, and their overcompensatory points are 0.38, 0.24, and 0.17 respectively(Fig.1 IIB). As far as precision calculation is concerned, we adopted the following method, let $y = 0$, x value is the compensatory point, and let $dy/dx = 0$, x value is the overcompensatory point. The results are shown in Table 3.

Table 3 The compensatory and overcompensatory points of *Picea mongolica* seedlings to defoliation rate

Types	Items	Compensatory points	Overcompensatory points
PM I	H_1(I)	0.7628	0.6056
	H_2(I)	0.7436	0.5802
	D (I)	0.5725	0.2909
PM II	H_1(II)	0.5012	0.4137
	H_2(II)	0.3421	0.2633
	D (II)	0.2488	0.0747

Notes: PM I. natural regeneration seedlings under *Picea mongolica* forest; PM II. artificial regeneration seedlings under *Betula platyphylla* forest; H_1. height in June 23; H_2. height in September 3; D. diameter at breast height

The results of the compensatory and overcompensatory points of different types *Picea mongolica* seedlings are identical with the mentioned analysis.

3 Discussion

Insects influence plants growth, and decrease their productivity, which is already emphasized by science. However, they can improve plants growth, and increase their yield, which is not understood by all people. There are many reports deal special with the co-evolutionary relationship between pests and their host plants. For example, do plants have compensatory ability (Paige, 1987; Sadras, 1996); morphological characteristic, physiological nature, and environmental factors may limit compensatory effects of plants (Vander, 1988); what conditions are beneficial to evolution of population compensatory ability (Crawley, 1987; Yano, 1993). in some cases, pests are truly useful to plants (Belsky, 1986; 1993). These researches proved that the compensatory and overcompensatory effects exist in plants extensively. Sheng (Sheng, 1990), Harris (Harris, 1974) reported that under certain conditions crop could increase production after browse by pests; Xia *et al*. (Xia, 1993) thought that volume of *Pinus tabulaeformis* had increasing tendency after damage by caterpillar; Arthur *et al*. (Arthur, 1993), Mark *et al*. (Mark, 1993) found that the resistance of individuals would enhance after damage. Those reports buffeted the traditional conception in pest-control, and revealed the forgotten facts followed directly perceived through the senses. That is in ecosystems level, we should consider pest-control systems according to co-evolutionary relationship between pests and their host plants (Ding, 1993). Then, what causes lead to the compensatory and overcompensatory effects on earth? Harris thought that pests browsed the vigorous growth top of plants, and broke top growth advantage, which make plants utilize environmental conditions effectively. Someone surmised that browse of pests may stimulate increase of hormone by some chemical matter (Mark, 1993; Cline, 1994), and improved metabolize activities of plants (Aarssen, 1991; Harris, 1974; Vaughton, 1993). It produce plenty of fruit bud for browse of pests such as shieldbug, and finally increase yield; Paige *et al*. (Paige, 1987) thought that pests could increase the fitness of plants; Juha *et al*. (Juha, 1994) thought some plants had plenty of dormant buds, and they could compensate even overcompensate the damage after browse by pests; Sheng (Sheng, 1990) thought that some crops such as cotton reproductive growth was earlier, number of reproduce organs was overmuch, which was unfavorable to yield. Pests browsed the superfluous growth and came forth higher yield.

As to the compensatory and overcompensatory effects of long-live woody plants, there are few reports at present. Someone studied the compensatory and overcompensatory effects of Scots pine based on their biomass (Lars, 1993); Xia *et al*. studied co-evolutionary relationship between *Pinus tabulaeformis* and caterpillar according to volume increase, and discuss mechanism of the compensatory and overcompensatory effects based on its physiological indexes (Xia, 1993). In nature, most plants have the compensatory and overcompensatory ability, which is the result of natural selection and co-evolution between plants system and pests system. In a point of view of eco-economics, the compensatory specialty of *Picea mongolica* can be applied to pest-control. A reasonable control objective could be look for, and not only could avoid explosion of insect pest, but also improve tree growth rate, and elaborate integer function of ecosystems, and save plenty of manpower, resources and financial input.

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