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Effects of root pruning on the growth and rhizosphere soil characteristics of short-rotation closed-canopy poplar

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Abstract

When poplar trees planted at a high density are canopy-closed in plantation after 4-5 years of growth, the roots of adjacent trees will inevitably intermingle together, which possibly restricts the nutrient uptake by root system. Root pruning might stimulate the emergence of fine roots and benefit the tree growth of short-rotation poplar at the stage of canopy closing. The aim of this study is to evaluate the effects of root pruning on DBH (diameter at breast height, 1.3 m), tree height, nutrients (N, P and K) and hormones (indoleacetic acid and cytokinin) in poplar leaves, gas exchange variables (photosynthetic rate and stomatal conductance), and rhizosphere soil characteristics. Field experiment was carried out with four-year-old poplar (*Populus* × *euramericana* cv. 'Neva') planted in a fluvo-aquic loam soil in Shandong province, China in early April, 2008. Three root pruning treatments (severe, moderate and light degree) were conducted at the distances of 6, 8 and 10 times DBH on both inter-row sides of the trees to the depth of 30 cm, respectively. The results showed that the growth performance was obtained in the following order of treatments: moderate > light = control > severe. In the rhizophere soil, moderate and light pruning increased the microbial populations, enzymatic activities, and the concentrations of available N, P, K and organic matter. Generally, root pruning to improve tree growth and rhizosphere soil fertility can be recommended in canopy-closed poplar plantation. The appropriate selection of root pruning intensity is a pivotal factor for the effectiveness of this technique.

Key words: root pruning method; poplar plantation; growth performance; rhizosphere soil fertility.

Resumen

Efectos de la poda de raíces sobre el crecimiento y las características de la rizosfera del suelo de los álamos de corta rotación en la etapa del dosel cerrado

Cuando los chopos plantados a alta densidad cierran el dosel de copas después de 4-5 años, las raíces de árboles adyacentes inevitablemente se mezclan, lo que posiblemente limita la absorción de nutrientes por el sistema radicular. La poda de raíces podría estimular la aparición de raíces finas y beneficiar al crecimiento de los álamos de corta rotación en la etapa del dosel cerrado. El objetivo de este estudio es evaluar los efectos de la poda de raíces en el DAP (diámetro a la altura del pecho, 1,3 m), altura de los árboles, los nutrientes (N, P y K) y las hormonas (ácido indolacético y citoquininas) en las hojas, variables de intercambio gaseoso (tasa de fotosíntesis y conductancia estomática) y características de la rizosfera del suelo. El experimento de campo se llevó a cabo con chopos (*Populus* × *euramericana* cv. 'Neva') de cuatro años de edad plantadas en un suelo franco fluvo-ácuico en la provincia de Shandong, China, a principios de abril de 2008. Se efectuaron tres tratamientos de poda de raíces (severa, moderada y el grado de luz) a distancias de 6, 8 y 10 veces DAP en ambos lados entre las filas de los árboles a la profundidad de 30 cm. Los resultados mostraron que el crecimiento se obtuvo en el siguiente orden de los tratamientos: moderada > suave = control > fuerte. En el suelo de la rizosfera, las podas moderada y suave aumentaron las poblaciones microbianas, las actividades enzimáticas y las concentraciones de N, P y K disponibles y materia orgánica. En general, se puede recomendar la poda de las raíces para mejorar el crecimiento del árbol y la fertilidad del suelo de la rizosfera en plantaciones de chopo con dosel cerrado. La selección adecuada de la intensidad de la poda de raíz es un factor fundamental para la eficacia de esta técnica.

Palabras clave: método de poda de raíz; plantación de chopo; crecimiento; fertilidad de la rizosfera.

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Abbreviations used: ANOVA, analysis of variance; DBH, diameter at breast height; IAA, indoleacetic acid; LSD, least significant difference.

Introduction

In several areas of the world, the fast-growing tree species of choice belong to the genus *Populus* (Pontailler *et al.,* 1999; Christersson, 1996; Bilodeau-Gauthier, 2011). Poplar has many characteristics such as fast growth, adaptability to different environmental conditions, and to different silvicultural systems. All of above features enable the production of large quantities of wood in short periods of time, which can be used for different forms of processing in the timber industry, in the pulp and paper industry and as a source of energy (Fang *et al.,* 1999). With the economic incentives and interests in fast-growing poplar hybrids for short-rotation production for pulp wood, fiber and veneer, poplar plantations have been recently established in northern plain and southwestern upland areas of China. High biomass production can be achieved by the use of intensive cultural management (Fang *et al.,* 2008). Frequently applied agricultural management practices are careful site preparation, selected tree species, dense design, short rotation, irrigation and fertilization throughout the whole rotation period.

Root pruning is a common technique that can reduce vegetative growth of fruit trees (Geisler and Ferree, 1984; Schupp and Ferree, 1990; Asín *et al.,* 2007). It not only assists in dwarfing, but also stimulates the emergence of new roots necessary to sustain growth (Yashiroda, 1960). Specifically, root pruning destroys the old growth balances of trees and changes their assimilation abilities, nutrient distributions, and hormone levels. The combined action of these elements caused different effects on growth and fruit quality (Yang *et al.,* 2009). Root pruning is also used in poplar tree transplanting. The root system is trimmed to a manageable size (usually to a diameter of about 20 cm) after lifting in prevision for storage and planting the following spring (DesRochers and Tremblay, 2009). Reducing the size of planting material is also interesting to practitioners to reduce lifting, packing, shipping and planting costs (South, 1996).

After 4-5 years of growth the poplar trees planted at a high density are usually canopy-closed in plantation. At the same time, the roots of adjacent trees will inevitably intermingle together, which possibly restricts the nutrient uptake by root system. The application of root pruning might stimulate the emergence of fine roots from the cutting site, which could be of advantage for poplar tree due to improved uptake of water and nutrients. At the same time, the reduction of root system can possibly decrease the poplar growth. If the root pruning with appropriate intensity is applied for poplar trees at the growth stage of canopy closing, the poplar growth might be improved as a result of increasing the uptake of water and nutrients by new fine roots from soils at the expense of some old roots. However, no research is available on the effects of root pruning on the growth of canopy-closed poplar trees. Is root pruning helpful to enhance the growth of poplar trees? If so, what pruning severity of root system is suitable to be applied in poplar plantation? How will the method influence the poplar growth? Therefore, it is desirable to determine the performances of root pruning in the management of poplar trees. Since auxin is known to be implicated in the control of root initiation (Torrey, 1976), it was of interest to explore indoleacetic acid (IAA) content in plants after excision of part of the root system. Roots are believed to be the main site of cytokinin synthesis. Measurement of the content of both IAA and cytokinin is important for understanding the effects of root pruning on the poplar growth (Vysotskaya *et al.,* 2001).

The rhizosphere is the zone of soil surrounding a plant root where the biology and chemistry of the soil are significantly influenced by living roots. This zone is about 1-2 mm wide, but has no distinct edge (Bertin *et al.,* 2003). Rather, it is an area of intense biological and chemical activity influenced by compounds exuded by the root, and by microorganisms feeding on the compounds. The chemical components of rhizosphere can be very different from that of bulk soil due to root exudation, nutrient uptake and microorganism activity (Wang and Zabowski, 1998). Root pruning may affect the physio-chemical characteristics and biological properties of poplar rhizopshere soil. However, less information is available on the fertility variation of rhizopshere soil as a result of root pruning.

In this study, we investigated the effects of root pruning on poplar growth, photosynthesis, hormone levels, leaf nutrient status and rhizopshere soil characteristics in the plain areas of the northern China. We hypothesized that the application of root pruning would increase tree growth and improve soil fertility. The objective was to determine the feasibility of implementing root pruning to increase the growth of short-rotation poplar at the stage of canopy closing.

Material and methods

Site description and plant material

The experiment was conducted in a poplar plantation located in Shuizai township, Zhangqiu city, Shandong province, north China (28°15’30”N latitude, 116°55´30”E longitude, and 19 m above sea level). The region has a temperate monsoon climate, with rainfall mainly concentrated in the summer (mean 600.8 mm per year). Mean minimum temperature is 11.7 °C, and mean maximum temperature is 13.6 °C. The morphology of the region is flat and the soil texture is fluvo-aquic loam. Main soil characteristics in the research site included 4.21 g/kg organic matter, available nitrogen (N) 30.18 mg/kg, available phosphorus (P) 9.95 mg/kg and available potassium (K) 101.02 mg/kg (Lu 1999). Soil pH was 7.7 (1: 2.5 soil/water suspension). The poplar plantation was established on the experimental site in 2005 by hand planting one-year-old seedlings of poplar ‘I-107’ clone (*Populus* × *euramericana* cv. ‘Neva’). Initially, plant density was 833 plant per hectare with distances of 4 m between rows and 3 m within rows. These trees are carefully managed and grown as short rotation (5-6 years) poplar mainly for pulp wood.

Experimental design and root pruning treatments

The experiment involved a randomized complete block design with four treatments and three replications. A total 12 plots were established and each replication of every treatment contained a plot with 30 trees arrayed in 5 rows, but only the innermost twelve trees, that were identical to the plot mean, were used for detailed measurements. The average DBH (diameter at breast height, 1.3 m) and height of the poplar trees were 10.03 cm and 10.28 m, respectively. Shortly after the leaves fully developed, four treatments were applied to the poplar trees at the start of the growing season on April 17, 2008: (1) control, with intact root system; (2) severe, removing a part of root system at 6 times DBH distance from trunk, 60 cm; (3) moderate, removing a part of root system at 8 times DBH distance from trunk, 80 cm; (4) light, removing a part of root system at 10 times DBH distance from trunk, 100 cm. Root system was cut with a sharp spade at different distances from the trunk on both inter-row sides of poplar trees to the depth of 30 cm. The treated trees were managed in accordance with routine methods. Nitrogen, phosphorus and potassium were applied annually at rates of 82, 13 and 25 kg per hectare respectively. Irrigation was provided four times during each season (late March, May, August and late November) with an irrigation capacity of 600 m^3 water ha^{-1} per time.

Growth measurement and leaf analysis

Tree height and DBH were measured at the beginning of experiment (early April), and the end of growing season of 2008 and 2009 (late November). The increment of tree height or DBH in 2008 was calculated as the amount of tree height or DBH measured in late November of 2008 minus that in early April of 2008. Similarly, the amounts of tree height and DBH measured in late November of 2009 exceeding the values obtained in late November of 2008 were assumed to increment of tree height and DBH in 2009, respectively. The innermost twelve trees of each plot were individually measured and the mean annual increment of tree height and DBH were calculated.

At the outset and the end of poplar fast-growing period, in late May and late September of 2008 and 2009 respectively, mature leaves were sampled in 3 to 5 trees randomly selected from each plot and fresh weights were recorded. After collected leaves were rinsed twice in deionized water, a portion of leaves were stored in liquid nitrogen for hormone analysis. Another portion of leaves were put into oven to deactivate enzymes for 15 minutes at 105 °C and then dried to constant weight at 80 °C. After drying, the leaves were ground through a 30-mesh screen and analyzed for total N, P, and K. Total N content was determined using Kjeldahl procedure (Lu, 1999). Total P content was measured as molybdovanadophosphoric acid and was read at 470 nm on a visible light spectrophotometer and total K content was determined by a flame spectrophotometer (Lu, 1999). The contents of IAA and cytokinin in leaves were analyzed using the method of Vysotskaya *et al*. (2001).

Measurements of photosynthetic rate and stomatal conductance of poplar leaves were undertaken between the hours 10:30-14:30 in late May and late September of 2008 and 2009, and five measurements per plot were measured with a Portable Photosynthesis System (Model Lci, ADC Biosientifc, Hoddedson, UK). The average values of photosynthetic rate and stomatal conductance in each plot were calculated.

Rhizosphere soil sampling and analysis

In late September of 2008 and 2009, rhizosphere soil was collected according to the procedures described by Wang and Zabowski (1998). Rhizosphere soil was collected in the following way: taking the whole seedling out of the soil with minimum injury to its roots, generally shaking the roots until the soil not tightly adhering to roots was removed and then collecting the soil closely adhering to the root system by putting the roots into a paper bag and vigorously shaking the roots.

Available N content in rhizosphere soil was determined by an indophenol blue colourimetric method (Lu, 1999). Available P content in rhizosphere soil was extracted by 0.5 M $NaHCO_3$ and measured using ascorbic acid-ammonium molybdate method of Murphy and Riley (1962). To determine available K, rhizosphere soil was extracted by ammonium acetate and determined with a flame spectrophotometer (Lu, 1999).

Soil enzymatic activities were assayed in triplicate air-dried samples as described by Guan (1986). Briefly, urease activity was determined using urea as substrate, and the soil mixture was incubated at 37 °C for 24 h, the produced NH_3-N was determined by a colorimetric method, and urease activity was expressed as mg NH_3-N g^{-1} h^{-1}. Invertase activity was determined using sucrose as a substrate and incubation at 37 °C for 24 h, measuring the produced glucose with the colorimetric method, and invertase activity was expressed as mg glucose g^{-1} h^{-1}. Catalase activity was measured using H_2O_2 as a substrate, shaked for 20 min and the filtrate was titrated with 0.1 M $KMnO_4$. Catalase activity was expressed as ml 0.1 M $KMnO_4$ g^{-1} h^{-1}.

Microbial populations were determined with dilution plate method (Zhang *et al.,* 1983). Colonies were counted after incubation at 28 °C for 7 to 10 days for growth of bacteria and actinomyces and at 25 °C for 3 to 5 days for growth of fungi. Microorganisms populations were expressed as colony-forming units g^{-1} soil DW.

Statistical analysis

The data were analyzed as a completely randomized design. The analysis of variance (ANOVA) was carried out to evaluate the effects of root pruning treatment on different variables measured regarding the poplar growth and rhizosphere soil characteristics. When the ANOVA analysis found significant differences between treatments, the LSD (Least significant difference) test was conducted to detect differences between individual treatment level means. All statistical analyses were performed at a significant level of $p < 0.05$. ANOVA and multiple comparisons were performed using SPSS software (version 15.0; SPSS Inc., Chicago, Illinois). All results in figures 1-3 and tables 1-4 were given as means of three replicates.

Results

Tree height and DBH growth

Root pruning treatments significantly affected the tree height and DBH growth of poplar trees (Fig. 1). Compared to the control, the increment of DBH was significantly increased after moderate root pruning. At the end of 2008 and 2009 growing season, the DBH increment of poplar trees treated by moderate root pruning were 7.38% and 4.59% higher than that of untreated trees ($p < 0.05$), respectively. For the increment of tree height, significant increase ($p < 0.05$) was also observed in contrast to the control in both years. Contrary to the moderate root pruning, the DBH increment was significantly decreased by the severe root pruning, which had no effect on the height growth. However, the light root pruning treatment showed no evident influences on the growth of tree height and DBH. In general, the best growth was obtained in the following order of root pruning treatment:

moderate > light = unpruned (control) > severe.

Total N, P and K contents in the leaves

Table 1 shows total N, P and K contents in the leaves of poplar trees during last two years of rotation after root pruning. In late May of 2008, about a month after root pruning, all three root pruning treatments decreased the contents of total N, P and K in leaves in comparison to the control. The lowest content of total N or P was associated with the severe root pruning. No significant difference was found among root pruning treatments. With the time delayed, the contents of total N and K in leaves were significantly increased by moderate root pruning in comparison to the control, whereas total P content was slightly enhanced without statistically significant difference. Unlike the performances in late May of 2008, the inhibition effects of severe root pruning on the contents of total N, P and K in the

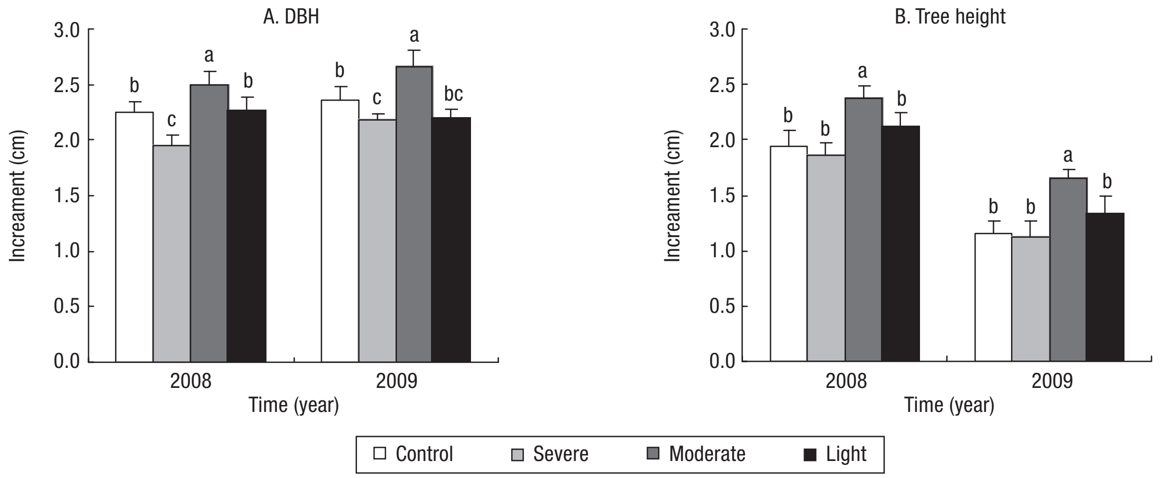

Figure 1. DBH and tree height growth following root pruning treatments in poplar plantation in two growing seasons. Bars are means and error bars are standard deviations (n = 3). The different letters above bars in the same year represent significantly different means at $p = 0.05$.

leaves were not observed in the experiment at subsequent three investigation times. The results indicated that root pruning of different intensities had entirely different effects on the mineral nutrient status of poplar trees.

IAA and cytokinin contents in the leaves

Both IAA and cytokinin are important in the restoration of plant growth after root pruning (Vysotskaya *et al.,* 2001). There was a similar pattern of variation for IAA and cytokinin contents of poplar leaves among different treatments (Fig. 2). In late May of 2008, the IAA and cytokinin contents were significantly reduced by root pruning in contrast to the untreated control ($p < 0.05$). The lowest value was measured in the severe pruning treatment. As the distances of root pruning from trunk increased, the inhibition effects declined. However, the moderate and light root pruning evidently raised the contents of IAA and cytokinin in late September of the same year, late May and late September of the next year. The highest value was found in the treatment of moderate root pruning. Compared with the control, the contents of the two hormones were still lower in the leaves of poplar trees treated by severe root pruning.

Photosynthetic rate and stomatal conductance

Photosynthetic rate of poplar leaves responded to root pruning very similarly to stomatal conductance

Table 1. The effects of root pruning on total N, P and K contents in poplar leaves

Treatment	N (g kg^{-1} DW)		P (g kg^{-1} DW)		K g kg^{-1} DW)	
	May	Sept.	May	Sept.	May	Sept.
The growing season of 2008						
Control	22.98 a	12.32 b	2.41 a	2.76 a	10.1 a	8.12 b
Severe	21.11 b	12.31 b	2.25 b	2.75 a	9.78 b	8.13 b
Moderate	22.23 b	12.61 a	2.33 b	2.86 a	9.72 b	8.31 a
Light	21.81 b	12.44 a	2.35 b	2.83 a	9.69 b	8.13 b
The growing season of 2009						
Control	20.82 b	11.36 b	2.17 b	2.53 a	9.21 b	7.34 b
Severe	20.68 b	11.32 b	2.15 b	2.49 a	9.21 b	7.27 b
Moderate	22.33 a	11.62 a	2.26 a	2.60 a	9.39 a	7.55 a
Light	20.71 b	11.41 b	2.19 b	2.57 a	9.28 b	7.38 b

Note: In the same growing season, means in the same column followed by different letters are significantly different at $p < 0.05$ by LSD.

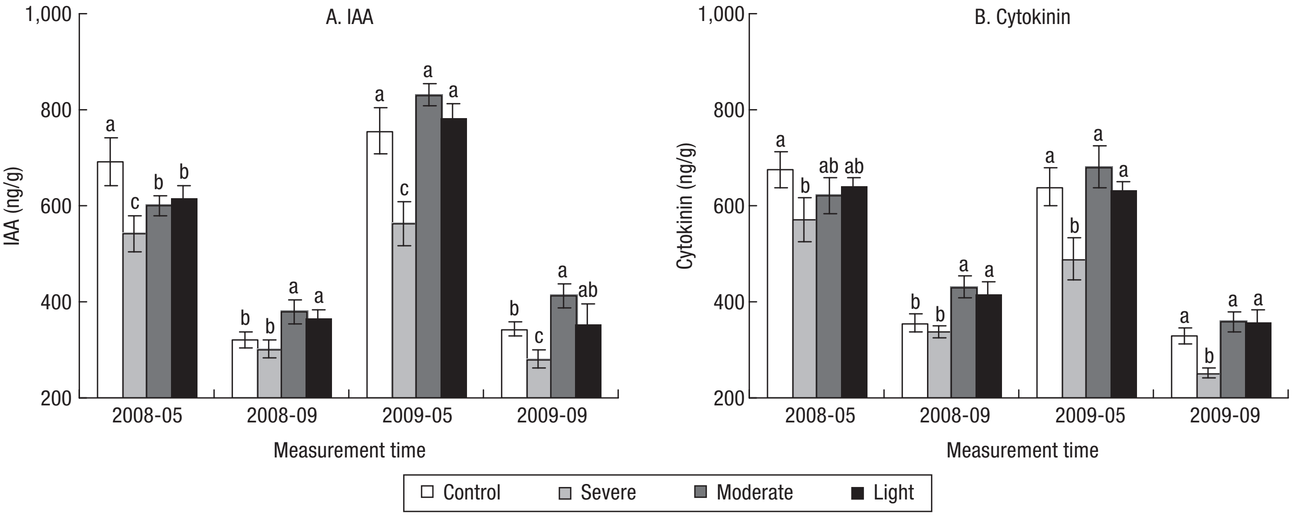

Figure 2. Effects of different root pruning on the conents of IAA and cytokinin in poplar leaves. The results are expressed as means on a basis of dry weight, and error bars are standard deviations (n = 3). The different letters above bars in the same measurement time represent significantly different means at $p = 0.05$.

(Fig. 3). One month after root pruning, the photosynthetic rate and stomatal conductance of the untreated control were significantly higher than the other treatments in late May of 2008. Among three root pruning treatments, the lowest value was obtained in the plot treated with severe root pruning for the two gas exchange variables. Whereas at any subsequent measurement time, photosynthetic rate and stomatal conductance of poplar leaves in plots with moderate or light root pruning treatment were significantly higher than the control plot. Compared with the control, a decrease of photosynthetic parameters was also observed for the treatment of severe root pruning at the second, third or fourth assessment.

Nutrient status in rhizosphere soil

The nutrient status of rhizosphere soil mainly depended on fertilizers added in current growing season, and was also affected by the intensity of root pruning. The concentrations of available N, P, K and organic matter in rhizosphere soil of different treatments at the end of the last two growing seasons are shown in Table 2.

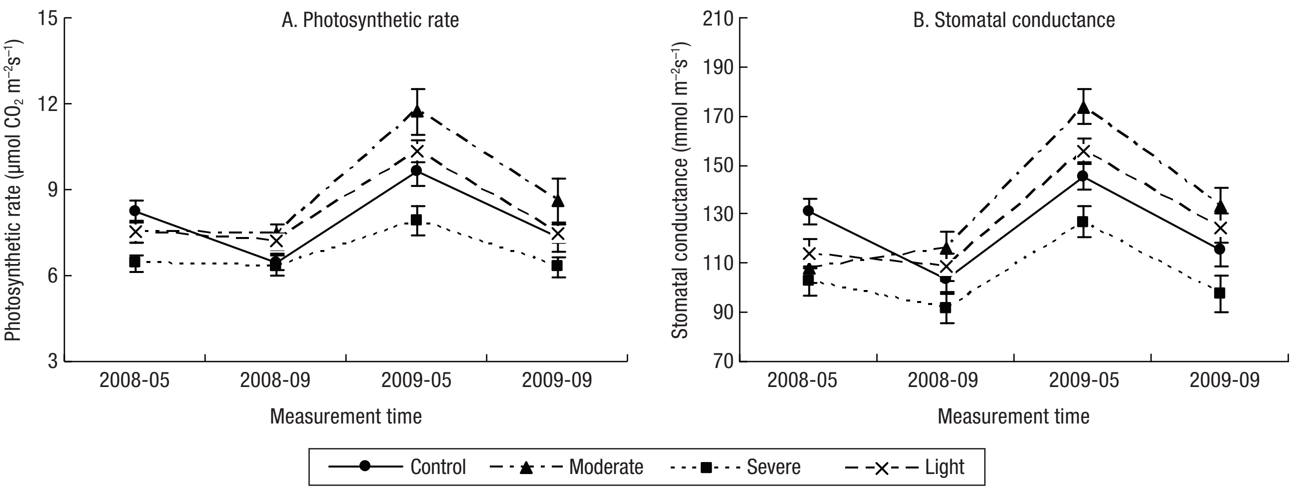

Figure 3. Effects of different root pruning on photosynthetic rate (A) and stomatal conductance (B) of poplar leaves. The results are expressed as means and error bars are standard deviations (n = 3).

Table 2. The concentrations of available N, P K and organic matter in rhizosphere soil of different treatments

Treatment	Available N ($mg\ kg^{-1}$ DW)	Available P ($mg\ kg^{-1}$ DW)	Available K ($mg\ kg^{-1}$ DW)	Organic matter ($g\ kg^{-1}$ DW)
The growing season of 2008				
Control	34.37 b	13.27 b	105 b	0.832 b
Severe	23.46 c	11.53 c	92 c	0.831 b
Moderate	44.91 a	16.02 a	135 a	0.911 a
Light	42.87 a	15.87 a	129 a	0.909 a
The growing season of 2009				
Control	37.11 b	13.36 b	109.41 b	0.93 b
Severe	34.70 c	12.91 c	94.12 c	0.89 b
Moderate	48.58 a	18.15 a	141.63 a	1.07 a
Light	38.82 b	13.55 b	111.23 b	0.94 b

Note: In the same growing season, means in the same column followed by different letters are significantly different at $p < 0.05$ by LSD.

The concentrations of available N, P and K in rhizosphere soil of lightly or moderately root-pruned poplar trees were higher than those of the control, the highest of which were obtained in moderate root pruning treatment. However, the concentrations of available N, P and K in rhizosphere soil were significantly reduced by the severe root pruning, which displayed no impact on the concentration of organic matter. The results of ANOVA analysis indicated that root pruning caused significant changes of nutrient status in rhizosphere soil.

Enzymatic activities in rhizosphere soil

The activities of soil enzymes could be used as an important index for evaluation of soil fertility. The enzymatic activities of rhizosphere soil, sampled from approximately 0 to 2 mm away from the root surface, was significantly influenced by living root system of poplar tree in the growing seasons of 2008 and 2009 (Table 3). The activities of three enzymes, namely, invertase, catalase and urease were significantly increased in rhizosphere soil as affected by moderate or light root pruning in contrast to those of the control. Among all the treatments, the activities of invertase, catalase, phosphatase and urease in rhizosphere soil of severely root pruned poplar trees were the lowest, but which had no statistical significant difference with the control. The results indicated that enzymatic activities were affected by root pruning. Both moderate and light root pruning could contribute to evident enhancement of enzymatic activities in rhizosphere soil.

Table 3. The effects of root pruning on enzymatic activities in rhizosphere soil

Treatment	Urease ($mg\ NH_3\text{-}N\ g^{-1}\ h^{-1}$)	Invertase (mg glucose $g^{-1}\ h^{-1}$)	Catalase (ml 0.1 M $KMnO_4\ g^{-1}\ h^{-1}$)
The growing season of 2008			
Control	0.124 b	4.46 b	0.89 b
Severe	0.116 b	3.74 b	0.80 b
Moderate	0.187 a	6.12 a	1.23 a
Light	0.184 a	6.03 a	1.17 a
The growing season of 2009			
Control	0.13 c	4.68 c	0.89 b
Severe	0.13 c	4.55 c	0.83 b
Moderate	0.18 a	6.92 a	1.34 a
Light	0.15 b	5.72 b	1.24 a

Note: In the same growing season, means in the same column followed by different letters are significantly different at $p < 0.05$ by LSD.

Microbial populations in rhizosphere soil

After root pruning, the populations of bacteria, actinomyces and fungi in rhizosphere soil of poplar trees were tested in late September of 2008 and 2009. The effects of root pruning on microbial populations are presented in Table 4. The amounts of bacteria, actinomyces, and fungi were significantly increased by moderate or light root pruning in comparison to the control, but reduced by severe pruning treatment. The amounts of microorganism population ranged from 240 $\times 10^5$ g^{-1} to 540 $\times 10^5$ g^{-1} and differed apparently between treatments. The results demonstrated that root pruning could play remarkable impacts on microbial populations in rhizosphere soil of poplar trees and the effects were dependent on root pruning strength.

Discussion

Populus × *euramericana* cv. 'Neva' has been found to be one of the most promising suitable species for afforestation and woody production in the arid and semi-arid areas of China. The successful establishment and rapid growth of trees are dependent on fast growth and excellent nutrient absorbing ability of root system. In the experiment, a portion of lateral roots was removed through root pruning, which resulted in some variations relating to the growth and rhizosphere soil characteristics of poplar trees. Unlike intact roots of unpruned trees, a large number of fine roots occurred on the cutting site of lateral roots of root-pruned trees (Fig. 4). Even though all three root pruning treatments resulted in the emergence of many fine roots, which may benefit the uptakes of nutrients and water by root system, the growth performances of poplar trees varied much under different root pruning intensities. The experimental results indicated that severe root pruning inhibited the growth of DBH ($p < 0.05$) in the first growing season. The reason probably was that poplar trees were unable to uptake adequate water and nutrients for the growth of aboveground organs due to existing root surface areas relatively much decreased by root pruning. With time extension, the inhibition effect was weakened, close to the control next year. However, the moderate or light root pruning significantly promoted the growth of poplar trees in the growing seasons of both 2008 and 2009. The moderate one showed the best growth performance. The results indicated that appropriate intensity of root pruning was critical for poplar trees, which possibly promoted the absorbing ability of root system at the expense of some lateral roots. Some researches also found that moderate root-pruning did not decrease hardwood survival or growth (Russell, 1973; Zaczek *et al.,* 1997). While others found that root-pruning to be detrimental to hardwood survival and growth (Sterling and Lane, 1975; Brantley and Conner, 1997; Khan *et al.,* 1998). The differences between these studies in the effects of root pruning on hardwood growth can be attributed to the different tree species, pruning degree, stand age and other factors (Brantley and Conner, 1997).

Significant increases in the mineral nutrient status, hormones contents, photosynthetic parameters of poplar leaves were also found by moderate and light root pruning. These results are in agreement with some previous researches applying root restriction to apple (Bar-Yosef *et al.,* 1988), beans (Carmi and Heuer,

Table 4. The effects of root pruning on microbial populations in rhizosphere soil of different treatments ($\times 10^5$ g^{-1} soil DW)

Treatment	Bacteria	Actinomyces	Fungi population	Total population
The growing season of 2008				
Control	367.9 b	8.4 b	1.7 b	378.0 b
Severe	236.2 b	7.3 b	1.4 b	244.9 b
Moderate	498.1 a	13.2 a	3.3 a	514.6 a
Light	476.4 a	11.4 a	3.0 a	490.8 a
The growing season of 2009				
Control	392.8 b	9.2 c	1.9 b	419.2 b
Severe	258.4 c	8.2 d	1.5 c	267.0 c
Moderate	541.7 a	13.3 a	2.5 a	536.6 a
Light	447.9 b	11.1 b	2.1 b	454.2 b

Note: In the same growing season, means in the same column followed by different letters are significantly different at $p < 0.05$ by LSD.

(a) Severe root pruning and control

(b) Moderate root pruning and control

(c) Light root pruning and control

Figure 4. Morphological changes of roots as affected by different pruning intensities.

1981) and tomato (Bar-Tal *et al.,* 1994). These studies showed that restricted root system was more efficient in N uptake rate per root unit. Many physiological processes associated with plant growth are enhanced by nutrient supply (Correia *et al.,* 2005). Higher correlation between photosynthetic rate and stomatal conductance was found in an experiment of sweet corn carried out by Efthimiadou *et al.* (2009). In this paper, we also observed that photosynthetic rate and stomatal conductance of poplar leaves were increased by moderate or light root pruning, which was in accordance with the increase of total N, P and K contents in leaves. Since IAA is well-known to be involved in the initiation of lateral roots (Blakesley *et al.,* 1991; Torrey, 1976), the increase in hormone concentration following root pruning of moderate or light intensity might be the cause of acceleration of lateral root emergence. Cytokinin production is believed to be associated with the division of root cells. Initiation of lateral roots might be responsible for the increase in the ability of roots to supply the shoot with cytokinins (Evans, 1984). Cytokinin is vey helpful to control shoot growth (Beck, 1996). Consequently the ability of poplar tree to maintain a high cytokinin content in aboveground organs after root pruning might be important for enabling the observed growth increase.

Plant roots can induce changes in nutrient composition in the rhizosphere solution directly through root uptake and indirectly through their effects on rhizosphere microorganisms (Drever and Vance, 1994). Under moderate and light root pruning, the photosynthesis of poplar trees was enhanced, which would indicate that the leaves of moderately or lightly root-pruned trees possibly allocated more photosynthate into roots. As a result, the microorganism population, enzymatic activities and nutrient status in rhizosphere soil were increased at the same time. The rhizosphere microorganisms play an important role in processing and retention of nutrients in plant-soil systems (O'Neil and Reichle, 1980). A higher population of microorganism can increase the decomposition of organic matter and therefore may increase nutrient concentrations of the rhizosphere solution (Wang and Zabowski, 1998). Compared to the control, higher nutrient concentrations in rhizosphere soil of moderate and light root pruning treatments could result in the increase of N, P and K contents in leaves and consequently the improvement of photosynthesis. Thus, a virtuous circle relating to soil nutrients and photosynthate was possibly created in poplar trees after appropriate root pruning.

Conclusions

In conclusion, it is evident from this study that the application of root pruning is an effective way to improve poplar growth and rhizosphere soil fertility at the stage of canopy closing, a late period of short rotation. The selection of root pruning intensity is a pivotal factor for the effectiveness of this technique for management of poplar plantation. The optimum distances from trunk of root pruning should be determined through required experiments for poplar plantations with different species, stand age, planting densities and soil properties.

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