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## Effects of aqueous leaf extracts of *Populus tomentosa* at different ages on the growth and photosynthetic characteristics of its own seedlings

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**Abstract** Through the outdoor potted plant trials, the allelopathic potential of *Populus tomentosa* was tested against its species in the growth, chlorophyll content, and photosynthetic and chlorophyll fluorescence characteristics with aqueous extracts (0.01, 0.02, 0.05, and 0.1 g·mL<sup>-1</sup>) obtained from leaves at different individual ages (1, 20, and 45 years old). The results showed that seedling height, basal diameter, fresh and dry weights, quantity of chlorophyll, the ratio of chlorophyll a/b, net photosynthetic rate ( $P_n$ ), stomatal conductance ( $G_s$ ), transpiration rate ( $T_r$ ), efficiency of primary conversion of light energy of PSII ( $F_v/F_m$ ), potential activity of PSII ( $F_v/F_0$ ), and photochemical quenching ( $q_p$ ) of the seedlings gradually decreased with the increase of extract concentration of all three ages when compared with the controls. The older the *P. tomentosa* used for extract preparation, the greater the percentage declined in the aforementioned parameters. Moreover, at the four concentrations used, there was a significant difference between treatments with the extracts from 1- and 45-year-old plants (except for  $q_p$ ), but occasionally, the effects were not obvious between the 1- and the 20-year-old plants, or the 20- and 45-year-old plants. The intercellular CO<sub>2</sub> concentration ( $C_i$ ) treated with the extracts from the 1-year-old decreased at the lowest concentration, whereas it increased at higher concentrations. The  $C_i$  treated with aqueous leaf extracts from the 20-year-old decreased at the lower concentrations and increased to similar levels to that of the control at the higher concentrations.  $C_i$  was always close to control levels in 45-year-old extract treatments. All the aqueous leaf extracts of *P. tomentosa* at all ages caused an increase

of the initial fluorescence ( $F_0$ ). The older *P. tomentosa* used for the preparation of aqueous leaf extracts caused a greater percentage decline in  $F_0$ . The nonphotochemical quenching ( $q_N$ ) increased significantly at lower concentrations of all *P. tomentosa* extracts, whereas it decreased significantly at higher concentrations. It seemed that aqueous leaf extracts from *P. tomentosa* were harmful to the photosynthetic structure of its own seedlings, inhibited seedling growth, and led to an eventual decrease of biomass. Extracts from older *P. tomentosa* leaves had more negative effects on the seedling growth of poplar. The effects on photosynthesis are the more important mechanism of the allelopathy of poplar.

**Keywords** *Populus tomentosa*, aqueous leaf extracts, photosynthesis, chlorophyll fluorescence

### 1 Introduction

Rice defined allelopathy as the effect of one plant (including microorganism) on growth of another plant through the release of chemical compounds into the environment. Both positive and negative effects are included in this definition (Rice, 1984). It was classified into two main forms including interspecific allelopathy (self-toxicity) and intraspecific allelopathy. Self-toxicity is an important obstacle in tree plantations that are used continuously and has been reported to occur in China fir, several species of *Eucalyptus*, *Cunninghamia*, and *Pinus* among others (Zeng and Li, 1997; Chen et al., 2002; Wang et al., 2002; Chen and Wang, 2003; Wang, 2004; Wang et al., 2006). Poplar is one of the most important afforestation tree species in North China. In poplar stands, soil degradation has occurred with increasing generations of trees, resulting in a decline in yield, the occurrence of diseases and insect pests, and a decrease in afforestation survival rate (Fang et al., 2007). It is assumed that

Received November 4, 2008; accepted December 11, 2008

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permanent poplar plantations have led to significant changes in the physical and chemical properties, nutrient content, enzyme activities, and the number and structure of the microbial community of the soil (Fan et al., 2007; Tan et al., 2008). There are few baseline studies on the allelopathy of poplars. Although a number of poplars as *Populus balsamifera*, *P. tremuloides*, *P. delto*, *P. pruinosa*, *P. aldatomentosa*, *P. tomentosa* have been reported to possess an inhibitory and stimulatory effect on herbs or crops (Olsen et al., 1971; Qin et al., 1999; Sharma et al., 2000; Kaushal et al., 2003; Luo et al., 2003, 2004; Jack et al., 2006), there is little information about the allelopathic effect of *Populus* on the growth of its own seedlings. Chinese white poplar (*P. tomentosa*) is an important tree species in industrial and shelter-timber forests in China with a large planting area. It is therefore important to study whether *P. tomentosa* possesses self-allelopathy so as to assure the sustainable management of *P. tomentosa* stands. Accordingly, we conducted an experiment to investigate the growth, photosynthesis, and fluorescence characteristics of *P. tomentosa* under stress from aqueous leaf extracts of this species at different ages.

## 2 Materials and methods

### 2.1 Materials

Cuttings of 1-year-old seedlings of *Populus tomentosa* and fresh leaves (2-month leaf age) obtained from trees of different ages (1-, 20-, and 45-year old) were collected from the Qing Xiling Urban Forest Demonstration of the Agriculture University, Baoding, China, in June 2007. The climate in this area is semiarid with an annual average rainfall of 760 mm and an active accumulated temperature of 4021°C. The soil type is cinnamon soil.

### 2.2 Preparation of aqueous leaf extracts

Aqueous extracts of each tree age were obtained by macerating leaves for 48 h in distilled water at 25°C. The extracts contained 1 g of leaves per 10 mL of water and were used as stock solutions after being filtered through gauze. Three other concentrations of 0.01, 0.02, and 0.05 g·mL<sup>-1</sup> were obtained by diluting the stock solutions in water, and all extracts were stored at 4°C for later use.

### 2.3 Test design and measurement methods

#### 2.3.1 Experimental design

The experiment was carried out in a greenhouse at the Agricultural University of Hebei during May to August, 2008. The washed and sterilized sand was used as cultural

medium. The completely randomized block design was applied with 12 testing blocks, one control block in the experiment, and six replications in each block. On May 1, 2008, the uniform 1-year-old *P. tomentosa* seedlings were transplanted into 30cm×40 cm plastic pots (one seedling per pot) with 10 kg sterilized sand and then cultured in the greenhouse. Forty-five days after transplantation, the different concentrations of extracts (1 L per pot) and Hoagland nutrient solution (0.5 L) were applied separately to each testing pot twice per month. Equal volumes of water, instead of extracts, and Hoagland nutrient solution were applied to each control pot. During cultivation, the same quantity of water and nutrient solution was poured into each pot according to the requirement of the experimental design.

#### 2.3.2 Measurement methods

On August 23, 2008, net photosynthetic rate ( $P_n$ ), stomatal conductance ( $G_s$ ), transpiration rate ( $T_r$ ), and intercellular CO<sub>2</sub> concentration ( $C_i$ ) were measured by a portable photosynthesis system (LCI, England) under open flow conditions during 8:00–10:00 on a sunny day. The wholly expanded leaves (the 3rd and 4th leaves from the top) were measured, with six replications in each test. The wholly expanded leaves were also used to measure the fluorescence parameter by a modulated chlorophyll fluorometer (OS52FL, America) after a 30-min dark treatment.

Chlorophyll content was measured by the method of equally mixing ethanol and acetone (Li et al., 2000). After their height and basal diameter were measured, the experimental seedlings were removed from each pot and washed in running water. The seedlings were blotted dry with filter paper before measuring their fresh weight. Dry weights were measured after deactivation of enzymes (about 15 min at 150–160°C) and drying for 48 h at 70°C. All data were analyzed by one-way ANOVA and LSD tests to compare multiple means using SPSS12.0 software.

## 3 Results and analysis

### 3.1 Effects of aqueous leaf extracts on the growth of seedlings of *P. tomentosa*

#### 3.1.1 Effect of aqueous leaf extract on height and basal diameter of seedlings

At 0.01 g·mL<sup>-1</sup>, the height and basal diameter of the seedlings were 1.72% and 3.38% smaller than those of the controls (Fig. 1), although there were no significant differences ( $P < 0.05$ ) between the control and treatment of the 1-year-old. However, the seedlings treated with extracts from 20- and 45-year-old trees were significantly smaller in height (6.55% and 10.34%, respectively) and basal diameter (15.68% and 19.08%, respectively) than the

controls. At  $0.02 \text{ g} \cdot \text{mL}^{-1}$ , seedling height was significantly ( $P < 0.05$ ) decreased by 14.83%, 20.34%, and 30%, with basal diameter significantly decreased by 6.27%, 22.70%, and 30.92% in 1-, 20- and 45-year-old treatments, respectively, compared with the controls. There were significant differences in both seedling height and basal diameter between the three age treatments at 0.01 and  $0.02 \text{ g} \cdot \text{mL}^{-1}$  concentration. The higher the concentration of the extracts, the stronger the inhibitory effects on both seedling height and basal diameter in all the three age treatments. This indicated that the aqueous leaf extracts from the trees of three different ages decreased the growth of *P. tomentosa* seedlings in terms of height and basal diameter at all the concentrations tested. The inhibitory effect was stronger on the basal diameter of seedlings when compared with the height.

### 3.1.2 Effect of aqueous leaf extract on fresh and dry weight of seedlings

For all concentrations of aqueous leaf extracts, the fresh weight was lowered by 5.48%–42.23%, and the dry weight

was lowered by 4.97%–38.17% in the 1-year-old treatment (Fig. 2). In the 20-year-old treatment, the fresh and dry weights were 14.01%–51.62% and 13.03%–46.79% lower, respectively. In the 45-year-old treatment, the fresh and dry weights were 17.34%–63.74% and 18.19%–58.97% lower, respectively. There were significant differences ( $P < 0.05$ ) in the fresh and dry weights in the three age treatments of extracts at all concentrations, except  $0.05 \text{ g} \cdot \text{mL}^{-1}$ , where there was no significant difference ( $P < 0.05$ ) in the fresh weight of the seedlings between 1- and 20-year-old treatments. It indicated that the fresh and dry weights of the seedlings were inhibited obviously by the extracts from *P. tomentosa* of the three ages at all concentrations. Furthermore, the greater the concentration of aqueous leaf extracts, the lower the fresh and dry weight of seedlings when compared with the controls. The older the *P. tomentosa* used for the preparation of aqueous leaf extracts, the lower the fresh and dry weight of the seedlings when compared with the controls. In comparison with the dry weight of the seedlings, the inhibitory effect was greater on fresh weight.

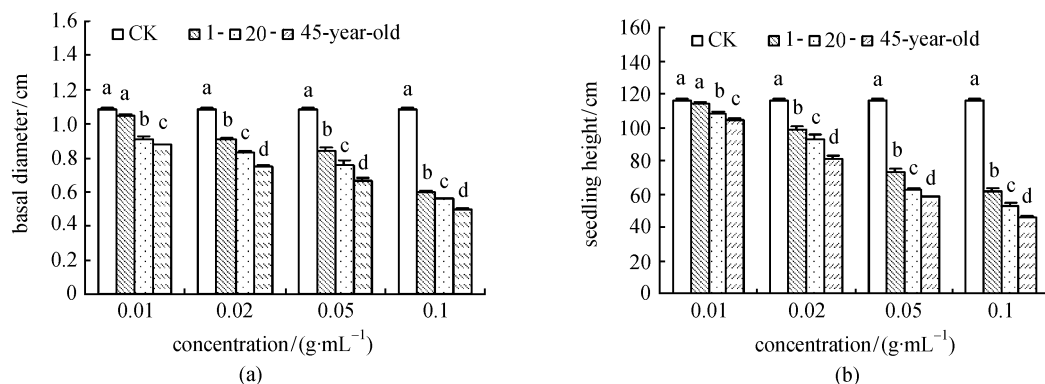


Fig. 1 Effects of aqueous leaf extracts from *P. tomentosa* on the basal diameter (a) and height (b) of *P. tomentosa* seedlings

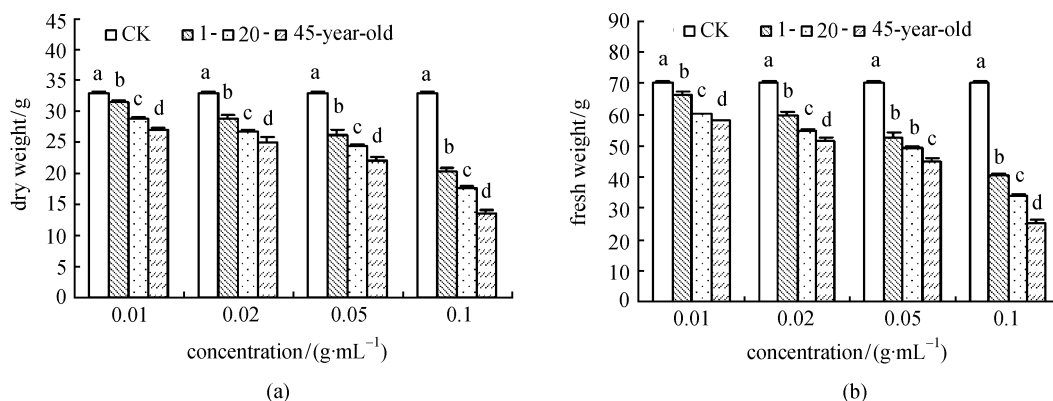


Fig. 2 Effects of aqueous leaf extracts from *P. tomentosa* on the dry weight (a) and fresh weight (b) of the seedlings of *P. tomentosa*. Note: Different letters above the square column indicate significant difference at the same concentration among different ages (including control) ( $P < 0.05$ ).

### 3.2 Effect of aqueous leaf extract on seedling leaf chlorophyll

An increase in the concentration of aqueous leaf extracts of various ages caused a decrease in chlorophyll content and the ratio of chlorophyll a/b (Fig. 3). At each concentration, there was a negative correlation between the two indexes and the age of the tree from which leaf extract was obtained. At 0.01 and 0.02 g·mL<sup>-1</sup>, the extracts of 1-year-old *P. tomentosa* had little effect on chlorophyll content. By contrast, at these concentrations, the chlorophyll content of 20- and 45-year-old *P. tomentosa* decreased by 7.53% and 8.63%, and 13.26% and 13.51%, respectively, when compared with that of the control. The chlorophyll content of the seedlings was significantly lower when treated with all aqueous leaf extracts of *P. tomentosa* at concentrations of 0.05 and 0.1 g·mL<sup>-1</sup>. Ratio of chlorophyll a/b decreased slightly when treated with extracts of 1-year-old *P. tomentosa* at 0.01–0.05 g·mL<sup>-1</sup>, and it significantly decreased by 10.53% compared with that of the control at 0.1 g·mL<sup>-1</sup>. Both the extracts of 20-year-old *P. tomentosa* at 0.05 g·mL<sup>-1</sup> and those of 45-year-old *P. tomentosa* at 0.02 g·mL<sup>-1</sup> caused a significant decrease in ratio of chlorophyll a/b. At the same concentration, although there was no significant difference between treatments of 20- and 45-year-old *P. tomentosa*, the differences were significant between the treatments of 1- and 20-year-old, and 1- and 45-year-old *P. tomentosa* in chlorophyll contents and the ratio of chlorophyll a/b.

### 3.3 Effect of aqueous leaf extract on photosynthetic and fluorescence characteristics

#### 3.3.1 Effect of aqueous leaf extracts on photosynthetic characteristics

Net photosynthetic rate ( $P_n$ ) of the seedlings exhibited a descending trend with increasing concentrations of aqueous

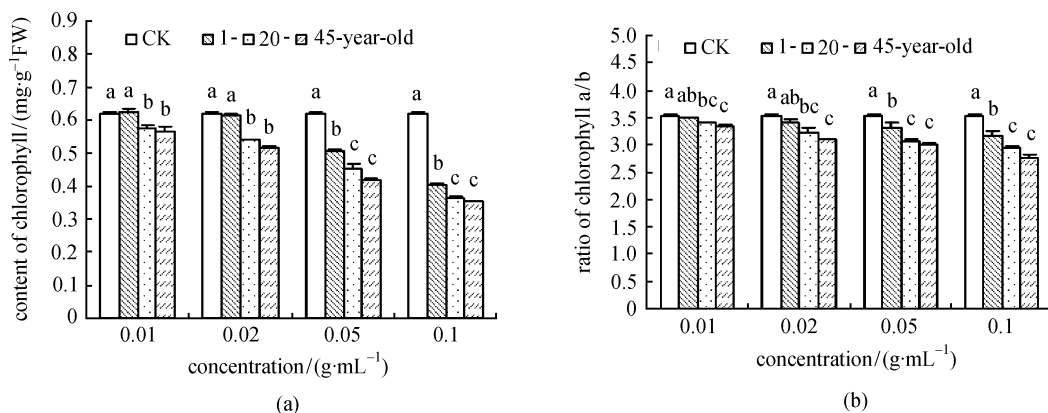
leaf extracts from the three age groups of *P. tomentosa* (Fig. 4 (a)). The extracts of the four concentrations of 1-year-old *P. tomentosa* caused the decrease in net photosynthetic rate of 6.89%–38.72%, whereas those of 20- and 45-year-old *P. tomentosa* caused decreases in  $P_n$  of 11.88%–43.13% and 19.08%–45.16%, respectively. The differences were significant between all the treatments and control. At the same concentration, among the extracts of the three ages of *P. tomentosa*, those of the 45-year-old exhibited the most severe inhibition effect in  $P_n$ , followed by those of the 20-year-old and those of the 1-year-old. There were significant differences between 1-year-old and 45-year-old extracts of *P. tomentosa*. This indicated that the older *P. tomentosa* extracts had a greater inhibitory effect on  $P_n$ .

At 0.01 g·mL<sup>-1</sup>, stomatal conductance ( $G_s$ ) decreased with  $C_i$  significant reduction with the application of extracts of 1-year-old *P. tomentosa* (Fig. 4 (b) and (c)). Whereas an increase in the concentration of extracts of 1-year-old *P. tomentosa* caused a further decrease in  $G_s$ ,  $C_i$  increased significantly. This response pattern was similar to the 20-year-old group. However,  $C_i$  kept to the levels of the control at all the concentrations in application of extracts of the 45-year-old.

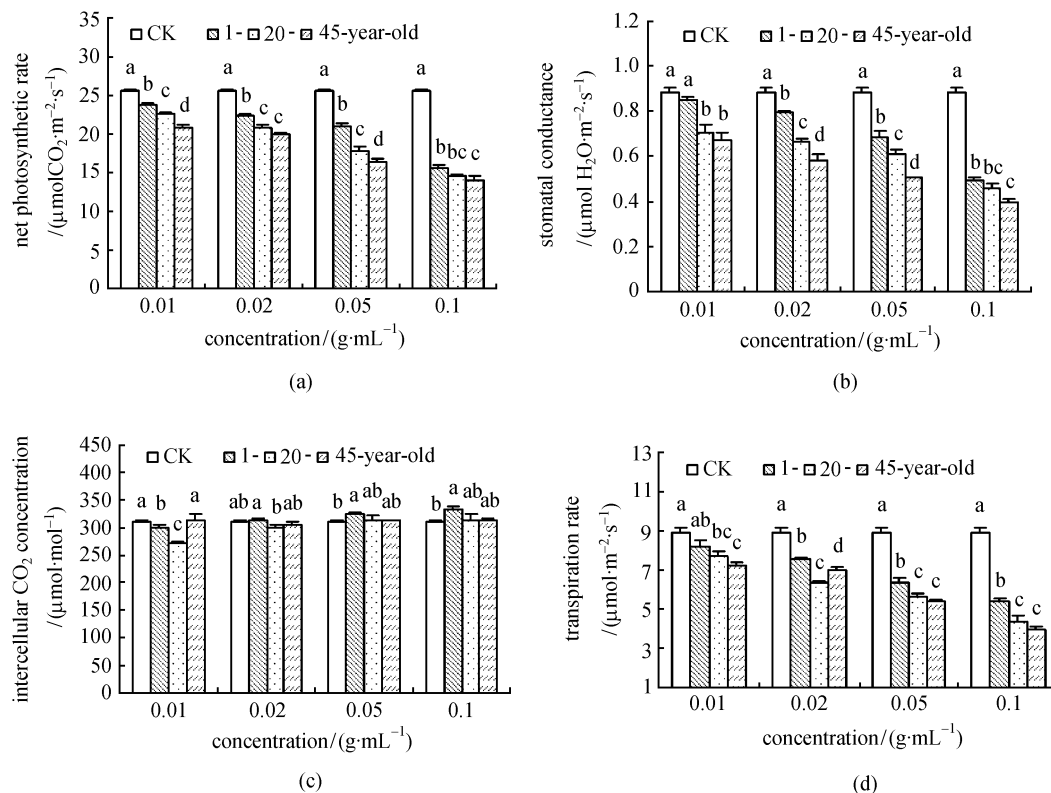
Similar to the effects on  $G_s$ ,  $T_r$  decreased to some extent with increasing extract concentrations (Fig. 4 (d)). The older the trees were, the more significantly  $T_r$  decreased. At 0.02 g·mL<sup>-1</sup>, there were significant differences among the extracts of all the three ages of *P. tomentosa*.

#### 3.3.2 Effect of aqueous leaf extracts on fluorescence characteristics

Chlorophyll fluorescence could reflect the effect of any environmental stress on photosynthesis (Yu et al., 2007). Initial fluorescence  $F_0$  increased in proportion to the concentration of the three age extracts of *P. tomentosa* (Fig. 5 (a)). At 0.05 g·mL<sup>-1</sup>,  $F_0$  increased significantly by



**Fig. 3** Effects of aqueous leaf extracts from *P. tomentosa* on the chlorophyll content (a) and the ratio of chlorophyll a/b (b) of *P. tomentosa*. Note: Different letters above the square column indicate significant difference at the same concentration among different ages (including control) ( $P < 0.05$ ).



**Fig. 4** Effects of aqueous leaf extracts of *P. tomentosa* on the photosynthetic characteristics of *P. tomentosa* seedlings

Note: (a), (b), (c), and (d) represent net photosynthetic rate, stomatal conductance, intercellular CO<sub>2</sub> concentration, and transpiration rate, respectively. Different letters above the square column indicate significant difference at the same concentration of different ages (including control) ( $P < 0.05$ ).

17.58% (1 year old), 26.80% (20 years old), and 35.38% (45 years old) when compared with that in the control. In addition, for each concentration, extracts from 1-, 20- and 45-year-old resulted in a progressive increase in  $F_0$ . At higher concentrations (0.05 and 0.1 g·mL<sup>-1</sup>), the differences between the three age treatments were significant.

Both  $F_v/F_m$  and  $F_v/F_0$  are important parameters that may reflect photochemical reaction, where  $F_v/F_m$  reflects the efficiency of primary conversion of light energy of PSII and  $F_v/F_0$  is the potential activity of PSII.  $F_v/F_m$  decreased at all the concentrations of the three age extracts, especially in the higher concentrations. At 0.02 g·mL<sup>-1</sup> in all the age treatments, the differences were significant (Fig. 5(b)). This showed that aqueous leaf extracts from 1-, 20- and 45-year-old treatments inhibited the efficiency of primary conversion of light energy of PSII. At each concentration, we also observed a direct correlation between the percentage of inhibition and the age of the material used in the tests. Moreover, there was a significant difference between 1- and 45-year-old treatments in  $F_v/F_m$ .

Similar to the effects of  $F_v/F_m$ ,  $F_v/F_0$  decreased significantly in all the treatments compared with the control (Fig. 5(c)). The inhibitory effects were proportional to age, and there were significant differences between 1- and 45-year-old treatments.

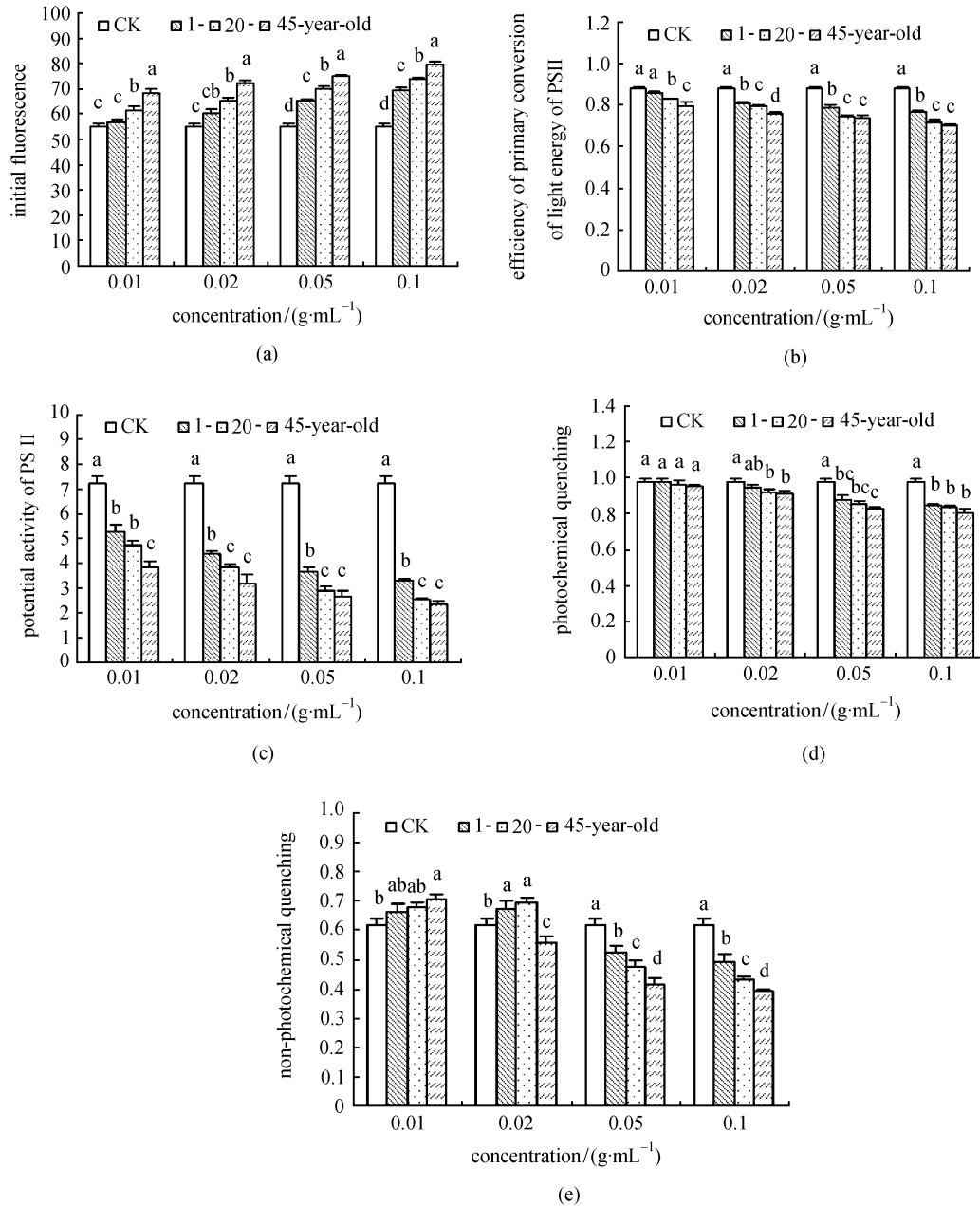
Increasing concentrations of extracts of *P. tomentosa* of

various ages caused a gradual reduction in  $q_P$  (Fig. 5 (d)). At 0.01 and 0.02 g·mL<sup>-1</sup>, application of extracts of the 1-year-old trees caused a slight decrease in  $q_P$ , and a significant decrease of 10.24% at 0.05 g·mL<sup>-1</sup>. Application of 20- and 45-year-old tree extracts at 0.02 g·mL<sup>-1</sup> significantly decreased  $q_P$  by 10.71% and 15.81%, respectively. At these concentrations, inhibition of  $q_P$  gradually increased with an increase in age, although the differences among all age treatments were not significant.

With an increase in the concentration of the extract of *P. tomentosa* of individual age,  $q_N$  increased at first and then decreased (Fig. 5 (e)). Extracts of the 1- and 20-year-old trees caused  $q_N$  to increase by 7.62% and 9.08%, respectively, at 0.01 g·mL<sup>-1</sup> and by 10.53% and 12.96%, respectively, at 0.02 g·mL<sup>-1</sup>. There was a significant decrease in  $q_N$  at 0.05 g·mL<sup>-1</sup>. However,  $q_N$  increased significantly by 14.26% at 0.01 g·mL<sup>-1</sup> in 45-year-old treatment, compared with that in the control, but sharply declined at 0.02 g·mL<sup>-1</sup>.

## 4 Discussion

A number of researches on autotoxicity were reported worldwide (Lin and Huang, 1999; Huang et al., 2002). It has been suggested that some allelopathic compounds may



**Fig. 5** Effects of aqueous leaf extracts of *P. tomentosa* on the chlorophyll fluorescence parameters of its seedlings

Note: (a), (b), (c), (d) and (e) represent initial fluorescence, efficiency of primary conversion of light energy of PSII, potential activity of PSII, photochemical quenching, and nonphotochemical quenching, respectively. Different letters above the square column indicate significant difference at the same concentration among different ages (including control) ( $P < 0.05$ ).

affect the synthesis and application of hormones; alter cell division, elongation and ultrastructure, and influence of membrane permeability or chlorophyll content; and interfere with metabolism of protein and nucleic acid (Rice, 1984). The silvicultural methods in our experiment showed that the aqueous leaf extracts of the 1-, 20- and 45-year-old trees had an equal sense with allelochemicals and resulted in a reduction in the growth (as reflected by height, basal diameter, and fresh and dry weight) of *P. tomentosa*

seedlings. It indicated that aqueous leaf extracts of *P. tomentosa* inhibited the growth of its own seedlings, with more susceptible diameter and fresh weight.

Other researchers reported that ferulic acid, caffeic acid, and vanillin were capable of inhibiting the growth of the seedlings by decreasing the net photosynthetic rate, chlorophyll content, and the ratio of chlorophyll a/b, as well as stomatal conductance (Einblling et al., 1979). Vanillin and  $\rho$ -hydroxybenzoic acid showed inhibitory

effects on the chlorophyll content, net photosynthetic rate, and stomatal conductance of the Chinese fir (Chen et al., 2002). Furthermore, aqueous litter extracts of *Pinus tabulaeformis* and *Quercus liaotungensis* reduced the chlorophyll content, net photosynthetic rate, and stomatal conductance of *P. tabulaeformis* seedlings (Jia et al., 2003). In our study, the net photosynthetic rate, stomatal conductance, chlorophyll content, and the ratio of chlorophyll a/b decreased to some extent, which was generally consistent with previous findings.  $F_0$  increased, and  $F_v/F_m$  and  $F_v/F_0$  constantly declined in all the treatments. This showed that aqueous leaf extracts of *P. tomentosa* decreased the efficiency of primary conversion of light energy of PSII and damaged the PSII reaction centers, eventually resulting in a decline in net photosynthetic rate. However, the reasons were various in the decreasing of net photosynthetic rate in treatments of different ages. Stomatal limitation led to a decrease in net photosynthetic rate at lower concentrations of 1- and 20-year-old tree extracts. In contrast, nonstomatal limitation was the major reason at higher concentrations (Farquhar and Sharkey, 1982; Guo and Zhao, 2001; Shi et al., 2004). Nonstomatal limitation was the major reason at all the concentrations of 45-year-old extract (Shi et al., 2004).

Tree age significantly affected the allelopathic potential of *P. tomentosa*. At similar concentrations, the height, basal diameter, fresh weight, dry weight, chlorophyll content, and net photosynthetic rate decreased with the increasing age. We suggest that the allelopathic potential is enhanced with *P. tomentosa* development. Allelochemicals are secondary metabolites, and their category and quantity may vary with environmental alteration or plant development (Wallstedt et al., 1997; Huang et al., 2002). For example, the inhibitory effects of *Eupatorium adenophorum* leaf extracts on native plants gradually increased with the increase in developmental stage (Han and Feng, 2007). *Ageratum houstonianum* had a stronger inhibitory effect on other plants during the reproductive growth period when compared with the vegetative period (Hu and Kong, 1997). The inhibition effect of grafted eggplant root exudates on its own seedlings increased at later growth stages (Zhang et al., 2005). Sharam (2000) found that the inhibitory effect of litter extracts of *P. deltoids* was enhanced with the prolonging of age. In this study, the leaves used were obtained from the same clones of trees of different ages grown at same plantation site; environmental effects on allelopathy should therefore be minimal. Consequently, age was responsible for the result that the treatment with 45-year-old tree extract caused the most severe inhibition effect, followed by the 20-year-old treatment and 1-year-old treatment. Further study is needed in our laboratory to separate and determine precisely the allelochemical in *P. tomentosa* of different ages.

In conclusion, aqueous leaf extracts damage the photosynthetic center, decrease the net photosynthetic rate, and inhibit seedling growth of *P. tomentosa*, which

may lead to a decline in biomass. Therefore, allelopathy is one reason for decreasing productivity in continuous plantations of *P. tomentosa*. The potential use of other species especially nitrogen fixing ones for resolving the decrease in biomass production has been recently applied in *P. tomentosa* stands. In addition, allelochemicals can be eliminated through the following two measures. For one thing, the allelochemicals can be decomposed or diminished at high temperature (Gentle and Duggin, 1997; Kaur and Inderjit Kaushik, 2005). For another thing, the allelochemicals can be absorbed through the addition of activated carbon to the soil in poplar plantation to increase productivity (Prati and Bossdorf, 2004).

**Acknowledgements** This study was financially supported by the Natural Science Foundation of Hebei Province, China (No. 20061124001).

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