EFFECT OF ALUMINIUM TOXICITY ON THE DEVELOPMENT OF POPLAR (*POPULUS TREMULA* L. $\times$ *P. ALBA* L.) CULTURED IN VITRO

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ABSTRACT

Adventitious bud cultures were established using vegetative buds from selected clones of poplar (*Populus tremula* L. $\times$ *P. alba* L.) as initial explants. For multiplication of shoots a modified Murashige and Skoog medium (MS) was used. Aluminium salts (aluminium sulphate and aluminium chloride) were added to the media.

It was found that the pH of the medium had no effect on the development of cultures at low concentrations of nutrients (1/2 or 1/4 MS). Low concentrations of aluminium (Al 25 mg·dm⁻³ supplied as aluminium sulphate, Al 15 mg·dm⁻³ as aluminium chloride) had no inhibitory effect on shoot development but decreased regeneration of adventitious roots. High concentrations of aluminium inhibited the development of shoots and roots, especially in a medium at pH 4.5.

Microcuttings rooted in the highest percentage and formed the strongest rooting system on 1/4 strength MS medium at pH 4.5. It was found that there was no difference between the rooting of shoots excised from cultures cultivated with or without Al in this medium at pH 5.5.

KEY WORDS: *Populus tremula* L. $\times$ *P. alba* L., in vitro culture, aluminium, development.

INTRODUCTION

Environmental pollution contributes to inhibition of the growth of trees and shrubs. In extreme situations it may result in decline of whole forest stands. One of the causes of tree decline is soil pollution, which has a negative effect on root system development and, consequently, results in impaired growth of the aboveground parts of the plant (Gabara 1992; Boudot et al. 1994).

Aluminium is one of the most troublesome metals present in the soil. Its accessibility to plants increases as soil pH decreases (Greger et al. 1992; Oleksyn et al. 1996). The most frequent cause of soil contamination and lowering of soil pH is the effect of acid rain and salts of toxic metals (Vilkka et al. 1990; Reich et al. 1994). High concentrations of the toxic aluminium ions lead to limited uptake of some macronutrients and micronutrients, which results in slower plant growth (Henriksen et al. 1992; Bojarczuk and Oleksyn 1994).

The mechanism of tree defence against industrial pollution is poorly understood. Broad-leaved trees are more tolerant to environmental pollution than conifers. Nevertheless, decline of many broad-leaved tree species has recently been observed in the vicinity of industrial plants. Scientific investigations revealed large differences in plant tolerance to industrial pollution between species and even between clones of trees and shrubs of the same species (Ernst et al. 1992; Oleksyn et al. 1996). Plant tolerance to toxic metal ions is genetically controlled (Ślaski 1992).

In vitro cultures had been used in studies on plant responses to toxic metal ions for a long time (Meredith 1978). Effects

of high concentrations of metal ions on root and shoot development were observed in plants tolerant and susceptible to industrial pollution (Arnold et al. 1994).

The purpose of the experiments, carried out at the Institute of Dendrology of the Polish Academy of Sciences in Kórnik, was to investigate the effect of aluminium on shoot and root development in three poplar clones cultured in vitro. Studies of this type may broaden our knowledge of the mechanisms of plant susceptibility to toxic compounds, and allow to select plants with a higher tolerance to industrial pollution.

MATERIAL AND METHODS

Explants, i.e. apical and lateral buds with shoot fragments, were excised from 1-year-old and 2-year-old plants (grafted on roots of *Populus tremula* L.) between June and September. The mother plants were grown in a greenhouse. The explants were cultured on media containing 1/2 or 1/4 strength MS medium (Murashige and Skoog 1962) or a modified medium (A) with 1/4 phosphorus, calcium and iron, as compared to the standard medium (MS). Casein hydrolysate (0.25-0.5 mg·dm⁻³) and vitamins (thiamine 1 mg·dm⁻³, pyridoxine 0.5 mg·dm⁻³, nicotinic acid 0.5 mg·dm⁻³, calcium pantothenate 0.1 mg·dm⁻³ and ascorbic acid 0.1 mg·dm⁻³) were added to the media. Poplar cultures were grown on media solidified with Bactoagar supplemented with hormones: 6-benzylaminopurine – BAP 0.5-5 mg·dm⁻³, 1-naphthaleneacetic acid – NAA 0.05-0.5 mg·dm⁻³ and indole-3-butyric acid – IBA 0.2-1 mg·dm⁻³. Microcuttings (about 2 cm long) were taken from 6-

8-month cultures of adventitious shoots and placed in perlite saturated with a liquid medium containing 1/4 MS medium. Aluminium was added to the media as aluminium sulphate $\text{Al}_2(\text{SO}_4)_3 \cdot 18 \text{ H}_2\text{O}$ (Al 25-100 $\text{mg}\cdot\text{dm}^{-3}$) or aluminium chloride $\text{AlCl}_3 \cdot 6 \text{ H}_2\text{O}$ (Al 7.5-30 $\text{mg}\cdot\text{dm}^{-3}$). The pH of media used for culture and rooting of microcuttings were 4.5 and 5.5.

Jars with poplar cultures and rooting microcuttings were incubated at 22-23°C, in a culture room irradiated 16 h/day with mercury-discharge lamps (7500 $\text{mW}\cdot\text{m}^{-2}$).

When transplanting the cultures to new media, i.e. every 5-6 weeks, and after 4 weeks of in vitro rooting of the microcuttings, the development of the formed shoots was evaluated. The evaluation involved measurements of shoot length, shoot and leaf number, degree of chlorosis and browning on a scale of 0-3 (0, lack of chlorosis or browning; 1, poor, 1-20% of chlorosis or browning; 2, moderate, with 21-60% of chlorosis or browning; 3, substantial, with 61-100% of chlorosis or browning) and degree of culture development or necrosis on a scale of 0-5, for example (0, lack of necrosis; 1, very slight, with 1-20% of necrosis; 2, slight, with 21-40% of necrosis; 3, moderate, with 41-60% of necrosis; 4, great, with 61-80% of necrosis; 5, very great, with 81-100% of necrosis).

The process of formation of adventitious roots on the microcuttings lasted about four weeks. After this period, the degree of root system development was measured (on a scale of 0-5) or root number and length were assessed, and root tip

growth was evaluated on a scale of 0-3 (0, lack of tip growth; 1, poor tip growth, with 1-20% of growing tips; 2, moderate tip growth, with 21-60% of growing tips; 3, substantial tip growth, with 61-100% of growing tips).

Shoot number, degree of culture necrosis and culture quality, i.e. chlorosis and browning, are expressed in tables and graphs as a mean value per one culture vessel, whereas the other parameters (shoot length, root length and number, root tip growth) as a mean value per one microcutting.

All the experiments were established in randomized designs with four replications. The statistical significance of the differences between individual combinations was assessed using the new Duncan's range test for 5% of limit values. In tables and figures values marked with the same letter do not differ from each other statistically ($P=0.05$).

RESULTS

The effect of media with various concentrations of mineral and organic compounds on poplar development was studied in the experiments. The strongest development of poplar cultures was observed in the culture with a complete composition of minerals and an admixture of casein hydrolysate and hormones: BAP 0.5 $\text{mg}\cdot\text{dm}^{-3}$ and NAA 0.2 $\text{mg}\cdot\text{dm}^{-3}$ (Table 1). These hormones were next added to the media in all experiments. It was found that individual poplar clones are charac-

TABLE 1. Effect of media on the development of three poplar clones (P-1, P-2, P-3) cultured in vitro. The cultures were grown on Murashige and Skoog medium (MS) or on a medium with a reduced concentration of calcium, phosphorus and iron (A), both supplemented with casein hydrolysate (Hk).

Poplar Clons	MS + casein hydrolysate (Hk)					A + casein hydrolysate (Hk)				
	Shoot number	Shoot length cm	Degree of culture development (scale 0-5)	Degree of chlorosis (scale 0-3)	Degree of browning (scale 0-3)	Shoot number	Shoot length cm	Degree of culture development (scale 0-5)	Degree of chlorosis (scale 0-3)	Degree of browning (scale 0-3)
P-1	14.5 b	3.2 c	2.8 b	0.5 b	0.5 a	9.7 a	2.6 c	2.0 b	0.9 a	0.7 a
P-2	9.2 a	1.8 b	1.5 a	0.2 a	0.6 a	11.1 a	1.6 b	1.3 a	1.0 a	0.9 a
P-3	10.2 a	0.8 a	1.3 a	0.5 b	1.2 b	8.6 a	0.5 a	1.0 a	2.0 b	1.6 b

Fig. 1. Effect of medium composition and pH on the development of poplar (*Populus tremula* L. $\times$ *P. alba* L.) cultured in vitro. 1 - MS medium + vitamins, 2 - 1/2 MS medium + vitamins.

TABLE 2. Effect of media and aluminium on the development of poplar (*Populus tremula* L. $\times$ *P. alba* L.) cultured in vitro. The cultures were grown on Murashige and Skoog medium with a complete nutrient composition (MS) or with 1/4 of the complete composition (MS 4). Aluminium as $\text{Al}_2(\text{SO}_4)_3 \cdot 18 \text{ H}_2\text{O}$ (Al 1).

Medium	pH	Shoot number	Shoot length cm	Leaf number	Degree of root development (scale 0-5)	Degree of necrosis (scale 0-5)
MS	5.5	8.8 c	2.6 c	8.5 d	3.7 c	0.4 a
MS	4.5	7.9 c	1.5 b	6.1 c	2.6 bc	0.9 b
MS 4	5.5	6.4 b	1.4 b	5.8 c	2.2 b	1.2 b
MS 4	4.5	6.1 b	1.4 b	4.9 b	2.0 b	1.6 bc
MS 4 + Al 1 25 $\text{mg}\cdot\text{dm}^{-3}$	4.5	4.9 b	1.3 b	4.8 b	0.8 a	2.7 c
MS 4 + Al 1 50 $\text{mg}\cdot\text{dm}^{-3}$	4.5	2.6 a	1.0 a	3.1 a	0.6 a	4.1 d

TABLE 3. Effect of medium composition, pH and aluminium on the development of poplar (*Populus tremula* L. $\times$ *P. alba* L.) cultured in vitro. The cultures were grown on Murashige and Skoog medium with a complete nutrient composition (MS) or with 1/2 of the complete composition (MS 2). Aluminium as $\text{Al}_2(\text{SO}_4)_3 \cdot 18 \text{ H}_2\text{O}$ (Al 1).

Medium	pH	Shoot number	Shoot length cm	Leaf number	Degree of root development (scale 0-5)	Degree of necrosis (scale 0-5)
MS	5.5	11.6 e	3.8 f	8.6 f	1.8 b	1.0 a
MS	4.5	10.2 d	2.9 e	6.7 e	2.0 c	1.1 a
MS 2	5.5	9.6 cd	2.2 de	6.3 e	3.0 d	1.0 a
MS 2	4.5	9.2 c	1.9 cd	5.2 d	3.5 d	1.5 a
MS 2 + Al 1 50 $\text{mg}\cdot\text{dm}^{-3}$	5.5	4.6 b	1.7 bc	3.9 bc	1.7 b	2.6 bc
MS 2 + Al 1 50 $\text{mg}\cdot\text{dm}^{-3}$	4.5	3.2 a	1.2 ab	3.1 a	1.4 b	3.1 cd
MS 2 + Al 1 100 $\text{mg}\cdot\text{dm}^{-3}$	5.5	3.6 ab	1.4 ab	4.1 c	1.5 b	2.5 b
MS 2 + Al 1 100 $\text{mg}\cdot\text{dm}^{-3}$	4.5	2.5 a	1.0 a	3.4 ab	0.4 a	3.4 d

TABLE 4. Effect of medium composition, pH and aluminium on the development of poplar (*Populus tremula* L. $\times$ *P. alba* L.) cultured in vitro. The cultures were grown on Murashige and Skoog medium with a complete nutrient composition (MS) or with 1/2 of the complete composition (MS 2). Aluminium as aluminium chloride $\text{AlCl}_3 \cdot 6 \text{ H}_2\text{O}$ (Al 2).

Medium	pH	Shoot number	Shoot length cm	Leaf number	Degree of root development (scale 0-5)	Degree of necrosis (scale 0-5)
MS	5.5	13.6 d	3.8 d	8.7 e	2.9 bc	1.0 a
MS	4.5	11.2 c	2.7 c	6.6 d	2.6 b	1.2 a
MS 2	5.5	9.6 b	2.2 b	6.3 cd	3.5 d	1.0 a
MS 2	4.5	9.2 b	1.9 b	6.1 cd	3.1 cd	1.5 ab
MS 2 + Al 2 15 $\text{mg}\cdot\text{dm}^{-3}$	5.5	10.3 b	2.0 b	5.7 bc	2.8 bc	1.1 a
MS 2 + Al 2 15 $\text{mg}\cdot\text{dm}^{-3}$	4.5	9.9 b	1.9 b	5.1 b	2.5 b	1.3 a
MS 2 + Al 2 30 $\text{mg}\cdot\text{dm}^{-3}$	5.5	9.7 b	1.9 b	5.2 b	2.7 b	1.1 a
MS 2 + Al 2 30 $\text{mg}\cdot\text{dm}^{-3}$	4.5	7.2 a	1.1 a	4.6 a	2.0 a	2.0 b

terized by a varied capacity to regenerate shoots. The strongest development of cultures and intensive formation of adventitious shoots was recorded in clone P-1 (Table 1).

The influence of medium pH on poplar development was also studied. In the medium with a complete nutrient composition (MS medium) more acidic conditions (pH 4.5) retarded poplar shoot development, i.e. resulted mainly in diminished shoot length and leaf number (Tables 2-4). Reduction of nutrient levels in the medium had an obvious negative effect on culture quality, i.e. decreased the degree of culture development and increased chlorosis and browning (Fig. 1). In media with a reduced concentration of macronutrients and micronutrients (1/2 and 1/4 MS) more acidic conditions (pH 4.5) did not exert any significant influence on culture development, i.e. the number and length of the formed shoots (Tables 2-4). Poplar root system developed most quickly in 1/2 MS medium solidified with agar (Tables 3 and 4).

Low concentrations of aluminium (Al 25 $\text{mg}\cdot\text{dm}^{-3}$ as aluminium sulphate or Al 15 $\text{mg}\cdot\text{dm}^{-3}$ as aluminium chloride) did

not affect poplar shoot development, especially at pH 5.5 (Tables 2 and 4). At pH 4.5, however, low concentrations of aluminium inhibited root system development (Tables 2 and 4). High concentrations of aluminium (Al 30 $\text{mg}\cdot\text{dm}^{-3}$ as aluminium chloride or Al 50-100 $\text{mg}\cdot\text{dm}^{-3}$ as aluminium sulphate) at pH 4.5 inhibited strongly both shoot and root development (Tables 2-4). Moreover, high concentrations of aluminium had a marked impact on culture quality, i.e. decreased the number and length of the formed shoots and increased the degree of culture necrosis (Tables 2-4).

Shoots of about 2 cm in length were taken from cultures grown on media with or without aluminium and planted in perlite saturated with a liquid 1/4 MS medium. Within 4-5 weeks the shoots produced adventitious roots. The longest and most numerous roots were formed by poplar microcuttings rooted at pH 4.5 (Fig. 2). It was found that medium pH did not affect on the development of the rooted shoots, i.e. shoot growth and the number of produced leaves (Fig. 3).

Fig. 2. Development of microcuttings of poplar (*Populus tremula* L. × *P. alba* L.) derived from cultures grown in media with aluminium (Al – 50 mg·dm⁻³, as aluminium sulphate) or without aluminium (K). The microcuttings were rooted in perlite with a liquid medium (1/4 MS).

Fig. 3. Development of microcuttings of poplar (*Populus tremula* L. × *P. alba* L.) derived from cultures grown in media with aluminium (Al – 50 mg·dm⁻³, as aluminium sulphate) or without aluminium (K). The microcuttings were rooted in perlite with a liquid medium (1/4 MS).

Shoots produced in cultures grown on media with aluminium formed smaller root systems at pH 4.5 (Fig. 2). At pH 5.5 no differences in root system development were observed between shoots derived from media with and without aluminium (Fig. 2). Microcuttings taken from cultures grown in media with aluminium and rooted at pH 4.5 were characterized by a slightly lower quality (i.e. produced a lower number of leaves and were characterized by a higher degree of necrosis) than shoots derived from cultures without aluminium (Fig. 3).

DISCUSSION

Aluminium is an important component of the sorptive complex of the soil but its availability depends mostly on soil pH. In alkaline conditions aluminium is present exclusively in the

form of anions, in neutral substrates the dominant form is inactive aluminium hydroxide, whereas in an acidic environment (pH below 5.0) the mobile cationic form prevails (Borkowska 1988; Wilkins and Hodson 1989). The dependence of the toxicity of aluminium on substrate acidity was also confirmed in these experiments on in vitro regeneration of several poplar clones. At pH 4.5 the toxic effect of aluminium was observed even at low concentrations (Al 25 mg·dm⁻³ as aluminium sulphate or Al 15 mg·dm⁻³ as aluminium chloride), whereas at pH 5.5 aluminium did not inhibit shoot and root growth (Tables 2 and 4). Lack of the toxic effect of low concentrations of aluminium and frequently even its stimulating effect on root and shoot development may consist in its impact on the solubility and availability of some nutrients, e.g. iron, calcium and magnesium (Keltjens and Loenen 1989; Bojarczuk 1997). In the experiments aluminium was applied as aluminium sulphate or aluminium chloride. Earlier investi-

gations have shown that if the same concentration of aluminium was used ($50 \text{ mg} \cdot \text{dm}^{-3}$), aluminium chloride was more toxic to the plants cultured in vitro than aluminium sulphate. In this study the smaller toxic effect of aluminium chloride on poplar development was probably caused by a lower concentration of aluminium (Tables 3 and 4).

A strong inhibiting effect on poplar growth in vitro was noticed at high concentrations of aluminium, particularly in more acidic media (pH 4.5). Aluminium toxicity was observed both in shoot cultures on the agar medium and during rooting of shoots in liquid media (Tables 2-4, Figs 2 and 3). It was found that aluminium had a particularly inhibiting effect on root system development. Roots are directly exposed to the toxic effect of aluminium. As a result, tips of main and lateral roots turn brown and stop growing (Gabara 1992; Lima and Copeland 1994). These damages may be caused by shortages of calcium, phosphorus and magnesium. This is because high concentrations of aluminium both limit the uptake of those nutrients by plants (Göransson and Eldhuset 1991; Kochian 1995) and block their transportation and utilization in metabolic processes (Borkowska 1988; Farid 1991). This is followed by an adverse change of the ratio Ca/Al (in favour of Al) and a reduction of magnesium concentration in plants (Keltjens and Loenen 1989; Henriksen et al. 1992). This, in turn, results in inhibition of plant growth and development, and in so important physiological processes as photosynthesis (Rengel 1992; Reich et al. 1994; Oleksyn et al. 1996) and respiration (Lima and Copland 1994).

Studies of aluminium phytotoxicity in vitro are conducted with the use of media with many components. It was found that some components of the media, e.g. chelate compounds of phosphorus, calcium and iron, may protect plants by lowering aluminium toxicity. Because of this, media with a diminished concentration of some nutrients or diluted media have usually been applied in those studies (Borkowska 1988). In these experiments on poplar regeneration in vitro, media with lower nutrient concentrations than standard media (1/2 or 1/4 MS) were used, so that the effect of aluminium on plants should not be alleviated. The results show that medium pH affects plant development in media with a complete composition of nutrients, whereas no inhibiting effect of low pH was observed in media with lower nutrient levels. The major factor inhibiting shoot and root development at pH 4.5 were toxic aluminium ions.

Addition of aluminium to the media resulted in inhibition of culture development and formation of adventitious buds. Shoots of about 2 cm in length, taken from these cultures and transplanted to perlite saturated with a liquid medium, were characterized by the same capacity to regenerate roots as shoots grown on control media (i.e. without aluminium) at pH 5.5. (Fig. 2). Plant culture in vitro may be also used for selection of plants with a higher tolerance to ions of aluminium or other toxic metals (Meredith 1978; Conner and Meredith 1985; Samantaray et al. 1994).

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WPLYW TOKSYCZNEGO DZIAŁANIA GLINU
NA ROZWÓJ TOPOLI (*POPULUS TREMULA* L. × *POPULUS ALBA* L.)
W KULTURACH IN VITRO

STRESZCZENIE

Kultury pędów przybyszowych uzyskano z pąków wegetatywnych wyselekcjonowanych klonów topoli (*Populus tremula* L. × *P. alba* L.). Do namnażania pędów zastosowano zmodyfikowaną pożywkę Murashige i Skoog (MS), do której dodawano glin, w postaci siarczanu i chlorku glinu. Stwierdzono, że odczyn pożywki nie miał wpływu na rozwój kultur topoli przy zastosowaniu pożywek o zmniejszonym poziomie związków mineralnych (1/2 i 1/4 MS). Glin w niskim stężeniu w pożywce nie hamował rozwoju pędów, natomiast ograniczał rozwój korzeni przybyszowych. Wysokie stężenie glinu wpływało hamująco na rozwój korzeni i pędów, szczególnie w pożywkach o pH 4,5. Mikrosadzonki topoli ukorzeniły się w najwyższym procencie i wytworzyły najsilniejszy system korzeniowy w pożywce 1/4 MS o pH 4,5. Nie stwierdzono różnic w ukorzenianiu się mikrosadzonek pozyskanych z kultur hodowanych z glinem i bez glinu, w pożywce 1/4 MS o pH 5,5.

Hodowla roślin w kulturach in vitro może być sposobem do uzyskania roślin o zwiększonej tolerancji na jony glinu lub innych toksycznych metali.

SŁOWA KLUCZOWE: *Populus tremula* L. × *P. alba* L., glin, rozwój roślin, kultury in vitro.