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Effects of manganese in solution culture on the growth of five deciduous broad-leaved tree species with different successional characters from northern Japan

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Abstract

The effects of four manganese (Mn) concentrations (1, 10, 50, and 100 g m^{-3} = Mn_1, Mn_{10}, Mn_{50}, Mn_{100}) in solution culture on growth variables were studied for seedlings of five deciduous broad-leaved trees with different successional characteristics and shoot development patterns in northern Japan. The five species were: *Betula ermanii*, *Betula platyphylla* var. *japonica,* and *Alnus hirsuta* (early-successional species with continuous leaf development), *Ulmus davidiana* var. *japonica* (mid-successional species with flush and continuous leaf development), and *Acer mono* (late-successional species with a flush type leaf development). In plants grown in the Mn environment for about 45 d, relative growth rate (RGR) decreased with increasing Mn supply. Between the 1 and 100 g(Mn) m^{-3}, RGR decreased by 20 % for *B. ermanii* and *B. platyphylla,* by 40 % for *A. hirsuta* and *A. mono,* and by 80 % for *U. davidiana.* Specific leaf area (SLA) and leaf mass ratio (LMR) of all species were little affected by high Mn supply. In *U. davidiana*, however, there was a 67 % decrease in LMR in Mn_{100} plants. Leaf area ratio (LAR) was higher in early-successional species than in mid- and late-successional ones but differed little among Mn treatments within species, except for *U. davidiana* where LAR declined substantially with increased Mn supply. While LAR, which represents the relative size of assimilatory apparatus, was little affected, net photosynthetic rate (P_N)

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saturated with radiant energy decreased with increasing Mn supply in all species. Thus P_N was adversely affected by high accumulation of Mn in leaves, which resulted in an overall reduction in biomass production. However, the proportional allocation of photosynthates to the assimilatory apparatus was not affected by different Mn toxicity in hardwood tree seedlings.

Additional key words: alder; birch; elm; leaf area ratio; maple; net photosynthetic rate; shoot development pattern; successional types.

Introduction

Manganese (Mn) toxicity is one of the major factors limiting plant growth in acid soils of pH<5.5 (Foy *et al.* 1978, Horst 1988, Sumner *et al.* 1991). The effects of high Mn on plant growth are further exacerbated by lower growth temperature (Heenan and Carter 1977, Rufty *et al.* 1979). Therefore, the forests of northern Japan, located in the cool temperate zones, may be more vulnerable to Mn toxicity from soils modified by acid deposition.

In northern Japan, there are many types of cool temperate forest composed of various broad-leaved tree species (Kikuzawa 1983). The forest composition on genus level in this area is similar to that in northern America and in Europe (Schulze *et al.* 1996), where forest decline due to acid deposition has been reported (Krahl-Urban *et al.* 1988). Because broad-leaved trees of different successional status have associated differences in growth patterns and photosynthetic properties, they may also have different sensitivities to increased Mn. Leaves of early-successional species generally emerge successively through the entire growing period. Mid-successional species flush several leaves in the spring and then continue to produce new leaves successively. Late-successional species flush several leaves usually only once in the spring (Kikuzawa 1983). Early-successional species have a higher photosynthetic capacity under high irradiance while late-successional species attain relatively higher P_N under low irradiance, and mid-successional species show intermediate properties (Koike 1988, 1990).

In several deciduous trees from northern Japan, a marked decline in photosynthetic rate has been observed in leaves high in Mn (Kitao *et al.* 1997a,b). Based on the photosynthetic response to high leaf Mn concentrations, early-successional species exhibited higher Mn tolerance than mid- and late-successional species. However, growth is determined not solely by P_N, but also by the partitioning of photosynthates to various tissues including new carbon assimilatory apparatus (Lambers and Poorter 1992, Potter and Jones 1977). We hypothesize that shoot development patterns among species of different successional status respond differently to the effect of Mn toxicity on growth through differences in biomass allocation of photosynthates. The present study reports the effects of high Mn treatments on the RGR of seedlings of five deciduous broad-leaved trees of early-, mid-, and late-successional types in northern Japan. We will address how leaf and whole-plant structural traits might influence differences in growth response to Mn toxicity among species.

Materials and methods

We used five deciduous broad-leaved tree species of different successional traits and leaf emergence types according to Kikuzawa (1983). Three are early-successional species: *Betula ermanii* Cham., *Betula platyphylla* Sukatchev var. *japonica* (Miq.) Hara, and *Alnus hirsuta* Turcz. with a succeeding type leaf emergence, one mid-successional species: *Ulmus davidiana* Planch. var. *japonica* (Rehder) Nakai with a flush and succeeding type, and one late-successional species of *Acer mono* Maxim. var. *glabrum* (Lév. et Van't.) Hara with a flush type leaf development. Two-year-old seedlings of *B. ermanii*, *B. platyphylla*, *A. hirsuta*, and *U. davidiana*, and 3-year-old seedlings of *A. mono* from a tree nursery (*Oji Forestry and Landscaping Co.*, Sapporo, Japan) were used. The initial height of bare root seedlings was 200-300 mm. Seedlings were cultivated hydroponically in trays of well-aerated nutrient solution containing [g m^{-3}]: 94.3 $(NH_4)_2SO_4$, 91.1 $NaNO_3$, 47.2 KH_2PO_4, 26.1 KCl, 61.5 $MgSO_4 \times 7\,H_2O$, 42.1 $Ca(NO_3)_2 \times 4\,H_2O$, 26.2 $CaCl_2 \times 2\,H_2O$, 1.1 H_3BO_3, 5 Fe (in the form of ferric citrate), and [mg m^{-3}]: 41.8 $ZnCl_2$, 78.5 $CuSO_4 \times 5\,H_2O$, 50.4 $Na_2MoO_4 \times 2\,H_2O$.

After a 2-week period of seedling establishment in the hydroponic trays, four Mn treatments at the following concentrations were applied: 1 (control), 10, 50, and 100 g m^{-3} (= Mn_1, Mn_{10}, Mn_{50}, Mn_{100}) in the form of $MnCl_2 \times 2\,H_2O$. The nutrient solution including Mn was completely replaced every 10 d. The initial pH of the solution was about 5. Seedlings were grown between late May and early August for totally about 60 d in trays set in a glasshouse exposed to natural daylight up to 2 mmol m^{-2} s^{-1} PPFD. Temperature range was 21 ± 5 °C (mean ± SD) during the experiment.

The number of newly-emerged leaves on leader shoots was counted several times during the experiment. Leaves of all species had flushed at about the same time before the experiment started. However, subsequently early- and mid-successional species continued to produce new leaves while the late-successional species *A. mono* did not. These are natural phenological differences among species (Kikuzawa 1983, Koike 1988) unrelated to Mn treatments. Leaves of *A. mono* and *U. davidiana* were at the early stages of expansion at the onset of Mn treatments, therefore they were equally subjected to Mn treatments during the maturation phase of leaf development as other species. We suggest that all species were in a similar physiological state at the initial stage of the experiment and later differences in growth are an integration of the morphological and physiological responses to both the species-specific phenological patterns and Mn tolerance.

Relative growth rate (RGR) was calculated as

$$\mathrm{RGR} = \frac{\ln W_2 - \ln W_1}{t_2 - t_1}$$

where W_2 [g] is the dry mass at harvesting; W_1 [g] is the dry mass at the start of this experiment; t_1-t_2 [d] is the growth period (56 to 59 d for all species). W_1 was estimated by using dry mass:fresh mass ratio derived from the average of 10 seedlings of each species at the start. The dry masses of roots, stems, and leaves were measured separately. The ratio of leaf to total dry mass (LMR) was calculated for individual plants. A leaf about 25-d-old from the leader shoot of each plant was used for measurement of P_N saturated with radiant energy. The same leaf was later used for the calculation of specific leaf area (SLA) and determination of Mn concentration. P_N of about 25-d-old leaves was measured, which could indicate physiological activity per unit leaf area (Koike 1990). P_N was measured at saturating irradiance (1100 μmol m^{-2} s^{-1} PPFD) and ambient CO_2 pressure of 35 Pa with an open system infra-red gas analyzer (model *H-3*, *Analytical Development Co.*, Hoddesdon, UK). Subsequently, leaves were rinsed with deionized water and oven dried. Leaves were wet ashed in a HNO_3 and $HClO_3$ mixture. Manganese concentration was determined using an atomic absorption spectrophotometer (model *180-50*, *Hitachi*, Tokyo, Japan) for individual leaves. Leaf area ratio (LAR) was calculated as

Table 1. Effects of Mn supply on growth and structural variables, *i.e.*, relative growth rate, RGR [g kg^{-1} d^{-1}], specific leaf area, SLA [m^2 kg^{-1}], leaf mass ratio [g kg^{-1}(d.m.)], and leaf area ratio, LAR [m^2 kg^{-1}(d.m.)], of 2-year-old seedlings of *Betula ermanii*, *Betula platyphylla* var. *japonica*, *Alnus hirsuta*, and *Ulmus davidiana* var. *japonica*, and of 3-year-old seedlings of *Acer mono*. Values are means ± SE. Mann-Whitney test (difference with the control): * significant at $p < 0.05$, ** significant at $p < 0.01$.

	Mn	*B. ermanii*	*B. platyphylla*	*A. hirsuta*	*U. davidiana*	*A. mono*
RGR	Mn_1	30.5±1.5	42.6±2.2	32.7±1.6	16.8±1.9	9.5±1.4
	Mn_{10}	30.7±1.9	42.2±1.9	29.4±2.7	16.0±2.0	10.8±0.9
	Mn_{50}	25.9±1.3	37.3±1.2	23.8±2.3**	5.7±0.5**	7.0±0.9
	Mn_{100}	25.1±1.3*	33.5±1.1**	18.9±2.4**	3.3±0.5**	5.7±0.7
SLA	Mn_1	36.9±1.8	41.3±1.9	33.4±1.2	30.1±0.8	24.6±1.7
	Mn_{10}	39.4±1.4	45.1±1.3	37.8±0.8	28.6±0.8	24.6±0.9
	Mn_{50}	36.7±1.4	38.7±2.9	36.5±1.9	28.2±1.0	22.0±1.6
	Mn_{100}	33.2±2.2	34.1±1.7	36.4±1.0	29.1±1.7	21.0±1.7
LMR	Mn_1	388±11	471±6	422±31	324±23	258±13
	Mn_{10}	402±9	465±6	408±45	306±36	269±28
	Mn_{50}	415±14	519±9**	395±26	142±15**	255±21
	Mn_{100}	449±14*	520±14*	416±19	109±10**	334±18**
LAR	Mn_1	14.3±0.4	19.5±0.3	14.1±1.0	9.8±0.7	6.4±0.3
	Mn_{10}	15.8±0.3*	21.0±0.3**	15.4±1.7	8.8±1.0	6.6±0.7
	Mn_{50}	15.2±0.5	20.1±0.3	14.4±1.0	4.0±0.4**	5.6±0.5
	Mn_{100}	14.9±0.5	17.7±0.5*	15.1±0.7	3.2±0.3**	7.0±0.4

$$\text{LAR} = \text{LMR} \times \text{SLA}.$$

For *A. hirsuta*, Mn concentration was measured for all leaves on the leader shoot of a typical plant from each treatment. Leaf age was estimated by the date when each leaf emerged.

Statistics: All measurements were made with 4-10 plants per treatment, except for the measurements of P_N, SLA, and leaf Mn at Mn_{100} treatment for *A. hirsuta* (*n*=3) and *U. davidiana* (*n*=2). Significance of differences compared to the control was estimated by the Mann-Whitney test (Sokal and Rohlf 1981).

Results

Effects of Mn supply on growth: RGR was the highest for *B. platyphylla* and the lowest for *A. mono*, both in the Mn_1 treatment. The RGR for all species decreased at higher Mn treatments (Table 1). Between Mn_1 and Mn_{100}, the decline in RGR was smallest (20 %) for *B. ermanii* and *B. platyphylla*, intermediate for *A. hirsuta* and *A. mono* (40 %), and largest for *U. davidiana* (80 %).

Within species, SLA was little affected by high Mn treatments. However, for the same treatment, SLA of early-successional species of *B. ermanii*, *B. platyphylla*, and *A. hirsuta* were higher than that of mid- and late-successional species of *U. davidiana* and *A. mono*. The LMR also varied little among Mn treatments except for *U. davidiana* under Mn_{50} and Mn_{100} (Table 1). Early-successional species had higher LMR compared with mid- and late-successional species. Similarly, the LAR was higher in early-successional species but similar among treatments except for *U. davidiana* at Mn_{50} and Mn_{100}.

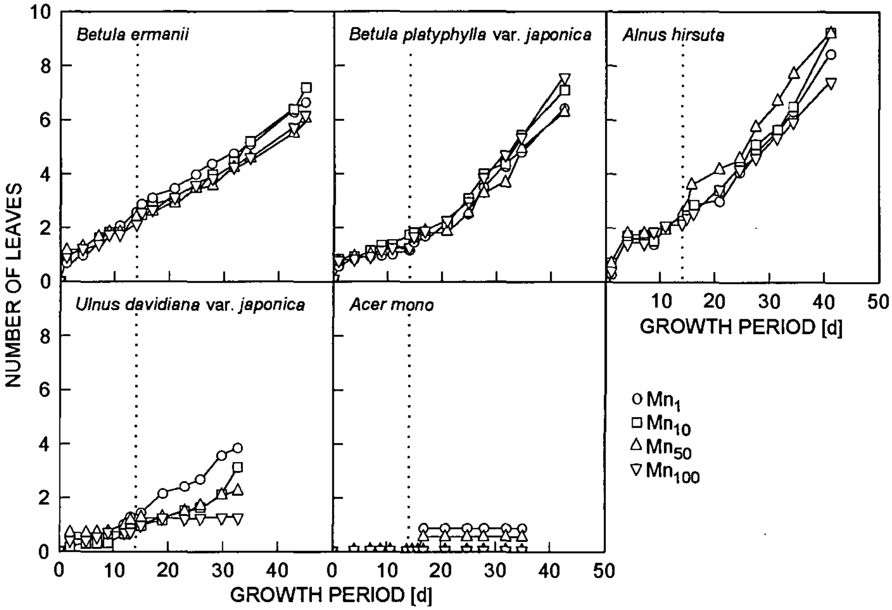

Fig. 1. Effects of Mn treatments on leaf emergence of five deciduous broad-leaved trees from northern Japan grown in solution culture. Dotted lines indicate the onset of Mn treatments (Mn_1, Mn_{10}, Mn_{50}, Mn_{100}; the index gives Mn concentration [g m^{-3}]) after an initial two-weeks establishment period. Values are means of 5 to 10 plants for each treatment.

Effects of Mn-treatment on leaf emergence: The tree species with the succeeding type of leaf emergence (*B. ermanii*, *B. platyphylla*, and *A. hirsuta*) produced new leaves continuously, especially after the 2-week establishment period (Fig. 1). There was little effect of Mn-treatments on their patterns of leaf emergence. For the flush and succeeding type (*U. davidiana*), the number of newly emerged leaves was depressed by the Mn_{50} treatment, and completely halted at Mn_{100}. For *Acer mono*, 7 to 9 leaves flushed before transplanting and no new leaves emerged after transplantation due to its intrinsic pattern of shoot development. Therefore, we could not test the effects of Mn treatment on leaf emergence in this species.

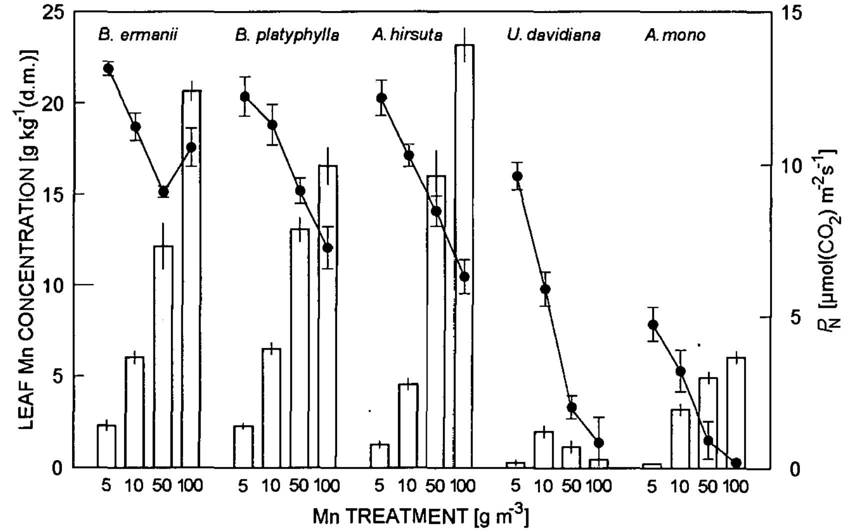

Fig. 2. Manganese concentration in *ca*. 25-d-old leaves (*open bars*) and radiant energy-saturated net photosynthetic rate (P_N) at ambient air (●) of *Betula ermanii*, *Betula platyphylla* var. *japonica*, *Alnus hirsuta*, *Ulmus davidiana* var. *japonica*, and *Acer mono*. Values are means ± SE.

Mn concentration in leaves and P_N: At the same Mn treatment and the same age (about 25 d, Fig. 2), the early-successional species (*B. ermanii*, *B. platyphylla*, and *A. hirsuta*) tended to accumulate more Mn in the leaves than the mid- and late-successional species of *U. davidiana* and *A. mono*. The Mn concentration in 25-d-old leaves increased with higher Mn treatments in all species except *U. davidiana* at Mn_{50} and Mn_{100}. P_N saturated with radiant energy showed decreasing trends at high Mn treatments in all species (Fig. 2). The extent of P_N decrease was much larger in *U. davidiana* and *A. mono* than in the early-successional species (*B. ermanii*, *B. platyphylla*, and *A. hirsuta*). Age-dependent Mn concentrations in *A. hirsuta* leaves increased with leaf age (Fig. 3). Higher Mn concentrations were observed at higher Mn treatments at the same leaf ages.

Discussion

Excessive Mn accumulation in leaves results in a reduction of photosynthetic activities (Ohki 1985, Nable *et al.* 1988, Kitao *et al.* 1997a,b). Such reduction in photosynthesis is expected to lead to a subsequent reduction in growth. In this study, the decline of RGR (Table 1) for five deciduous broad-leaved tree species with increasing Mn supply was observed as well as the decline in P_N (Fig. 2).

However, plant growth is also determined by various factors directly or indirectly linked to P_N (Poorter 1990, Lambers and Poorter 1992). SLA represents leaf thickness and the relative proportions of assimilatory to conductive or mechanical tissues in leaves (Květ *et al.* 1971, Björkman 1981, Poorter 1990, Lambers and Poorter 1992). Although SLA within species was little affected by Mn treatments, higher SLA observed in early-successional species than in mid- or late-successional species suggests a higher radiant energy utilization capacity per unit leaf mass in the former under high irradiance. The pattern of continuous leaf development in early-successional species could result in higher values of LMR, suggesting a greater allocation of photosynthates to photosynthetic (*i.e.*, leaf) *vs.* non-photosynthetic tissue (Květ *et al.* 1971, Björkman 1981, Poorter 1989, Lambers and Poorter 1992). Within species, the lack of differences in LMR among Mn treatments could be explained by the small effect of Mn treatments on leaf emergence, except for *U. davidiana* at Mn_{50} and Mn_{100}. Since LAR (the relative size of assimilatory apparatus to total plant) is the product of LMR and SLA (Květ *et al.* 1971, Poorter 1990, Lambers and Poorter 1992), it also shows no effect among different Mn treatments in all tree species except for *U. davidiana* at Mn_{50} and Mn_{100}. Compared with other species, the significantly lower LAR of *U. davidiana* at Mn_{50} and Mn_{100} is mainly caused by the decline of LMR in these treatments rather than that of SLA as found in other species. The decline of LMR for *U. davidiana* under Mn_{50} and Mn_{100} is probably associated with the reduced number of newly emerging leaves under high Mn treatments (Fig. 1). We also observed the cessation of root growth in *U. davidiana* at Mn_{100}. The reduced root activity likely resulted in the depression of nutrient and/or water supply for shoot development. The lower leaf Mn concentration at Mn_{50} and Mn_{100} than at Mn_1 and Mn_{10} is consistent with the root limitation assumption (Fig. 2). In other species, the higher Mn concentrations observed in leaves grown at higher Mn treatments (Fig. 2) indicate that nutrient/water uptake by the root is still functional. If Mn toxicity acts primarily on the root, with the secondary effect of reducing water and/or nutrient uptake leading to a decline in shoot growth, then modifications in SLA and LMR should have been observed in a manner similar to the effect of nitrogen deficiency (McDonald 1990) and water deficits (Begg 1980, Passioura *et al.* 1993). Therefore, it is more likely that accumulation of Mn in the shoot is the primary cause of changes in shoot growth. Although there could be a possible reduction of the size of assimilatory apparatus with prolonged Mn treatments, reduced RGR observed with this relatively short-term exposure to high Mn treatments may result primarily from the declined photosynthetic rate in highly Mn accumulated leaves.

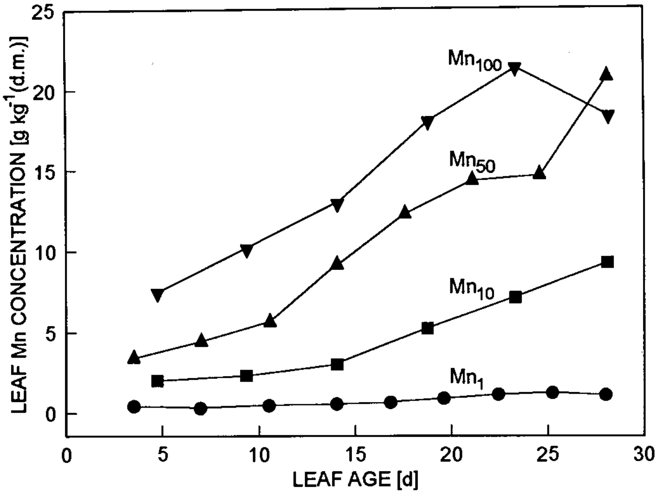

Fig. 3. Manganese concentration in leaves of various leaf age (estimated by the date of emergence for each leaf) of *Alnus hirsuta* plants grown under various Mn treatments (Mn_1, Mn_{10}, Mn_{50}, Mn_{100}; the index gives Mn concentration [g m^{-3}]).

The accumulation of Mn in the leaf appears to be cumulative in *A. hirsuta* where Mn concentration increased with leaf age (Fig. 3). Since Mn is readily transported from root to shoot through the transpiration stream but not readily remobilized through phloem to other organs after reaching the leaves (Nable and Loneragan 1984, Loneragan 1988), Mn concentrations in leaves should reflect the cumulative amount of transpiration, leading to higher Mn concentrations in older leaves. If this is the case, then even within the same Mn treatment we ought to find higher leaf Mn concentrations in early-successional than mid- and late-successional species (Fig. 2) given by their generally higher transpiration rate *via* higher stomatal conductance (Ike 1982, Schulze and Hall 1982, Berninger *et al.* 1996). This relationship should lead to a direct correlation between higher photosynthetic capacity and greater leaf Mn concentration, and should result in a larger toxicity effect of greater photosynthetic decline. But by virtue of their leaf phenology, early-successional species can allocate greater amounts of photosynthates to new leaves of lower initial Mn load, thereby mitigating the effect of Mn toxicity. While mid- and late-successional species are also capable of circumventing high leaf Mn accumulation, they do so through their inherently lower P_N and lower Mn uptake.

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