Ecophysiological evaluation of the potential invasiveness of *Rhus typhina* in its non-native habitats

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Received April 9, 2009; accepted July 29, 2009; published online 4 September 2009

Summary *Rhus typhina* L. (staghorn sumac) is a clonal woody species that is considered potentially invasive in its non-native habitats. It is slow growing as seedlings, but grows fast once established. Its growth in the early stages is limited by many abiotic factors, including light intensity. To evaluate its potential of becoming invasive in areas it has been introduced into, we conducted a field experiment to investigate the effects of light intensity on the physiology and growth of *R. typhina*. Two-month-old *R. typhina* seedlings were examined under five light levels, that is, 100% full sunlight (unlimited light), moderate stress (50% or 25% of full sunlight) and severe stress (10% or 5% of full sunlight), for 60 days in Hunshandak Sandland, China. Net photosynthetic rate ($P_N$) was reduced significantly under severe light stress, but $P_N$ of the moderately stressed seedlings was unaffected. Light stress also led to a reduction in saturated light intensity of the moderately stressed seedlings by 20% and of the severely stressed seedlings by 40%, although the light saturation points were as high as 800 and 600 $\text{l} \text{mol m}^{-2} \text{s}^{-1}$ for the moderately and severely stressed seedlings, respectively. Under severe light stress, the maximum quantum yield of Photosystem II ($F_v/F_m$) decreased significantly, but the minimal fluorescence yield ($F_0$) increased compared to that of the control plants. The number of newly produced leaves and the stem height, however, decreased as the light intensity became lower. Root length and leaf area decreased, whereas specific leaf area significantly increased as light became increasingly lower. Biomass production was significantly reduced by light stress, but the allocation pattern was unaffected. Our results demonstrated that *R. typhina* seedlings can survive low light and grow well in other light conditions. That is, becoming invasive, we urge caution when it comes to introducing *R. typhina* into its non-native habitats, despite its many ecological benefits.

Keywords: biomass allocation, biomass production, chlorophyll fluorescence, gas exchange, growth, light intensity.

Introduction

*Rhus typhina* L. (staghorn sumac), a native of the eastern United States, is a shrub or a small tree that reproduces by rhizomes and seeds (Uva et al. 1997). This fast-growing species can not only grow under environmental stresses, such as drought, low temperature and low soil nutrient environments (Radford et al. 1968, Chapman and Bessette 1990, Kudish 1992), but is also highly effective in retaining water and soil due to its colony-forming growing pattern. *Rhus typhina* is also valued by many for its brightly colored foliage during fall (Uva et al. 1997). Because of its ecological benefits and horticultural uses, *R. typhina* has been introduced from its native North America to many other countries, including China. As its distribution keeps expanding, it is being increasingly realized that the very characteristics that make *R. typhina* a species of choice for soil conservation and urban forestation may enable it to escape from cultivation and become a problem species in its introduced habitats. It is therefore essential to better understand how the physiology and growth of *R. typhina* seedlings, a key stage in its life cycle, will be affected by the environmental factors in its non-native habitats where it is widely planted.

In recent years, *R. typhina* has been regularly introduced into the Hunshandak Sandland (HS), a semi-arid area in Inner Mongolia, China, to stabilize sand and to restore the degraded environment. The HS is one of the most seriously degraded and desertified sandlands in the world resulting primarily from frequent biotic disturbances,
particularly overgrazing by livestock (Jiang et al. 2003). The HS has thus been considered one major source of the serious sandstorms that occurred lately in North China, including its capital Beijing (Liu et al. 2004). Soil deterioration has also restricted the growth of native plants and restoration of the native ecosystems, thus further reducing the productivity of these important ecosystems. To prevent the accelerating environmental degradation and to eventually restore the native ecosystems in the sandland, much effort has been spent in identifying and introducing plant species into the HS. *Rhus typhina* is a species that has been regularly introduced and widely cultivated in and around the HS for such a purpose.

The fast vegetative and reproductive growth of this non-native species, however, has led some to believe that it may become invasive and out of control if cultivated in large numbers (Zhang et al. 2005, Wang et al. 2008). Because of the numerous adverse effects of invasive species on native ecosystems, there have been attempts to understand the biology of this potential invasive species. Most studies so far have focused on the morphology (Brown and Brown 1972, Duncan and Dancan 1988), phytochemistry (Brigitte et al. 2002, Werner et al. 2004, Ruth and Geory 2005) and reproductive biology (Jon and Lesley 1988, Lukan 1990, Zhang et al. 2005) of this species. Little is understood about the physiology and growth of *R. typhina* seedlings as affected by the environmental factors, such as light level, in the field.

A key process for an exotic species to become established and subsequently invasive is how it adapts to the local environmental conditions, such as light (Dwyer et al. 2000, Hertling and Lubke 2000, Wang et al. 2004). Among the exotic species that have had adverse effects on important grassland ecosystems in China, for example, *Eupatorium adenophorum* Spreng., *Gynura sp.*, *Plantago virginica* L. and *Solidago canadensis* L., a common denominator is their plasticity to growing under a wide range of light intensities (Wang et al. 2004). The ability to survive low light conditions is in fact one of the most important reasons that allow a non-native species to become established and eventually invasive (Standish et al. 2001, Yamashita et al. 2002, Niinemets et al. 2003).

In a field experiment conducted in the HS, we examined the effects of varying light intensities on the physiology and growth of *R. typhina* seedlings. These light levels represented the range of light intensities that cultivated *R. typhina* seedlings may be exposed to in the HS. Seedlings may see light intensity as high as 2500 μmol m⁻² s⁻¹ in the open, or may face low light conditions if grown under the dense *R. typhina* canopies or if planted under the shading of the sporadic native plant species. By examining the morphological, physiological and growth characteristics of *R. typhina* under the different light conditions in the field, we will be able to assess its growth plasticity at different light intensities and to improve our mechanistic understanding of the survival and growth of *R. typhina* individuals in its introduced habitats. We hypothesized that the CO₂-fixing capacity of *R. typhina* would be adversely affected by low light levels; the characteristics of photosynthesis and growth in *R. typhina* seedlings would be extensively investigated under the wide range of light intensities encountered in the HS in the first growing season, thus, to reveal whether *R. typhina* would be a potential invasive species.

**Materials and methods**

**Experimental sites**

The experiment was conducted in the Grass Cultivation Station of Zhenglan Banner, Inner Mongolia, China (42°16′ N and 115°57′ E). This Station is located in the east of HS, which covers an area of 30,000 km² (Eerdun 1987). The prevailing climate is of a cold-temperate arid and a semiarid type. The average annual temperature is about 1.1 °C with the mean maximum in July (16.6 °C) and with the mean minimum in January (~−24.1 °C). The annual total radiation time is 3000~3200 h. The annual accumulated temperature of > 10 °C is 2000~2600 °C, and the frostless period is about 100 days (Zhu et al. 1980, Wang 1990). The average annual precipitation is 185–392 mm, and the annual potential evaporation is about 1643–2969 mm. Maximum precipitation is observed from June to August and the minimum values from March to May. In addition, rainfall fluctuates greatly among years and can be as low as 150 mm in dry years and as high as 400 mm in rainy years (Zhu et al. 1980, Wang 1990).

**Study species**

*Rhus typhina*, a large perennial shrub that can grow up to 10–12 m in height, is a dioecious species of the family Anacardiaceae. Although populations comprise male and female individuals, asexual reproduction is the main way to reproduce offspring and sexual reproduction is low under natural conditions (< 10%) (Lovett and Doust 1988, Chapman and Bessette 1990). Individuals may have a clonal growth through the production of rhizomes to form large and dense dome-shaped canopies with progressively younger ramets around the periphery.

**Experimental design**

Plant materials for this study were started from seeds, which were collected from *R. typhina* trees on the campus of the Institute of Botany, Chinese Academy of Sciences in Beijing, China. The seeds were germinated in April 2007 at the Grass Cultivation Station, where the field experiment was conducted. Two-month-old *R. typhina* seedlings of similar size were planted individually in plastic pots of 0.2 m height and 0.22 m diameter in June 2007. The pots were filled with sandy soil taken from nearby dunes and sieved to remove debris and seeds. Two weeks later, potted seedlings were
randomly divided into five groups of 24 seedlings each. These 24 seedlings were divided into subgroups for morphological, physiological and growth measurements. Based on the full sunlight of the experiment region, we designed five light intensity levels, that is, 100% full sunlight (control), moderate stress (50% and 25% full sunlight) and severe stress (10% and 5% full sunlight). The five light levels represented the full range of light levels that *R. typhina* seedlings could be exposed to in the HS, ranging from unobstructed sandland (100% sunlight) to deep shade created by dense canopy of *R. typhina* plants. Different black plastic nets were used to control the light intensity, and the quantum sensor attached to the Li-Cor 6400 system (Li-Cor Inc., Lincoln, NE) was used to check the light levels. The light intensities in the 50, 25, 10 and 5% full sunlight treatments were close to the target percentages in the days when light was measured inside the cubes. The seedlings were grown inside the cubes (2.0 m width × 2.0 m length × 1.0 m height). While the top panel of each cube was fixed, the four side panels could be opened for better ventilation. We typically kept the sides open before sunrise and after sunset to keep the temperature difference among treatments at a minimum. The cubes were placed 2.0 m from one another in all directions to avoid mutual shading. On June 20, 2007, we placed the five groups of seedlings into their respective light levels. All pots were kept at the same soil water content of 70% field capacity during the experimental period.

**Leaf gas exchange measurements**

Three seedlings from each light treatment were measured every 2 h from 0600–2000 h on August 12, 2007, to determine the photosynthetic rate (*P*$_{N}$), stomatal conductance (*g*$_{s}$) and intercellular CO$_{2}$ concentration (*C*$_{i}$) using a portable photosynthesis system LI-6400. Stomatal limitation (*L*$_{a}$) was calculated as 1 – *C*$_{i}$/*C*$_{a}$, where *C*$_{i}$ is the intercellular CO$_{2}$ concentration and *C*$_{a}$ is the atmospheric CO$_{2}$ concentration. Youngest fully expanded leaves in upper shoots were selected for all physiological measurements. We measured three leaves for each light treatment on the day of measurement.

**Irradiance effects on *P*$_{N}$**

Response of *P*$_{N}$ to stepwise changes in photosynthetic photon flux density (PPFD) was examined in the field using the method of Jiang and He (1999). A series of PPFD (2500, 2200, 2000, 1500, 1000, 800, 600, 400, 200, 100, 50 and 0 μmol m$^{-2}$ s$^{-1}$) was produced using LI-6400-02B red-blue light-emitting diodes. Each PPFD level was maintained for at least 5 min before the *P*$_{N}$ was recorded. The reference CO$_{2}$ concentration in the leaf cuvette was 350 ± 20 μmol mol$^{-1}$ and the temperature was 25 ± 0.5 °C. The *P*$_{N}$ was plotted against PPFD and the light response curves were fitted using the non-rectangular hyperbola model of Thornley (1976). Light-saturated photosynthesis (*P*$_{\text{max}}$) and light saturation points were then calculated from the fitted curves in a similar way as used by Quero et al. (2006).

**Chlorophyll fluorescence measurements**

In vivo chlorophyll fluorescence was measured on three leaves from three different seedlings at each light level using an LI-6400-02B fluorometer as described by Gomez-Aparicio et al. (2006). Leaves were kept in darkness for 12 h for dark adaptation before measurement. After the measurement of minimal Chl fluorescence yield (*F*$_{0}$) under low modulated measuring light, a 0.7-s pulse of saturating white light (> 3000 μmol m$^{-2}$ s$^{-1}$) was applied to determine maximal Chl fluorescence yield (*F*$_{m}$). Maximal Photosystem (PS) II quantum yield (*F*$_{v}$/*F*$_{m}$) was calculated as the ratio of variable fluorescence *F*$_{v}$ to *F*$_{m}$ where *F*$_{v}$ = *F*$_{m}$ – *F*$_{0}$.

**Growth measurements**

Stem height and leaf number of all seedlings were recorded at 10-day intervals throughout the experiment. Relative growth rate (RGR) of the newly produced leaves and stems was calculated using the following formula: RGR = (ln(final seedling data at the final harvest) – ln(initial seedling data)/time in treatment (day)) (Pattison et al. 1998). All seedlings were harvested on August 20, 2007. Seedlings were carefully washed out of pots and separated into leaves, shoots and roots before being dried at 80 ± 1 °C to a constant weight. Three weight ratios were calculated using the following formulae: leaf weight ratio (LWR) = leaf biomass/total plant biomass; stem weight ratio (SWR) = stem biomass/total plant biomass; and root weight ratio (RWR) = root biomass/plant biomass. Root length was the sum of total length of all roots with a diameter of < 0.2 cm. Leaf area was measured using a leaf area meter (AM100, ADC, Hoddesdon, England).

**Leaf characteristic and pigment determination**

Leaf samples of 10 cm$^{2}$ were used to determine the specific leaf area (SLA) (cm$^{2}$ g$^{-1}$ dw). To measure the leaf pigment content, we used leaf discs of 1 cm in diameter punched from the youngest fully expanded leaves. Chlorophylls a and b and carotenoids were extracted with 80% acetone using the method of Arnon (1949) and determined using a UV-120 system spectrophotometer (Shimadzu, Kyoto, Japan). The plate of leaf transverse structure was finished using the normal paraffin section technology, using the method of Jodie and Deborah (1985).

**Data analysis**

Analysis of variance was carried out using SPSS 10.0 package (SPSS, Chicago, IL). Mean values were compared using least significant differences (LSD) test at 95% confidence level.
Results

Gas exchange and chlorophyll fluorescence

All seedlings grown under the five light levels had similar patterns of change in \( P_N \) during the day, that is, a gradual decline from morning to late afternoon hours (Figure 1A). The time when \( P_N \) peaked, however, was different for seedlings under different light environments. For seedlings exposed to full sunlight, the peak appeared at about 0800 h. For seedlings exposed to all other light levels, the peaks appeared at about 1000 h. \( P_N, g_s \) and \( L_s \) became significantly lower with decreasing light intensity (Figure 1A, B and D). In contrast, \( C_i \) increased in response to a lower light intensity (Figure 1C).

Photosynthetic light response curves for seedlings grown under different light environments showed that low light significantly reduced light-saturated photosynthetic rates (\( P_{\text{max}} \)) of \( R. \ typhina \) seedlings. Light saturation points of the moderately stressed seedlings (50% and 25% full sunlight) and severely stressed plants (10% and 5% full sunlight) were 800 and 600 \( \mu \text{mol} \text{m}^{-2} \text{s}^{-1} \), respectively, which were 20% and 40% lower than those grown under full sunlight (Figure 2).

Different light intensities significantly influenced the fluorescence parameters in \( R. \ typhina \) seedlings (Figure 3). Maximum quantum yield of PS II (\( F_v/F_m \)) and maximum fluorescence yield (\( F_m \)) decreased with decreasing light intensity (Figure 3A and B), whereas minimal fluorescence yield (\( F_0 \)) increased significantly at lower compared to higher light levels (Figure 3C).

Growth characteristics

All seedlings grown under five light levels survived the 60-day experiment. Different light intensities, however, significantly affected the growth characteristics of the seedlings. All plants grew substantially larger by the end of the experiment, but the magnitude of increase in leaf number and stem height was different among the seedlings grown under different light levels (Figure 4). The RGR of the newly produced leaves and stem height in the 5% and

Figure 1. Changes in net photosynthetic rate \( P_N \) (A), stomatal conductance \( g_s \) (B), intercellular CO\(_2\) concentration \( C_i \) (C) and stomatal limitation \( L_s \) (D) in \( R. \ typhina \) seedlings grown under five levels of light intensity. Mean ± 1 SEM, \( n = 3 \). Vertical bars represent the LSD (\( P < 0.05 \)).

Figure 2. Net photosynthetic rate (\( P_N \)) response curves to light intensity (PPFD) in \( R. \ typhina \) seedlings. Mean ± 1 SEM, \( n = 3 \).
10% light treatments were significantly lower than those of the control and the moderately stressed seedlings (50% and 25% full sunlight) (Figure 5). Root length and leaf areas were also affected by light intensity. Root length decreased significantly from higher to lower light levels (Figure 6A). Leaf area did not differ between the control and the moderately stressed seedlings, but the leaf area in the severely stressed seedlings was significantly lower than in those grown under the three higher light levels (Figure 6B).

**Leaf characteristics and chlorophyll levels**

Leaves were larger and thinner and thus had a significantly higher SLA in the seedlings grown under low light (Table 1). Specific leaf area was only 143.8 cm² g⁻¹ dw in the seedlings under the full sun, but was as high as 690.6 cm² g⁻¹ dw in those under 5% full sunlight. Pigment content was also greatly affected by light intensity. Total chl a+b and carotenoid levels and the pigment ratios of chl a/b significantly decreased and chl a+b/carotenoids significantly increased as light intensity decreased (Table 1). Leaf morphological change was particularly evident when the seedlings were grown under severely stressed conditions (10% and 5% of full sunlight). The thickness of leaves was only half of that in the control plants (Table 1). Mesophyll cells also became less dense as the light intensity became increasingly lower (Figure 7).

**Biomass accumulation and allocation**

Biomass production in *R. typhina* seedlings was greatly affected by change in light intensity. Leaf, stem and root biomass was significantly lower at lower than higher light levels (Figure 8A). Biomass accumulations of moderately stressed seedlings (50% and 25% full sunlight) were lower than those of the control, but significantly higher than the severely stressed seedlings (10% and 5% full sunlight). Stem weight ratio of the severely stressed seedlings was significantly lower than those of the control and the moderately...
stressed seedlings. Leaf weight ratio and root weight ratio were unaffected by light levels (Figure 8B). Despite the large differences in total biomass production, allocation of biomass to the above- and below-ground components, as indicated by root/shoot ratio, was similar among the seedlings grown under different light levels (Figure 8B).

Discussion

Gas exchange characteristics

Our results demonstrated a high degree of photosynthetic plasticity in *R. typhina* seedlings at light levels ranging from full sunlight to low light (5–10% of full sunlight). *Rhus typhina* seedlings exposed to full sunlight had $P_N$ as high as 14 $\mu$mol m$^{-2}$ s$^{-1}$ during morning hours and could maintain a relatively high level of $P_N$ ($> 5$ $\mu$mol m$^{-2}$ s$^{-1}$) at dawn and dusk when the light level was low. Although $P_{max}$ of the severely stressed plants was reduced, it was still 21% of the $P_{max}$ in the seedlings exposed to ambient light (3 versus 14 $\mu$mol m$^{-2}$ s$^{-1}$). The high light saturation point in the severely stressed plants (600 $\mu$mol photon m$^{-2}$ s$^{-1}$) indicates that the plants grown under low light have the capability to use high light level, for example, sunflecks or when sunlight is at a particular angle during the day. These results demonstrated that *R. typhina* seedlings are photosynthetically plastic when it comes to using the solar energy available in the environment. They are able to maintain high $P_N$ when grown under natural light in the sandland. More importantly, they are able to maintain their potential photosynthetic ability when the light is low. Our results are consistent with those of Wang et al. (2004), who found similar responses to variations in light intensities in the seedlings of *Ageratina adenophora* (Spreng.) R.M. King & H. Rob., an invasive species that has caused enormous damage to the agricultural systems in China.

Chlorophyll fluorescence

Chlorophyll fluorescence parameters, such as $F_0$ and $F_{v}/F_{m}$, are often used to assess the activity of original photochemistry of PS II (Hulsebosch and Hoff 1996). Our chlorophyll results revealed significant effect of light stress on the photochemical activity of PS II. In the severely stressed seedlings, $F_0$ increased, whereas $F_{v}/F_{m}$ decreased compared to those that were exposed to higher levels of light, indicating a reduction in potential PS II efficiency and a loss of activation or destruction in the reaction center of PS II (Massimo and Namachevayam 2004). These results are in disagreement with those from previous studies that showed lower $F_0$ and higher $F_{v}/F_{m}$ with reduced light intensity (Long et al. 1994, Sarijeva et al. 2007). In *R. typhina*, $F_0$ did not
differ among seedlings exposed to high and moderate light levels, but was much lower than that of the seedlings under severe light stress. Values of $F_v/F_m$ varied little within a narrow range of 0.76–0.82 for all plants, although the severely stressed seedlings had a statistically lower $F_v/F_m$. Our results indicated that little photoinhibition occurred in the reaction center of PS II in *R. typhina* seedlings exposed to high light levels in the HS. *Rhus typhina* seedlings grown under severe stress, despite the somewhat damaged photosynthetic apparatus as indicated by increased $F_0$ and decreased $F_v/F_m$, were able to maintain photosynthesis at a high enough level to survive and grow under low light levels.

**Leaf morphology and photosynthetic pigments**

Leaf morphology differed greatly among *R. typhina* seedlings that were exposed to different levels of light. The leaves of seedlings grown under low light levels had much thinner leaves than those grown under higher light levels.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Normal light level</th>
<th>Moderate light level</th>
<th>Lower light level</th>
</tr>
</thead>
<tbody>
<tr>
<td>SLA (cm$^2$ g$^{-1}$ dw)</td>
<td>143.8 ± 18.5 e</td>
<td>163.6 ± 16.4 d</td>
<td>196.7 ± 20.4 c</td>
</tr>
<tr>
<td>Chl a + b (mg cm$^{-2}$)</td>
<td>612 ± 44 a</td>
<td>601 ± 38 ab</td>
<td>558 ± 29 b</td>
</tr>
<tr>
<td>Carotenoids (mg cm$^{-2}$)</td>
<td>139 ± 12 a</td>
<td>119 ± 9 b</td>
<td>96 ± 7 c</td>
</tr>
<tr>
<td>Chl a/b</td>
<td>3.95 ± 0.35 a</td>
<td>3.63 ± 0.44 b</td>
<td>3.38 ± 0.13 c</td>
</tr>
<tr>
<td>Chl a + b/cars</td>
<td>4.41 ± 0.52 d</td>
<td>5.06 ± 0.24 c</td>
<td>5.80 ± 0.37 b</td>
</tr>
<tr>
<td>Thickness of leaf (µm)</td>
<td>287.61 ± 21.2 a</td>
<td>224.81 ± 19.4 b</td>
<td>220.9 ± 17.3 b</td>
</tr>
<tr>
<td>Density of palisade tissue cell/100 µm</td>
<td>4.8 ± 0.24 a</td>
<td>4.1 ± 0.37 b</td>
<td>3.9 ± 0.47 b</td>
</tr>
</tbody>
</table>

Figure 7. Transverse section of palisade (PT) and sponge (ST) tissues of *R. typhina* leaves from seedlings grown under different light intensities. The five levels of light intensity are 100% (CK), 50% (T1), 25% (T2), 10% (T3) and 5% (T4) of full sunlight, respectively; 1 bar = 50 µm.
as indicated by the greatly increased SLA. These morphological responses are typical of plants grown or acclimated to low light intensity (Kitao et al. 2000). Thinner leaves and hence less leaf mass per unit area increase the relative proportion of assimilatory tissue to conductive and structural tissues in leaves (Björkman 1981, Poorter 1989, Lambers and Poorter 1992). A higher SLA may also contribute to the net CO₂ assimilation in the shade-acclimated plants through a decrease in dark respiration (Björkman 1981, Pearcy and Sims 1994). A higher SLA in low-light grown plants as found in our study thus suggested that *R. typhina* seedlings had high capability to capture light efficiently when the light is limited.

Like leaf morphological characteristics, leaf pigments were highly responsive to varying light levels. *Rhus typhina* seedlings grown under full sunlight had 2.4–3.8 times more chlorophylls and 3.2–5.4 times more carotenoids than those grown under the severely stressed conditions (5% and 10% of full sunlight). The wide range of pigment content, particularly of carotenoids, has significant ecological implications for *R. typhina* growing in the HS. On one hand, the high content of carotenoids in sun-grown seedlings allows plants to enhance the antioxidation and thermal dissipation ability of leaves to avoid photodamage and photoinhibition under full sunlight (Frank and Cogdell 1996, Bungard et al. 1999). On the other hand, the low level of carotenoids in plants under low light levels allows plants to allocate carbohydrates, which is typically limited in plants under low light, for other uses, thus increasing its chance of surviving in the first growing season.

**Biomass production and allocation**

It is well understood that plants change biomass allocation as a strategy to adapt to environmental changes (Poorter and Nagel 2000, Tao and Zhong 2003). Our study found that the biomass production of *R. typhina* seedlings became increasingly lower as light intensity became lower. Biomass distribution pattern, however, was unaffected by light levels. These results are inconsistent with those of previous studies on other species (Poorter 1999, Poorter and Nagel 2000), who found that plants allocate more biomass to leaves to capture more light energy under lower light conditions. The unusual biomass allocation pattern in *R. typhina* demonstrated that it may acclimate to a wider range of soil conditions than other species. In our study, all *R. typhina* seedlings survived under the severely light stressed treatment (5% full sunlight). In contrast, no seedlings of *Gynura* sp., an invasive species, survived under low light environment (4.5% full sunlight) during the first year (Wang and Feng 2004). The unresponsiveness to light in its biomass allocation and its ability to assimilate sufficient carbon to survive may be related to its life history characteristics. *Rhus typhina* is adapted to poor, dry soil and is often found in areas too hostile to other plant species (Uva et al. 1997). Additionally, *R. typhina* is found to form a highly dense unitary population through agamogenesis. Dense canopy creates contrasting light environments within and outside the canopy. Sprouts can often be found inside the dense canopy as well as far away from the center of population. Its adaptability to poor soil conditions and high tolerance of shade will increase its chance of survival and outcompete other species that may not adapt to low light conditions.

**Conclusion**

Our results demonstrated that change in light intensity affected photosynthesis, growth and biomass accumulation in *R. typhina* seedlings. *Rhus typhina* seedlings are highly plastic when it comes to using the available light energy. The seedlings could maintain a high P₅ and a high growth rate under full sunlight and moderately low light conditions (50% and 25% full sunlight). *Rhus typhina* seedlings were able to assimilate sufficient carbon to survive severely low light intensity environment (10% and 5% full sunlight). These physiological and growth traits will likely confer an advantage of surviving and growing over a wide range of light environments in the HS and elsewhere. *Rhus typhina* thus has a potential advantage in competing for light and soil resources with native species. Accordingly, we urge caution when it comes to introducing *R. typhina* to its non-native habitats, despite its many ecological benefits.
The authors thank two anonymous reviewers for valuable suggestions on an earlier version of this manuscript. They thank Dr. Xianzhong Wang (Department of Biology, Indiana University–Purdue University, Indianapolis, USA) for help with the analysis and the interpretation of the manuscript and its revision. This work was supported in part by a Key Innovation Project of the Chinese Academy of Sciences (KSCX2-YW-N-52) and Combating Desertification Research Project of the Ministry of Science and Technology of China (2006BAD26B0101 and 2006GB24910475).

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