

Morphological and physiological responses of the invasive weed *Isatis tinctoria* to contrasting light, soil-nitrogen and water

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Summary

We evaluated the morphological and physiological responses to contrasting above- and below-ground resources for the invasive weed, *Isatis tinctoria* L. (dyer's woad). Plants were grown under low and high levels of light [shade (50% of ambient) and full sun], soil water (50 and 100 mL day⁻¹), and soil nitrogen (N) (0 and 20 mg N kg⁻¹ soil) in 8 L pots in 63 day glasshouse experiments conducted during winter and spring. Soil-N enrichment did not increase any of the growth variables (shoot and root dry mass, shoot:root ratio, leaf area, and specific leaf area) or physiological variables (stomatal conductance and ¹³C discrimination) in either experiment. The absence of plasticity in response to changes in soil-N supply suggests that *I. tinctoria* may

survive and persist in nutrient-poor conditions by having low-N requirements, low-N productivity, or both. In contrast, plants compensated for shaded conditions by altering leaf area, specific leaf area, and shoot:root ratio to improve light capture. We discuss the potential mechanisms whereby response to these variable resources may be associated with a series of adaptations that favour the ability to tolerate and colonize harsh, nutrient-poor conditions, as well as invade shaded and undisturbed sites.

Keywords: shade, carbon isotope composition, stomatal conductance, specific leaf area, invasive weed, Great Basin, root growth, multiple limiting resources, phenotypic plasticity.

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Introduction

No single trait or group of traits can completely explain or predict the invasive ability of a plant species (Thompson *et al.*, 1995; Rejmánek, 1996; Pysek *et al.*, 2004) because the success of an invader often depends on complex interactions between the species and its target community (D'Antonio, 1993; Radford & Cousens, 2000). Consequently, physiological and morphological adaptations of invasive species to specialized environments may be better predictors of the success of invaders than specific traits (Thebaud *et al.*, 1996; Radford & Cousens, 2000). For example, adaptive adjustments of physiology and morphology in response to variable

environments and resources, i.e. phenotypic plasticity (Givnish, 1988; Agrawal, 2001; Sultan, 2003), are believed to enable invasive plants to successfully colonize a broad range of habitats (Baker, 1974; Pattison *et al.*, 1998). However, if a species is to become truly invasive, it must not only have an effective means of dispersal and establishment, but also mechanisms for demographic expansion (Kolar & Lodge, 2001).

The recent expansion of the exotic biennial herb, *Isatis tinctoria* L. (dyer's woad; Brassicaceae), from disturbed, sparse, and rocky slopes that are unsuitable for most species into relatively non-disturbed, dense plant communities is a major concern in the western United States (Farah *et al.*, 1988; Dewey *et al.*, 1991).

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The mechanisms of invasion are not well understood for this weed, but its success may be partly attributed to several factors, including allelopathic effects on native species germination (Young & Evans, 1971), high reproductive output, and a two-layered rooting pattern (Farah *et al.*, 1988). High genetic diversity and phenological and morphological variability have also been observed in its landraces (Callihan *et al.*, 1984; Gilbert *et al.*, 2002). Nonetheless, its expansion into undisturbed sites is puzzling because conventional life-history descriptions suggest that facultative biennials such as *I. tinctoria*, primarily occupy fertile, early successional and disturbed sites (Kelly, 1985). In addition, the life history of *I. tinctoria* suggests more of a stress-tolerant ruderal strategy as opposed to adaptations to low-light environments of undisturbed plant communities (Grime, 1979).

Greater understanding of the ecology of *I. tinctoria* may help identify potential limits in ecological breadth and could lead to improved control methods for this species. Because stress-tolerant species typically dominate nutrient-poor sites and demonstrate low plasticity in allocation to root and shoot biomass with nutrient enrichment (Monk, 1966; Lambers & Poorter, 1992; Aerts, 1995), we hypothesized that *I. tinctoria* would exhibit low plasticity in growth and physiology in response to variable soil nitrogen. We also hypothesized that the ability of *I. tinctoria* to expand into undisturbed and shaded sites necessarily requires relatively high morphological or physiological plasticity in response to variable light and water. We conducted glasshouse experiments with rosettes of *I. tinctoria* to assess these possibilities by evaluating gas exchange, biomass allocation, and morphology in response to low and high levels of soil nitrogen, water and light.

Materials and methods

Winged fruits (siliques) of *I. tinctoria* were collected from a disturbed big sagebrush (*Artemisia tridentata* ssp. *wyomingensis* Beetle & A.W. Young) shrub-steppe plant community (41°46'10"N, 111°46'47"W) in the summer of 2002. Soil for both experiments was collected from an infertile plant community, and was classified as a coarse-loamy, mixed, calcareous, superactive, mesic Xeric Torriorthent. This soil contained <1 g total N kg⁻¹, and <5 mg total mineral N kg⁻¹.

Two 63 day experiments were conducted in a glasshouse under natural lighting with temperatures maintained between 18 and 23°C. A winter experiment was conducted between 6 December 2002 and 6 February 2003 and a spring experiment between 7 February and 10 April 2003. The two experiments were identical except that the winter experiment exposed plants to

shorter day lengths with c. 60% lower net solar radiation compared with the spring experiment. Plants remained as vegetative rosettes during both experiments, because without a vernalization event, rosettes will not flower (Asghari *et al.*, 1992). Experiments were conducted with rosettes because it is widely recognized that rosette size is highly correlated with fecundity in facultative biennials (Lacey, 1986; Bloom *et al.*, 2002). A total of 64 8 L pots were filled with 7.5 kg of dry soil. In each pot, a total of seven siliques were planted 1 cm deep in a circular pattern, with the pedicel (stipe) pointing down. The soil surface was then covered with 1 cm of vermiculite (laminar magnesium–aluminum–ironsilicate) to buffer environmental influences of germinating seeds and minimize potential soil disturbance associated with watering pots. Pots were weighed daily, and the appropriate amount of water was added to achieve field capacity. Seedlings emerged after 7 days. At 21 days (four-leaf stage), seedlings were thinned to four uniformly sized plants per pot and randomly assigned to a treatment.

The plants were exposed to one of the eight possible combinations of high and low levels of light, soil water, and soil N. Both experiments had eight replications of each treatment combination. A neutral-density shade structure was placed above four individual pots to produce the low light level (i.e. shade = 50% of ambient level; Monaco & Briske, 1999). Pots assigned to the high light level (full sun) were similarly arranged on the glasshouse bench in groups of four, but received ambient light. Each four-pot group remained together, but was systematically moved to different locations within the glasshouse each day. The four-pot groups were adequately spaced on the glasshouse benches so that the shading structures did not interfere with the light environment of other four-pot groups.

The four pots within a light level were randomly assigned one of the following soil water and soil N treatment combinations: (1) low water–low N, (2) low water–high N, (3) high water–low N, and (4) high water–high N. The low and high soil water levels were 50 and 100 mL of water, respectively, each day from day 21 until the experiments ended. Pots in the high soil-N treatment received 20 mg N kg⁻¹ soil as NH₄NO₃ (10 on days 21 and 40 of the experiments). Pots assigned to the low soil-N treatment did not receive supplemental N during the experiments. Previous experimentation with this soil revealed that growth of annual and perennial grasses from habitats that are frequently invaded by *I. tinctoria* was drastically reduced when not amended with additional N (Monaco *et al.*, 2003).

After 8 weeks, stomatal conductance was measured for one plant in each pot. These measurements were made over four consecutive days between 11:00 and

13:00 hours when the intensity of solar radiation was most consistent, using a portable photosynthesis system (LI-6400; Li-Cor Corp., Lincoln, NE, USA). The leaf chamber environment maintained the following conditions during measurements: block temperature 24°C; CO₂ concentration 400 µmol mol⁻¹; airflow 500 µmol s⁻¹; and photosynthetically active radiation (PAR) 600 µmol m⁻² s⁻¹. Stomatal conductance was expressed on a leaf-area basis.

Plants were harvested at the end of experiments to determine the treatment effects on above- and below-ground vegetative growth. Shoots were immediately clipped at ground level and passed through a leaf-area meter (LI-3000; Li-Cor Corp.) and then dried to determine shoot mass. Roots were sieved (2 mm mesh) gently in water, dried and then weighed. Dry masses were obtained after drying plants in a convective oven at 60°C for 48 h. Specific leaf area (SLA) was calculated by dividing the leaf area by the respective dry leaf mass.

Shoot material from the same plants used for determination of stomatal conductance was ground to pass a 0.5 mm screen and analysed to determine δ¹³C values (the ratio of ¹³C/¹²C relative to that of the Pee Dee Belemnite standard) using an isotope ratioing mass spectrometer (SIRA 10; Fisons Instruments, Altrincham, UK). Precision for the δ¹³C values was better than 0.01‰ (1 in a million). The δ¹³C values were converted to ¹³C discrimination values (Farquhar *et al.*, 1989). Experiments were analysed using a split-plot design with light as the main plot, and water and nitrogen combinations as the split plot. The mean square error for the replicate by light interaction was used to test the effects of light. All statistical analyses were evaluated with α = 0.01.

Results

Augmenting soil with N did not significantly affect any of the variables. There were very few variables where interaction between N and either light or water was significant (not shown), apart from the addition of soil-N that increased shoot dry mass in the winter under low water conditions (Fig. 1). In contrast, water and light treatments affected nearly all growth variables in winter and spring experiments, and several variables showed dynamic interactive responses to light and water (Table 1).

Shoot and root dry mass

Shading plants did not alter shoot dry mass relative to full sun in either season (Table 1). Shoot dry mass under low water conditions was less ($P < 0.01$) than that under high water conditions in both winter ($n = 32$; 0.22

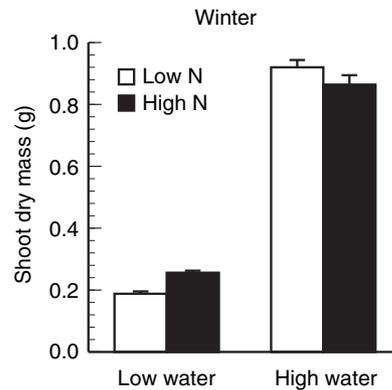


Fig. 1 Mean (± 1 SEM; $n = 16$) shoot dry mass (g) of *I. tinctoria* plants when grown in low and high levels of soil-N and water in the winter experiment.

Table 1 Results of ANOVA for shoot and root dry mass, shoot:root ratio, leaf area, specific leaf area, stomatal conductance, and ¹³C discrimination

Factor:		Light (<i>P</i> -value)	Water (<i>P</i> -value)	L × W (<i>P</i> -value)
df:	Season	1, 7	1, 42	1, 42
Shoot dry mass	Winter	ns	<0.01	ns
	Spring	ns	<0.01	ns
Root dry mass	Winter	<0.01	<0.01	<0.01
	Spring	<0.01	<0.01	<0.01
Shoot:root ratio	Winter	<0.01	<0.01	<0.01
	Spring	<0.01	<0.01	ns
Leaf area	Winter	<0.01	<0.01	<0.01
	Spring	<0.01	<0.01	<0.01
Specific leaf area	Winter	<0.01	<0.01	<0.01
	Spring	ns	<0.01	ns
Stomatal conductance	Winter	ns	ns	ns
	Spring	ns	<0.01	ns
¹³ C discrimination	Winter	<0.01	ns	ns
	Spring	<0.01	<0.01	ns

ns, not significant; df, numerator and denominator degrees of freedom for *F*-tests of dependent variables.

vs. 0.89 g; Fig. 2) and spring ($n = 32$; 0.58 vs. 1.18 g). In spring, shoot dry mass was generally greater (> 30%) than that in winter. In both seasons, root dry mass was significantly higher under full sun than shade (Fig. 2). Providing plants with more water resulted in significantly greater increases in root dry mass under full sun than under shade in winter and spring (Table 1).

Leaf area, SLA, and shoot:root ratio

The pattern and magnitude of leaf-area responses to light and water were consistent in winter and spring (Table 1; Fig. 2). Leaf area was at least twofold greater under high than low water conditions ($P < 0.01$), and plants produced more leaf area under shade than

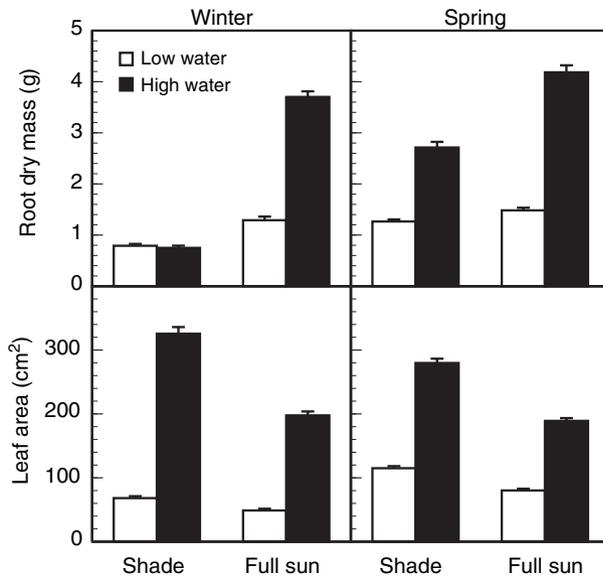


Fig. 2 Mean (± 1 SEM; $n = 16$) root dry mass (g) and leaf area (cm^2) of *I. tinctoria* plants when grown in low and high levels of water and under shade or full sun in the winter and spring experiments.

full sun ($P < 0.01$) in both seasons. Water-mediated increases in leaf area were substantially greater in shade than full sun. Specific leaf area was primarily controlled by light in winter and by water in spring. In winter, plants grown under shade had nearly 40% greater specific leaf area than in full sun (Fig. 3). Specific leaf

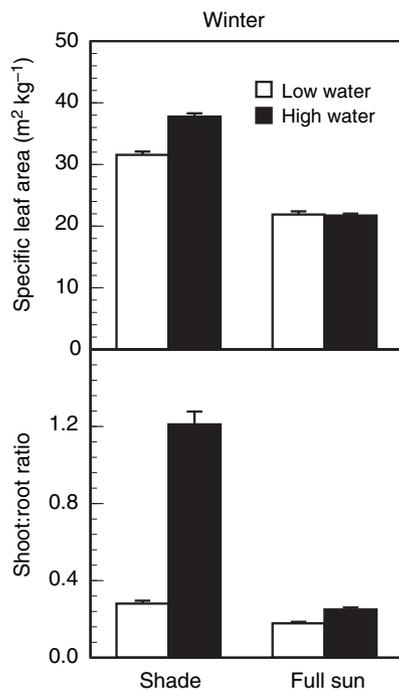


Fig. 3 Mean (± 1 SEM; $n = 16$) specific leaf area ($\text{m}^2 \text{kg}^{-1}$) and shoot:root ratio of *I. tinctoria* plants when grown in low and high levels of water and under shade or full sun in the winter experiment.

area increased significantly in the winter with additional water under shade, but not under full sun. In contrast, specific leaf area in high water conditions was nearly threefold greater than that in low water conditions in the spring experiment ($n = 32$; 23 vs. $66 \text{ m}^2 \text{kg}^{-1}$).

Shade induced significantly greater shoot:root ratios (SRR) relative to full sun in both winter and spring (Table 1; Fig. 3). However, on average, the magnitude in which shade increased SRR relative to full sun was much larger in winter ($n = 32$; 0.7 vs. 0.2) than in spring ($n = 32$; 0.5 vs. 0.3). In winter, plants grown in high water conditions had significantly greater SRR in both shade and full sun, but the magnitude of this increase was much larger under shade than in full sun. In contrast, SRR declined (Table 1; $P < 0.01$) under high water relative to low water conditions in spring ($n = 32$; 0.43 vs. 0.34 respectively).

Stomatal conductance and ^{13}C discrimination

Stomatal conductance was not significantly influenced by light or water in the winter experiment. However, mean stomatal conductance for winter was 62% greater than in spring ($n = 64$; 0.29 vs. $0.11 \text{ mol m}^{-2} \text{ s}^{-1}$). In spring, plants under low water conditions had significantly lower stomatal conductance than those under high water conditions ($n = 32$; 0.07 vs. $0.14 \text{ mol m}^{-2} \text{ s}^{-1}$). Likewise, ^{13}C discrimination was generally greater in winter than in spring ($n = 64$; 24.37 vs. 21.23‰). In spring, low water induced significant decreases in ^{13}C discrimination relative to the high water treatment ($n = 32$; 21.79 vs. 20.67‰). Values of ^{13}C discrimination were significantly lower in full sun than under shade in winter ($n = 32$; 23.69 vs. 25.05‰) and spring ($n = 32$; 20.53 vs. 21.94‰).

Discussion

Our results confirm that *I. tinctoria* exhibits low plasticity in growth and physiology in response to variable soil nitrogen. Results of this study also support the hypothesis that the ability of *I. tinctoria* to expand its range into undisturbed and shaded sites necessarily requires relatively high plasticity in response to variable light and water. The absence of plasticity in responses to changes in soil-N supply suggests that *I. tinctoria* may possess low-N requirements, low-N productivity, or both. Interestingly, all three characteristics are associated with the ability of species to survive and persist under stressed, nutrient-poor conditions (Grime & Campbell, 1991; van der Werf *et al.*, 1993; Craine *et al.*, 2002). These results also agree with those of others who found that early succession on disturbed, harsh sites is determined by colonizing ability, not competitive ability

for soil-N (Huston & Smith, 1987; Tilman & Wedin, 1991).

Isatis tinctoria compensated for low light primarily through modifying morphology as opposed to shoot biomass and physiology, as was observed in shade-tolerant tree seedlings (Bloor & Grubb, 2004). It is surprising that shoot biomass was unaltered by low light, given that plants typically respond to decreases in above-ground resources through increases in allocation to shoots (Hirose, 1987; Poorter & Nagel, 2000). Instead, shade enhanced *I. tinctoria*'s light-harvesting efficiency by increasing leaf area in both seasons and SLA in the winter. Shade-induced increase in SLA is a well-known morphological plastic response (Fitter & Hay, 2002) that enables plants to compensate the growth-limiting effects of shading (Patterson, 1995; Ryser & Eek, 2000). Light-demanding species generally have more variable SLA than shade-tolerant species when grown under contrasting light conditions (Walters & Reich, 1999). Greater SLA may help compensate in shaded conditions by increasing the capacity to assimilate CO₂, because more leaf area is produced for a given leaf mass invested in photosynthetic tissues. *I. tinctoria* also compensated low-light conditions by producing significantly lower root mass and demonstrating marked flexibility in shoot:root ratio under shaded conditions relative to full sun, particularly in the winter. Flexible root production probably facilitated the ability of *I. tinctoria* to maintain shoot dry mass, even under unfavourable shade conditions. Similarly, plasticity in biomass allocation assisted the invasive biennials, *Alliaria petiolata* (Bieb.) Cavara & Grande (garlic mustard) and *Centaurea solstitialis* L. (yellow starthistle), to respond favourably to variable light environments and possibly grow in a wider range of environmental conditions (Meekins & McCarthy, 2000; Gerlach & Rice, 2003). *I. tinctoria* thus appears to compensate for reduced light by altering dry mass allocation, so as to perform equally well under variable light conditions, as opposed to growing fast and allocating growth primarily to produce shade and suppress neighbours (e.g. Weiner, 1990; Bengtsson *et al.*, 1994).

With the addition of water, *I. tinctoria* plants exhibited typical growth responses by increasing overall productivity (Wilson, 1998; Noda *et al.*, 2004). Although root mass generally decreased under low water conditions, an increase in root mass relative to shoot mass was evident by decreases in the shoot:root ratio, particularly under shade in the winter experiment. Low shoot:root ratios have been associated with competitive ability when water is a limiting factor (Brewer *et al.*, 1998). The magnitude of water-facilitated increases in leaf area, SLA, and shoot:root ratio was

consistently greater under shade than full sun. According to the 'influential trade-off hypothesis' (Smith & Huston, 1989), plasticity in shade may intensify dynamic changes to variable water because shoot mass allocation to improve light capture may occur at the expense of allocation to root mass. Greater root mass allocation and morphological plasticity in response to water in shade than full sun was also likely a result of the growth limitations imposed by water stress in full sun, as indicated by significantly higher ¹³C discrimination in leaves relative to shade in both seasons.

The hypothesized greater plasticity in response to water and light relative to soil-N appears to be associated with several adaptations. These favour the ability to tolerate and colonise harsh, nutrient-poor environments, as well as dealing with variability in light and water that exists when invading more productive sites. Species such as *I. tinctoria* that have wide environmental tolerances are likely to succeed in new habitats (Goodwin *et al.*, 1999) because of the advantages of high plasticity in heterogeneous environments (Rice & Bazzaz, 1989; Pattison *et al.*, 1998). More detailed characterization of the adaptive nature of plasticity in *I. tinctoria* and other invasive weeds, compared with the morphological and physiological plasticity of the native species they displace, should be a research priority, because this form of variation may allow certain species to colonize environmentally diverse sites without the lag time required for local adaptation (Sultan, 2004).

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