

# Plant–soil relationships of the invasive annual grass *Taeniatherum caput-medusae*: a reciprocal transplant experiment

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**Abstract** The annual grass *Taeniatherum caput-medusae* (L.) Nevski (medusahead) is highly invasive on rangelands of the western United States. It originates from the Mediterranean basin and was introduced accidentally into North America in the late 1800s. To increase our knowledge of the soil factors that may contribute to its invasiveness, we conducted a reciprocal transplant experiment. Seed sources used were from an invasive population in northeastern California, USA and from a native population in southern France. Four soils were used: two from northeastern California, invaded (USI) and non-invaded (USN) by *T. caput-medusae*; two from southern France, with *T. caput-medusae* occupied (FR+) and a similar soil presently unoccupied (FR–) by *T. caput-medusae*. Treatments were control and autoclaved. Seeds were sown in containers (six replicates) for each soil and treatment combination of the reciprocal planting matrix and allowed to grow for 60 days. Following harvest, above-ground and below-

ground tissue was dried and weight recorded separately. Above-ground tissue was analyzed for nutrient concentrations and various soil nutrient pools were quantified. Above-ground mass of *T. caput-medusae* was greatest in the USN soil and least in the FR- soil. Growth was affected by significant seed source × soil and treatment × soil interactions. French seed produced larger plants than did US seed when grown in the USN soil. For the USI soil, plant growth was significantly greater in the autoclaved soil than control. Availability of soil Fe, Mn, and ortho-P were significant predictors of plant growth as shown by stepwise regression. Moreover, the positive effect on growth of *T. caput-medusae*, due to autoclaving of USI soil, may be partially a consequence of elevated nutrient availability. Our data also suggests that US seed may have evolved a greater ability to uptake Mn from soil than French seed. Elevated soil nutrient availability in our western United States study area is a potential factor explaining the invasiveness of *T. caput-medusae*.

**Keywords** Invasion processes · Medusahead · Microorganisms · Soil fertility

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## Introduction

The annual grass *Taeniatherum caput-medusae* (L.) Nevski (medusahead) was first collected in the U.S. in Oregon in 1887. It spread rapidly in the 1930s (Young and Evans 1982) and has become a major

invasive species across millions of hectares on clay-rich, arid to semi-arid rangelands of the western United States (Young and Evans 1970; Dahl and Tisdale 1975). *Taeniatherum caput-medusae*, like the invasive annual grass *Bromus tectorum* L., increases the risk and scale of catastrophic wildfires (D'Antonio and Vitousek 1992). By creating a near continuous fuel on clay-textured soils occupied by widely spaced and low-statured *Artemisia* spp., *T. caput-medusae* brings the chance of wildfire into communities rarely affected by wildfire. This species is generally thought to be unpalatable to grazing animals (Lusk et al. 1961), but will be consumed when green (Miller et al. 1999). Once invaded, however, rangeland livestock carrying capacity can be reduced by 50% (Hironaka 1961). Herbicides for the control of *T. caput-medusae* are available, but are expensive and continual application is necessary for long-term suppression. Recently, a list of potential bio-control agents for *T. caput-medusae* has been identified for host specificity testing (Siegwart et al. 2003; Sforza et al. 2004; Widmer and Sforza 2004).

Myriad theories have been offered to explain why particular exotic plants become invasive in their new host environment (Mack et al. 2000). Mechanisms offered include: (1) some invasive plants are allelopathic and displace competing vegetation by exuding phytotoxins (Callaway and Ridenour 1999); (2) elevated atmospheric carbon dioxide confers greater advantage to faster growing weedy species (Ziska 2003); (3) increased atmospheric deposition of nitrogen increases competitive ability of some weeds (Fenn et al. 2003); (4) alteration of soil food webs may confer advantage to some weeds (Belnap and Phillips 2001); (5) some invasive plants engineer the soil to increase nutrient availability (Blank 2002); and (6) lack of negative feedback between an exotic plant and new soil microflora (Klironomos 2002). Unfortunately, it is nearly impossible to solely attribute any one of the above mechanisms, let alone other potentially important mechanisms, as the critical determinant in explaining plant invasiveness. Complicating causality is the reality that mechanisms are often site specific and influenced temporally via vegetation and soil microbial dynamics as affected by climate. Reciprocal transplant methodology is particularly useful to decipher factors that facilitate exotic plant invasion (Hinz and Schwarzlaender 2004).

Our purpose is to use reciprocal transplant methodology to elucidate soil and germplasm factors that have enabled *T. caput-medusae* to become invasive in its new host range. Our working null hypotheses are:

- (1) Growth of *T. caput-medusae* will be similar in native and introduced soils—there are no inherent soil differences, between its native and new host environment that explains why *T. caput-medusae* has become invasive in the western United States.
- (2) Growth of *T. caput-medusae* will be similar in control and autoclaved soil—autoclaving kills all organisms; thus, similar growth suggests lack of pathogenic organisms in its new host environment does not explain its invasiveness.
- (3) Seeds of *T. caput-medusae* from native and exotic populations will grow and uptake soil nutrients similarly in soil from native and introduced areas—its new host environment has not promoted evolutionary adaptations to become more invasive.

## Materials and methods

Four soils were chosen for the experiment; two from the United States (*T. caput-medusae* (L.) Nevski invaded (USI), *T. caput-medusae* non-invaded (USN)) and two from southern France where *T. caput-medusae* is considered a native (*T. caput-medusae* occupied (FR+), *T. caput-medusae* unoccupied (FR−)). Soils from the United States were collected from the volcanic tablelands of northeastern CA (Fig. 1) and are classified as fine, smectitic, mesic, aridic Haploxererts and fine, smectitic, mesic, xerertic Haplargids. These soils developed in lake-laid volcanic tephra and consequently have a high content of smectitic clays (40–60% by weight). Based on long-term climatic records at nearby sites, the average annual precipitation is 230 mm and the mean annual *T* is 6.8°C. The volcanic tablelands have had a long history of invasion by *T. caput-medusae*, facilitated by the movement of sheep (Young et al. 1972). In the US soil collection areas, however, invasion by *T. caput-medusae* began in the late 1980's (Personal observation, R.R. Blank). Native vegetation includes *Artemisia arbuscula* Nutt. ssp. *longicaulis* (Lahontan sagebrush), *A. tridentata* Nutt.



**Fig. 1** Top two photos are of the volcanic tablelands of northeastern California, USA. Top shows area not yet extensively invaded by *T. caput-medusae*. Dominating the landscape is low growing shrub sp. *Artemisia arbuscula* ssp. *longicaulis*. Center photo taken in Oct. of 2004 shows landscape invaded by *T. caput-medusae* where soils were collected. It is about 10 km northeast of the non-invaded area. The taller more yellowish grass is *Bromus tectorum*. Only small areas of native shrubs remain. Bottom photo is of a vineyard in southern France where *T. caput-medusae* is native and soil was collected from.

ssp. *tridentata* (Basin big sagebrush), *Chrysothamnus viscidiflorus* (Hook.) Nutt. (Green rabbitbrush), *Tetradymia glabrata* Torrey & A. Gray (Littleleaf horsebrush), *Poa sanbergii* J. Presl. (Sandberg bluegrass), *Pseudoroegneria spicata* (Pursh) A. Love

(bluebunch wheatgrass) and *Eriogonum* sp. Another invasive annual grass, *Bromus tectorum* L. (cheatgrass) is also present over the entire tablelands sometimes forming dense monocultures. In June 2004 we collected soil from 0 to 20 cm, which corresponds to the A and upper Bt horizons, from both *T. caput-medusae* invaded (elevation = 1,446 m; 40°30.35' N, 120°07.06' W) and nearby non-invaded areas (elevation = 1,432 m; 40°29.48' N, 120°06.26' W). We homogenized samples from multiple areas over 10 m apart—over 100 separate points were sampled. The soil was returned to the glasshouse and large cobbles and live plant material were removed. The soil was stored in closed containers until the soil from France arrived.

In May 2004, soil from France was collected similarly near the valley of Herault river in the northeastern part of Languedoc Roussillon region in the vicinity of Montpellier (Fig. 1). For Montpellier, mean annual *T* is 14.2°C and average annual precipitation is 700 mm. The selected sites are located in a typical Mediterranean landscape called “garrigues”. Native vegetation in the two selected sites is dominated by *Thymus vulgaris* L. (thyme), *Rosmarinus officinalis* L. (rosemary), and *Ficus carica* L. (fig tree). The *T. caput-medusae* occupied site is an abandoned vineyard near Murviel-lès-Montpellier (elevation = 110 m; 43°36.09' N, 03°45.11' E) and the non-occupied *T. caput-medusae* site is fallow land surrounded by *Olea europaea* L. (wild olive) and *Pinus* spp. (pine trees) near Prades-le-Lez (elevation = 120 m; 43°43.48' N, 03°52.02' E). Both soils developed in limestone marl. In southern France, *T. caput-medusae* is not invasive. It is listed as a weed in vineyards, without causing much crop damage.

When soils and seeds from France arrived in Reno in July 2004, all soils were split, one-half left as control, one-half autoclaved for 40 min at 121°C at 2 atmospheres pressure. For the experiment, small plastic containers were filled with 300 g soil for 6 replications of all soil by treatment by seed source combinations. The US and French seeds were collected the previous year from near the soil collection sites and stored prior to use. Seeds were sown on 7/9/04 and grown in a glasshouse in Reno, Nevada, USA (elevation = 1,351 m; 39°32.295' N, 119°48.377' W). We watered (deionized) daily as needed. Six replicate unplanted containers of each

soil  $\times$  treatment combination were watered similarly as soil control. Plant height, number of leaves, and other observations were recorded twice weekly. Plants were harvested on 9/7/04.

Plant tissue was dried for 48 h at 70°C, separated into above-ground and below-ground components, and weighed. Above-ground tissue was milled and a subsample ashed then solublized in 1 N HCl (Miller 1998). Iron, Mn, and Mg were quantified by atomic absorption spectroscopy; K by atomic emission spectroscopy; ortho-P by vanomolybdate chemistry using an autoanalyzer. Following harvest, soil in containers was homogenized and subsamples taken for moisture content and various nutrient analyses. The following attributes were measured: KCl-extractable  $\text{NO}_3^-$  and  $\text{NH}_4^+$ —readily available N (Bundy and Meisinger 1994), DTPA-extractable Fe, Mn, and Cu—measure of micronutrient availability (Lindsay and Norvell 1978), immiscibly displaced anions and cations—measure of solutes in the soil-solution (Mubarek and Olsen 1976), and alkaline phosphatase enzyme activity (Tabatabai 1994). DTPA-extractable micronutrients and cations in the soil-solution were quantified using atomic absorption spectroscopy. Anions in the soil-solution were quantified using ion chromatography. All data were converted to an oven-dry soil basis. On selected subsamples, we also determined resin-extractable ortho-P as follows: to 4 g of soil, 40 ml deionized  $\text{H}_2\text{O}$  was added, a commercial resin capsule (Unibest) was inserted and the mixture shaken for 16 h. The resin capsules were then pulled, washed with deionized water, dried and adsorbed ortho-P was released by shaking for 1 h in 1 N HCl. Ortho-P was quantified with an autoanalyzer using vanomolybdate chemistry (Lachat Corp.).

The experimental design was completely randomized, as throughout plant growth, pots were relocated on glasshouse benches. Categorical variables were SOIL (US invaded by *T. caput-medusae*, US non-invaded, French occupied by *T. caput-medusae*, French unoccupied), TREATMENT (control, autoclaved), and SEED SOURCE (US seed, French seed). We also included unplanted soils in the SEED categorical variable to test the effect of plant growth on soil nutrient availability. We used (6 replicates)  $\times$  (4 soils)  $\times$  (2 treatments)  $\times$  (2 seed sources + 1 unplanted) = 144 pots. Data were analyzed using PROC MIXED (SAS 1999). Some variables were log transformed to assure normality. Statistical compar-

ison among means used Tukey's honest significant difference test. All soil and plant nutrient concentration variables were used in stepwise regression with final above-ground plant mass.

## Results

### Plant growth and tissue nutrient concentrations

Growth of *T. caput-medusae* was affected by significant ( $P \leq 0.05$ ) soil  $\times$  treatment and soil  $\times$  seed source interactions (Table 1, Fig. 2). Above-ground and root mass were greatest for seeds sown in the US non-invaded soil (USN) and least for the French soil unoccupied by *T. caput-medusae* (FR-). For the US invaded soil (USI), above-ground mass increased significantly when grown in the autoclaved treatment compared to the control treatment. In autoclaved soil, root mass was significantly greater when grown in the French soil occupied by *T. caput-medusae* (FR+) and USI soil, and significantly less when grown in the USN soil compared to their respective controls. Seed source affected plant growth: for the USN soil, above-ground and root mass from French seed were significantly greater than those from US seed. Above-ground/root mass ratios were affected by a significant soil  $\times$  treatment interaction and a significant main effect due to seed source (Table 1, Fig. 2). For the FR+ soil, above-ground/root mass ratios were significantly greater in the control treatment compared to the autoclaved treatment. For the FR-, USI, and USN soils, above-ground/root mass ratios were significantly greater in the autoclaved treatment. The above-ground/root mass ratio from the French seed source was significantly less than that of the US seed source.

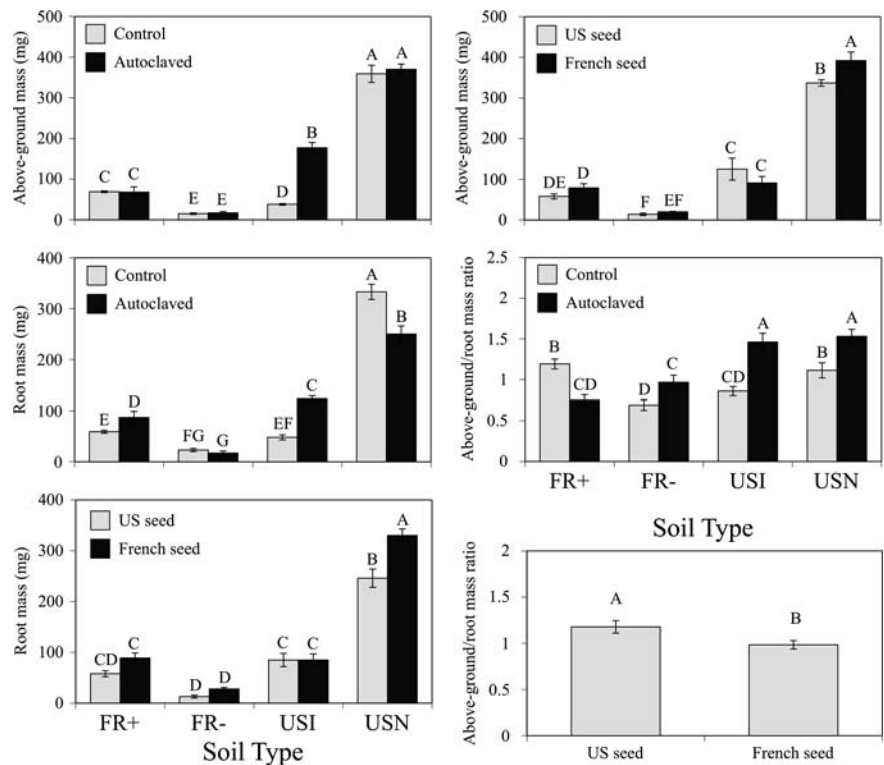
Above-ground plant Mg concentration was affected by a significant interaction among soil, seed source, and treatment (Table 1). Plants grown from French seed had significantly higher Mg concentrations than did plants grown from US seeds, but only for the control US invaded soil and the autoclaved US soils (Table 2). Overall, plants grown in US soil had significantly greater concentrations of Mg (pooled mean = 75  $\text{mmol kg}^{-1}$ ) than plants grown in French soil (pooled mean = 56  $\text{mmol kg}^{-1}$ ). Overall, plant Mg was not affected by soil treatment (control = 64  $\text{mmol kg}^{-1}$ ; autoclaved = 68  $\text{mmol kg}^{-1}$ ).

**Table 1** Results of ANOVA analyses<sup>a</sup>

Attribute	Soil	Seed	Soil*seed	Trt	Soil*Trt	Trt*seed	Soil*Trt*seed
Above-ground mass	<0.0001	0.0858	0.0002	0.0001	<0.0001	0.2308	0.0663
Root mass	<0.0001	<0.0001	<0.0001	0.3571	<0.0001	0.1824	0.3533
Shoot/root	0.3048	0.0302	0.0938	0.0261	0.0312	0.0699	0.0976
Plant Mg	<0.0001	<0.0001	0.0003	0.1126	0.0003	0.7856	0.0112
Plant K	<0.0001	0.0008	<0.0001	0.0002	0.0325	0.0006	<0.0001
Plant P	<0.0001	0.5345	0.0022	0.0012	0.0539	0.1925	0.5511
Plant Mn	<0.0001	<0.0001	0.0028	<0.0001	<0.0001	0.1718	0.0100
Soil DTPA Fe	<0.0001	<0.0001	0.0006	<0.0001	<0.0001	0.0081	0.0249
Soil DTPA Mn	<0.0001	<0.0001	0.1365	<0.0001	<0.0001	0.0190	0.1386
Soil DTPA Cu	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
Soil-solution ortho-P	<0.0001	<0.0001	0.0067	0.1710	0.0032	<0.0001	0.0017
Soil-solution Mg <sup>2+</sup>	<0.0001	0.0220	0.0010	0.0001	0.0041	0.0432	0.0033
Soil-solution K <sup>+</sup>	<0.0001	<0.0001	<0.0001	0.6868	0.0073	0.0164	0.0360
Soil-solution SO <sub>4</sub> <sup>2-</sup>	0.0233	<0.0001	<0.0001	<0.0001	0.1203	<0.0001	0.0053
Soil phosphatase	<0.0001	0.0003	0.6448	<0.0001	<0.0001	0.6779	0.6804
Soil KCl-NH <sub>4</sub> <sup>+</sup>	<0.0001	<0.0001	<0.0001	<0.0001	0.0019	<0.0001	<0.0001
Soil KCl-NO <sub>3</sub> <sup>-</sup>	<0.0001	<0.0001	<0.0001	0.6593	0.0013	0.3031	0.0007
Soil resin P	<0.0001	0.8452	0.1632	0.0084	0.0111	0.6296	0.6081

<sup>a</sup> Trt, treatment (control, autoclaved)

**Fig. 2** Above-ground mass, root mass, and shoot/root ratios of *T. caput-medusae* by soil, treatment, and seed source. For each individual panel, bars with different letters above are significantly different at the  $P < 0.05$  level



**Table 2** Above-ground plant tissue nutrient concentrations by soil, treatment, and seed source<sup>a</sup>

Soil	Control soil		Autoclaved soil	
	French seed	US seed	French seed	US seed
Plant Mg (mmol kg <sup>-1</sup> )				
FR+	63(13) <sup>C-G</sup>	53(6) <sup>F-H</sup>	49(8) <sup>GH</sup>	56(11) <sup>E-H</sup>
FR-	58(9) <sup>D-H</sup>	46(3) <sup>H</sup>	70(4) <sup>B-E</sup>	59(5) <sup>C-H</sup>
USI	76(7) <sup>A-D</sup>	55(8) <sup>E-H</sup>	90(12) <sup>A</sup>	62(8) <sup>D-G</sup>
USN	86(6) <sup>AB</sup>	80(5) <sup>A-C</sup>	88(6) <sup>A</sup>	67(8) <sup>C-F</sup>
Plant K (mmol kg <sup>-1</sup> )				
FR+	418(54) <sup>B</sup>	359(38) <sup>B-D</sup>	373(59) <sup>B-D</sup>	408(52) <sup>BC</sup>
FR-	354(32) <sup>B-E</sup>	360(3) <sup>B-D</sup>	519(57) <sup>A</sup>	287(68) <sup>D-E</sup>
USI	214(48) <sup>G</sup>	224(22) <sup>G</sup>	324(58) <sup>C-F</sup>	262(21) <sup>F-G</sup>
USN	218(17) <sup>G</sup>	267(24) <sup>E-G</sup>	256(18) <sup>FG</sup>	304(22) <sup>D-G</sup>
Plant P (mmol kg <sup>-1</sup> )				
FR+	44(5)	52(10)	33(13)	61(60)
FR-	28(14)	45(32)	23(9)	89(36)
USI	86(20)	69(4)	108(52)	100(40)
USN	80(9)	54(5)	128(29)	94(17)
Soil × seed source interaction			Treatment main effect	
Soil	French seed	US seed	Control	57(23) <sup>B</sup>
FR+	39(11) <sup>DE</sup>	57(41) <sup>CD</sup>	Autoclaved	81(49) <sup>A</sup>
FR-	26(11) <sup>E</sup>	51(34) <sup>C-E</sup>		
USI	98(40) <sup>AB</sup>	84(32) <sup>AB</sup>		
USN	104(32) <sup>A</sup>	74(24) <sup>BC</sup>		
Plant Mn (mmol kg <sup>-1</sup> )				
FR+	1.6(0.3) <sup>EF</sup>	2.1(0.2) <sup>D-F</sup>	2.0(0.6) <sup>D-F</sup>	3.4(0.8) <sup>DE</sup>
FR-	1.1(0.4) <sup>F</sup>	1.8(0.4) <sup>D-F</sup>	3.6(1.0) <sup>D</sup>	2.5(2.6) <sup>D-F</sup>
USI	2.3(0.4) <sup>D-F</sup>	3.5(0.4) <sup>D</sup>	8.1(0.9) <sup>B</sup>	10.6(2.0) <sup>A</sup>
USN	2.0(0.4) <sup>D-F</sup>	3.0(0.3) <sup>D-F</sup>	6.1(1.2) <sup>C</sup>	8.8(1.0) <sup>AB</sup>

<sup>a</sup> FR+, French soil collection site occupied by *T. caput-medusae*; FR-, French soil collection site unoccupied by *T. caput-medusae*. USI and USN refer to invaded and non-invaded United States sites, respectively. Standard deviations are presented in parentheses. For each attribute, means followed by different superscripted letters are significantly different at the  $P \leq 0.05$  level

A significant soil × treatment by seed source interaction affected above-ground plant concentration of K (Table 1). Overall, K was significantly greater when plants were grown in the French soil (pooled mean = 398 mmol kg<sup>-1</sup>) compared to the US soils (pooled mean = 260 mmol kg<sup>-1</sup>) (Table 2). Plant growth in autoclaved soil had slightly higher K concentration (pooled mean = 347 mmol kg<sup>-1</sup>) than plants grown in control soil (pooled mean = 303 mmol kg<sup>-1</sup>). Seed source was a significant factor in plant K concentration only for the FR- soil and only for the autoclave treatment (pooled mean French seed = 519 mmol kg<sup>-1</sup>; pooled mean US seed = 287 mmol kg<sup>-1</sup>).

Plant P concentration was influenced by a significant soil × seed source interaction and a significant treatment main effect (Table 1). Plants grown in US soils had over double the P concentration (pooled mean = 90 mmol kg<sup>-1</sup>) than plants grown in French soils (pooled mean = 43 mmol kg<sup>-1</sup>) (Table 2). Plants from French seed had significantly greater leaf tissue P than plants from US seed, but only when grown in USN soil. When grown in French soils, however, plants from French seed had less leaf tissue P than plants from US seed. Plants grown in autoclaved soil had significantly greater above-ground P concentrations than plants grown in control soil.

A significant soil  $\times$  treatment  $\times$  seed source interaction affected plant Mn concentration (Table 1). Overall, plants grown in autoclave treated soil had significantly more tissue Mn compared to plants grown in controls (Table 2). The effect was most pronounced for US soils (autoclaved = 8.4 mmol kg<sup>-1</sup>; control = 2.7 mmol kg<sup>-1</sup>), but also significant for French soils (autoclaved = 2.8 mmol kg<sup>-1</sup>; control = 1.7 mmol kg<sup>-1</sup>). Plants grown in US soil had over double the tissue Mn (pooled mean = 5.6 mmol kg<sup>-1</sup>) than plants grown in French soil (pooled mean = 2.2 mmol kg<sup>-1</sup>). Seed source mattered when grown in the US soils; plants from French seed had significantly less tissue Mn (pooled mean = 4.7 mmol kg<sup>-1</sup>) than plants grown from US seed (pooled mean = 6.5 mmol kg<sup>-1</sup>).

#### Soil attributes

Following plant harvest, availability of soil Fe and Cu were significantly affected by soil type  $\times$  treatment  $\times$  seed source interactions (the statistical model used evaluated the effect of unplanted controls) and treatment  $\times$  seed source and soil  $\times$  treatment interactions influenced Mn availability (Table 1). Relative to the other soils, the US invaded soil had inherently higher Fe availability, which declined significantly in the autoclaved treatment (Table 3). Plant growth significantly increased Fe availability, compared to the unplanted soil, but only for the control treatment. Seed source did not influence Fe availability. The French soils had significantly greater Cu availability than the US soils (Table 3). Relative to unplanted pots, both US and French seeds enhanced Cu availability for the control treatment. For the autoclaved treatment, only the French seeds enhanced Cu availability. Overall, the US soils had significantly greater Mn availability (pooled mean = 535  $\mu\text{mol kg}^{-1}$ ) than the French soils (pooled mean = 72  $\mu\text{mol kg}^{-1}$ ) (Table 3). Relative to the control treatment, autoclaving significantly increased the availability of Mn for US soils, but did not significantly affect Mn availability for the French soils. Although Mn availability increased with autoclaving in unplanted soil, both French and US seed sources resulted in a very large increase in Mn availability relative to controls.

Nutrients in the soil-solution were affected by a significant interaction among soil, treatment, and seed source/planting regime (Tables 1 and 4). Of the

soil-solution nutrients measured, only ortho-P was significantly affected by seed source. For the autoclaved US invaded soil, ortho-P was significantly less for soils sown with French seed compared to the corresponding soils sown with US seed. As might be expected, plant growth generally reduced soil-solution nutrient concentrations relative to the unplanted control, but not universally so. For example, post-harvest soil-solution ortho-P actually increased relative to that in unplanted pots for the control US non-invaded soil. Similarly, static or increasing soil-solution nutrients, compared to unplanted pots, occurred for Mg<sup>2+</sup> (US invaded soil) and SO<sub>4</sub><sup>2-</sup> (French control soil occupied by *T. caput-medusae*). Soil origin had a large effect on post-harvest soil-solution nutrient concentrations. Compared to the French soils, the US soils had far greater ortho-P (pooled means = 25.6 vs. 1.1  $\mu\text{mol l}^{-1}$ ), Mg<sup>2+</sup> (pooled means = 197 vs. 49  $\mu\text{mol l}^{-1}$ ) and K<sup>+</sup> (pooled means = 168 vs. 55  $\mu\text{mol l}^{-1}$ ). Compared to the control, soil autoclaving had relatively minor effects on soil-solution ortho-P and K<sup>+</sup>. For the French seed source growing in US invaded soil, post-harvest ortho-P was significantly less in the autoclaved soil versus the control soil. For the US non-invaded soil in unplanted pots, autoclaving significantly reduced soil-solution K<sup>+</sup> relative the control treatment. Soil autoclaving had a more generalized effect on soil-solution Mg<sup>2+</sup> and SO<sub>4</sub><sup>2-</sup>. Soil-solution Mg<sup>2+</sup> was significantly greater for the control US soil (pooled mean = 311  $\mu\text{mol l}^{-1}$ ) than the corresponding autoclaved soils (pooled mean = 162  $\mu\text{mol l}^{-1}$ ). Unplanted control soil had significantly less soil-solution SO<sub>4</sub><sup>2-</sup> (pooled mean = 56  $\mu\text{mol l}^{-1}$ ) than unplanted autoclaved soil (pooled mean = 186  $\mu\text{mol l}^{-1}$ ).

Phosphatase activity was affected by a significant soil  $\times$  treatment interaction and a significant main effect due to seeding regime (Table 1). Autoclaving significantly reduced phosphatase activity, but only for the USN soil (Table 5). For the control treatment, phosphatase activity was greatest for the US non-invaded soil. Plant growth significantly increased phosphatase activity relative to unplanted pots.

An interaction among soil, treatment, and seed affected concentrations of KCl-extractable NH<sub>4</sub><sup>+</sup> and NO<sub>3</sub><sup>-</sup> (Table 1). Compared to soil in unplanted pots, growth of *T. caput-medusae* had variable effects on KCl-extractable NH<sub>4</sub><sup>+</sup> and NO<sub>3</sub><sup>-</sup> (Table 5). In the control treatment, planting did not affect NH<sub>4</sub><sup>+</sup>, but

**Table 3** DTPA-extractable Fe, Mn, and Cu, by soil, treatment, and seed<sup>a</sup>

Soil	Control soil			Autoclaved soil		
	Unplanted	French seed	US seed	Unplanted	French seed	US seed
DTPA-Fe ( $\mu\text{mol kg}^{-1}$ )						
FR+	46(5) <sup>E-I</sup>	73(5) <sup>C-F</sup>	76(11) <sup>C-E</sup>	52(7) <sup>E-I</sup>	65(11) <sup>D-H</sup>	56(16) <sup>E-I</sup>
FR-	36(7) <sup>G-I</sup>	53(11) <sup>E-I</sup>	52(14) <sup>E-I</sup>	41(2) <sup>E-I</sup>	44(7) <sup>E-I</sup>	40(11) <sup>F-I</sup>
USI	28(3) <sup>HI</sup>	43(22) <sup>E-I</sup>	64(20) <sup>D-G</sup>	26(4) <sup>I</sup>	54(16) <sup>E-I</sup>	46(8) <sup>E-I</sup>
USN	131(19) <sup>B</sup>	219(38) <sup>A</sup>	223(33) <sup>E-H</sup>	60(8) <sup>E-H</sup>	97(15) <sup>CD</sup>	105(8) <sup>BC</sup>
DTPA-Mn ( $\mu\text{mol kg}^{-1}$ )						
FR+	16(3)	48(8)	47(8)	51(11)	72(27)	39(12)
FR-	35(23)	61(14)	62(34)	86(31)	95(44)	72(15)
USI	70(36)	159(57)	161(66)	481(146)	932(476)	1212(91)
USN	183(19)	420(150)	404(132)	441(60)	911(134)	986(92)
Soil $\times$ treatment interaction				Seeding regime $\times$ treatment interaction		
Soil	Control	Autoclaved		Seeding regime	Control	Autoclaved
FR+	37(16) <sup>C</sup>	54(20) <sup>C</sup>		Unplanted	76(70) <sup>B</sup>	265(215) <sup>B</sup>
FR-	52(27) <sup>C</sup>	84(31) <sup>C</sup>		French seed	177(172) <sup>B</sup>	563(493) <sup>A</sup>
USI	130(67) <sup>C</sup>	875(414) <sup>A</sup>		US seed	163(157) <sup>B</sup>	653(539) <sup>A</sup>
USN	332(156) <sup>B</sup>	780(266) <sup>A</sup>				
DTPA-Cu ( $\mu\text{mol kg}^{-1}$ )						
FR+	112(11) <sup>BC</sup>	186(6) <sup>A</sup>	181(20) <sup>A</sup>	102(6) <sup>C</sup>	131(25) <sup>B</sup>	106(11) <sup>C</sup>
FR-	35(6) <sup>D</sup>	46(6) <sup>D</sup>	45(12) <sup>D</sup>	34(4) <sup>D</sup>	40(8) <sup>D</sup>	41(8) <sup>D</sup>
USI	9(1) <sup>E</sup>	13(6) <sup>E</sup>	16(5) <sup>E</sup>	8(1) <sup>E</sup>	16(4) <sup>E</sup>	16(2) <sup>E</sup>
USN	10(1) <sup>E</sup>	13(4) <sup>E</sup>	15(3) <sup>E</sup>	8(1) <sup>E</sup>	13(3) <sup>E</sup>	14(2) <sup>E</sup>

<sup>a</sup> FR+, French soil collection site occupied by *T. caput-medusae*; FR-, French soil collection site unoccupied by *T. caput-medusae*. USI and USN refer to invaded and non-invaded United States sites, respectively. Standard deviations are presented in parentheses. For each attribute, means followed by different superscripted letters are significantly different at the  $P \leq 0.05$  level

significantly reduced  $\text{NO}_3^-$ , for the French soils and the US non-invaded soil. For the autoclave treatment, plant growth significantly reduced  $\text{NH}_4^+$  for the French unoccupied soil and the US soils, but only reduced  $\text{NO}_3^-$  for the French soil occupied by *T. caput-medusae*. Overall, autoclaving led to higher post-harvest KCl-extractable  $\text{NH}_4^+$  (pooled mean =  $1.07 \mu\text{mol kg}^{-1}$ ) compared to the control treatment (pooled mean =  $0.66 \mu\text{mol kg}^{-1}$ ). In general, seed source did not affect KCl-extractable  $\text{NH}_4^+$  or  $\text{NO}_3^-$ ; for the autoclaved French soil unoccupied by *T. caput-medusae*, soil sown with French seed had significantly higher  $\text{NH}_4^+$  than soil sown with US seed. The French soil unoccupied by *T. caput-medusae* had the greatest total KCl extractable N (pooled mean =  $2.27 \mu\text{mol kg}^{-1}$ ), followed by the

French soil occupied by *T. caput-medusae* (pooled mean =  $1.50 \mu\text{mol kg}^{-1}$ ), the US non-invaded soil (pooled mean =  $1.43 \mu\text{mol kg}^{-1}$ ), and the US invaded soil (pooled mean =  $1.17 \mu\text{mol kg}^{-1}$ ).

Resin extractable ortho-P was affected by a significant soil  $\times$  treatment interaction (Table 1). The US invaded soil had over 7 times more resin-extractable ortho-P than the other soils (Table 6). For the US invaded soil, resin-extractable ortho-P was significantly less in the control treatment than the autoclaved soil.

When all data were included in a stepwise analysis to predict what variables explained the growth of *T. caput-medusae*, soil variables most strongly predictive were DTPA-extractable Fe, DTPA-extractable Mn, and ortho-P in the soil-solution (Table 7).

**Table 4** Soil-solution ortho-P, Mg<sup>2+</sup>, K<sup>+</sup>, and SO<sub>4</sub><sup>2-</sup> by soil, treatment, and seed<sup>a</sup>

Soil	Control soil			Autoclaved soil		
	Unplanted	French seed	US seed	Unplanted	French seed	US seed
Soil-solution ortho-P ( $\mu\text{mol l}^{-1}$ )						
FR+	2.6(2.2) <sup>F</sup>	2.4(0.6) <sup>F</sup>	1.9(1.1) <sup>F</sup>	3.3(2.0) <sup>F</sup>	1.0(0.8) <sup>F</sup>	1.0(0.5) <sup>F</sup>
FR–	4.5(3.8) <sup>F</sup>	0.6(0.5) <sup>F</sup>	0.4(0.6) <sup>F</sup>	2.2(2.9) <sup>F</sup>	0.5(0.4) <sup>F</sup>	0.5(0.3) <sup>F</sup>
USI	31.7(5.1) <sup>A–C</sup>	27.5(9.3) <sup>B–D</sup>	23.1(7.9) <sup>C–E</sup>	34.2(2.9) <sup>AB</sup>	14.8(7.6) <sup>E</sup>	21.3(3.3) <sup>DE</sup>
USN	20.8(1.4) <sup>DE</sup>	30.4(6.8) <sup>A–D</sup>	26.6(3.6) <sup>B–D</sup>	38.5(6.5) <sup>A</sup>	22.9(4.2) <sup>C–E</sup>	32.9(3.5) <sup>AB</sup>
Soil-solution Mg <sup>2+</sup> ( $\mu\text{mol l}^{-1}$ )						
FR+	66(15) <sup>BC</sup>	58(18) <sup>C</sup>	53(14) <sup>C</sup>	63(20) <sup>C</sup>	41(6) <sup>C</sup>	51(10) <sup>BC</sup>
FR–	60(8) <sup>C</sup>	51(9) <sup>C</sup>	44(12) <sup>C</sup>	51(23) <sup>C</sup>	43(16) <sup>C</sup>	46(9) <sup>C</sup>
USI	237(229) <sup>BC</sup>	298(308) <sup>B</sup>	235(200) <sup>BC</sup>	120(46) <sup>BC</sup>	155(64) <sup>BC</sup>	129(18) <sup>BC</sup>
USN	616(192) <sup>A</sup>	239(70) <sup>BC</sup>	183(106) <sup>BC</sup>	193(29) <sup>BC</sup>	196(96) <sup>BC</sup>	170(76) <sup>BC</sup>
Soil-solution K <sup>+</sup> ( $\mu\text{mol l}^{-1}$ )						
FR+	58(3) <sup>EF</sup>	66(16) <sup>EF</sup>	60(15) <sup>EF</sup>	71(8) <sup>EF</sup>	48(11) <sup>D–H</sup>	54(40) <sup>EF</sup>
FR–	49(5) <sup>EF</sup>	59(28) <sup>EF</sup>	36(9) <sup>F</sup>	79(27) <sup>D–F</sup>	59(5) <sup>EF</sup>	53(16) <sup>EF</sup>
USI	185(99) <sup>CD</sup>	138(48) <sup>C–F</sup>	143(31) <sup>C–F</sup>	187(70) <sup>CD</sup>	150(40) <sup>C–E</sup>	144(16) <sup>C–E</sup>
USN	499(117) <sup>A</sup>	196(67) <sup>C</sup>	180(55) <sup>CD</sup>	309(28) <sup>B</sup>	196(45) <sup>C</sup>	190(59) <sup>C</sup>
Soil-solution SO <sub>4</sub> <sup>2-</sup> ( $\mu\text{mol l}^{-1}$ )						
FR+	59(14) <sup>D–F</sup>	66(52) <sup>D–F</sup>	95(76) <sup>C–E</sup>	174(57) <sup>BC</sup>	101(35) <sup>C–E</sup>	110(92) <sup>B–D</sup>
FR–	51(18) <sup>D–F</sup>	46(3) <sup>D–F</sup>	42(10) <sup>D–F</sup>	110(36) <sup>B–D</sup>	91(14) <sup>C–F</sup>	99(56) <sup>B–F</sup>
USI	37(15) <sup>D–F</sup>	31(17) <sup>D–F</sup>	22(7) <sup>D–F</sup>	193(63) <sup>B</sup>	82(25) <sup>D–F</sup>	94(22) <sup>C–F</sup>
USN	80(17) <sup>D–F</sup>	9(3) <sup>EF</sup>	11(3) <sup>F</sup>	282(71) <sup>A</sup>	48(19) <sup>D–F</sup>	32(19) <sup>D–F</sup>

<sup>a</sup> FR+, French soil collection site occupied by *T. caput-medusae*; FR–, French soil collection site unoccupied by *T. caput-medusae*. USI and USN refer to invaded and non-invaded United States sites, respectively. Standard deviations are presented in parentheses. For each attribute, means followed by different superscripted letters are significantly different at the  $P \leq 0.05$  level

## Discussion

Growth of *T. caput-medusae* was significantly greater in the USN soil and the autoclaved USI soil compared to both French soils tested (native), which refutes hypothesis 1, growth of *T. caput-medusae* will be similar in native and introduced soils. Invasive plants are often larger and more successful in their introduced environments than their native environments (Elton 1958; Crawley 1987; Willis and Blossey 1999; Thebaud and Simberloff 2001; Buckley et al. 2003). Multiple theories have been evoked to explain this phenomenon and causality is linked to myriad factors that vary in relative importance depending on the characteristics of the invasive plant and plant–soil relationships in its new host environment (Elton 1958; Herbold and Moyle 1986; Crawley 1987; Callaway and Aschehoug 2000; Davis et al. 2000; Mack et al. 2000; Bais et al. 2003; Beckstead and

Parker 2003; Hierro and Callaway 2003; Mitchell and Power 2003; Callaway et al. 2004).

Reciprocal transplants are potentially a robust experimental design to determine underlying mechanisms of successful invasive plants (Hierro et al. 2005). Our reciprocal transplant experiment offers compelling evidence that elevated nutrient availability in the United States study area is potentially a partial explanation of why *T. caput-medusae* is invasive. Stepwise regression indicates that DTPA-extractable Fe and Mn and ortho-P in the soil-solution explains over 80% of the variation in above-ground mass and these nutrients are more available in the US soils we examined compared to the French soils. Invasion success of plants is often correlated with high soil fertility levels (Burke and Grime 1996) and N and P availability are of paramount importance (Brooks 2003; Green and Galatowitsch 2001; Monaco et al. 2003; Suding et al. 2004). Indeed, by

**Table 5** Alkaline phosphatase enzyme activities and KCl-extractable  $\text{NH}_4^+$  and  $\text{NO}_3^-$  by soil, treatment, and seed<sup>a</sup>

Soil	Control soil			Autoclaved soil		
	Unplanted	French seed	US seed	Unplanted	French seed	US seed
Phosphatase activity ( $\mu\text{mol g}^{-1} \text{h}^{-1}$ )						
FR+	0.39(0.04)	0.58(0.55)	0.84(0.61)	0.10(0.11)	0.19(0.18)	0.41(0.35)
FR–	0.30(0.04)	0.45(0.45)	0.57(0.27)	0.05(0.11)	0.38(0.23)	0.34(0.05)
USI	0.64(0.06)	1.12(0.69)	0.76(0.60)	0.34(0.05)	0.72(0.50)	0.85(0.36)
USN	1.73(0.02)	1.71(0.09)	1.80(0.27)	0.31(0.17)	0.52(0.34)	0.65(0.30)
Soil $\times$ treatment interaction			Seeding regime main effect			
Soil	Control	Autoclaved	Unplanted	0.48(0.51) <sup>C</sup>		
FR+	0.59(0.47) <sup>BC</sup>	0.23(0.26) <sup>C</sup>	French seed	0.76(0.61) <sup>A</sup>		
FR–	0.43(0.26) <sup>BC</sup>	0.25(0.21) <sup>C</sup>	US seed	0.70(0.50) <sup>AB</sup>		
USI	0.83(0.52) <sup>B</sup>	0.63(0.40) <sup>B</sup>				
USN	1.73(0.10) <sup>A</sup>	0.49(0.29) <sup>BC</sup>				
KCl- $\text{NH}_4^+$ ( $\text{mmol kg}^{-1}$ )						
FR+	0.33(0.19) <sup>D</sup>	0.66(0.03) <sup>D</sup>	0.66(0.12) <sup>D</sup>	1.07(1.0) <sup>CD</sup>	0.86(0.09) <sup>D</sup>	0.61(0.10) <sup>D</sup>
FR–	0.66(0.66) <sup>D</sup>	0.76(0.12) <sup>D</sup>	0.66(0.17) <sup>D</sup>	2.56(0.43) <sup>A</sup>	1.67(0.64) <sup>BC</sup>	0.41(0.20) <sup>D</sup>
USI	0.61(0.12) <sup>D</sup>	0.57(0.23) <sup>D</sup>	0.54(0.16) <sup>D</sup>	2.06(0.31) <sup>ABC</sup>	0.49(0.10) <sup>D</sup>	0.58(0.05) <sup>D</sup>
USN	0.41(0.23) <sup>D</sup>	0.69(0.26) <sup>D</sup>	0.69(0.20) <sup>D</sup>	2.34(0.01) <sup>AB</sup>	0.74(0.15) <sup>D</sup>	0.76(0.12) <sup>D</sup>
KCl- $\text{NO}_3^-$ ( $\text{mmol kg}^{-1}$ )						
FR+	1.28(0.26) <sup>B-D</sup>	0.57(0.20) <sup>D-G</sup>	0.69(0.35) <sup>D-G</sup>	2.37(2.05) <sup>AB</sup>	0.58(0.06) <sup>D-G</sup>	0.85(0.33) <sup>C-G</sup>
FR–	1.54(0.78) <sup>A-C</sup>	1.00(0.15) <sup>C-G</sup>	1.13(0.17) <sup>B-E</sup>	1.04(0.49) <sup>B-G</sup>	1.06(0.58) <sup>C-F</sup>	1.36(0.63) <sup>A-D</sup>
USI	0.60(0.05) <sup>D-G</sup>	0.45(0.13) <sup>E-G</sup>	0.48(0.12) <sup>E-G</sup>	0.57(0.11) <sup>D-G</sup>	0.34(0.07) <sup>G</sup>	0.38(0.03) <sup>E-G</sup>
USN	2.18(0.12) <sup>A</sup>	0.43(0.16) <sup>E-G</sup>	0.40(0.10) <sup>E-G</sup>	0.93(0.12) <sup>C-G</sup>	0.45(0.09) <sup>E-G</sup>	0.40(0.09) <sup>E-G</sup>

<sup>a</sup> FR+, French soil collection site occupied by *T. caput-medusae*; FR–, French soil collection site unoccupied by *T. caput-medusae*. USI and USN refer to invaded and non-invaded United States sites, respectively. Standard deviations are presented in parentheses. For each attribute, means followed by different superscripted letters are significantly different at the  $P \leq 0.05$  level

**Table 6** Resin-extractable ortho-P by soil, treatment, and seed source<sup>a</sup>

Soil	Control soil		Autoclaved soil	
	French seed	US seed	French seed	US seed
Resin-extractable ortho-P ( $\text{mmol kg}^{-1}$ )				
FR+	0.61(0.46)	0.54(0.20)	0.58(0.17)	0.91(0.25)
FR–	0.14(0.05)	0.29(0.29)	0.16(0.01)	0.17(0.01)
USI	7.66(1.80)	7.76(1.49)	8.04(0.76)	9.00(1.22)
USN	1.03(0.73)	0.63(0.28)	2.24(0.49)	1.49(0.97)
Soil $\times$ treatment interaction				
Soil	Control	Autoclaved		
FR+	0.58(0.32) <sup>D</sup>	0.76(0.27) <sup>D</sup>		
FR–	0.22(0.21) <sup>D</sup>	0.18(0.02) <sup>D</sup>		
USI	7.79(1.58) <sup>B</sup>	8.59(1.09) <sup>A</sup>		
USN	0.84(0.57) <sup>D</sup>	1.85(0.86) <sup>C</sup>		

<sup>a</sup> FR+, French soil collection site occupied by *T. caput-medusae*; FR–, French soil collection site unoccupied by *T. caput-medusae*. USI and USN refer to invaded and non-invaded United States sites, respectively. Standard deviations are presented in parentheses. For each attribute, means followed by different superscripted letters are significantly different at the  $P \leq 0.05$  level

**Table 7** Results of stepwise regression relating above-ground plant growth with measured soil nutrient pools

Step	Variable	$R^2$	$F$	$P$
1	DTPA Fe	0.48	48.82	<0.0001
2	DTPA Mn	0.80	27.42	<0.0001
3	Soil-solution ortho-P	0.81	6.59	0.0131

reducing soil N availability with the addition of the labile C source such as sucrose and microbial immobilization, one can extirpate *T. caput-medusae* and favor native perennials (Young et al. 1998). We are unaware, however, of any literature relating invasive success with soil availability of Fe or Mn.

Depending on soil type, autoclaving significantly affected above-ground mass, root mass, and above-ground/root mass ratios, relative to respective controls. These findings force rejection of hypothesis 2, growth of *T. caput-medusae* will be similar in control and autoclaved soil. The significant decrease in root mass exhibited for the autoclaved USN soil could be due to phytotoxins developed during heat-sterilization (Rovira and Bowen 1966). An autoclaved-caused increase in above-ground mass of *T. caput-medusae* for the USI soil and root mass for the FR+ and USI soils, at a first approximation, suggests pathogenic factors may have been reduced through sterilization. This suggestion must be tempered by the finding that autoclaving of the USI soil also significantly increased availability of DTPA-Mn, resin-extractable P, soil-solution  $\text{SO}_4^{-2}$ , and KCl-extractable  $\text{NH}_4^+$  and these increases may also have contributed to increased plant growth. Autoclaving soil can increase nutrient availability (Campillo et al. 2001; Anderson and Magdoff 2005). One conclusion that can be drawn from our data is that autoclaving soil may alter nutrient availability to such an extent as to obfuscate processes related to biological activity.

In measurements of plant growth and plant nutrient uptake, the US and French seed sources performed differently, thus forcing rejection of hypothesis 3. In USN soil, plants from US seed produced significantly less above-ground and root biomass than plants from French seed. This response is perplexing; one might suspect that US seed grown in its own adapted soil might perform better than French seed. Seed source had a significant effect of nutrient uptake of P and Mn. Plants from the French seed source were able to uptake significantly more P

from the USN soil than the US seed source. We hypothesize that, because *T. caput-medusae* from France evolved in soil with lower P availability than the US soils studied, it may have more efficient uptake mechanisms for P than the US seed source. For the control treatment, no matter the soil type, plants grown from US seed had greater Mn concentration than plants from French seed. Moreover, for the USI and USN soils, Mn concentration was significantly greater in plants from US seed than plants from French seed. These data, combined with the finding that autoclaving US soils greatly increased Mn availability, suggest that *T. caput-medusae*, in the crucible of its new environment, may have evolved a greater ability to uptake Mn. Studies have shown that invasive species can evolve rapidly (Reznick and Ghalambor 2001; Maron et al. 2004).

Overall, the reciprocal transplant design provided data, which suggests that elevated soil nutrient availability in soil beneath invasive populations of our western United States may *partially* explain why *T. caput-medusae* has become invasive. A more robust reciprocal transplant design encompassing multiple native sites throughout Eurasia and invasive populations in the western United States would be requisite to definitely determine what factors and their ratio of importance affects the invasiveness of *T. caput-medusae*.

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