

Medusahead: Available Soil N and Microbial Communities in Native and Invasive Soils

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Abstract—To better understand why medusahead (*Taeniatherum caput-medusae*) is invasive, we quantified soil N availability and characterized soil microbial communities between native and invasive populations. No consistent differences in soil N mineralization potentials were noted between native medusahead sites in Spain, Turkey, France, and Greece and two invaded sites on the volcanic tablelands of northeastern, California, U.S.A. The proportional makeup of the microbial community, as quantified by phospholipid fatty acid analysis (PLFA), did not differ appreciably between a native site in southern France and one site on the tablelands of northeastern, California sites. Microbial markers indicative of growth phase suggest soils of invasive populations have higher turnover rates than native soil. No useable DNA could be extracted from the native medusahead soil in southern France using bacterial S16 ribosomal DNA. Tablelands soil contained distinct bacterial DNA bands for bacteria that utilize methane and methanol, anaerobically reduce sulfur, catabolize aromatics, for symbiotic relationships with root nodules of legumes. In summary, there is no definitive evidence in the studies carried out to indicate why medusahead is invasive in the Western United States.

Introduction

Why do some exotic plants become invasive? The question has been and is being vigorously researched. Myriad mechanisms have been proposed whereby an exotic plant can gain a competitive advantage over native species. An influential hypothesis posits that exotic species, set free from native biological enemies, from microbes through arthropods, now flourish in their new environment (Keane and Crawley 2002; Torchin and others 2003). This hypothesis is the underpinning for introducing biological control agents from the exotic's home of origin. It has become clear, however, that the ultimate answer to how some exotic species become invasive is incredibly complex. Some invasive plants are allelopathic, capable of exuding powerful phytotoxins,

which displace competing native vegetation (Bais and others 2003). Other invasive weeds alter or “engineer” the soil to increase nutrient availability or are able to access a previously under-utilized nutrient niche and thereby increase their competitive profile (Blank 2002). Soil food webs can be changed by exotic plants to gain a competitive advantage (Belnap and Phillips 2001). Confounding explanations of why some exotic plants become invasive is the finding that anthropogenic elevated atmospheric carbon dioxide confers greater advantage to faster growing weedy species many of which are exotic (Ziska 2003).

A robust factor that explains invasive success is soil nutrient availability, particularly availability of N and P (Milbau and Nijs 2004). Indeed, increased atmospheric deposition of nitrogen increases competitive ability of some weeds (Fenn and others 2003). Two of the dominant invasive annual grasses in the Intermountain West, cheatgrass (*Bromus tectorum*) and medusahead (*Taeniatherum caput-medusae*) greatly increase their competitive stature upon soil additions of N (Paschke and others 2000, Monaco and others 2003). The present study on medusahead is linked to a larger program on invasion processes and biological control using natural enemies from Eurasia (Widmer and Sforza 2003, Sforza and others 2004).

Our purpose here was to compare soil N availability and the soil microbial community in native and exotic soils occupied by medusahead. Our working hypotheses were: 1) soil N availability is similar in native and exotic soils and 2) the soil microbial community is similar in native and exotic soils.

Materials and Methods

Hypothesis testing was accomplished by collecting soil, 0 to 20 cm, directly beneath native and exotic populations of medusahead (see fig. 1 for photographs of native and exotic landscapes). We collected native soil from Spain (3 sites), Turkey (4), Greece (2), and France (4) with 4 replications at each site. These soils were contrasted with exotic populations in two locations of northeastern California (fig. 1). The California sites were near Alturas and on the volcanic tablelands just north of the Honey Lake Valley. The European sites were in Andalusia, near Huelva, Cordoba, and Granada for Spain, in Central and Eastern Anatolia, near Göreme, Erzurum, Gaziantep, and Erzinçan for Turkey, in Northern Greece, near Thessaloniki, and in Southern France, near Montpellier. On the less than 2 mm soil fraction, available soil N was quantified using a 30 day aerobic incubation procedure (Hart and others 1994). In another experiment, freshly-collected soil (two replicates) from southern France

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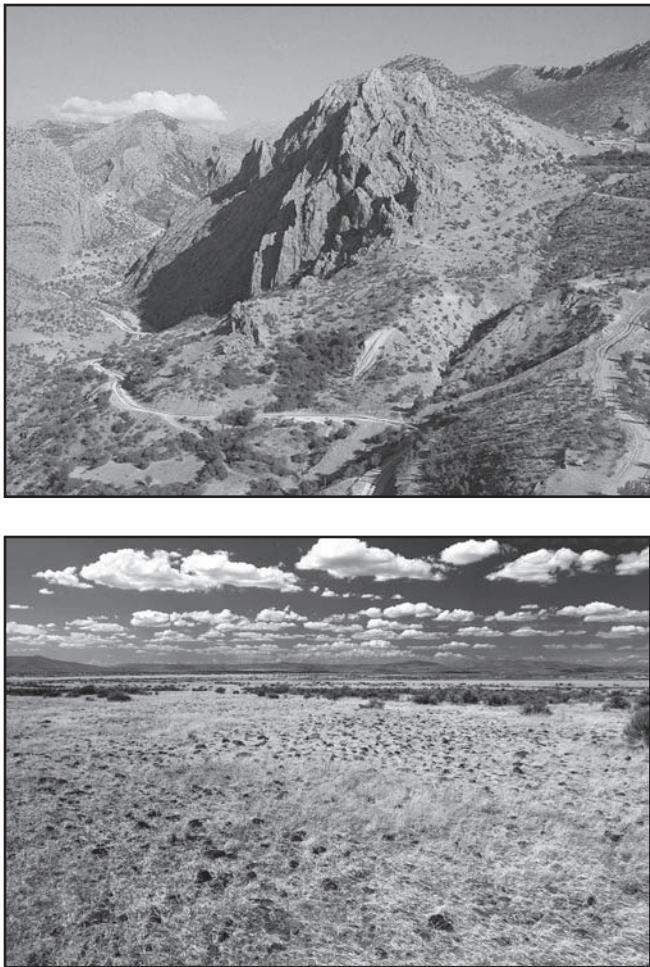


Figure 1—Top photo is from a native medusahead area in Nemrut national park in southwestern Turkey. Bottom photo is from a medusahead-invaded area in the volcanic tablelands of northeastern, California where the native low sage community has largely been extirpated.

(native) and from the volcanic tablelands of northeastern California (invasive) were sent in iced coolers to a commercial laboratory for phospholipid fatty acid analysis (PLFA) (Zelles and Bai 1993) and S-16 ribosomal DNA analysis using denaturing gradient gel electrophoresis (DGGE) (Stephen and others 1999).

Results and Discussion

Nitrogen Availability

There is no consistent trend in soil N availability after 30 day aerobic incubation between native and exotic populations of medusahead (fig. 2). Nitrogen availability is a robust predictor of ecosystem invasibility of exotic plant species (Huenneke and others 1990). Based on this relationship, one would suspect that the soil from Spain and three of the sites in Turkey would be at similar risk of invasion as the

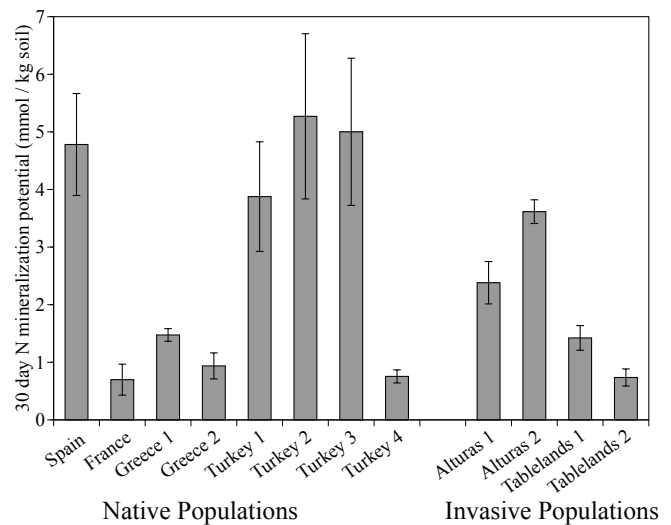


Figure 2—Total available N ($\text{NH}_4^+ + \text{NO}_3^-$) in soil following 30 day aerobic incubation.

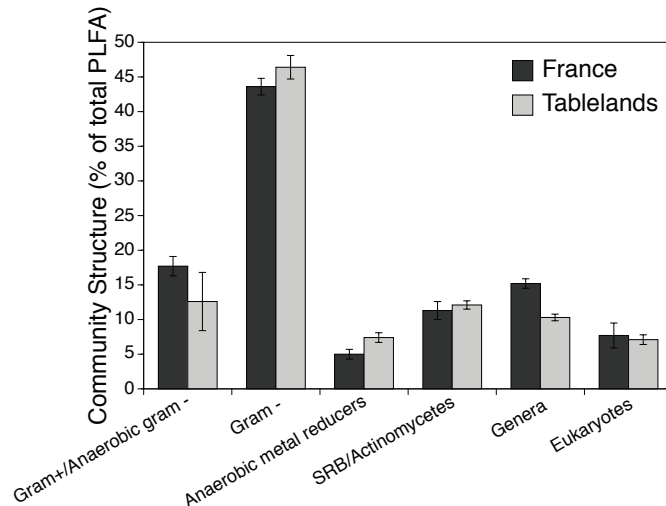
sites in the United States that are actively being invaded by medusahead. We are unaware, however, of any threshold of N availability that fosters plant invasion. In all likelihood, the growth of weedy species such as medusahead would respond differently to pulses of N availability through fertilizer addition versus the slow increases due to mineralization. None-the-less, similar soil N availability between native and exotic populations suggests that it is not the controlling factor explaining its invasiveness in western North America.

PLFA Analyses

Native medusahead soils from southern France have far greater total microbial, bacterial, and eukaryotic biomass than the invaded sites on the tablelands of northern California (table 1). These findings seem logical given that native soils of southern France are wetter and contain more organic matter than the tableland soils. Both invaded and non-invaded soils are bacteria-dominated and their ratios of bacterial to eukaryotic biomass are similar. Bacterial dominance may be indicative of a soil system that is not self-regulating — out of equilibrium (Bardgett and McAlister 1999). Ratios of fatty acid biomarkers, the growth phase (table 1), suggest that the tableland soils have higher microbial turnover rates than the native soils in France, which is logical given the greater climatic variability and harshness compared to the French sites. Despite the large differences in microbial biomass and site climatic condition between the two sites, the soil microbial community structure has only minor differences between the native and invasive sites (fig. 3). Given the marked difference in soils and climate, this finding seems remarkable. Moreover, invasive plants can alter microbial community structure promoting different classes of organisms presumably to increase plant fitness (Batten and others 2006).

Table 1—Results of PLFA analyses for native medusahead site in France and invasive site on the volcanic tablelands of northeastern, CA. Standard deviations in parentheses.

Attribute	France	Tablelands
	- - - pico moles PLFA g ⁻¹ soil - - -	
Microbial biomass	51996 (5206)	22995 (4773)
Bacteria biomass	48077 (5120)	21344 (4354)
Eukaryotic biomass	3916 (1017)	1654 (459)
Ratio Bacteria/Eukaryotes	12.3	12.9
Growth phase	0.635 (0.103)	0.363 (0.023)

**Figure 3**—Microbial community structure of native (France) and invasive (tablelands) soils as discerned by phospholipid fatty acid analyses (PLFA).

DNA Analyses

We were unable to obtain bacterial DNA from the native medusahead site in France. For the invaded tablelands site, six bands with useable sequence information were obtained (table 2). *Methylomonas* and *Sulfuricurvum* seem out of place in the semi-arid environment of the tablelands. In these lake-laid, clayey soils, however, there is the potential

at depth and in reduced microsites for methane production and sulfur reduction. *Caulobacter* generally live in dilute aquatic environments where the most common limiting nutrient is phosphorus. Certainly, availability of P in these soils is reduced by sorption to clay, but it is hardly an aquatic environment? The genus *Sphingomonas* is known for its ability to catabolize complex organics and is used to remediate contaminated sites. Its presence in tableland soil may be a reflection of the complex biochemistry of *Artemisia*? The tablelands have legumes, thus the presence of *Bradyrhizobium* is logical.

Conclusions

Available N does not appear to be the controlling factor in medusahead invasion. Soil microbial community structure does not appreciably differ between native and invasive medusahead populations. Does this fact imply that community structure cannot explain the invasive nature of medusahead in the Western United States? Alternatively, do microbial populations between native and invasive sites differ at the genus and species level and does this difference explain invasibility? We would additionally suggest testing these hypotheses with closely-related cheatgrass because it invades some of the same habitats in the Western United States, and it originates from similar habitats in Eurasia.

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Table 2—Bacterial DNA analyses of medusahead invaded areas on the tablelands.

Genus	Function	% Match
Methylomonas	utilize methane and methanol	97
Sulfuricurvum	anaerobe – sulfur reducing	100
Eubacterium	biphenyl-contaminated site	96
Sphingomonas	aerobe – broad catabolic potential (aromatics)	100
Caulobacter	specialized for oligotrophic environments	100
Bradyrhizobium	root nodules legumes	97

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