Medusahead (*Taeniatherum caput-medusae*) Distribution and Genetics: Morphological and Genetic Differentiation Among Subspecies

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TAXONOMIC COMPLEXITY: RECOGNIZING DIFFERENT SUBSPECIES
Central Question in the Study of Taxonomic Complexity: Identification of Multiple, Morphologically Similar Subspecies

- Recognize invasive and non-invasive subspecies in their native range (e.g., *Acacia nilotica*, Kriticos et al. 2003)
- Identify native and non-native subspecies in the invasive range (e.g., *Phragmites australis* in N.A., Saltonstall et al. 2004)
- Identify different invasive subspecies of the same species (e.g., *Lepidium draba*, Gaskin et al. 2005)
- Detection of a cryptic invasion through the identification of a previously unrecognized invasive subspecies (Bickford et al. 2006)
- Aids in the search for the most specific and effective biological control agents in the native range (Wardill et al. 2005, Palmer et al. 2010)
Medusahead

*Taeniatherum caput-medusae* (L.) Nevski
Medusahead

- Annual grass
- Triticeae “wheat tribe”
- Diploid (2n = 14)
- Primarily self-pollinating
- Occupies semi-arid habitats
- Found on disturbed sites
- Widely distributed in Eurasia
- Three subspecies
- Invasive in western USA
- Detailed collection history
Medusahead
Native Range Distribution

(from Frederiksen, 1986)
Three Subspecies in Eurasia

“Apparently, the correct taxon for the medusahead of western North America is *Taeniatherum caput-medusae* ssp. *asperum*”

Young 1992 SRM
Objectives of the Study

1) Determine the utility of morphological characters to distinguish the three subspecies of medusahead

2) Assess morphological differentiation among native populations of the three subspecies

3) Determine genetic differentiation among native populations of the three subspecies
Medusahead
Native Range

Macedonia, 2011

Spain, 2009

Romania, 2011

Portugal, 2009
Dracula’s Castle
Bram, Romania
Results: Morphological Characters

- **Glume Length**
  - ssp. asperum: A
  - ssp. caput-medusae: B
  - ssp. crinitum: C

- **Glume Angle**
  - ssp. asperum: A
  - ssp. caput-medusae: B
  - ssp. crinitum: C

- **Palea Length**
  - ssp. asperum: A
  - ssp. caput-medusae: A
  - ssp. crinitum: B
Results: Morphological Differentiation

Taeniatherum caput-medusae Subspecies Assignment
Morphological Measurements

Conical cell and surface hair data not shown
## Results: Genetic Diversity

<table>
<thead>
<tr>
<th></th>
<th>ssp. asperum (n=34)</th>
<th>ssp. caput-medusae (n=20)</th>
<th>ssp. crinitum (n=28)</th>
<th>Overall</th>
</tr>
</thead>
<tbody>
<tr>
<td># Alleles</td>
<td>48</td>
<td>36</td>
<td>33</td>
<td>50</td>
</tr>
<tr>
<td>Alleles/Locus</td>
<td>2.09</td>
<td>1.57</td>
<td>1.43</td>
<td>2.17</td>
</tr>
<tr>
<td># Polymorphic Loci</td>
<td>15</td>
<td>10</td>
<td>9</td>
<td>16</td>
</tr>
<tr>
<td>%Polymorphic Loci</td>
<td>65.22%</td>
<td>43.48%</td>
<td>39.13%</td>
<td>69.57%</td>
</tr>
<tr>
<td>%Polymorphic Populations</td>
<td>67.64%</td>
<td>50.00%</td>
<td>39.29%</td>
<td>53.66%</td>
</tr>
<tr>
<td>Nei’s Expected mean Heterozygosity (H_{exp})</td>
<td>0.1408</td>
<td>0.0725</td>
<td>0.0258</td>
<td>0.1314</td>
</tr>
<tr>
<td>Mean observed Expected Heterozygosity (H_{obs})</td>
<td>0.0126</td>
<td>0.0126</td>
<td>0.0126</td>
<td>0.0126</td>
</tr>
<tr>
<td>Fst</td>
<td>0.8423</td>
<td>0.8663</td>
<td>0.8285</td>
<td>0.9081</td>
</tr>
<tr>
<td>Nm</td>
<td>0.0468</td>
<td>0.0386</td>
<td>0.0518</td>
<td>0.0253</td>
</tr>
<tr>
<td># of Multilocus Genotypes</td>
<td>66</td>
<td>22</td>
<td>11</td>
<td>93</td>
</tr>
</tbody>
</table>
Genetic Structure of Native Populations of Medusahead

AMOVA:

<table>
<thead>
<tr>
<th></th>
<th>d.f.</th>
<th>Sum of Squares</th>
<th>Variance Components</th>
<th>Percentage Variation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Among subspecies</td>
<td>2</td>
<td>2651.552</td>
<td>0.86506</td>
<td>48.38</td>
</tr>
<tr>
<td>Among populations</td>
<td>75</td>
<td>3455.088</td>
<td>0.79073</td>
<td>44.22</td>
</tr>
<tr>
<td>within subspecies</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Among individuals</td>
<td>2194</td>
<td>571.854</td>
<td>0.12845</td>
<td>7.18</td>
</tr>
<tr>
<td>within populations</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Within individuals</td>
<td>2272</td>
<td>8.5</td>
<td>0.00374</td>
<td>0.21</td>
</tr>
<tr>
<td>Total</td>
<td>4543</td>
<td>6686.994</td>
<td>1.78799</td>
<td>--</td>
</tr>
</tbody>
</table>
Results: Genetic Differentiation
Conclusions: Morphological Differentiation

1) Means for glume length and glume angle are significantly different among all three subspecies; whereas ssp. *crinitum* has significantly longer palea length.

2) In combination, these three morphological characters clearly differentiate populations of the three subspecies.


4) Morphological overlap among some subspecies is not surprising because intermediate forms have been reported.
Conclusions: Genetic Differentiation

1) Subspecies *asperum* possesses the highest amount of genetic diversity; ssp. *caput-medusae* has intermediate values, and ssp. *crinitum* has the lowest values.

2) Four distinct clusters of populations were observed; with populations of ssp. *asperum* occurring in several clusters.

3) Subspecies *crinitum* is genetically differentiated from the other two (Cluster 3); some populations of ssp. *asperum* and ssp. *caput-medusae* co-occur within Cluster 2.

4) Co-occurrence of some individuals of these two subspecies within the same cluster may reflect past hybridization events.
GEOGRAPHIC ORIGINS, MULTIPLE INTRODUCTIONS AND FOUNDER EFFECTS
Central Question in the Study of Insight from the Combined Analysis of Native and Invasive Populations

- Identify geographic origins (source populations)
- Assess introduction dynamics (multiple vs. single introductions) and mechanism of range expansion (local vs. widespread)
- Genetic consequences of introduction events (founder effects?)
- Role of post-immigration evolution vs. pre-adaptation in invasion
- Implemented in management of invasive species (biological control programs)

Medusahead

- Annual grass
- Triticeae “wheat tribe”
- Diploid (2n = 14)
- Primarily self-pollinating
- Occupies semi-arid habitats
- Found on disturbed sites
- Widely distributed in Eurasia
- Three subspecies
- Invasive in western USA
- Detailed collection history
Results

- 45 populations (1663 indivs.)
- 15 enzyme systems (29 loci)
- 5 variable loci (\textit{Pgi-2, Mdh-2, Adh, 6Pgd-2, Pgm-2})
- 7 homozygous multilocus genotypes (MLG)
- 4 MLG associated with early collection sites

Multiple Introductions
Objectives of the Study

1) Determine the geographic origins for the invasion of medusahead in western US

2) Assess the introduction dynamics (single vs. multiple) of medusahead

3) Determine whether medusahead has experienced founder effects during its invasion in western USA
Medusahead
Native Range

Romania, 2011

Spain, 2009

Bulgaria, 2011

Italy, 2009
Medusahead
Native Range Sampling
Results: Morphological Characters

Glume Length

- ssp. asperum: A
- invasive asperum: B
- ssp. caput-medusae: C
- ssp. crinitum: D

Glume Angle

- ssp. asperum: A
- invasive asperum: A
- ssp. caput-medusae: B
- ssp. crinitum: C

Palea Length

- ssp. asperum: A
- invasive asperum: B
- ssp. caput-medusae: A
- ssp. crinitum: C
Results: Morphological Differentiation

Taeniatherum caput-medusae Subspecies Assignment
Morphological Measurements

Conical cell and surface hair data not shown.
Results: Genetic Differentiation
Five multilocus genotypes matched those in western USA
Source populations: France, Sardinia, Greece and Turkey
## Genetic Diversity Across Populations of Medusahead: Founder Effects

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>All native pops.</td>
<td>34</td>
<td>48</td>
<td>2.09</td>
<td>15</td>
<td>65.2</td>
<td>67.6</td>
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<tr>
<td>Putative source pops.</td>
<td>10</td>
<td>38</td>
<td>1.65</td>
<td>10</td>
<td>43.5</td>
<td>80.0</td>
</tr>
<tr>
<td>Invasive pops.</td>
<td>45</td>
<td>28</td>
<td>1.22</td>
<td>5</td>
<td>21.7</td>
<td>37.8</td>
</tr>
</tbody>
</table>
## Genetic Diversity Within Populations of Medusahead: Founder Effects

<table>
<thead>
<tr>
<th></th>
<th>Alleles/locus</th>
<th>% Poly. Loci</th>
<th>$H_{\text{obs}}$</th>
<th>$H_{\text{exp}}$</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>All native pops.</strong></td>
<td>1.10</td>
<td>9.08</td>
<td>0.00003</td>
<td>0.0246</td>
</tr>
<tr>
<td><strong>Putative source pops.</strong></td>
<td>1.14</td>
<td>12.18</td>
<td>0.00000</td>
<td>0.0361</td>
</tr>
<tr>
<td><strong>Invasive pops.</strong></td>
<td>1.02</td>
<td>1.90</td>
<td>0.00010</td>
<td>0.0040</td>
</tr>
</tbody>
</table>
Conclusions: Geographic Origins, Introduction Dynamics and Founder Effects

1) Geographic origins of the invasion of medusahead in western US could have been drawn from across much of the native range = France, Sardinia, Greece and Turkey

2) Pattern of allozyme diversity in medusahead is consistent with the multiple introduction hypothesis = minimum of 7 introductions

3) Founder effects appear to have reduced genetic diversity both across and within invasive populations = genetically depauperate
Conclusions: Genetic Diversity and Management

1) Because invasive populations are genetically depauperate, highly adapted biocontrol agents are likely to be quite effective

2) Approximately 38% of invasive populations have two or more native genotypes = genetic admixtures

3) Thus, complex management strategies may be needed to control invasive populations of medusahead that are admixtures = multiple biological control agents

4) The search for biocontrol agents should occur broadly across the Mediterranean, where putative source populations have been identified
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European Biological Control Laboratory
M.J. Murdock Charitable Trust
Boise State University
Genetic Structure of Medusahead

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<th>Variance Components</th>
<th>Percentage Variation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Among regions</td>
<td>3</td>
<td>172.366</td>
<td>0.010692</td>
<td>22.21</td>
</tr>
<tr>
<td>Among populations within regions</td>
<td>30</td>
<td>387.291</td>
<td>0.23378</td>
<td>48.57</td>
</tr>
<tr>
<td>Among individuals within populations</td>
<td>892</td>
<td>250.433</td>
<td>0.14011</td>
<td>29.11</td>
</tr>
<tr>
<td>Within individuals</td>
<td>926</td>
<td>0.5</td>
<td>0.00054</td>
<td>0.11</td>
</tr>
<tr>
<td>Total</td>
<td>1851</td>
<td>810.589</td>
<td>0.48135</td>
<td>--</td>
</tr>
</tbody>
</table>

Nei’s Gene Diversity Statistics:

<table>
<thead>
<tr>
<th>Range</th>
<th>$H_T$</th>
<th>$H_S$</th>
<th>$G_{ST}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Native</td>
<td>0.262</td>
<td>0.043</td>
<td>0.745</td>
</tr>
<tr>
<td>Invasive</td>
<td>0.224</td>
<td>0.028</td>
<td>0.906</td>
</tr>
</tbody>
</table>