Clonal plants as invasive species in a changing world

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The defining feature of clonal growth in plants is multiple connections between root and shoot.

The consequences of this feature include increased ability to space areas of resource uptake, increased ability to respond to spatial patterns, reduced risk of mortality, indefinite spread, and immortality.
invasive – entering a place and harming things there; spreading, becoming abundant

non-invasive

**introduced** – brought to a new place by humans  
**native**  

**not introduced**,
The 10 species considered invasive in the most countries:

- Rattus rattus
- Rattus norvegicus
- Felis catus
- Ricinus communis
- Eichhornia crassipes
- Lantana camara
- Capra hircus
- Mustela vison
- Cyperus rotundus
- Mus musculus
Cyperus rotundus (purple nutsedge, 香附子)
Studies of the distribution and traits of introduced, invasive, clonal plant species:

none – until later today.

Studies of the distribution and traits of introduced, invasive plant species that include clonal growth as a trait:


Daehler. 1998. Biological Conservation. In the world, climbers tend to be invasive in natural areas.

Jakobs et al. 2004. Diversity & Distribution. Populations of Solidago gigantea in the introduced range have more rhizomes than populations in the native range.
Suehs et al. 2004. *Heredity.* In the Hyères Islands, the more invasive of 2 species of *Carpobrotus* relies more on vegetative reproduction.

Sutherland. 2004. *Oecologia.* In the U.S., weeds are more likely to have vegetative reproduction than non-weeds, but only because they tend to be perennial.


Burns. 2006. *Ecological Applications.* In 6 species in the Commeliaceae, invasiveness is associated with high production of nodes in response to high N and water.

Cadotte et al. 2006. *Biological Invasions.* Comparison of 19 studies suggests that presence of clonal organs is associated with invader success.
Cadotte et al. 2006. *Ecoscience*. In Ontario in Canada, introduced plant species tend to have vegetative reproduction.

Thuiller et al. 2006. *Ecology*. In South Africa, invasive species in wet tropical and disturbed habitats have very small seeds or vegetative reproduction.

Herron et al. 2007 *Diversity & Distribution*. In woody plants in New England, invasiveness is associated with vegetative reproduction.

Küster et al. 2008. In German neophytes, vegetative reproduction explains 2% of invasiveness. Species with runners are more invasive if they flower earlier; species with rhizomes are more invasive if they flower later.

Gasso et al. 2009. *Diversity & Distribution*. In Spain, clonality is not associated with invasiveness in plants.

Thuiller et al. 2012. *Biological Invasions*. In Spain, clonal invasive species are associated with *human disturbance near the coast*, and annual and biennial clonal species introduced through agriculture have a relatively *high tolerance of climate and landscape conditions*.

These 14 studies suggest that invasiveness in introduced plant species is associated with clonal growth, but sometimes only in certain habitats.

Clonal growth does not seem to explain a large proportion of variation in the invasiveness of introduced plant species, but neither does any other trait.
How may clonal growth interact with these effects on and of biological invasions?

Bradley et al. 2010. TREE.

Effects of Elevated Atmospheric CO$_2$ on Invasive Plants: Comparison of Purple and Yellow Nutsedge (Cyperus rotundus L. and C. esculentus L.)

D. H. Gjerstad Auburn University

<table>
<thead>
<tr>
<th>CO$_2$</th>
<th>375 ppm</th>
<th>575 ppm</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Aboveground mass (g):</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>leaf</td>
<td>89</td>
<td>107</td>
</tr>
<tr>
<td>seed head</td>
<td>7.0</td>
<td>6.6</td>
</tr>
<tr>
<td><strong>Belowground mass (g):</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>root</td>
<td>81</td>
<td>104</td>
</tr>
<tr>
<td>tuber</td>
<td>122</td>
<td>156</td>
</tr>
<tr>
<td><strong>Water use efficiency (mmol CO$_2$ / mol H$_2$O):</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>3.3</td>
<td>4.6</td>
</tr>
</tbody>
</table>

P > 0.05
P = 0.01-0.05
P < 0.01

Rogers *et al.* 2008. *J. Env. Quality*
Adaptation to flooding in upland and lowland ecotypes of *Cyperus rotundus*, a troublesome sedge weed of rice: tuber morphology and carbohydrate metabolism

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**Figure A**

- **A.** Bar graph showing soluble sugar content (% by weight) in upland and lowland ecotypes.
  - Upland: 10%, 20%, 30%
  - Lowland: 20%, 30%, 40%

- **B.** Bar graph showing starch content (% by weight) in different fields.
  - Field 1: 30%
  - Field 2: 20%

**Figure B**

- **Pyruvate decarboxylase (PDC) activity (U)** over time under hypoxia (h).
  - Legend: Upland field 1, Upland field 2, Lowland field 1, Lowland field 2.

In *Cyperus rotundus*,

- > tolerance of flooding

- > tubers
Eichhornia crassipes
(water hyacinth, 风眼莲)
Six populations of *Eichhornia crassipes* in southern China showed no polymorphisms in RAPDs or ISSRs, and may be just one clone.

Li *et al.* 2006. *Aquatic Bot.*
Elevated CO$_2$ decreased import of C by offspring from 10% of parental assimilation to 8%. Only import to leaves was affected.

(Even under uniform conditions, parent and offspring exported C to each other and to new offspring.)

Eichhornia crassipes grown at 2 levels of light (70 or 350 μmol m^{-2} s^{-1}) x 2 levels of N (0.5 or 5 mM NO_3)

<table>
<thead>
<tr>
<th>light (μmol m^{-2} s^{-1})</th>
<th>350</th>
<th>70</th>
</tr>
</thead>
<tbody>
<tr>
<td>N (mM NO_3)</td>
<td>5</td>
<td>0.5</td>
</tr>
<tr>
<td>(P)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Root/leaf mass:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>parent</td>
<td>0.29</td>
<td>0.60</td>
</tr>
<tr>
<td>offspring</td>
<td>0.23</td>
<td>0.20</td>
</tr>
<tr>
<td>Offspring/parent mass</td>
<td>0.79</td>
<td>0.71</td>
</tr>
<tr>
<td>Offspring</td>
<td>4.5</td>
<td>3.5</td>
</tr>
<tr>
<td>g /offspring</td>
<td>0.30</td>
<td>0.23</td>
</tr>
<tr>
<td>μmol N / g leaf:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>parent</td>
<td>287</td>
<td>80</td>
</tr>
<tr>
<td>offspring</td>
<td>125</td>
<td>77</td>
</tr>
</tbody>
</table>

Eichhornia crassipes grown at 2 levels of light (70 or 350 μmol m\(^{-2}\) s\(^{-1}\)) x 2 levels of N (0.5 or 5 mM NO\(_3\))

Division of labor in clonal plants

*Non-clonal* plants typically specialize to acquire *scarce* resources, e.g., by having more leaves when light is low.

*Connected plants* within clones often specialize to acquire *abundant* resources.
Reciprocal resource *patchiness* and clonal integration induce specialization to acquire abundant resources in *pairs* of connected, *sibling* ramets.

Uniform resource *limitation* and clonal integration induce specialization to acquire abundant resources in *offspring* connected to parental ramets.

- **Low N**
- **Low light**
- **Division of labor**

**Non-clonal**

**Clonal**

**Subsidized specialization**
Rodriguez et al. 2012. 
In *Eichhornia crassipes*, high propagule success

> allocation to offspring, subsidized specialization

< parental export of C

What may be the ecological consequences of interactions between clonal growth, global change, and biological invasion?

... intensive study of particular species as models;
Alternanthera philoxeroides (alligator weed, 空心莲子草) is a likely model species in China.
Much of the answer is likely to involve the high probability of establishment of vegetative offspring compared to sexual ones.
Cymodocea nodosa, a Mediterranean seagrass

New ramets may be much higher in N and P than seedlings are.

Duarte et al. 1996. Aquatic Bot.
Increased N may increase invasiveness of clonal species with widely spaced ramets.
In Europe, rhizomatous species whose rhizomes live 1-2 years are associated with higher moisture and soil fertility than species whose rhizomes live longer.

Height and spacer length are also positively associated with fertility.

In 10 grasslands, adding N increased the relative abundance of tall, clonal plants with widely spaced ramets.
In experimental communities, adding clonal species increased total mass but decreased mass of non-clonal species, and decreased species richness if nutrients were added as well.

A model suggested that increasing habitat richness favored longer duration of clonal integration.
