Biomass Allocation in Four Prairie Grasses under Drought Stress

Xuejun Dong, Eco-physiologist, and Janet Patton, Research Assistant
Central Grasslands Research Extension Center – NDSU, Streeter, North Dakota

Introduction
The invasion of exotic plants, such as Kentucky bluegrass and smooth brome, is posing challenges to land management in the northern Great Plains rangelands. Control of these species relies on our understanding of the eco-physiological mechanisms responsible for their spread as they compete with the native plants for soil resources.

In grasses, food reserves in crowns and rhizomes support herbage production and allow regrowth in the spring. One important factor leading to the relative competitiveness of Kentucky bluegrass and smooth brome is that they initiate spring regrowth earlier than their native counterparts in the mixed-grass prairie. It still remains to be tested if there is a greater biomass investment to crowns or rhizomes in the exotic grasses as compared to the native species. We report on a study of the effect of drought stress on vegetative biomass allocation in two native grass species, western wheatgrass (*Pascopyrum smithii* (Ryd.) A. Löve) and green needlegrass (*Nassella viridula* (Trin.) Barkworth), and two exotic species, Kentucky bluegrass (*Poa pratensis* L.) and smooth brome (*Bromus inermis* Leyss.). All four species are dominant in the mixed-grass prairie. Green needlegrass is a bunch-type grass while the remaining three species are strongly rhizomatous. We tested the following three hypotheses:

1. The two exotic grass species may have a higher proportion of biomass allocated to **roots**, as opposed to shoots, compared with two native species, which allow the former to more aggressively exploit soil water and nutrients.

2. The two exotic species may have a higher biomass allocation to **rhizomes** or **crowns** than the two native species, which may facilitate the initiation of new tillers following defoliation or in early spring regrowth.

3. Compared with the native species, the two exotic species may have a greater increase in biomass allocation to roots, rhizomes, or crowns under **drought stress**, so as to have a better chance of regrowth after drought.

We also expected that the only bunch-type grass (green needlegrass) would have a greater fraction of biomass allocation to crowns than the three rhizomatous species, in which both crowns and rhizomes serve as food reserves.

Materials and Methods
Plants of four grass species (Kentucky bluegrass, smooth brome, western wheatgrass and green needlegrass) were subjected to two treatments, control and drought.

![Figure 1. Picture taken on June 17, 2011, a week after sowing. Smooth brome (SB) seeds started to germinate three days earlier and seedlings grew faster than the other three species, i.e., Kentucky bluegrass (KB), western wheatgrass (WW) and green needlegrass (GN).](image-url)
Ninety-six pots, (3 ¾ inch\(^2\) X 9 ½ inch high), were filled with sieved native soil and planted on June 10, 2011. The pots were arranged randomly within the greenhouse (Fig. 1) and plants were thinned to about 30 stems per pot. The control group pots were watered twice a week, and the drought group pots every seven to 10 days, depending on drought stress. Each pot was given 150 ml water at each watering. During the course of the experiment, plants in the drought group experienced seven cycles of severe water stress. Plants were harvested from September 14 to 23, separated by plant part, dried and weighed (Fig. 2). The data were analyzed using the nonparametric Mann-Whitney test.

<table>
<thead>
<tr>
<th>Group of species</th>
<th>Shoots</th>
<th>Roots</th>
<th>Crowns</th>
<th>Rhizomes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Introduced</td>
<td>49.2</td>
<td>45.3</td>
<td>3.7</td>
<td>1.7</td>
</tr>
<tr>
<td>Native</td>
<td>61.8</td>
<td>31.4</td>
<td>6.7</td>
<td>0.2</td>
</tr>
</tbody>
</table>

Comparisons between introduced and native species are all highly significant for each column according to ANOVA on arcsine-transform data.

Results

The two exotic species (Kentucky bluegrass and smooth brome) had significantly higher biomass allocation to roots than the two native species (Table 1). Conversely, the two native species had a significantly higher biomass allocation to shoots than the two exotic species. Meanwhile, the two native species had a significantly higher biomass allocation to crowns than the two exotic species.

There were varied biomass allocations to rhizomes, with the highest investment observed in Kentucky bluegrass, followed by western wheatgrass, but smooth brome and green needlegrass had no rhizomes at all (Fig. 3, page 3). It is interesting to note that the strongly rhizomatous grass smooth brome did not produce rhizomes in the first season’s growth, regardless of the water stress level.

Contrary to our original expectation, neither allocation to roots nor allocation to shoots was affected significantly by drought stress for all species (\(p>0.05\)) except in root allocation of green needlegrass where severe drought marginally increased the biomass allocation to roots (\(p=0.053\)) (Fig. 3).

Of the two grasses that produced rhizomes, the effect of drought stress was to reduce the biomass allocation to rhizomes. In Kentucky bluegrass, the rhizome allocation decreased from 5.4% in the control group to 1.6% in the drought group. In western wheatgrass, the rhizome allocation decreased from 0.5% in the control group to less than 0.1% in the drought group.

The biomass allocation to crowns in smooth brome (4.2%) and western wheatgrass...
Figure 3. Biomass allocation (in accumulated percentages) to shoots, roots, rhizomes and crowns in four grass species growing under well-watered and drought treatment in a greenhouse in 2011. The four species are Kentucky bluegrass (kb), smooth brome (sb), western wheatgrass (ww) and green needlegrass (gn). “D” refers to drought treatment. For each species, the effect of drought on allocations to shoots, roots, rhizomes and crowns are indicated by symbols between the bars. The effect of drought may be positive (+), negative (-), or non-significant (0).

(5.3%) did not respond to drought stress ($p=0.14$ and $p=0.47$, respectively). However, in Kentucky bluegrass, the allocation to crowns increased to 4.0% from the control level of 2.5%, while in green needlegrass, the value decreased to 7.0% from 9.2% of the control group. Only green needlegrass had a significantly greater fraction of biomass allocated to the crowns ($p<0.0005$), compared with the three rhizomatous species.

**Discussion**

Our study suggests that invasive grasses are physiologically primed for exploiting soil resources through a heavy investment of biomass to roots. Kentucky bluegrass has a sensitivity of stomatal conductance to developing water stress along with a shallow rooting habit and high root density that reduces water infiltration to the deep soil profile. In our study, smooth brome had the largest root system, both in terms of absolute root mass per pot and the fractional allocation. The two native grass species tend to have deep root systems. This suggests that the invasive species employ a higher competitive ability in terms of root growth and potential water uptake capacity, as compared with their native counterparts.

The result that the biomass allocation to crowns was significantly lower in the invasive species than the native species does not explain their early initiation of spring growth. It is possible that the biochemistry
of bud-break is more important than the amount of food reserves. While the high rhizome allocation observed in Kentucky bluegrass may contribute to its aggressive growth, the fact that strongly rhizomatous smooth brome did not grow rhizomes in the first season does not explain the aggressive invasion of this species in the mixed-grass prairie. It appears that the competitive ability of smooth brome may not manifest itself fully in one season.

Our data indicate that the effect of drought stress on biomass allocation manifested itself more on rhizomes and crowns than on roots and shoots of the four grass species. It appears in our study that drought stress can weaken the vegetative growth potential of both the invasive Kentucky bluegrass and the native western wheatgrass. However, the mixed responses to drought among the four species suggest species-specific responses.

Our work suggests a distinction between the invasive and native species in potential competitiveness in soil resource use, as seen in the root/shoot allocation and allocation to crowns. However, we did not find a consistent trend in the response to drought that differentiates the invasive species from the native species. Further studies spanning multiple years are needed to fully identify the competitive ability of these perennial grasses in their biomass allocation and resource use strategies.

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