Allocation of clonal growth in goldenrod varies across species and environments

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Introduction

In the context of plants, the word reproduction is often associated with flowers. However, in the prairie, the most successful plants have evolved to reproduce without a dependency on seeds (Reichmann 1987). Rhizomes, although perhaps not as glamorous as flowers, provide prairie plants such as *Solidago altissima* with a dependable method of reproduction in the face of harsh competition. Because plants have a limited amount of energy, they must allocate energy to one method of reproduction over another. Biologists have found varied results as to whether there is a trade-off between clonal growth and sexual reproduction among species and environments (Schmid and Werner 1993).

Exploring the relationship between clonal growth and sexual reproduction is relevant to three current themes in prairie studies. The first of these is Wes Jackson's attempt to create an agricultural prairie by encouraging perennial prairie plants to increase sexual output. The second of these themes in prairie restoration is the importance of biodiversity, which necessitates the establishment of rarer species. Hartnett maintains that clonal growth is crucial to the establishment of a species within the prairie (1993).
Finally, the effects of fire are important in prairie restoration. Little is known about the effects of fire on below ground vegetation (Svejcar 1990). In general, belowground vegetation increases due to fire, but it is unknown whether this general increase is due to an increase in roots or rhizomes (Seastedt et al 1990). Understanding energy allocation will establish the importance of clonal growth to prairie restoration.

We designed our experiment in order to determine how much biomass three different species of goldenrod, *Solidago altissima, Solidago rigida, and Solidago speciosa*, allocate to their stem and leaves, roots, sexual reproduction, and clonal growth. We also examined the biomass allocation of *S. altissima* in burned and unburned plots.

S. altissima is one of the most prominent forbs at CERA, Grinnell College's experimental prairie, although it was never formally seeded (Delong, unpublished manuscript). It is a perennial forb that reproduces after establishment primarily through clonal growth (Abrahamson and Weis 1997). The other two species, although native to Iowa, are much more rare at CERA in general, but were easily found in Deaner Prairie as they were heavily seeded there (DeLong, unpublished manuscript). *S. rigida* can be found scattered in the dry or mesic soils of prairies and fields throughout Iowa. It is a very aggressive forb that inhibits the growth of other plants if it is not faced with considerable competition (Shirley 1994). *S. speciosa* grows in mesic and dry soil in the prairies and woods of Iowa. It becomes aggressive in moist soils (Shirley 1994).

Materials and Methods

During the beginning of October we sampled *S. rigida*, *S. altissima*, and *S. speciosa* at CERA's Deaner Prairie, which has been burned annually in spring and regularly seeded with forbs since 1990 (DeLong unpublished manuscript). At the time of sampling, the plants were in full bloom and just beginning to go to seed. In late October, we sampled solely *S. altissima* in the burned and unburned experimental plots at CERA. These experimental plots consist of twenty ten-by-ten meter plots. Every other plot is burned in the spring while the other plots remain unburned. These plots were never seeded with *S. altissima* (Brown pers. com.).

Sample Selection

At Deaner we collected ten samples of *S. rigida* and ten samples of *S. speciosa*. There were few specimens of *S. altissima* in this prairie, so we took only three samples. For the other two species, we randomly selected ten sampling points and then collected the individual of each species closest to that point.

At the experimental plots, we randomly selected a point and then located the *S. altissima* plant closest to that point. Since we were sampling after the majority of the plants had gone to seed, we attempted to use only samples which had retained the majority of their above ground reproductive matter.

Sample Treatment

We excavated each plant, taking precautions to include all of the belowground biomass. We divided the plant into four sections – sexual reproduction, stem and leaves, roots and clonal growth. In the case of sexual reproduction, we cut the flowers at the base of the last inflorescence. In order to separate the roots from the clonal growth, we carefully washed off all of the dirt and plant matter not belonging to our samples. We made careful note of the rhizomes' size and number before we clipped them from the base of the stem. Many of our samples were very closely connected to other stems. We included stems that were either right next to our sample stem or under five centimeters apart, directly connected by a thick rhizome. We dried all of our samples for forty-eight hours, and weighed them.

Data analysis

We calculated the percent biomass of each of the plant segments –vegetative growth, roots, rhizomes, and sexual reproduction. We compared the weight and percent biomass of each segment across burn treatments using a T-test. We compared the mean weight and percent biomass of every segment collected at Deaner among the three species using a one-way ANOVA. Due to a low sample size, we combined clonal growth data from Deaner Prairie and the Experimental Prairie.

Results

We found no significant difference among the mean weights or mean percentages in the biomass of *Solidago altissima, Solidago rigida*, and *Solidago speciosa* of Deaner Prairie concerning sexual reproduction, stem and leaves, and roots. However, there was a significant difference among the three species for both the mean weight and mean percent biomass of clonal growth (p .012, p .012, respectively). Every experimental group devoted the majority of energy to its stem and leaves, a moderate amount to sexual reproduction and roots, and the smallest amount to clonal reproduction (Figure 3).

For *Solidago altissima* in the Experimental Prairie, burning had no significant effect on the mean weights or percentages of sexual reproductive matter, stem and leaves, or roots. The mean weight for clonal growth, however, was marginally insignificant ($p = .073$). In the unburned plots, *Solidago altissima* allocated more energy to both sexual and clonal, while *Solidago altissima* in the burned plots allocated more energy to the stem, leaves, and roots (Figures 5-8).

Figure 1. Percent biomass of
growth in S. speciosa, S. al
and S. rigida in Deaner Pra

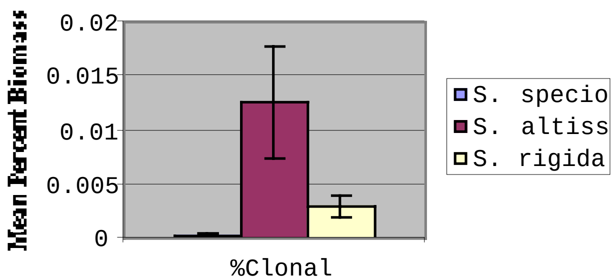


Figure 2. Mean weight of cl
growth of S. speciosa, S. al
and S. rigida in Deaner Pra

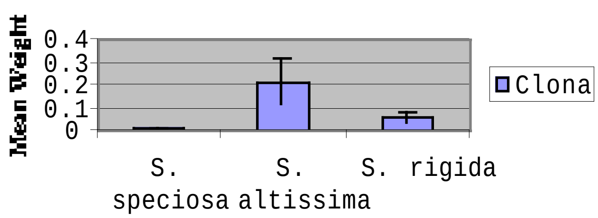


Figure 5. Mean weight of clonal
of S. altissima in burned and u
plots

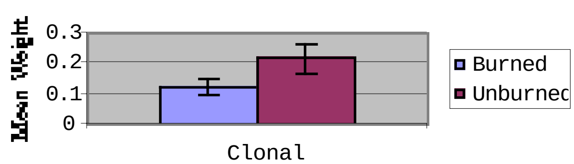


Figure 6. Percent weight of clona
of S. altissima in burned and un
plots

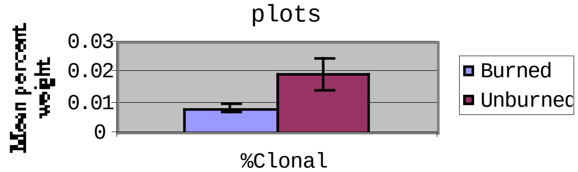


Figure 3. Weights of S. speciosa, S.
and S. rigida in Deaner Prairi

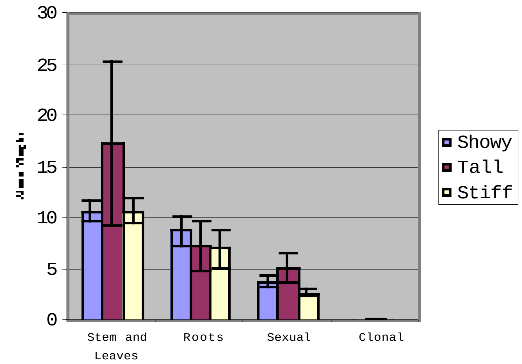


Figure 4. Percent biomass o
altissima, S. speciosa, and S
in Deaner Prairie

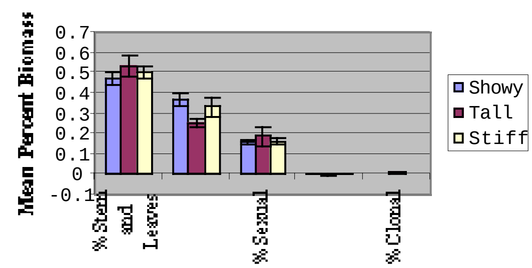


Figure 7. S. altissima in bu
unburned plots

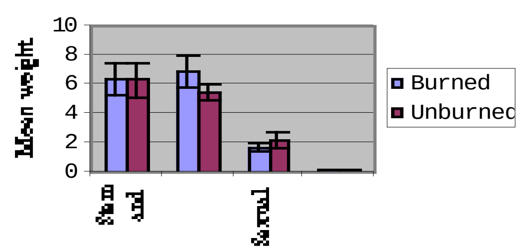
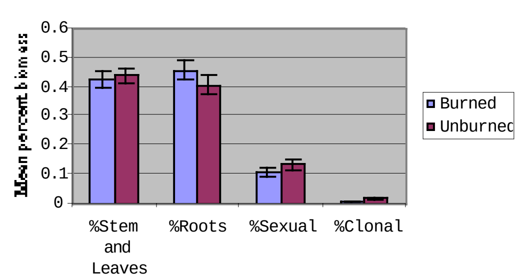


Figure 8. Percent biomass of S. altissima
and unburned plots



Discussion

In Deaner Prairie, we found that *S. altissima* allocated significantly more energy to clonal growth than *S. rigida* and *S. speciosa*. In the Experimental Prairie, we found that samples in the unburned plots had nearly significantly more clonal growth than the samples in the burned plots. However, we found no significant difference in sexual reproduction in the data we collected from either prairie. Our results do not illustrate any apparent trade-off between clonal and sexual growth. Rather, we found that the plants that had significantly more clonal growth also had slightly more sexual reproduction. This lack of a trade-off has implications for ecological dynamics within the prairie and prairie restoration. Determination of allocation between clonal growth and sexual reproduction has shown no consistent trend. For example, Schmid and Weiner (1993) found that there was a trade-off between clonal growth and sexual reproduction in *S. altissima*, but Weis et al. (1987) did not find such a trade-off.

First, we expected that there would be more clonal growth in the burned plots. However, we found that environment did seem to have an effect on how one species allocates its energy to clonal growth in that the unburned plots had an almost significantly larger amount of clonal growth than the burned plots (p=. 073). One potential reason for this is that *Solidago altissima* has a low tolerance for competition (Brown pers. com.). For example, Abrahamson and Weis (1993) found that the reproductive efforts of goldenrod populations generally declined with the increasing success of the surrounding vegetation. When a prairie is burned, underground vegetative mass increases by approximately twenty percent (Seastedt et al 1990). In one study by Kucera and Dahlman (1968), as found in Svejcar (1990), *Andropogon gerardii*, commonly known as big bluestem, was found to have a thirty-nine percent increase in underground biomass in burned as opposed to unburned plots. Thus, burned plots offer *S. altissima* increased competition which limits the clonal growth and expansion (Hartnett 1993).

As expected, we found the clonal growth of *Solidago altissima* to be greater than that of the two less dominant species. Abrahamson and Weis (1997) found that certain species of goldenrod stress sexual reproduction while others, such as *S. altissima*, emphasize clonal growth. During its secondary succession *S. altissima* becomes dominant primarily through clonal growth (Schmid et al. 1994, Abrahamson et al. 1997). We observed that rhizomes from *S. altissima* were very numerous and often up to twelve centimeters in length; while the rhizomes from the other two species were extremely short, often only a millimeter. Many of our *S. altissima* samples were connected to other stems by long, thick, old rhizomes; *S. rigida* and *S. speciosa* samples were almost always directly connected another stem.

Our findings on the differences in clonal growth within one species in different environments and among several species in one environment, provided us some insight into the three prairie restoration themes cited earlier. First, our results reveal that burning may not promote clonal growth in every prairie forb. Indeed, it seems to have had the opposite effect on *S. altissima*.

Furthermore, we had hoped that our results would provide us knowledge on the allotment of energy to sexual reproduction as opposed to clonal reproduction, and thus sexual reproduction could be encouraged. We determined, however, that *Solidago* is not a good model for prairie species due to the differences in allocation that exist among the separate species of *Solidago*. Also, we did not find a trade-off between sexual reproduction and clonal growth which is conducive to Jackson's efforts because plants that had more clonal growth did not have less sexual reproduction.

Towards the promotion of biodiversity, our study helped us to understand how rarer species of *Solidago* could be encouraged through clonal growth. Schmid and Weiner (1993) found that plants derived from rhizomes put more energy into storage. Additionally, Abrahamson and Weis (1997) found that *Solidago altissima* ramets that were severed from their mother clumps were forced to compensate for this lack of resources. As a result, they allocated significantly more of their biomass to roots and clonal growth over sexual reproduction and stems. Therefore, we suggest that in order to promote rarer species of *Solidago* in prairie restoration projects, one should grow the plants from rhizomes in a greenhouse. Then, one should remove the ramets from the mother clone and plant them in the prairie. Thus, the plants would be more likely to reproduce clonally, giving them a head-start over other prairie forbs and grasses.

Although our experiment answered many of our questions, it left us with many new questions. Firstly, we realized that we could not possibly generalize about how forbs allocate energy to clonal growth. Even within one genus, environmental variation and competition may alter allocation to clonal growth. Furthermore, even within one species, there may be varying allocations to clonal growth dependent upon environment and competition from neighboring species. This has led us to develop many ideas for further exploration. For example, we would be interested to find how the two rarer species would react to fire. We expect that they would have more clonal reproduction in the burned plots but this would depend upon other environmental factors. In order to determine this, we would set up an experiment similar to the experimental plots, except that we would plant all three species. We would also like to study the successive clonal growth for several years after establishment. We expect that clonal growth would decrease due to increased competition.

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