Impact of early root competition on fitness components of four semiarid species

Günther Reichenberger* and David A. Pyke

Department of Range Science and the Ecology Center, Utah State University, Logan, Utah 84322-5230, USA

Received December 19, 1989 / Accepted in revised form June 20, 1990

Summary. Plant demographic and root exclusion approaches were used to examine the influence of roots of adult Artemisia tridentata, Agropyron desertorum, and Agropyron spicatum individuals on seedling survival of four C₃ semiarid species, three perennials, Ar. tridentata, Ag. desertorum, Ag. spicatum, and an annual, Bromus tectorum. Furthermore, height of Ar. tridentata seedlings and seed production of B. tectorum were assessed. The probability of a seedling being alive significantly depended on the seedling species, the neighboring adult species, and on the depth to which root competition was excluded. As seedlings, survival of Agropyron species did not differ, whereas survival of Ar. tridentata seedlings was higher than Ag. desertorum and was similar to Ag. spicatum. Bromus tectorum maintained significantly higher survival rates than perennial seedlings. Established individuals of Ar. tridentata reduced seedling survival more than established individuals of either Agropyron species. Seedling survival significantly increased with greater depth of root exclusion for the perennials but did not significantly affect seedling survival of B. tectorum. Height of Ar. tridentata seedlings and seed production of B. tectorum significantly increased with depth of root exclusion. Seed production of B. tectorum was highest when competing with Ag. desertorum and was lowest with Ar. tridentata. Root competition decreased the seed population of B. tectorum in the next generation even though it had no impact on survival. Competition in the upper soil horizon occurs between seedlings and established adults early in the growing season and potentially restricts root growth of seedlings. In arid and semiarid ecosystems, soil moisture is depleted from the upper horizons first, resulting in the death of seedlings that do not have access to moisture.

Key words: Root competition – Seedling survival – Seedling height – Seed production – Semiarid ecosystem

The importance of competition in the development and persistence of plant populations that form plant communities has been debated recently (Tilman 1982; Connell 1983; Roughgarden 1983; Schoener 1983; Strong 1983). Competitive interference among plants for resources is often demonstrated by reductions in individual biomass with increases in the density of competitors (Harper 1977). However, little is known about the importance of competition on the abundance and dynamics of plant populations (Watkinson 1986).

Sufficient evidence exists that competition regulates growth of plants in arid and semiarid communities (Fowler 1986). Many of these studies assessed competition by removing potential competitors and comparing survival or reproduction against treatments where competitors were not removed. However, removal of competitors potentially removes other biotic agents, such as herbivores, therefore confounding the impact of competition (Parker and Root 1981).

When evaluating plant competition, it is therefore important to separate effects of competitors from those of other interactions. Root exclusion tubes provide an effective technique to evaluate the effects of root competition from established neighbors on seedling development without removing potential competitors (Cook and Ratcliffe 1984). This was the approach used in the current study to evaluate the effect of root competition on seedling establishment.

Within the Great Basin sagebrush ecosystem, mechanisms for belowground competition have been investigated for mature individuals of dominant species. Root systems of neighboring individuals commonly occur within the same soil volume, leading to a potential overlap of resource exploitation zones (Caldwell and Richards 1986). Adult individuals of Agropyron desertorum (Fisch. ex Link) Schult., a widely seeded Eurasian species, and of Agropyron spicatum (Pursh) Scribn. and Smith¹, a native species, differ in their ability to compete for water and nutrients with Artemisia tridentata Nutt., a dominant native shrub, due to differences in root growth and root morphology (Caldwell et al. 1983; Nowak and Caldwell 1984). Rooting density tends to be more important in acquisition of belowground resources than physiologic characteristics of roots (Clark-
son 1985). Roots of these established perennials in the Great Basin are most dense in the upper 15 cm of the soil (Caldwell and Richards 1986). Thus seedlings, during their early development, must compete for resources with established perennials in this upper horizon.

Harris and Wilson (1970) have shown that root elongation for seedlings was greatest for Bromus tectorum L., an alien annual grass that is common in the Great Basin, least for Ag. spicatum, and intermediate for Ag. desertorum. Root elongation of B. tectorum often exceeds depths of 15 cm in less than one month providing it the potential of obtaining resources at depths with fewer roots of established competitors and at an earlier time than seedlings of perennial species (Harris 1967; Aguirre 1989). However, little is known about the influence of root competition in this upper portion of the soil on seedling growth, survival and reproduction of these semiarid species.

The objective of our study was to evaluate the impact of root competition from established perennials in the upper 10 cm of the soil profile on fitness components of four C₄ seedlings, Ar. tridentata, Ag. desertorum, Ag. spicatum, and B. tectorum. We examined seedling survival of all four species, and seed production of B. tectorum. In addition, we used seedling height of Ar. tridentata rather than biomass as an early indicator of competitive impacts on plant growth because measuring height was nondestructive and it allowed us to simultaneously monitor the fate of individuals.

Study sites

The study was conducted at two sites in northern Utah. The first was located near Petersboro, about 15 km west of Logan, UT (41°46' N, 112°2' W, 1680 m elev.), on a south-facing slope (15%) that has been described as a Palouse grassland outlier in Utah (Stoddart 1941). Areas dominated either by Ar. tridentata ssp. vaseyana (Ryd.) Beetle, Ag. desertorum, or by Ag. spicatum are distributed in a mosaic pattern at this site.

The second site is located in Curlew Valley in northwestern Utah (41°56' N, 113°7' W, 1480 m elev.) within an Ar. tridentata ssp. wyomingensis Beetle & Young/Ag. spicatum habitat type (Hironaka et al. 1983). A large portion of this site was sprayed with 2,4-dichlorophenoxy acetic acid in 1968 and 1973 and was aerially seeded with Ag. desertorum, which resulted in a mosaic pattern of dominant established perennials similar to the Petersboro site. For further information about the Curlew site see Eisenstat and Caldwell (1988).

The dry air and moisture deficiency during the growing season make the region more arid than would be expected from climatological data. Long-term average annual precipitation is 490 mm and 305 mm at Logan, Utah, the closest climatological station to Petersboro, and at Snowville, the closest station to Curlew, respectively.

The Great Basin sagebrush ecosystem is characterized as a winter-wet and summer-dry region with large annual temperature amplitudes. Soil water recharge normally occurs in winter and early spring and is followed by depletion, beginning in upper and progressing to lower soil layers (Caldwell et al. 1977). About 50% of the annual precipitation occurs within the growing season, but summer rains are seldom beneficial for plant growth and do not significantly recharge the soil unless rain is atypically heavy.

Methods and materials

Thin-walled PVC pipes (3 mm wall thickness) were used to prevent roots of established perennial species that were outside tubes from competing with roots of seedlings that were inside tubes. Each tube had a diameter of 15 cm and was similar to those used by Cook and Ratcliff (1984). Three lengths of tubes provided one control (1 cm) and two depths (5 cm, 10 cm) of root exclusion of neighboring established plants. Tubes were pressed into the soil so the upper edge of the tube was slightly below the soil surface to ensure that tubes did not attract animals nor cause water to pond inside tubes.

Each site was split by background species since mosaics of dominant species occurred naturally at each site. Within each background species, 80 sets of the three tube lengths were located and one of the four seedling species was assigned randomly to each set.

The experimental design was a split-split-plot design with three wholeplots (established perennial species referred to henceforth as background species Ar. tridentata, Ag. desertorum, and Ag. spicatum). Subplots with four seedling species (Ar. tridentata, Ag. desertorum, Ag. spicatum, and B. tectorum) and subsubplots with three tube lengths (1 cm, 5 cm, and 10 cm) were completely randomized and replicated 20 times within each wholeplot. We realize that wholeplots were not replicated and we therefore cannot separate site effects from background species effects. However, we feel that the area, about 1 ha per background species, was large enough that we can infer that the major impact was caused by the background species.

Distribution of roots of background individuals relative to the 10-cm tubes was quantified to determine if roots from neighboring plants grew vertically into tubes. A pair of soil samples was removed from inside and outside each tube for 10 replicates with Ar. tridentata as the background vegetation and with either Agropyron species as the seedling species. Roots were separated from the soil, and 50 root segments were randomly selected from each sample.

Live roots of Ar. tridentata were distinguished from grass roots by using a fluorescence technique (Caldwell and Virginia 1988). Roots were placed on a glass plate, soaked in 2N NaOH, and covered with chromatography paper. The basic extract was dried and observed under a UV-A lamp. Artemisia roots were distinguished from grass roots by color and intensity of fluorescence. The percentage of Ar. tridentata roots in each sample was determined and a one-tailed t-test for paired comparisons was used to test if the percentage of roots outside tubes was significantly greater than inside.

Seeds of B. tectorum, of the two Agropyron species, and of Ar. tridentata were collected at each site from randomly chosen plants on 26 June 1987, on 17 August 1987, and on 4 November 1987, respectively. After cleaning, 50 seeds were sown into each tube in the first week of December 1987 and in the last week of November 1988. Seeds were sown at the same site from which they were collected. After germination, seedlings were thinned to 20 individuals per tube, giving a density of about 1100 seedlings m⁻². This density may be higher than natural densities for Ag. spicatum but is in the normal range of densities for the other three species (Mack and Pyke 1984; Owens and Norton 1989; Pyke 1990). Each seedling was marked with a wire hoop around its base to ensure that the same individual was monitored throughout its life.