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IMPACT OF ROOT COMPETITION ON SURVIVAL AND
GROWTH OF SEEDLINGS OF IMPORTANT
GREAT BASIN SPECIES

by

Günther Reichenberger

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Range Ecology

Approved:

Major Professor

Committee Member

Committee Member

Dean of Graduate Studies

UTAH STATE UNIVERSITY
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Günther Reichenberger

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ABSTRACT

Impact of Root Competition on Survival and
Growth of Seedlings of Important
Great Basin Species

by

Günther Reichenberger, Master of Science
Utah State University, 1989

Major Professor: Dr. David A. Pyke
Department: Range Science

Belowground competition is pronounced in the arid Great Basin sagebrush ecosystem. 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 Ar. tridentata, Ag. desertorum, Ag. spicatum, and Bromus tectorum. Furthermore, growth rates of Ar. tridentata seedlings and seed production of B. tectorum were assessed.

The probability of a seedling being alive versus dead significantly depended on the seedling species, the neighboring adult species, and on the depth to which root competition was excluded. As seedlings, Agropyron species did not differ in their competitive abilities, whereas Ar. tridentata seedlings showed higher survival rates than

either perennial grass. Bromus tectorum, on the other hand, maintained much higher survival rates than any perennial seedlings.

Established Ar. tridentata was more competitive in reducing seedling survivorship than either Agropyron species. Seedling survival significantly increased with greater depth of root exclusion for the perennials but had no significant effect on seedling survival of B. tectorum. Height and growth rates 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 lowest with Ar. tridentata.

Life cycle tables for B. tectorum showed that even though root exclusion had no impact on survivorship it did increase seed production and thereby increase the seed population of B. tectorum in the next generation.

(67 pages)

INTRODUCTION

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 density of inter- or intraspecific competitors (Harper 1977). However, little is known about the importance of competition on the abundance and dynamics of plant populations (Watkinson 1986). For competition to influence population dynamics of species that coexist within native communities, competition must negatively impact their reproduction or the survival. Inferences about the impact of competition on community dynamics can be made only when mechanisms of competition are understood (Strong 1983) and when the impacts of those mechanisms upon the population dynamics of species that makeup those communities are also understood.

Sufficient evidence exists to show that competition is important in regulating growth of plants in arid and semiarid communities (Fowler 1986). In many studies, competition was assessed by removing the potential competitor and comparing survival or reproduction against

treatments where competitors were not removed. However, Parker and Root (1981) have illustrated how plant removal may result in herbivore removal, thus confounding the effect of competition with the effect of herbivory on plant fitness.

When evaluating plant competition, it is important to separate effects of competition from other effects. Therefore, Cook and Ratcliff (1984) used a different approach to evaluate plant interactions. Rather than removing competitors, they used root exclusion tubes to evaluate the effects of root competition from established neighbors on seedling development. The advantage of this approach is that root competition can be evaluated without disturbing potential competitors. 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 dominant species of the same age. 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 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).

Differential survival of *Ar. tridentata* has been related to differences in water extraction among competitive species. Survival and reproduction of transplanted indicator plants of *Ar. tridentata* decreased when they competed with adult *Ag. desertorum* compared with those that competed with *Ag. spicatum* for water (Eissenstat and Caldwell 1988). However, little is known about the influence of competition on fitness components of species with overlapping life history stages (Owens and Norton 1989). Because competitive interference belowground is more pronounced than aboveground in the Great Basin sagebrush ecosystem (Caldwell and Fernandez 1975; Caldwell et al. 1983; Caldwell and Richards 1986), the importance of root competition from established plants on seedling survival and annual plant reproduction was emphasized in this study.

The objective of this study was to evaluate the

¹ Recent taxonomic revision of the North American Triticeae (Barkworth and Dewey 1985) recommends a name change to *Pseudoroegneria spicata* (Pursh) A. Löve subsp. spicata.

impact of root competition in the upper 10 cm of the soil profile on fitness components of seedlings of important Great Basin species. I compared seedling survival of Ar. tridentata, Ag. desertorum, Ag. spicatum, and Bromus tectorum L., an introduced annual grass, when competing with established perennials. In addition, growth rates of Ar. tridentata and seed production of B. tectorum were compared among individuals competing with the three established perennial species.

STUDY AREA

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 (Rydb.) Beetle or by one of the perennial grasses are distributed in a mosaic pattern at that 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 and was aeriually seeded with Ag. desertorum, which resulted in a mosaic pattern of

dominant established perennials similar to the Petersboro site. For further information about this site see Eissenstat and Caldwell (1988).

Both sites were dominated by Ar. tridentata, Ag. desertorum, and Ag. spicatum; but they differed in that Petersboro had greater species diversity and had a greater component of forbs in the community than the Curlew site.

The dryness of the air and the deficiency of moisture during the growing season make the region more arid than would be expected from climatological data. Long-term average annual precipitation at Logan, the closest station to Petersboro, is 490 mm but is only 305 mm at Snowville, the closest station to Curlew (Appendix A).

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 at the upper and progressing to the 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 (Appendix A). Soil layers below the uppermost layer are not significantly recharged during the summer unless there are atypically heavy rains.

METHODS

Thin-walled PVC pipes (3 mm wall thickness) were used to exclude roots of established perennial species outside tubes from competing with roots of seedlings 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 (1 cm, 5 cm, and 10 cm) 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 that 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 the 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 sub-subplots with three tube lengths (1 cm, 5 cm, and 10 cm) were completely randomized and replicated 20 times within

each wholeplot. I 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.

Artemisia tridentata roots were distinguished from grass roots by using a fluorescence technique that distinguishes live roots of Artemisia from those of grasses (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, paired t test 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 their sites 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. 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. Each seedling was marked with a wire hoop around its base to ensure tracking the same individuals throughout their life cycle.

Seed germinability for ten samples of 50 seeds of each species was tested in a growth chamber (Environmental Growth Chambers, Model M-13, Chagrin Falls, Ohio, USA) under 14/10 hours day/night time and 25/15°C day/night temperature. Differences in germination percentage were tested using ANOVA.

Censuses of populations in Curlew began with first emergence of seedlings on 27 March 1987. Seedlings were monitored biweekly for survival from germination to maturation for B. tectorum and from germination until spring of the second year or until all individuals died for the three other seedling species. The impact of root competition on the seed production of B. tectorum was measured by counting the seeds produced by each individual

that survived to the end of June, 1989, at both Curlew and Petersboro.

Seedling height of Ar. tridentata was measured several times at both sites during the growing season of 1989. Height was measured from the soil surface to the highest leaf tip. Specific growth rates (GR) were calculated as

$$GR = (H_{t+1} - H_t) * I^{-1}$$

where H_t is height of seedlings in mm at time t , and I is the time interval in days.

Differences in survival rates of seedlings among treatments were tested using Peto and Peto's logrank test ($P < 0.05$, Peto and Pike 1973; Pyke and Thompson 1986). A hierarchical logit model was calculated using the CATMOD procedure in SAS to test overall survival at the last date when all species had sufficient individuals alive to give an adequate fit of the model for all treatments. Since a maximum of only three factors occurred for each model, the most effective way of choosing a model was to calculate goodness-of-fit test statistics (likelihood ratio chi-square, G^2) for all possible models. The model fits the data well if G^2 has a large observed significance (P) value (Heisey 1985). The simplest model that fit the data was chosen according to the criteria of model selection in Fienberg (1980). The odds of being alive versus dead were calculated from the maximum likelihood

estimates of each treatment. Unplanned multiple comparison tests for the maximum likelihood estimates of each factor (seedling species, background species, and depth of root exclusion) were calculated for the main effects using the formula in Heisey (1985).

Differences in Ar. tridentata height during the first week of June and in seed production of B. tectorum were tested by a split-plot design ANOVA ($P < 0.05$) that was combined over sites for 1989 or over years for the Curlew site.

RESULTS

The root exclusion tubes appeared to be an effective barrier to roots of established Ar. tridentata. The percentage of Ar. tridentata roots outside 10-cm tubes was significantly higher than that inside tubes (Table B.1).

Annual precipitation at both sites in 1988 was about 40% below the long-term average (Appendix A), resulting in severe drought that limited the experimental results to data on Ar. tridentata seedlings in all three backgrounds at the Curlew site only. Germination of the grasses was very low (<1%). Those few B. tectorum individuals that survived until maturation were grazed by rodents before seed production. With higher winter and spring precipitation in 1989 (Fig. 1), overall germination was sufficient to establish individuals of all four

seedling species in all treatments in Curlew and of Ar. tridentata seedlings in all treatments in Petersboro.

In the first year, survivorship curves for Ar. tridentata seedlings significantly differed among tube depths in all backgrounds (Table B.2). For seedlings competing with adult Ar. tridentata, survival rates in the 10-cm and 5-cm tubes were similar until the end of June 1988; whereas survival rates of plants in controls showed increased mortality almost from the beginning of May (Fig. 2.a).

Established Ag. spicatum plants appeared to be the least competitive background species for seedlings of Ar. tridentata (Fig. 2.c). Artemisia tridentata seedlings had the highest survival rates when competing with established Ag. spicatum than with the other two background species. Even though seedling mortality over the summer was too high for statistical analyses of survival rates, the only individuals of Ar. tridentata that survived the summer drought were in 10-cm tubes in the Ag. spicatum background.

Survival rates for Ar. tridentata seedlings growing in Ag. desertorum backgrounds (Fig. 2.b) were slightly lower than survival rates for seedlings in the Ar. tridentata backgrounds (Fig. 2.a) in the two lengths of root exclusion but were similar in the controls.

Survival rates of Ar. tridentata in 1989 were similar

to those in 1988. Survival rates of Ar. tridentata seedlings significantly increased with greater depths of root exclusion (Figs. 3-6, Table B.2). Divergence of survivorship curves occurred later in the growing season in 1989 than in 1988, and the differences in survival rates among tube depths were generally not as pronounced in 1989 as in 1988 (c.f., Fig. 2 to Figs. 3.a, 4.a, 5.a, and 6).

The general pattern of survivorship with the greatest proportion of survivors in 10-cm tubes and fewest in controls was observed for all seedling species, although it was significant only for the perennial seedlings (Figs. 3-5) with Ag. spicatum seedlings competing with established conspecifics being the exception among perennials (Fig. 5.c and Table B.2). Differences in survival rates among tube depths for perennial seedlings may seem small due to the log scale, but they do exist based on the logrank test (Table B.2).

Depth of root exclusion did not significantly increase the survival rate of B. tectorum, although the same general pattern of survival that was noted for the perennial seedlings also occurred for B. tectorum.

Survival rates of Ar. tridentata seedlings differed among tube depths for all treatments in Petersboro (Table B.2) and was similar to survival rates in Curlew in the same year. The impact of depth of root exclusion on

survival (the diverging pattern of the curves) was more pronounced in the Ag. spicatum background (Fig. 6.c) in Petersboro than it was for Ar. tridentata seedlings in the Ag. spicatum background in Curlew in 1989 (Fig. 5.a).

Survival rates for seedling species were highest when seedlings grew in Ag. spicatum (Fig. 5) backgrounds than when seedlings competed with either of the other perennial species. Overall survival was higher for seedlings competing with adult Ag. desertorum (Fig. 4) than for those competing with adult Ar. tridentata (Fig. 3). Individuals of all four seedling species survived until October when competing with Ag. desertorum.

In Petersboro, background species had similar competitive impact on survival as in Curlew. Survival of Ar. tridentata seedlings was lowest in the controls in the Ar. tridentata background (no survivors) and highest both in Ag. desertorum and Ag. spicatum (Fig. 6).

For Curlew 1989, the simplest logit model that fit these data included all main effects (seedling species, background species, and tube depth) and all 2-way interactions. The 3-way interaction was not significant and was therefore eliminated from the saturated model during model formation (Table B.4).

For all perennial seedlings, the probability of dying by the end of the experiment in Curlew in 1989 was greater than the probability of surviving (Fig. 7). Artemisia

tridentata seedlings had a slightly better chance of surviving than Ag. desertorum seedlings but did not significantly differ from survival odds of Ag. spicatum. The two Agropyron species did not significantly differ in their survival odds. However, the annual species B. tectorum, was 22 times more likely to survive than to die (Fig. 7).

The competitive impact of adult perennials on seedling survival differed significantly among background species (Fig. 8). Only seedlings competing with Ag. spicatum had a slightly higher chance of surviving than dying (Table B.4). Seedlings that grew in the most competitive background, Ar. tridentata, had the highest odds of dying.

Seedlings showed significantly greater survival odds with increasing depth of root exclusion (Fig. 9). Eliminating root competition between seedlings and adult plants to a depth of 10 cm increased the odds of seedlings surviving until they equaled their odds of dying.

Although the interaction between seedling and background species was significant, all seedlings had equal odds of surviving versus dying when grown in backgrounds of Ag. spicatum. The maximum likelihood estimates for Ag. spicatum as a background species in combination with any seedling species explained no additional probability of surviving versus dying than the

seedling species main effect alone (Table B.3 and B.4). Artemisia tridentata, and to a lesser extent Ag. desertorum, are the background species that significantly affect the probability of seedling survival.

For Ar. tridentata seedlings in three backgrounds at Curlew and at Petersboro in 1989, the best model includes both main effects (site, background species, and tube depth) and two interaction terms (Table B.6). Seedlings competing with adult Ar. tridentata had lower chances of surviving versus dying than those competing with adult Agropyron species. Survival odds for Ar. tridentata seedlings competing with Ag. spicatum were lower than for seedlings competing with Ag. desertorum in Petersboro, but Ag. desertorum was more competitive than Ag. spicatum in Curlew (Fig. 10). However, the survival odds of Ar. tridentata seedlings competing with Ar. tridentata in Petersboro were 40-fold lower than of seedlings competing with either Agropyron species. Seedlings showed significantly greater survival odds with increasing depth of root exclusion in rank order to those in Curlew in 1989 but much lower in magnitude (Table B.4 and Table B.6).

A single height measurement of Ar. tridentata from the first week of June was used to make comparisons between Curlew in 1988 and 1989 and between Curlew and Petersboro in 1989 (c.f., Figs. 2-6 to Fig. 11). Artemisia tridentata height (Fig. 11) responded to

exclusion from root competition in a similar fashion as did survivorship. Seedlings of Ar. tridentata were significantly taller in the 10-cm tubes than in 5-cm tubes. Individuals in control tubes were significantly shorter than those in either of the two depths of root exclusion. This pattern was observed in both years as well as on both sites. Seedlings of Ar. tridentata in Curlew were taller in 1989 than in 1988; however, they were taller in Petersboro than in Curlew in 1989.

When Ar. tridentata seedlings competed with established Ar. tridentata, they were significantly shorter than seedlings that competed with either Agropyron species. However, heights of Ar. tridentata seedlings that competed with either Agropyron background did not significantly differ (Tables B.7 and B.8).

Growth rates of Ar. tridentata seedlings in Petersboro and in Curlew were lower in control tubes than in either depth of root exclusion until mid-June, when growth ceased. Growth rates in the latter part of the growing season were so low that depth of root exclusion no longer had an impact on plant development (Figs. 12 and 13).

Seed production of B. tectorum in 1989 increased significantly with depth of root exclusion on both sites (Fig. 14). Bromus tectorum in Curlew produced significantly more seeds per individual than in

Petersboro. Seed production in the Ar. tridentata background was the lowest on both sites but increased more in the other two backgrounds in Curlew than it did in Petersboro (Fig. 15). The ANOVA table for seed production of B. tectorum is presented in Table B.9.

Life cycle diagrams were constructed for B. tectorum from germination until maturation and seed production in the second year. A high proportion of plants were infected with the smut fungus Ustilago bullata Berk., which reduced the number of viable seeds. Overall seed production was calculated both for the population with smut infection and for an hypothesized case of no infection, assuming that the number of seeds produced per individual would be equal in both the uninfected and the infected populations (Figs. 16-18).

Even though survivorship did increase slightly with depth of root exclusion, total seed output after one growing season was driven mainly by seed production. In the controls, 1000 B. tectorum seeds produced only 147 seeds for the next generation when grown in the Ar. tridentata background and when smut infection was included in the calculation (Fig. 16). Even for the case of no U. bullata infection, an output of 312 seeds suggests a population decline when grown in an Ar. tridentata background. With the same background species, root exclusion of 10 cm increased the reproductive success of

B. tectorum, but even without fungus infection the population declined 20 % in the next generation.

Bromus tectorum competing with adult Agropyron species (Fig. 17 and 18) showed greater reproductive success in the controls and in all depths of root exclusion than when competing with adult Ar. tridentata. However, only the hypothesized case with no U. bullata infection would have resulted in a full replenishment of seeds in the controls. Seed output in the controls was lower in Ag. desertorum than in Ag. spicatum background regardless of smut infection. Excluding root competition to depths of 10 cm may result in stable populations of B. tectorum with U. bullata infection in the Ag. desertorum background and may result in increasing population sizes without infection in both Agropyron backgrounds.

DISCUSSION

Results of these experiments clearly showed that root competition had a major impact on fitness components of seedlings, namely survivorship of perennials and seed production of B. tectorum. The probability of plant survival depended not only on the seedling species itself but also on the species of established neighbors with which seedlings must compete and on the depth in which roots of the seedlings must compete with roots of their established neighbors.

The greatest differences in survival probabilities occurred when comparing B. tectorum seedlings with the three perennials. Considering only survivorship, B. tectorum competed better with established perennial plants than seedlings of these perennials competed among established conspecifics.

Differences in root growth and root phenology may enable B. tectorum seedlings to escape the zone of highest root competition more easily than perennial seedlings and therefore contribute to the explanation of why survival of B. tectorum was greater than survival of any perennial seedling species in any treatment. Primary roots of B. tectorum grow at lower temperatures than Ag. spicatum roots. Roots of B. tectorum grow to depths of 20 cm before branching while primary roots of seedlings of both Agropyron species branch near the surface (Harris 1967; Harris and Wilson 1970; Harris 1977) and therefore Agropyron seedlings compete with the background vegetation in the zone of highest root density of established perennials (Caldwell and Richards 1986). Aguirre (1989) showed that root length, root dry weight, and the number of seminal roots of B. tectorum seedlings are greater than those of competing Agropyron seedlings.

The ability of B. tectorum to coexist with established perennials and to successfully invade native vegetation in the Intermountain West is enhanced by its

multiple fecundity schedule and its annual life cycle (Mack and Pyke 1983). Being an annual, allows B. tectorum to complete its life cycle early and therefore avoid the summer drought that is responsible for the death of most perennial seedlings.

The greatest decline in survival rate for all perennials coincided with reduced precipitation in summer and was consistent with the period of greatest mortality for perennial seedlings in the sagebrush ecosystem noted by previous studies (Salihi and Norton 1987; Owens and Norton 1989; Pyke 1990). The later divergence of survivorship curves of Ar. tridentata seedlings at Curlew in 1989 when compared to 1988 indicated that resources became limited at an earlier time in 1988 than in 1989.

As seedlings, Agropyron species did not differ in their abilities to compete with established vegetation (Fig. 7, Table B.4). Pyke (1990) noted few differences in emergence and survival of seedlings of Aq. desertorum and Aq. spicatum. However, demographic factors other than seedling survival, such as seed dispersal time relative to seed predation, may influence replacement abilities of the Agropyron species.

However, this similarity in the competitive ability of the Agropyron species apparently changes as these grasses mature. Mature Aq. spicatum plants were more tolerant of seedling establishment than mature Aq.

desertorum in Curlew. The competitive advantage of established Ag. desertorum over established Ag. spicatum when competing for resources is attributed to its higher root density, a higher proportion of lateral roots, and the fact that its roots are thinner than roots of Ag. spicatum (Caldwell and Richards 1986).

The overall survival probability of Ar. tridentata seedlings was mainly affected by the site, the depth of root exclusion, and by established Ar. tridentata neighbors in Petersboro. The differences in survival odds of Ar. tridentata seedlings growing with established neighbors of Ar. tridentata and of Agropyron was much more pronounced in Petersboro than in Curlew (Fig. 10). Also, the order of Ar. tridentata survival between the two Agropyron backgrounds was reversed in Petersboro versus Curlew. The differences in the tolerance of Agropyron backgrounds to Ar. tridentata establishment may be related to the subspecies of Ar. tridentata at the two sites. The Petersboro site has ssp. vaseyana, while the Curlew site has ssp. wyomingensis. Most studies concerning the competitive ability of Ar. tridentata were conducted using ssp. vaseyana, and to our knowledge little is known about the differences in competitive abilities between ssp of Ar. tridentata.

The overall survival odds for Ar. tridentata seedlings were 6 times lower in Petersboro than in Curlew.

The greater probability of Ar. tridentata seedlings dying in Petersboro compared with Curlew may be related to the differences in subspecies between the sites. Even though Petersboro receives more precipitation, which seems to be reflected in the rapid increase of Ar. tridentata growth rates early in the growing season, the effect of the southfacing slope of this site may override other factors in influencing survival rates of seedlings later in the growing season.

Excluding root competition at depths of only 5 cm increased seedling survival. Root competition for resources in those shallow soil layers is intense early in the growing season when moisture is readily available. Reduced competition from neighbors at that time may help seedling roots penetrate to greater depths, and therefore more effectively exploit resources later in the growing season when moisture and nutrients are only available deeper in the soil profile. The decline of seedling survival rates in summer may be the effect of differential root growth in spring.

Soil disturbances may form gaps in the rooting zone that allow plants to establish and coexist. Gaps may therefore determine the relative abundances of species in a community (Denslow 1985). However, aboveground gaps may not coincide with belowground gaps, which lack root competition from neighbors. Belowground gaps may play a

more important role for seedling survival of perennials than for B. tectorum seedlings within this ecosystem.

Even though survivorship of B. tectorum was not affected by root competition as much as survivorship of the perennials, all major factors that contribute to the fitness of B. tectorum must be considered. Conclusions about the population dynamics of Bromus drawn from survivorship or seed production alone must be modified. Life cycle structograms include the major factors influencing overall fitness and indicate that Ar. tridentata withstands spread of B. tectorum better than adult Agropyron. In control treatments, B. tectorum produced more seeds when associated with Ag. spicatum, which has been shown to be more easily invaded by B. tectorum than Ag. desertorum.

Reproduction of B. tectorum is significantly affected by biotic interactions other than competition, such as grazing (Pyke 1986) or pathogens. Infection of B. tectorum with the smut fungus U. bullata was slightly higher than reported in previously published accounts ($\leq 45\%$, Hulbert 1955; Mack and Pyke 1984). The high infection rate of U. bullata may have resulted because seeds were stored in a single container before cleaning.

Besides the classical fitness components of survivorship and reproductive success, growth at the seedling stage significantly influences the ability of a

seedlings to successfully establish (Cook 1979). Height and growth rates of Ar. tridentata seedlings significantly increased with depth of root exclusion early in the growing season. The growth rates indicate that plants responded to reduced root competition during early growth. However, growth rate differences became more apparent as resources became more limited later in the growing season.

Height and growth rates of Ar. tridentata seedlings were significantly lower in the Ar. tridentata background than in either Agropyron background, even though roots of adult Agropyron species dominate the shallower portions of the soil profile (Caldwell and Richards 1986) and even though root density of adult Ar. tridentata is lower than that of Agropyron grasses (Caldwell et al. 1985). This was counterintuitive and suggests that mechanisms other than belowground competition may have been involved. Factors that should be considered in future studies include allelopathy, aboveground competition for light, and differential abilities of species to acquire resources independent of root density.

This study demonstrated that root competition impacts fitness components of seedlings of important Great Basin species. The degree of root competition and the established species that a seedling has to compete with determine the success of seedling establishment. Even though the response of a single fitness component may vary

among species, interspecific and intraspecific competition play major roles in determining the abundance of individuals on the population level.

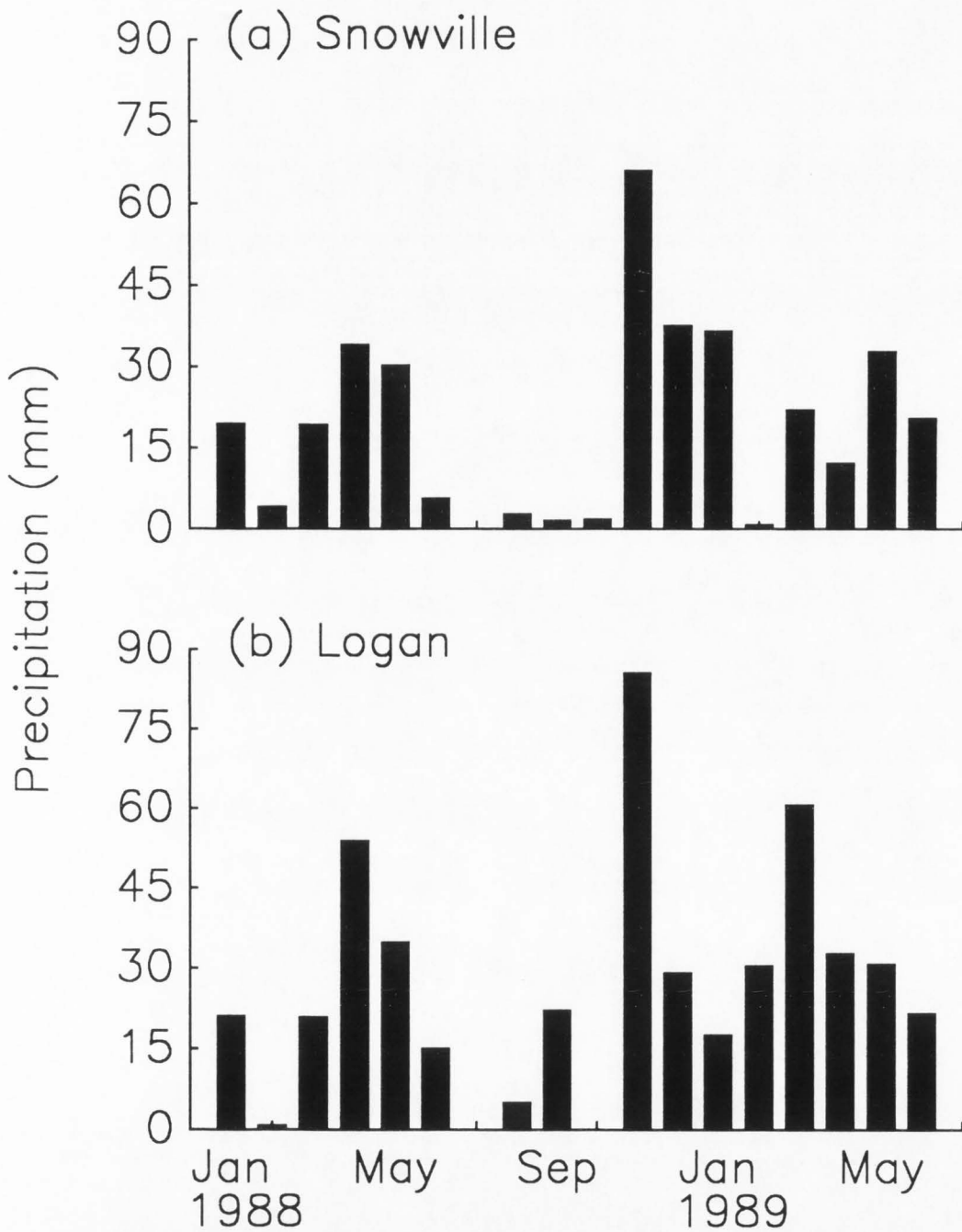


Fig. 1. Mean monthly precipitation for the Petersburg (station Logan) and Curlew sites (station Snowville) from January 1988 until June 1989.

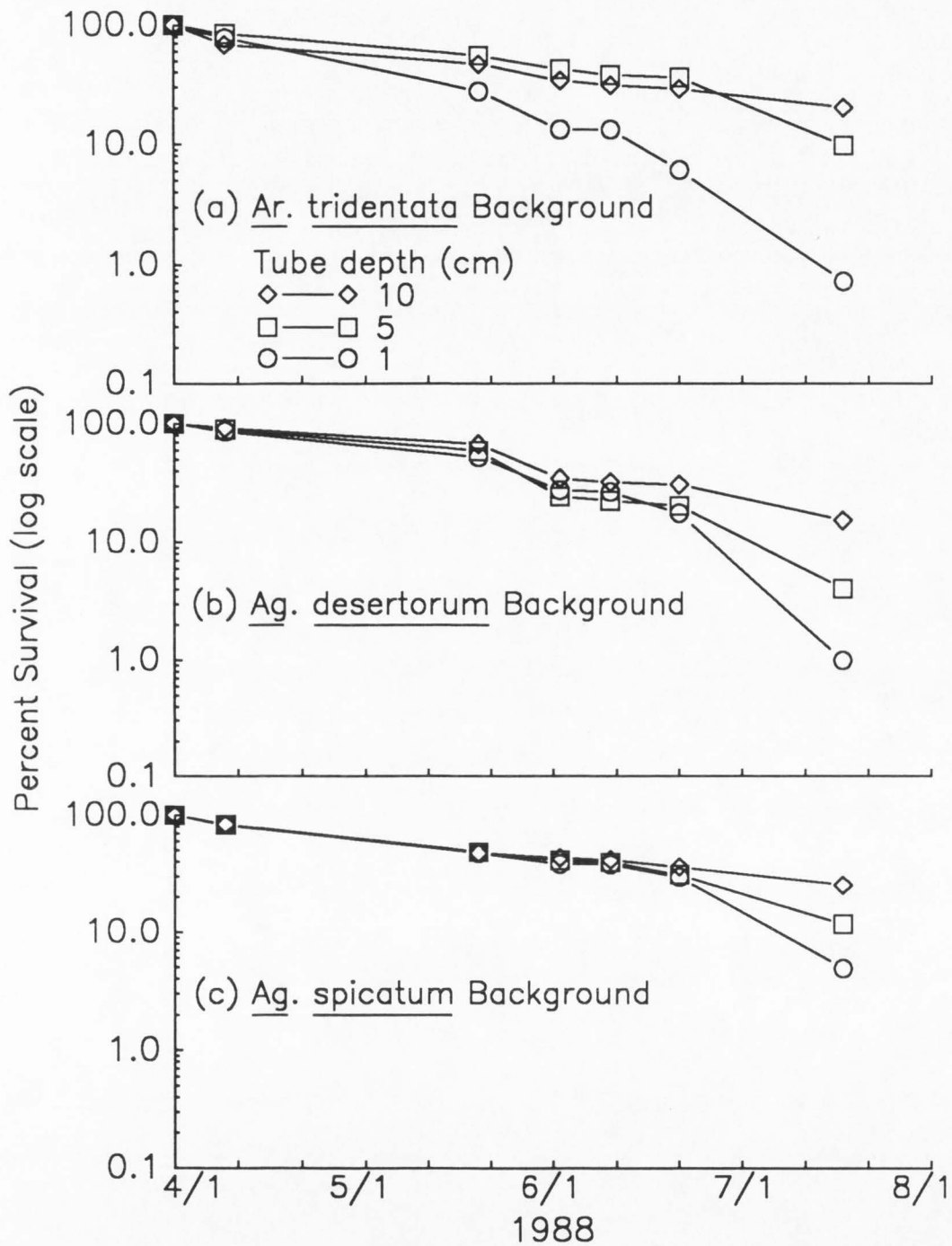


Fig. 2. Survivorship curves for *Ar. tridentata* seedlings competing with three established background species (a-c) at Curlew in 1988.

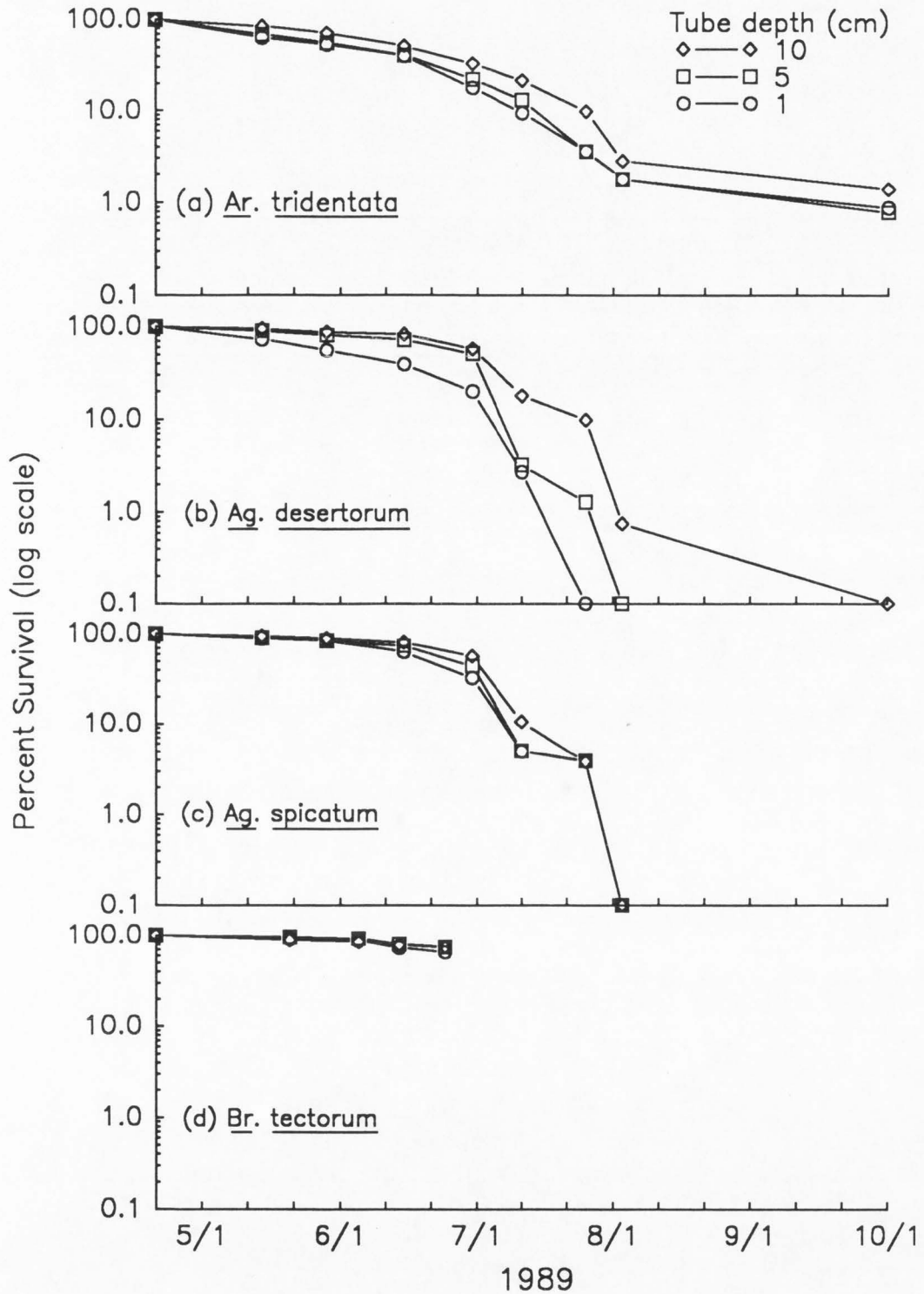


Fig. 3. Survivorship curves for four seedling species (a-d) competing with established *Ar. tridentata* at Curlew in 1989.

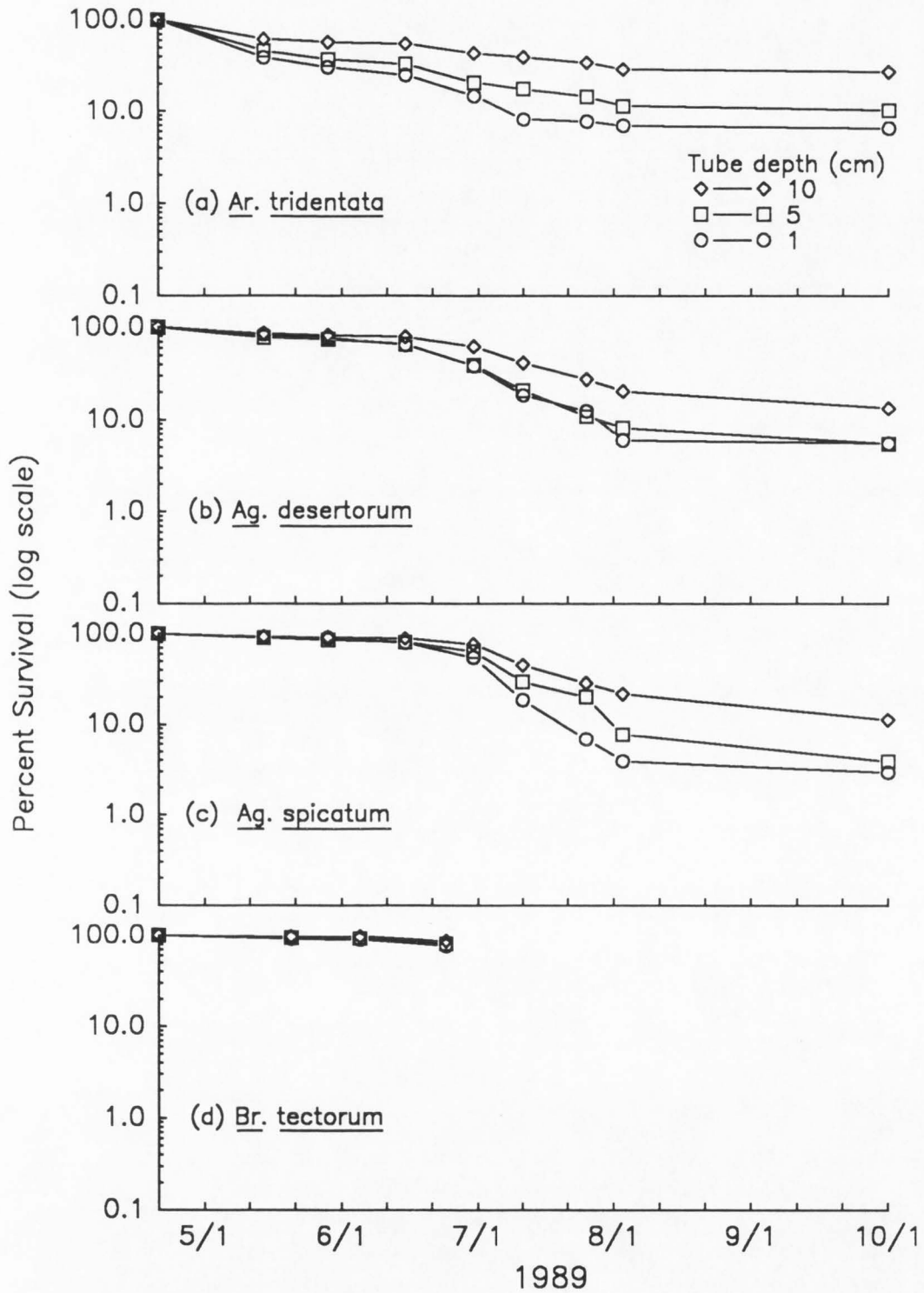


Fig. 4. Survivorship curves for four seedling species (a-d) competing with established *Ag. desertorum* at Curlew in 1989.

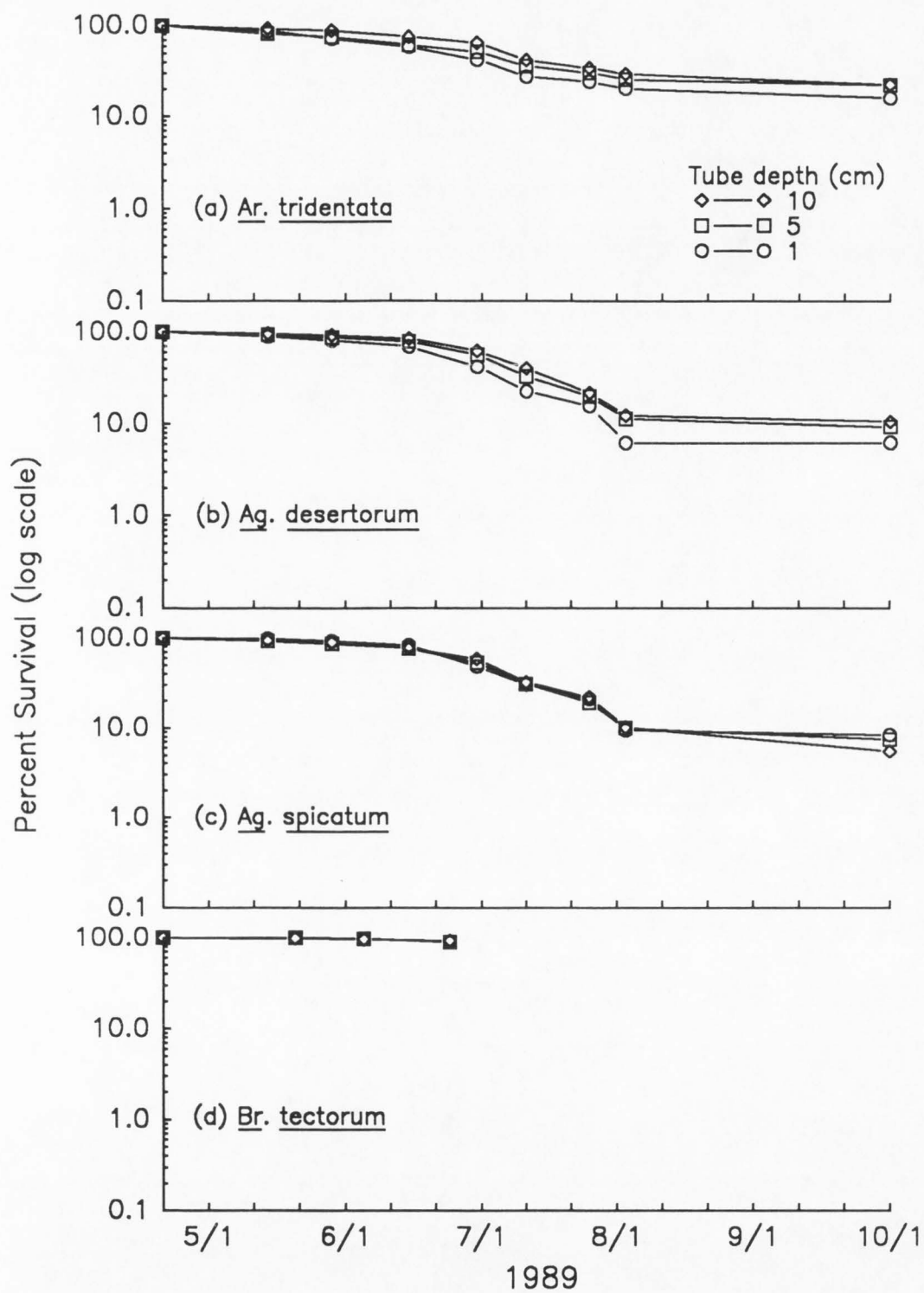


Fig. 5. Survivorship curves for four seedling species (a-d) competing with established *Ag. spicatum* at Curlew in 1989.

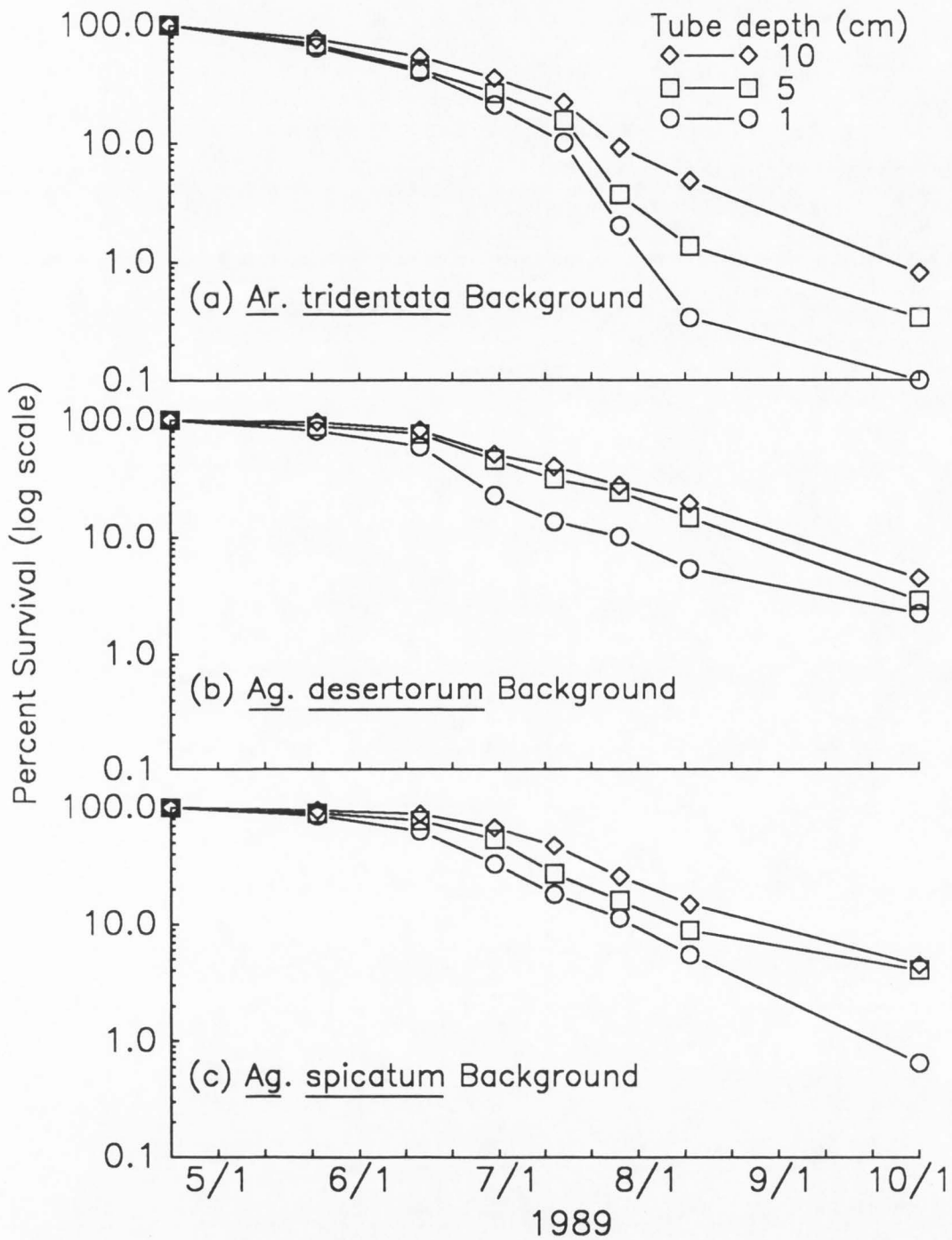


Fig. 6. Survivorship curves for *Ar. tridentata* seedlings competing with three established background species (a-c) at Petersboro in 1989.

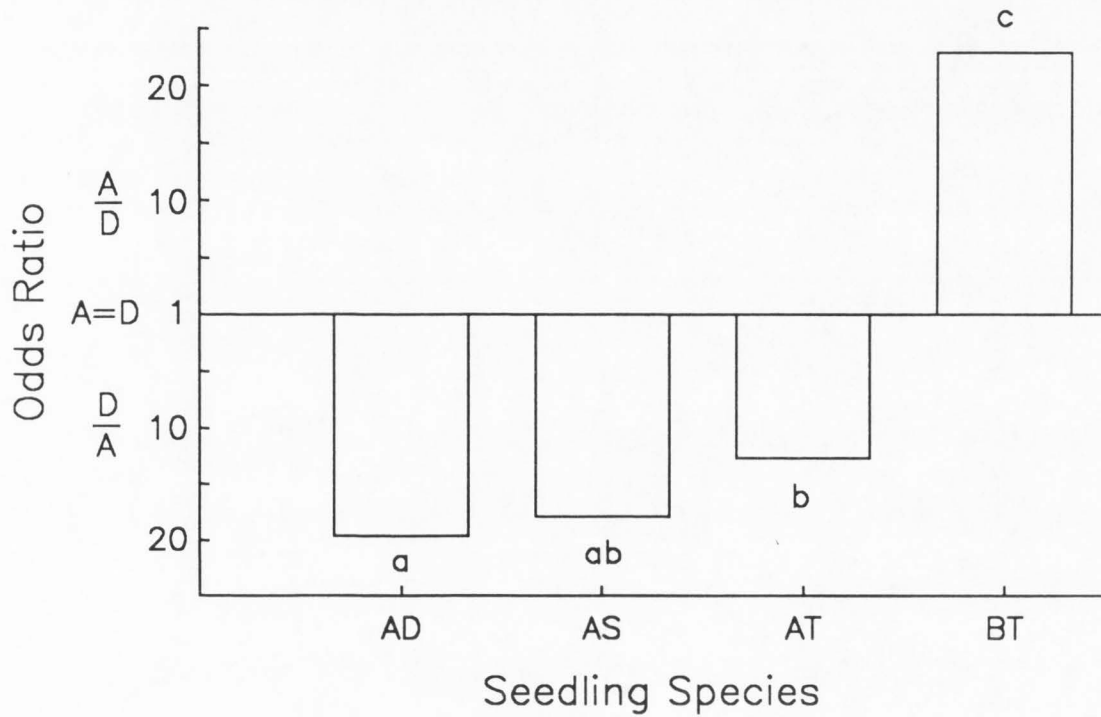


Fig. 7. Survival odds for four seedling species (AS=Ag. spicatum, AD=Ag. desertorum, AT=Ar. tridentata, BT=B. tectorum) at Curlew in 1989. Letter A represents the odds of being alive and letter D represents the odds of being dead at the end of the experiment. Different lower case letters associated with bars denote statistical differences at $P=0.05$.

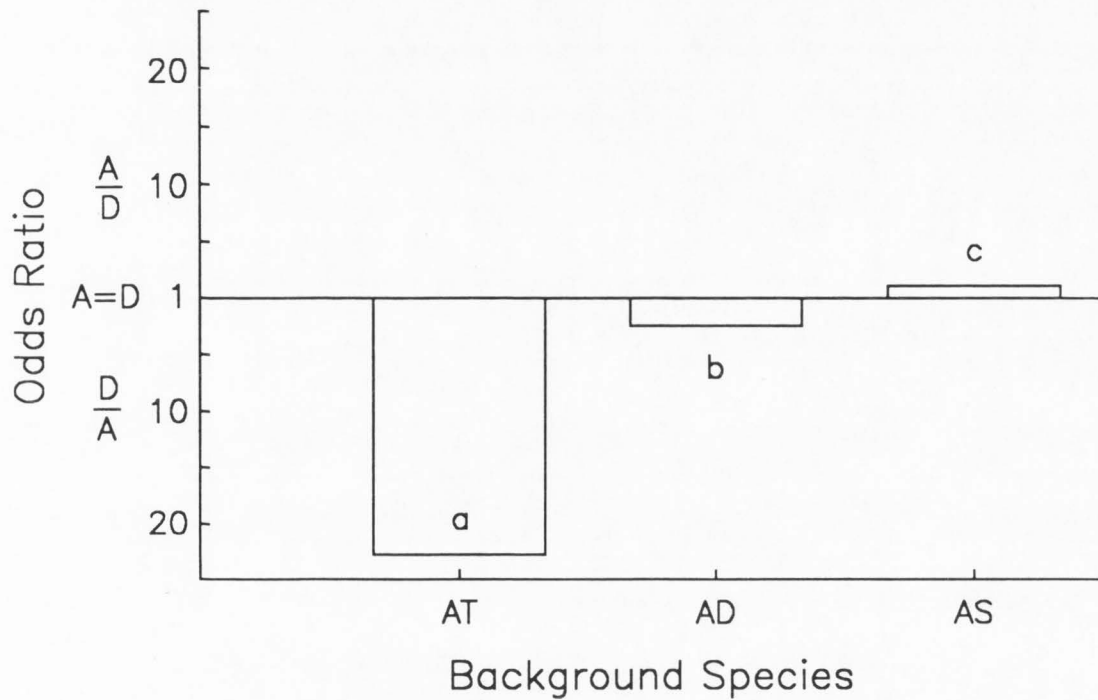


Fig. 8. Survival odds for four seedling species competing with three established background species (AS=Ag. spicatum, AD=Ag. desertorum, AT=Ar. tridentata) at Curlew in 1989. Letter A represents the odds of being alive and letter D represents the odds of being dead at the end of the experiment. Different lower case letters associated with bars denote statistical differences at $P=0.05$.

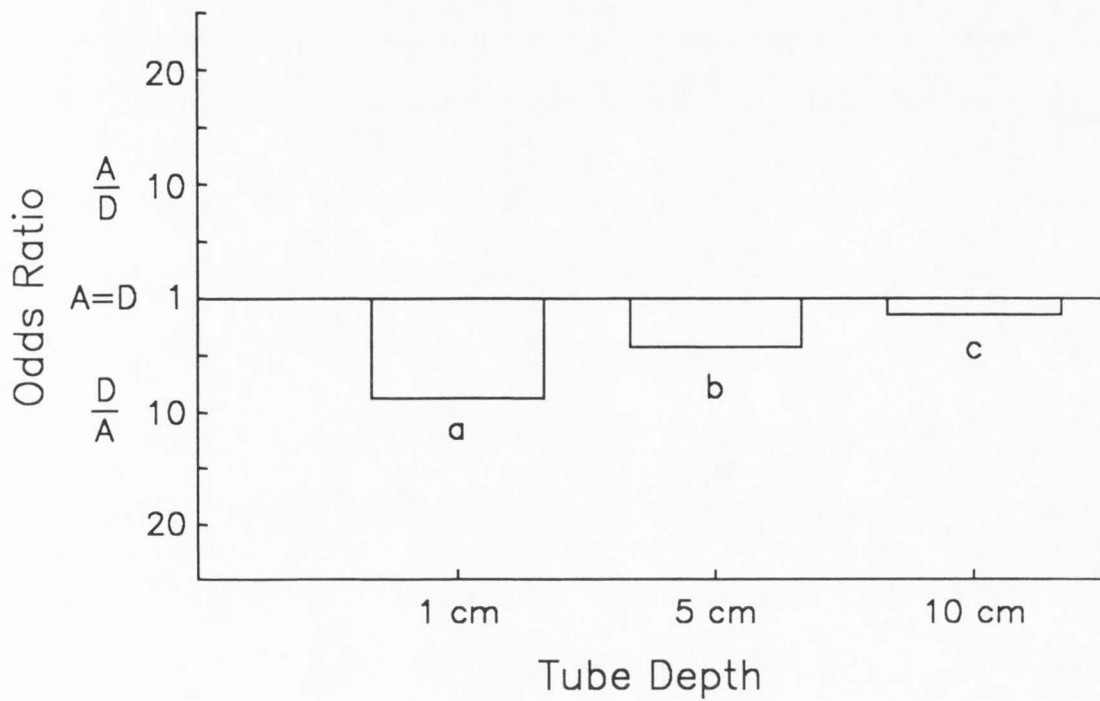


Fig. 9. Survival odds for four seedling species in three depths of root exclusion (1 cm control, 5 cm and 10 cm) at Curlew in 1989. Letter A represents the odds of being alive and letter D represents the odds of being dead at the end of the experiment. Different lower case letters associated with bars denote statistical differences at $P=0.05$.

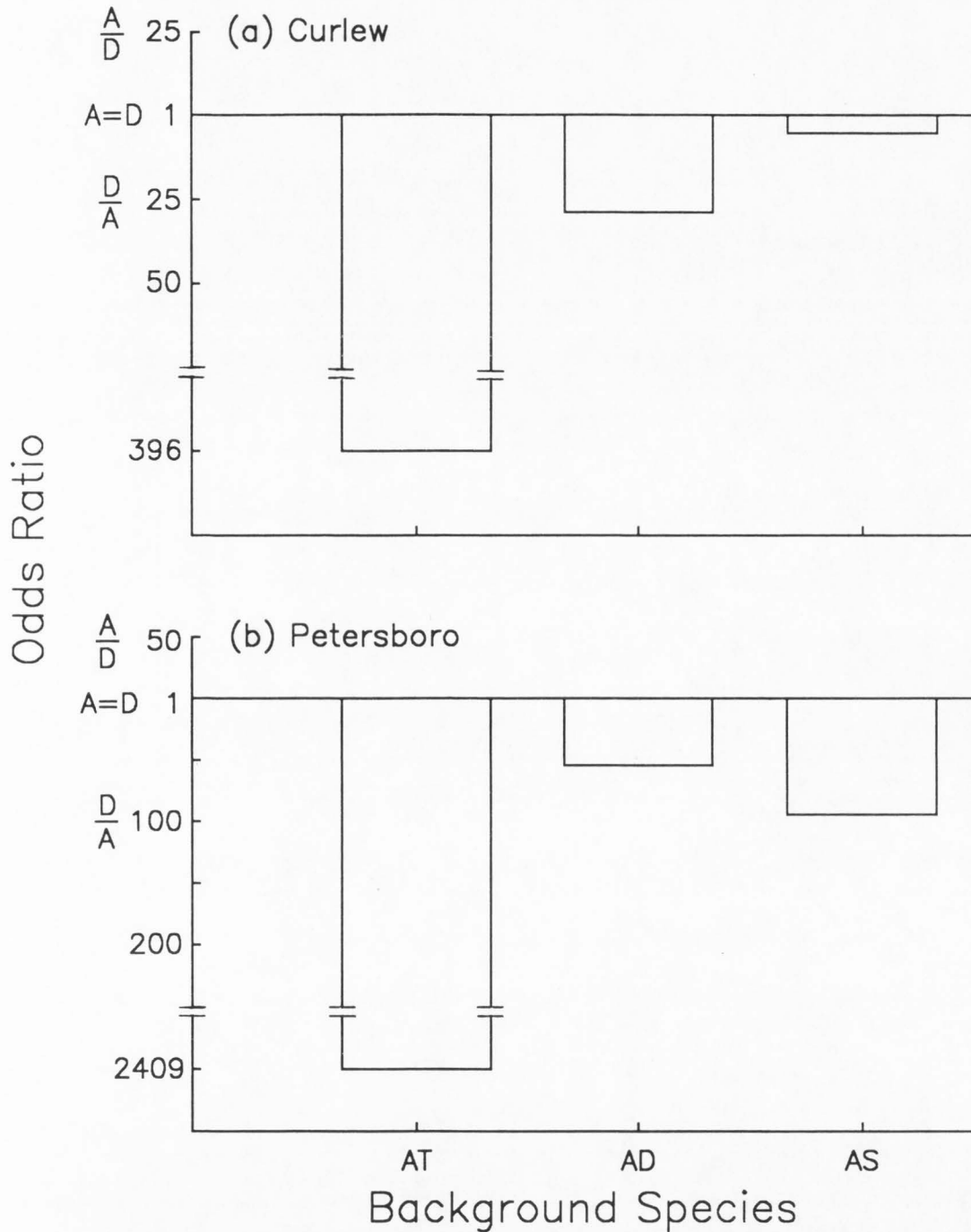


Fig. 10. Survival odds for *Ar. tridentata* seedlings competing with three established background species (AD=*Ag. desertorum*, AS=*Ag. spicatum*, AT=*Ar. tridentata*) at Curlew and at Petersboro in 1989. Letter A represents the odds of being alive and letter D represents the odds of being dead at the end of the experiment.

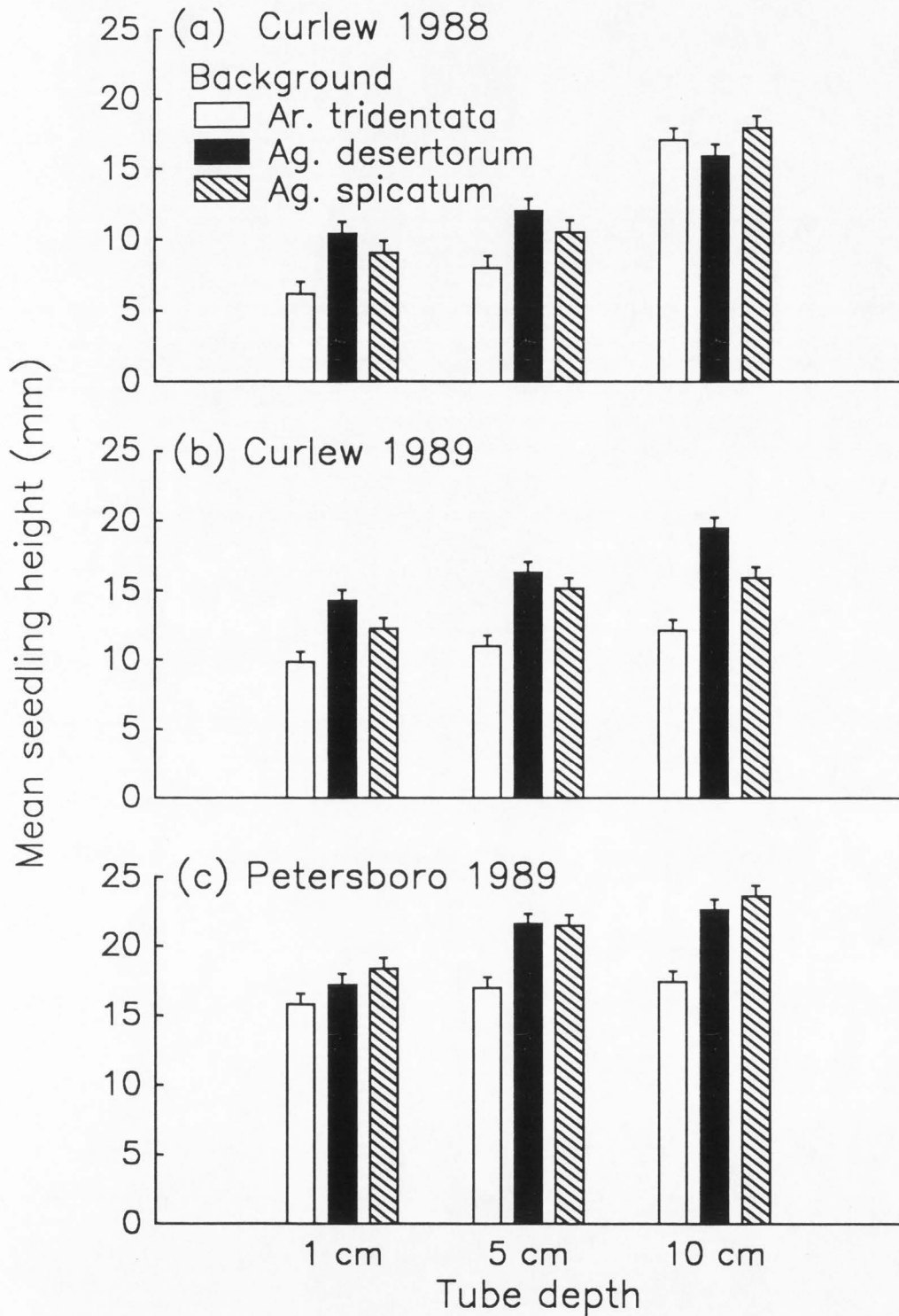


Fig. 11. Height of *Ar. tridentata* seedlings during the first week of June at Curlew in 1988 and 1989 and at Petersboro in 1989.

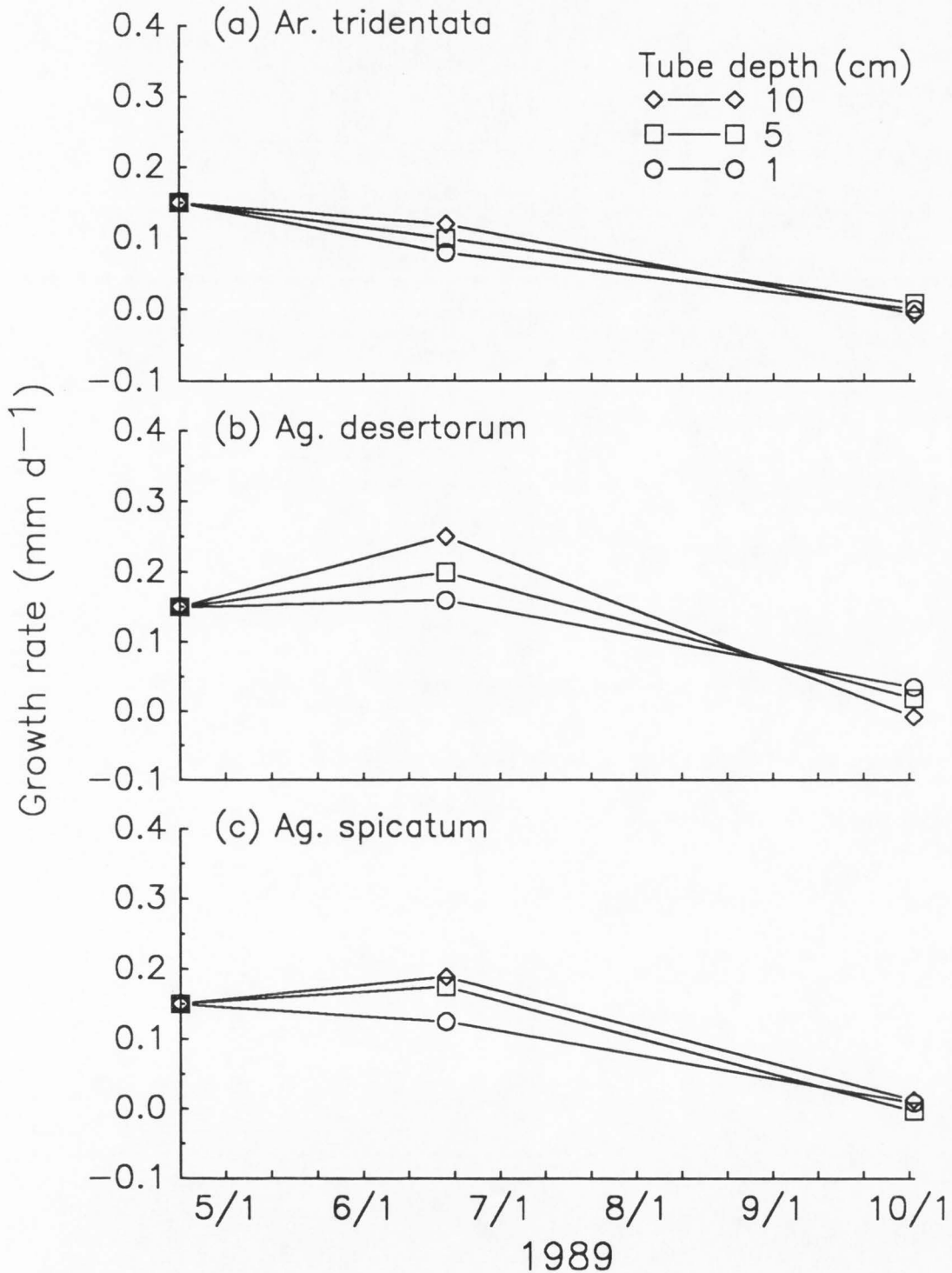


Fig. 12. Growth rates of *Ar. tridentata* seedlings competing with three established background species (a-c) at Curlew in 1989.

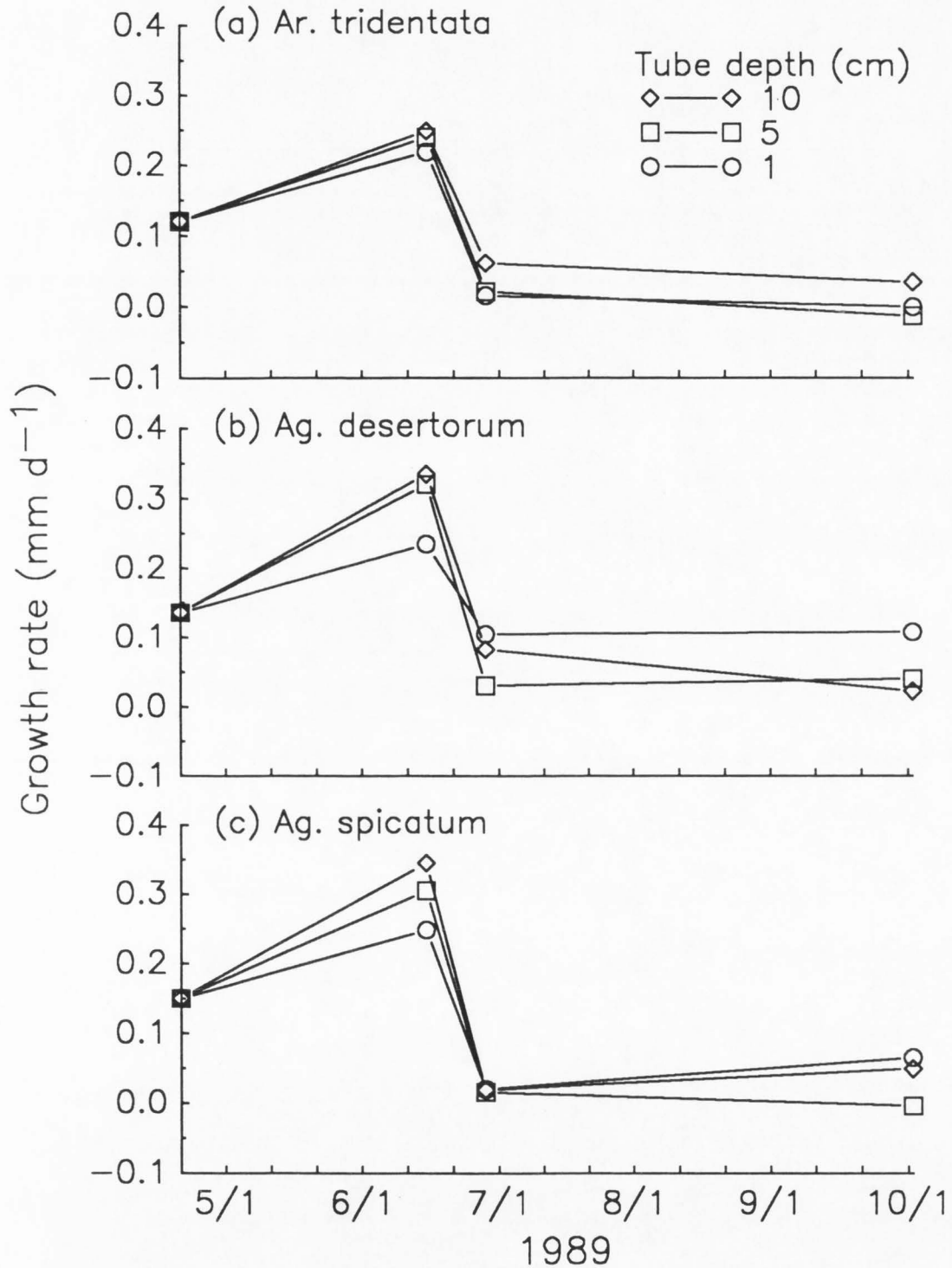


Fig. 13. Growth rates of *Ar. tridentata* seedlings competing with three established background species (a-c) at Petersboro in 1989.

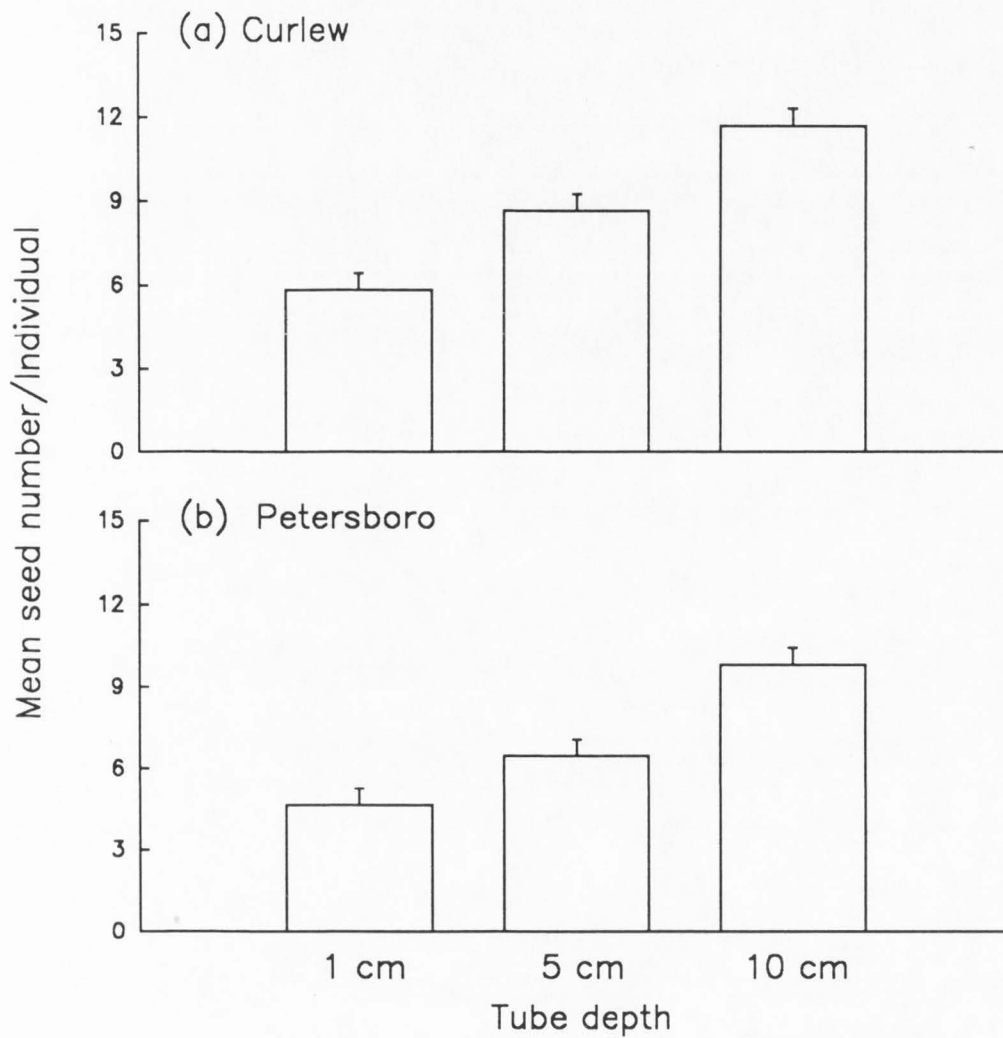


Fig. 14. Seed production of *B. tectorum* grown with three depths of root exclusion (1 cm control, 5 cm and 10 cm) at two sites (a-b) in 1989.

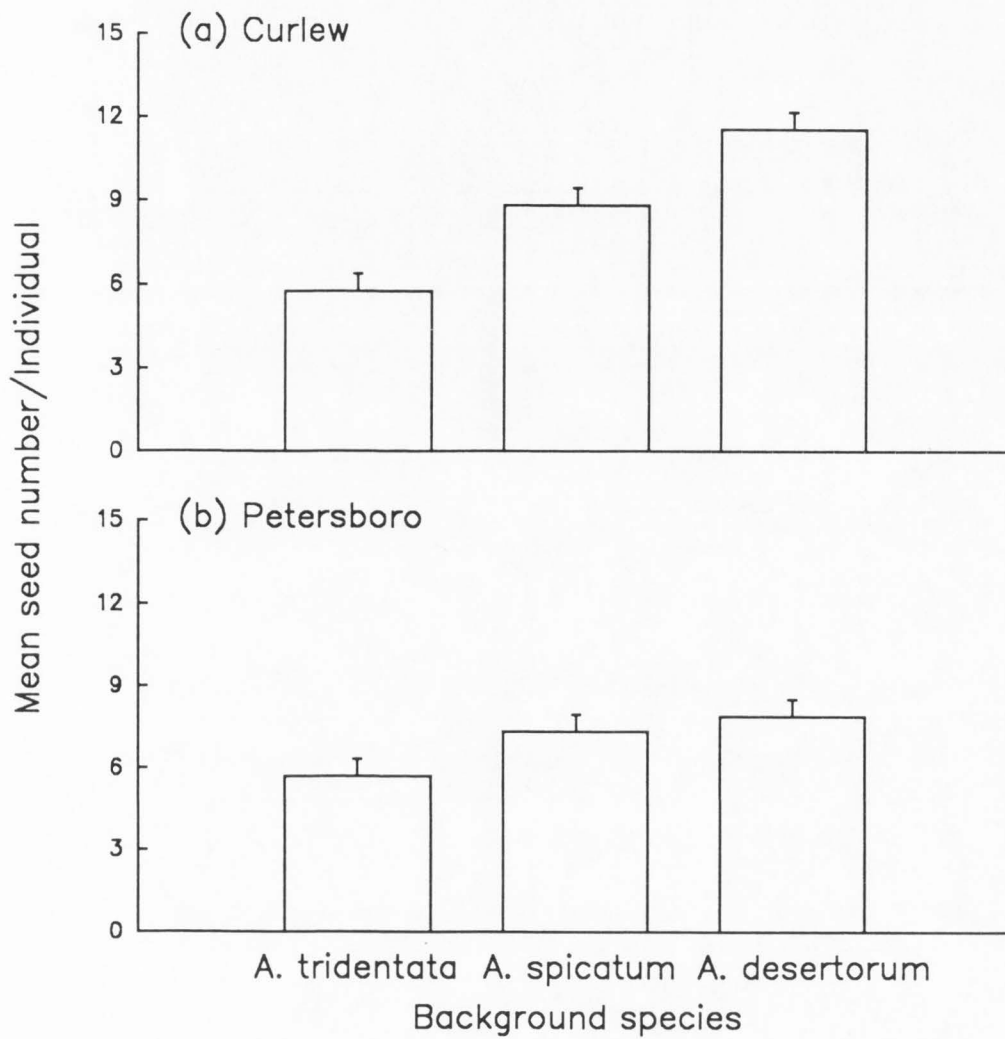


Fig. 15. Seed production of *B. tectorum* competing with three established background species at two sites (a-b) in 1989.

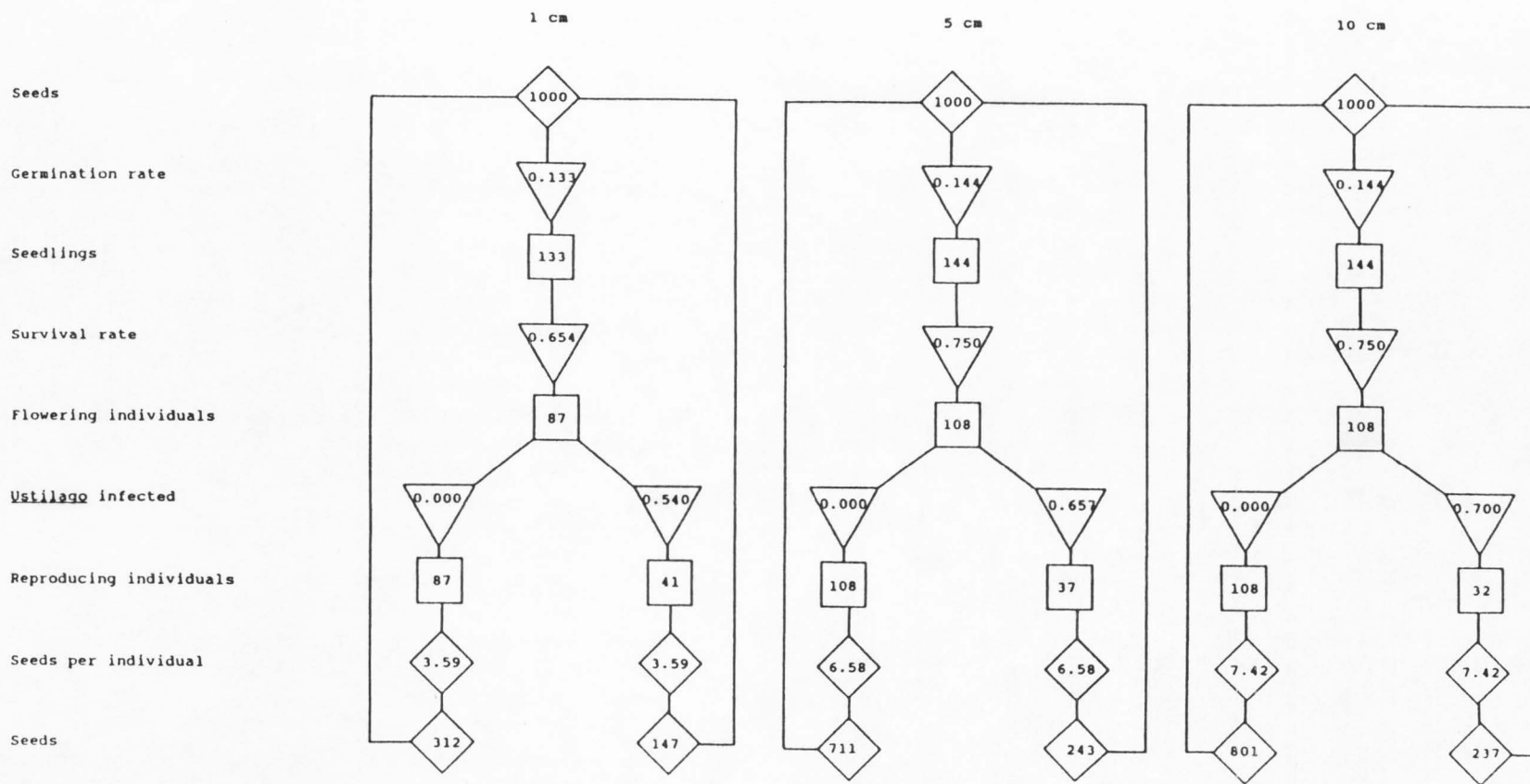


Fig. 16. Life cycle diagram of *B. tectorum* grown with three depths of root exclusion and with established *Ar. tridentata* as the background species at Curlew in 1989.

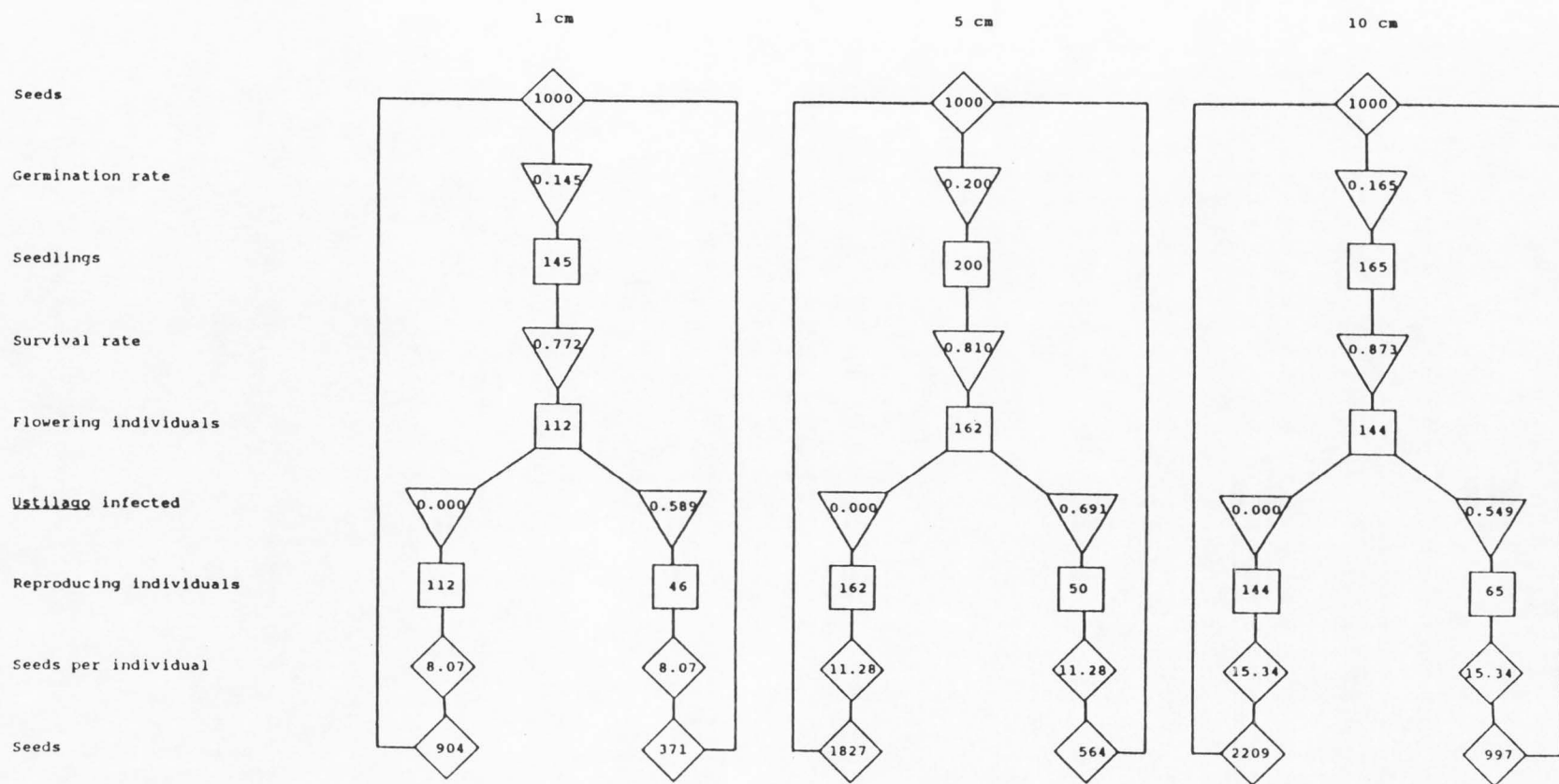


Fig. 17. Life cycle diagram of *B. tectorum* grown with three depths of root exclusion and with established *Ag. desertorum* as the background species at Curlew in 1989.

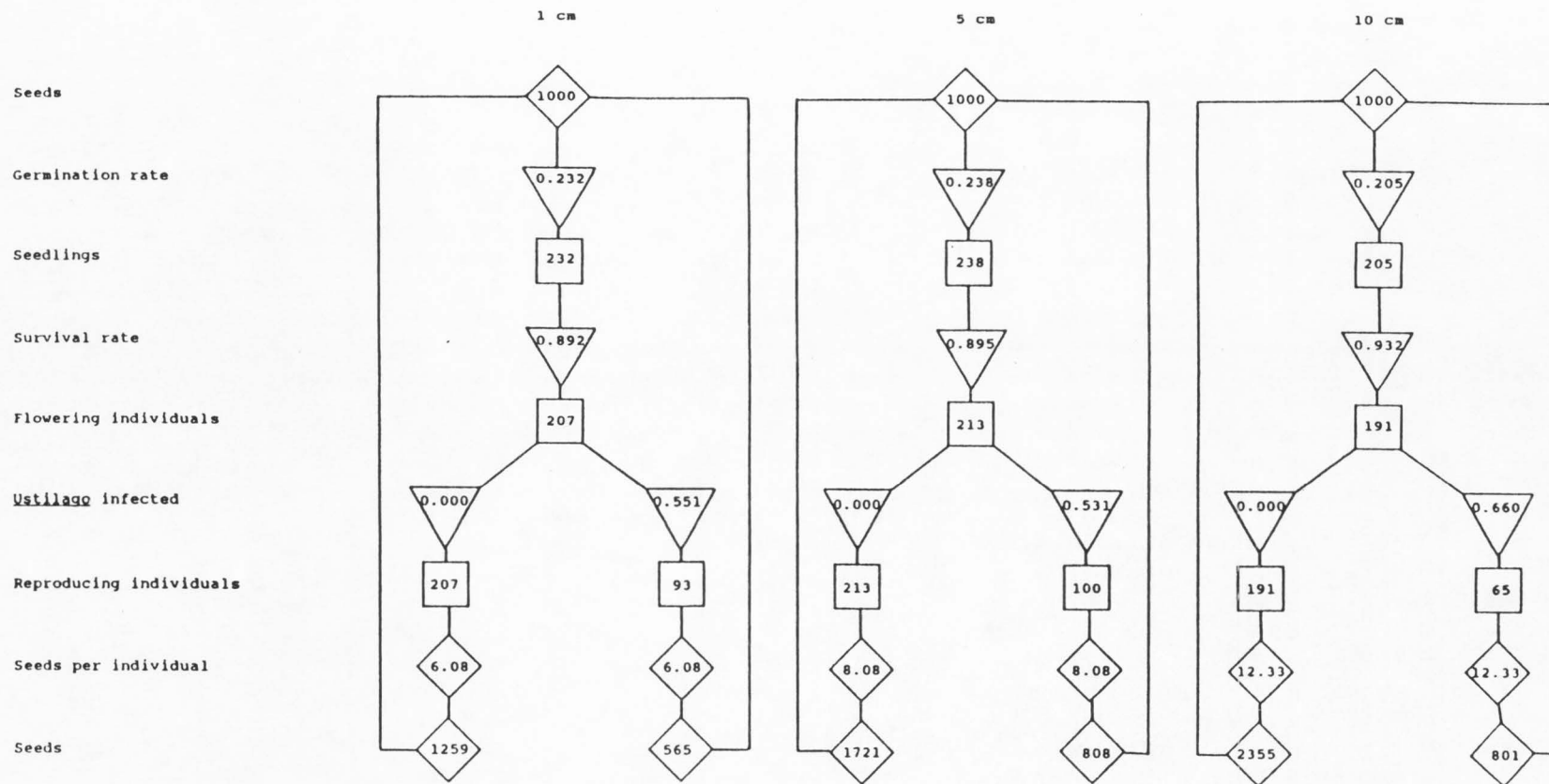


Fig. 18. Life cycle diagram of *B. tectorum* grown with three depths of root exclusion and with established *Ag. spicatum* as the background species at Curlew in 1989.

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APPENDICES

Appendix A. Climatological data
 Table A.1. Long-term climatological data and 1988 precipitation for the Petersboro (station Logan) and Curlew sites (station Snowville).

Long-term data	Logan (1969-1986)	Snowville (1948-1986)
<u>Ar. tridentata</u>	<u>ssp.vaseyana</u>	<u>ssp.wyomingensis</u>
avg ann temp	7.4 C	7.3 C
avg min Jan	-11.9 C	-12.4 C
avg max Jul	30.8 C	32.4 C
avg ann prec	490 mm	305 mm
avg prec		
Apr-Sep	221 mm	159 mm
% of annual	45 %	52 %
avg max prec/month	Apr 53.3 mm	May 41.7 mm
avg min prec/month	Aug 21.1 mm	Aug 19.8 mm

Year 1988

prec	228 mm	223 mm
% of long-term	59 %	73 %

Appendix B. Tables

Table B.1. Mean number (n=10) of live one-year-old Artemisia tridentata roots out of 50 randomly selected roots from inside versus outside 10-cm tubes with either Agropyron desertorum or Agropyron spicatum as a seedling species and with Ar. tridentata as the background species. Results for paired T-test of roots inside versus outside tubes.

	mean \pm SE	
Inside tubes	2.8 \pm 0.93	
Outside tubes	15.2 \pm 3.50	
	T value	<u>P</u>
	-3.61	0.0056

Table B.2. Logrank test among tube depths for four seedling species in three backgrounds at Curlew and at Petersboro in 1988 and 1989.

	χ^2	P
Year 1988		
Site Curlew		
Seedling species <u>Ar. tridentata</u>		
Background		
<u>Ar. tridentata</u>	50.30	< 0.001
<u>Ag. desertorum</u>	65.74	< 0.001
<u>Ag. spicatum</u>	35.89	< 0.001
Year 1989		
Site Curlew		
Background <u>Ar. tridentata</u>		
Seedling species		
<u>Ar. tridentata</u>	28.30	< 0.001
<u>Ag. desertorum</u>	133.18	< 0.001
<u>Ag. spicatum</u>	18.11	< 0.001
<u>Br. tectorum</u>	4.34	n.s.
Background <u>Ag. desertorum</u>		
Seedling species		
<u>Ar. tridentata</u>	109.04	< 0.001
<u>Ag. desertorum</u>	39.70	< 0.001
<u>Ag. spicatum</u>	36.63	< 0.001
<u>Br. tectorum</u>	5.18	n.s.
Background <u>Ag. spicatum</u>		
Seedling species		
<u>Ar. tridentata</u>	14.34	< 0.001
<u>Ag. desertorum</u>	14.04	< 0.001
<u>Ag. spicatum</u>	0.02	n.s.
<u>Br. tectorum</u>	2.44	n.s.
Site Petersboro		
Seedling species <u>Ar. tridentata</u>		
Background		
<u>Ar. tridentata</u>	53.79	< 0.001
<u>Ag. desertorum</u>	87.13	< 0.001
<u>Ag. spicatum</u>	91.67	< 0.001

Table B.3. Maximum likelihood estimates (α_i) for the main effects (seedling species, background species, and tube depth), their likelihood ratio chi-square (G^2) and significance value. Data for the best fit model for Curlew 1989. ($H_0: \alpha_i = 0$).

	α_i	G^2	<u>P</u>
Intercept	-0.6575	301.25	0.0000
Seedling species			
<u>Aq. desertorum</u>	-0.8294	148.36	0.0000
<u>Aq. spicatum</u>	-0.7830	111.21	0.0000
<u>Ar. tridentata</u>	-0.6104	123.70	0.0000
<u>Br. tectorum</u>	2.2228	1317.06	0.0000
Background			
<u>Ar. tridentata</u>	-0.9033	227.59	0.0000
<u>Aq. desertorum</u>	0.2122	19.17	0.0000
<u>Aq. spicatum</u>	0.6933	200.37	0.0000
Tube depth			
1 cm	-0.4221	64.21	0.0000
5 cm	-0.0682	1.97	0.1609
10 cm	0.4903	105.66	0.0000

Table B.4. Survival odds for four seedling species (Ar. tridentata, Ag. desertorum, Ag. spicatum, and B. tectorum) in three backgrounds (Ar. tridentata, Ag. desertorum, and Ag. spicatum) at Curlew in 1989. The 1-cm tubes represent controls, 5 cm and 10 cm are depths of root exclusion. Different letters following survival odds denote statistical differences at $P=0.05$.

	survival odds
Seedling species	
<u>Ag. desertorum</u>	0.051 a
<u>Ag. spicatum</u>	0.056 ab
<u>Ar. tridentata</u>	0.079 b
<u>Br. tectorum</u>	22.888 c
Background	
<u>Ar. tridentata</u>	0.044 a
<u>Ag. desertorum</u>	0.410 b
<u>Ag. spicatum</u>	1.074 c
Tube depth	
1 cm (control)	0.115 a
5 cm	0.234 b
10 cm	0.716 c

	df	G^2	\underline{P}
Intercept	1	301.25	0.0000
Seedling species	3	1347.87	0.0000
Background	2	264.87	0.0000
Tube depth	2	114.53	0.0000
Seedling species * Background	6	43.90	0.0000
Seedling species * Tube depth	6	13.90	0.0307
Background * Tube depth	4	19.34	0.0007
Likelihood ratio	12	18.72	0.0955

Table B.5. Maximum likelihood estimates (α_i) for the main effects (site, background species and tube depth) and the background * site interaction, their likelihood ratio chi-square (G^2) and significance value. Data for the best fit model for Ar. tridentata seedlings at Curlew and at Petersboro in 1989. ($H_0: \alpha_i = 0$).

	α_i	G^2	<u>P</u>
Intercept	-2.2920	1256.76	0.0000
Site			
Curlew	0.4573	64.24	0.0000
Petersboro	-0.4573	64.24	0.0000
Background			
<u>Ar. tridentata</u>	-1.1895	110.06	0.0000
<u>Ag. desertorum</u>	0.4533	33.17	0.0000
<u>Ag. spicatum</u>	0.7363	89.91	0.0000
Tube depth			
1 cm	-0.5727	33.46	0.0000
5 cm	-0.0824	0.86	0.3542
10 cm	0.6551	71.94	0.0000
Site * Background			
Cur * <u>Ar. tridentata</u>	0.0337	0.12	0.7291
Cur * <u>Ag. desertorum</u>	-0.2964	17.66	0.0000
Cur * <u>Ag. spicatum</u>	0.2627	13.53	0.0002
Pet * <u>Ar. tridentata</u>	-0.0337	0.12	0.7291
Pet * <u>Ag. spicatum</u>	-0.2627	13.53	0.0002
Pet * <u>Ag. desertorum</u>	0.2964	17.66	0.0000

Table B.6. Survival odds of Ar. tridentata seedlings in three backgrounds (Ar. tridentata, Ag. desertorum, and Ag. spicatum) at Curlew and at Petersboro in 1989. The 1-cm tubes represent controls, 5 cm and 10 cm are depths of root exclusion. Different letters following survival odds denote statistical differences at $P=0.05$.

	survival odds
Site	
Curlew	0.025492 a
Petersboro	0.004092 b
Background	
<u>Ar. tridentata</u>	0.000946 a
<u>Ag. desertorum</u>	0.025289 b
<u>Ag. spicatum</u>	0.044529 c
Tube depth	
1 cm (control)	0.003249 a
5 cm	0.008662 b
10 cm	0.037862 c
Site * Background	
Cur * <u>Ar. tridentata</u>	0.002524
Cur * <u>Ag. desertorum</u>	0.034888
Cur * <u>Ag. spicatum</u>	0.187946
Pet * <u>Ar. tridentata</u>	0.000354
Pet * <u>Ag. spicatum</u>	0.010550
Pet * <u>Ag. desertorum</u>	0.018330

	df	G ²	P
Intercept	1	1256.76	0.0000
Background	2	117.74	0.0000
Tube depth	2	74.70	0.0000
Site	1	64.24	0.0000
Background * Tube depth	4	16.89	0.0020
Site * Background	2	29.40	0.0000
Likelihood ratio	6	11.03	0.0874

Table B.7. Mean height (mm) of Ar. tridentata seedlings competing with three background species (Ar. tridentata, Ag. desertorum, and Ag. spicatum) at Curlew in 1988 and in 1989. The single height measurement was taken in the first part of June. Different letters following means denote statistical differences at $P=0.05$.

	mean \pm SE
Year	
Curlew 1988	11.9 \pm 0.42 a
Curlew 1989	14.0 \pm 0.39 b
Background	
<u>Ar. tridentata</u>	10.7 \pm 0.55 a
<u>Ag. spicatum</u>	13.5 \pm 0.45 b
<u>Ag. desertorum</u>	14.7 \pm 0.50 b
Tube depth	
1 cm	10.3 \pm 0.50 a
5 cm	12.2 \pm 0.49 b
10 cm	16.4 \pm 0.50 c

	df	MS	<u>P</u>
Year	1	405.43	< 0.001
Background	2	511.57	< 0.001
Year * Background	2	83.53	< 0.05
Error A	114	19.44	
Tube depth	2	1185.79	< 0.001
Year * Tube depth	2	247.25	< 0.001
Background * Tube depth	4	7.66	n.s.
Year * Background * Tube depth	4	55.89	< 0.05
Error B	126	22.03	

Table B.8. Mean height (mm) of Ar. tridentata seedlings competing with three background species (Ar. tridentata, Ag. desertorum, and Ag. spicatum) at Curlew in 1989 and at Petersboro in 1989. The single height measurement was taken in the first part of June. Different letters following means denote statistical differences at $P=0.05$.

	mean \pm SE
Site	
Curlew 1989	14.0 \pm 0.26 a
Petersboro 1989	19.5 \pm 0.26 b
Background	
<u>Ar. tridentata</u>	13.9 \pm 0.31 a
<u>Ag. spicatum</u>	17.8 \pm 0.31 b
<u>Ag. desertorum</u>	18.6 \pm 0.31 b
Tube depth	
1 cm	14.6 \pm 0.31 a
5 cm	17.1 \pm 0.31 b
10 cm	18.5 \pm 0.31 c

	df	MS	P
Site	1	2652.72	< 0.001
Background	2	772.93	< 0.001
Site * Background	2	64.04	< 0.05
Error A	114	20.61	
Tube depth	2	471.73	< 0.001
Site * Tube depth	2	6.12	n.s.
Background * Tube depth	4	31.53	< 0.01
Site * Background * Tube depth	4	11.18	n.s.
Error B	188	8.88	

Table B.9. Mean number of seeds produced per B. tectorum individual in three backgrounds (Ar. tridentata, Ag. desertorum, and Ag. spicatum) in three tube depths at Curlew and at Petersboro in 1989. The 1-cm tube represents the control, 5 cm and 10 cm are depths of root exclusion. Different letters following means denote statistical differences at $P=0.05$.

	mean \pm SE
Site	
Curlew	8.7 \pm 0.36 a
Petersboro	7.0 \pm 0.36 b
Background	
<u>Ar. tridentata</u>	6.6 \pm 0.44 a
<u>Ag. spicatum</u>	8.4 \pm 0.44 b
<u>Ag. desertorum</u>	8.6 \pm 0.44 b
Tube depth	
1 cm (control)	5.2 \pm 0.44 a
5 cm	7.6 \pm 0.44 b
10 cm	10.8 \pm 0.44 c

	df	MS	<u>P</u>
Site	1	271.56	< 0.01
Background	2	153.66	< 0.05
Site * Background	2	428.67	< 0.001
Error A	114	38.33	
Tube depth	2	925.35	< 0.001
Site * Tube depth	2	8.16	n.s.
Background * Tube depth	4	44.57	n.s.
Site * Background * Tube depth	4	16.75	n.s.
Error B	194	18.59	