THE EFFECTS OF SEEDING DENSITY ON SELF-THINNING AND NUTRIENT CYCLING DURING ESTABLISHMENT OF ORCHARDGRASS AND REED CANARYGRASS

MARSHALL W. MORALES
Swarthmore College, Swarthmore, PA 19081 USA

MENTOR SCIENTIST: DR. VALERIE T. EVINER
University of California, Davis, CA 95616 USA

Abstract. Seeding rates can have profound ecological impacts on agriculture and revegetation, but many differences between establishment at natural densities and at lower, recommended densities remain unclear. High densities are often assumed to increase competitive stress, but high seed density may also increase nutrient supply by promoting seedling thinning, and decrease nutrient leaching during establishment. In order to investigate the effects of sowing density on population and nutrient dynamics during establishment, Orchardgrass (*Dactylis glomerata*) and Reed Canarygrass (*Phalaris arundinacea*) were each planted at recommended, at natural, and at intermediate seeding rates. The highest densities resulted in greater thinning rates and greater aboveground biomass, but did not impact nitrogen supply or nitrogen leaching.

INTRODUCTION

Revegetation work seeks to restore a previous ecosystem or to replace it with a stable alternative, which requires a working knowledge of biotic and abiotic mechanisms. Agriculture is chiefly concerned with producing the most palatable or productive crop through management techniques. Whether we seek to restore an old pasture to native grass or produce a profitable hay meadow, the processes of plant establishment and nutrient cycling are essential. At times revegetation has been perceived as a process of swift establishment to produce a fixed community, excluding the effects of erratic factors such as disturbance, and climate (Call 1991). Plant communities are actually dynamic and changing, and even during establishment some elements of population dynamics and nutrient cycling may have long-term effects on the community (Wulff 1986).

The recommended seeding rates of managed ecosystems are set much lower than seed production in established adult stands and are often lower than natural mature plant density, thus minimizing self-thinning during stand establishment. Recommended seeding rates often minimize self-thinning of seedlings, which seems logical since sowing more seed than can survive seems wasteful, yet studies in California grasslands have shown that seedling thinning may be an important nutrient retention and supply mechanism (Eviner and Vaughn in prep). Though there may be more seedlings than can survive in natural grasslands, high-density stands should minimize leaching and may be an important N source for other seedlings.

During establishment of high-density stands, self-thinning plays a role in both population dynamics and nutrient cycling. The self-thinning rule states that aboveground plant biomass is related to initial plant density and to the amount of density-dependent mortality. A mathematical expression connects biomass to density:

$$\log w = \log K - 1.5(\log d)$$

Where w is mean biomass, d is the mean number of plants per unit area, and K is a constant. Seedling thinning may be an important early nutrient supply mechanism as it could match or surpass nutrient supply from litter alone.

Pyke (1991) described the benefits and costs to both low-density and high-density stands in terms of revegetation. Low-density stands tend to minimize stress to produce overall larger individuals but may allow unwanted plants to establish within space between sown plants. High-density stands experience more self-thinning and produce smaller individuals but also provide for greater soil stability, exclude unwanted plants, and decrease soil runoff. High-density stands then may be seen as proficient at weed control and soil stability, and low-density stands optimize individual size and production.

In this study, I investigated the effects of seeding rates on thinning and nutrient retention and supply during establishment. Plants were seeded at recommended, at natural, and at intermediate seeding rates, and these treatments were monitored for seedling establishment and nitrogen cycling. I hypothesize that increased seed density should increase stand uptake of soil water and nutrients, lowering the amount of leaching. In high-density stands, density-dependent mortality due to self-thinning is expected to increase, providing a nutrient supply to other seedlings.

MATERIALS AND METHODS

Experimental design.

This experiment took place at the Institute of Ecosystem Studies (Millbrook, NY), in a field that had a history of being mowed, but had no recent agricultural use. In late May, the field was plowed at a depth of 15cm and raked to remove existing biomass to mimic the condition of a newly seeded pasture. No measures were taken to minimize the seed bank of any other plants in the soil. My research focused on Orchardgrass (*Dactylis glomerata*) and Reed Canarygrass (*Phalaris arundinacea*), which are often used in pastures for grazing or restoration work and are noted for excellent erosion control and quick germination and establishment.

In order to determine natural density (post-thinning), six 49cm^2 quadrat samples were taken from adult stands in old fields in Millbrook, NY. The adult stand density was calculated to give a range from 4.96 X10^6 to 1.07 X10^7 individuals/acre. These numbers were assumed to represent the density at which thinning would not occur. Recommended seeding rates and the average number of seeds per pound for Orchardgrass and Reed Canarygrass were collected from Ernst Conservation Seeds (representative of the seeding industry) (Table 1). Using the average number of seeds per pound and recommended density from the supplier, the recommended seeding rate was found to be below the average number of adult plants in natural stands. In order to replicate a more natural stand, the high sowing densities were set at 10-fold and 25-fold the recommended rates to provide a gradient approaching the natural stand density based on the calculated adult stand densities.

Seeds were purchased from Ernst Conservation Seeds (Meadville, PA), and planted by hand-broadcasting in 50cm x 50cm plots. The germination rate of seeds was labeled as 85%. Each of the six treatments (2 species x 3 densities) was replicated 8 times in a randomized block design. There was a 20cm buffer between plots and a 1m buffer between blocks. After noting a high number of birds and ants feeding on the seeded plots, 25% of original seed number was added to each plot on the 6th day after seeding. The seeds for addition were allowed to germinate in wet paper before planting. The majority of seeds in each lot were observed to have germinated 10 days after seeding with daily watering.

Measurements and Statistics

At 1 week and 4 weeks after germination, seedlings were counted from a 49cm^2 quadrat. Seedlings from this sample were then clipped at their base, dried, and weighed to determine aboveground dry biomass. Two soil cores from 0-15cm and from 25-35cm were taken at both 1 week and 4 weeks after germination. Soils were placed in aluminum tins and weighed before and after 2 days of drying to determine soil moisture. Inorganic N concentrations at these two depths were determined using a KCl extraction. Soils from the 0-15cm samples were also incubated for one week in lab and then extracted with KCl to determine net Nitrogen mineralization and nitrification rates. KCl extracts were run on a Lachat autoanalyzer to determine NH_4 and NO_3 concentrations. Three sets of both 15cm and 35 cm deep soil cores were also taken from areas around the plots to gauge nutrient cycling in unseeded soil. Percent ground covered by weeds at 4 weeks after germination was also measured using a 49cm^2 quadrat. Statistical analyses were performed on JMP software and consisted of ANOVAs, using density and species as the independent variables, followed by Tukey-Kramer post-hoc tests.

RESULTS

Population Dynamics

For Orchardgrass, the number of established seedlings at both 1 week and 4 weeks in the low density was significantly lower than medium and high densities (Figure 1; $p<.05$), with no significant difference between medium and high densities. For Reed Canarygrass, the number of established seedlings at the high density was significantly higher than the medium and low treatments at 1 week (Figure 1; $p<.05$). The low density was significantly lower than the medium and high densities at 4 weeks (Figure 1; $p<.05$).

For Orchardgrass, the total stand biomass was significantly different across all densities at 1 week (Figure 1; $p<.05$), showing greater biomass with increasing density. At 4 weeks, the total stand biomass for the low density was significantly lower than medium and high densities (Figure 1; $p<.05$), and the medium density treatment tended to have higher biomass than the high density treatment, though this was not significantly different. For Reed Canarygrass, the total stand biomass for the high density was significantly higher than the low and medium densities at 1 week (Figure 1; $p<.05$), and the low density was significantly lower than the medium and high densities at 4 weeks (Figure 1; $p<.05$). There was no significant difference in the average individual weight of seedlings across density for either species at either time ($p>.05$).

For both species, there was a significant increase in thinning with planting density (Figure 1; $p<.05$). For Orchardgrass, the highest density thinned to numbers below the medium density. In Reed Canarygrass, the high density treatment had higher number of seedlings and total stand biomass than the medium density treatment, though not significantly different at 4 weeks. For both species, the low and medium densities treatments increased stand aboveground biomass between sampling intervals. The high-density treatments did not significantly differ in aboveground biomass between sampling intervals. The percent weed cover was not significantly different across densities for both species.

Soil nitrogen

At 1 week after germination, there was no significant difference across density treatments in soil moisture, [NH_4], [NO_3], net mineralization, or nitrification for either species at the 0-15cm level (Figure 2). There was also no significant difference in soil moisture, [NH_4], or [NO_3] for the 30-40cm level. At 4 weeks, plots of medium density Orchardgrass were significantly higher than the low density, with no significant difference between the high and low or medium densities. All other data at both depths for 4 weeks was not significantly different across density for either species (Figure 2). Nitrogen below the rooting zone results showed no significant difference across densities for either species (Figure 3).

DISCUSSION

Revegetation efforts often have only limited success, and this may be partly due to low seeding rates. An ecological strategy for this phenomenon proposed by Eviner (in preparation) suggests that seedling thinning provides nutrients to surviving neighbors. Therefore, the expected nutritive benefits from high competition stands are dependent on high seedling death. With the increase in seed density, both species showed higher rates of thinning. It is interesting that the highest density treatment in Orchardgrass averaged lower numbers of individuals by week 4 than the medium density treatment. This is likely due to increased competitive pressure, causing many seedlings to perish due to the stress, thinning to numbers below what the space and nutrients could support. Similarly, in natural stands, high densities result in a high amount of thinning in seedlings. The high-density treatments also produced a loss in living aboveground biomass, likely due to the extreme amounts of thinning, while both low and intermediate densities gained in aboveground biomass. Due to increased competition between seedlings, a difference in individual biomass was expected across density, but the results showed no significant difference. Belowground biomass also was planned to be measured, but time constraints prevented this data collection.

Elevated net N mineralization and nitrification were expected at higher densities, yet no significant differences were found. Higher densities were expected to decrease nutrient leaching, yet there was no difference in soil nitrogen concentrations below the rooting zone. The accumulation of dead biomass across the plots suggests that there was not enough time for dead biomass to decay and for those nutrients to become available in the soil. Other possibilities include herbivore consumption or that density-dependent mortality had no effect on nitrogen supply, but do not explain the dead biomass accumulation.

The majority of weeds that grew in the plots were from regenerating pieces that were not removed before the experiment. This weed regeneration probably provided more competitive pressure than had weeds not regenerated, yet the lack of a difference in weed cover across density suggests that each plot experienced comparable competition with weeds. The presence of weeds may have helped the realistic design of the experiment, in that natural stands must compete with other species, though it may have affected the population dynamics and nutrient cycling in the plots in unmeasured ways.

To create a more complete picture of seedling competition during establishment, it is also important to consider which seedlings were thinning. Some studies have presented systems in which less competitive seed types support larger seeds (Smith 1977, Wulff 1986), suggesting that some short-lived individuals could enhance early season nutrient retention and then supply nutrients to surviving plants later in the season. Much of the work done so far in seed size variation and the seed number vs. seed size tradeoff covers the effective differences between different species while there is still a good deal of seed size asymmetry within species and within a single plant (Wulff 1986). Larger seeds have been shown to have better survivorship during establishment (Turnbull 1999) and increase final plant yield (Wood 1977). These reasons warrant further investigation into the fates of various seed sizes and the implications on self-thinning and stand establishment.

Based on the nutrient information from Eviner, the results of increased self-thinning with higher densities in this experiment, and the doubts over an explanation for the nutrient supply and retention results the possibly of an important link between self-thinning and nutrient cycling warrants further study. Furthermore, nutrient data would be vital for fully evaluating seeding densities for restoration work. Though the nutritive benefits from thinning still need to be substantiated, the intermediate density poses the most beneficial seeding rate for management since it produced higher biomass gains and higher self-thinning than the low density.

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LITERATURE CITED

Call, C.A., B.A. Roundy. 1991. Perspectives and processes in revegetation of arid and semiarid rangelands. Journal of Range Management **44**: 543-549

Pyke, D., S. Archer. 1991. Plant-plant interactions affecting plant establishment and persistence on revegetated rangeland. Journal of Range Management **44**: 550-557.

Smith, A.P. 1977. Albinism in relation to competition in bamboo *Phyllostachys bambusoides*. Nature **266**: 527-529.

Turnbull, L.A., M.J. Crawley, M. Rees. 1999. Journal of Ecology **87**: 899-912

Wood, D.W., P.C. Longden, R.K. Scott. 1977. Seed size variation; its extent, source, and significance in field crops. Seed Science & Technology **5**: 337-352.

Wulff, R.D. 1986. Seed size variation in *Desmodium paniculatum*. Journal of Ecology **74**: 99-114.

Yadav, A.S., R.S. Tripathi. 1985. Effect of soil moisture and sowing density on population growth of *Eupatorium adenophorum* and *E. riparium*. Plant and Soil **88**: 441-447.

APPENDIX

TABLE 1. Seeding rates used in experiment. Low: rates recommended by Ernst Conservation Seeds, medium: 10-fold, and high: 25-fold. The average number of seeds per pound was used to determine the seeding rate in pounds per meter squared. OG= Orchard Grass, RC= Reed Canary grass

Species and seeding level	Seeding Rates (lbs/acre)	Average Seeds/lb	Seeds/acre	Seeds/m2
OG low	12	487,200	$5.85x10^6$	1,445
OG med	120	487,200	$5.85x10^7$	14,447
OG high	300	487,200	$1.46x10^8$	36,117
RC low	14	537,920	$7.53x10^6$	1,861
RC med	140	537,920	$7.53x10^7$	18,609
RC high	350	537,920	$1.88x10^8$	46,523

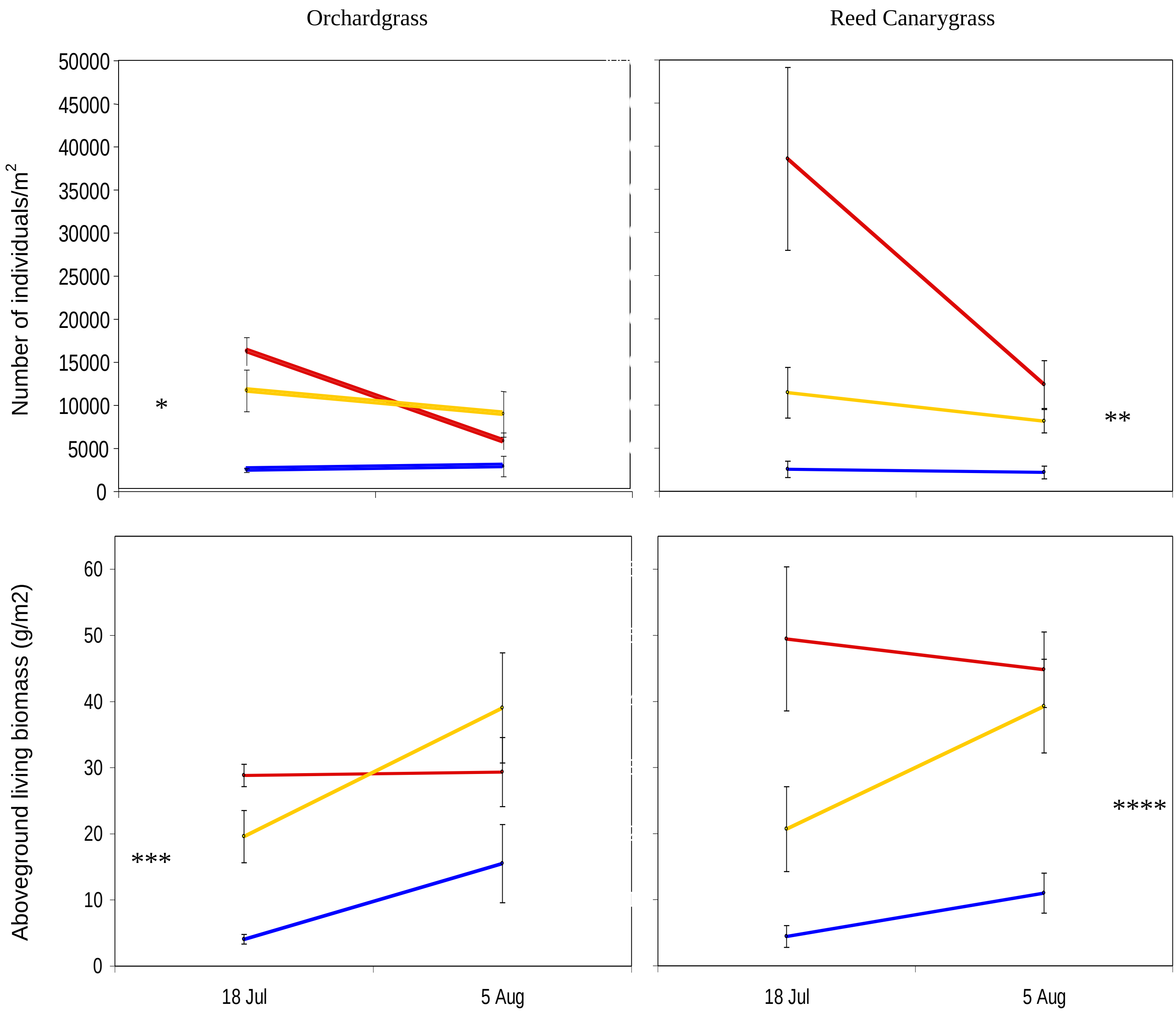

FIGURE 1. Average number of individuals/m^2 (top) and living aboveground biomass in grams /m2 (bottom) for both species. Red represents high-density treatments, yellow intermediate-density, and blue low-density. P values for number of individuals/m^2 represent change over time.

* p=.0084, high different from medium and low
** p=.03, high different from low
*** p<.0001, all densities different at 18 Jul; p=.019, medium different from low at 5 Aug
**** p=.011, high different from medium and low at 18 Jul; p-.006, low different from medium and high at 5 Aug

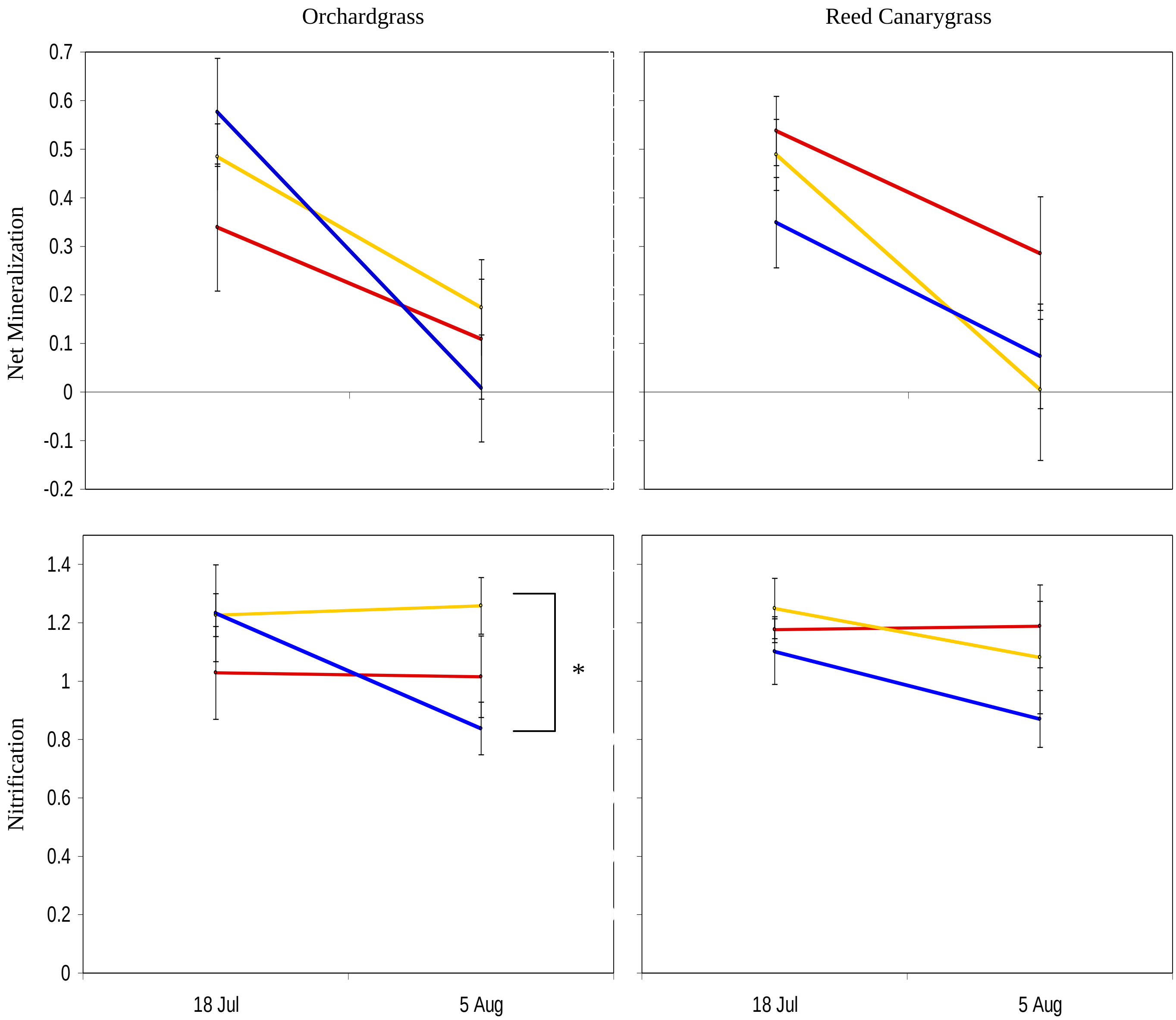

FIGURE 2. Average net mineralization (top) and nitrification (bottom) for both species in µg N/g dry soil. Red represents high-density treatments, yellow intermediate-density, and blue low-density.

*p=.05 low significantly lower than medium at 5 Aug

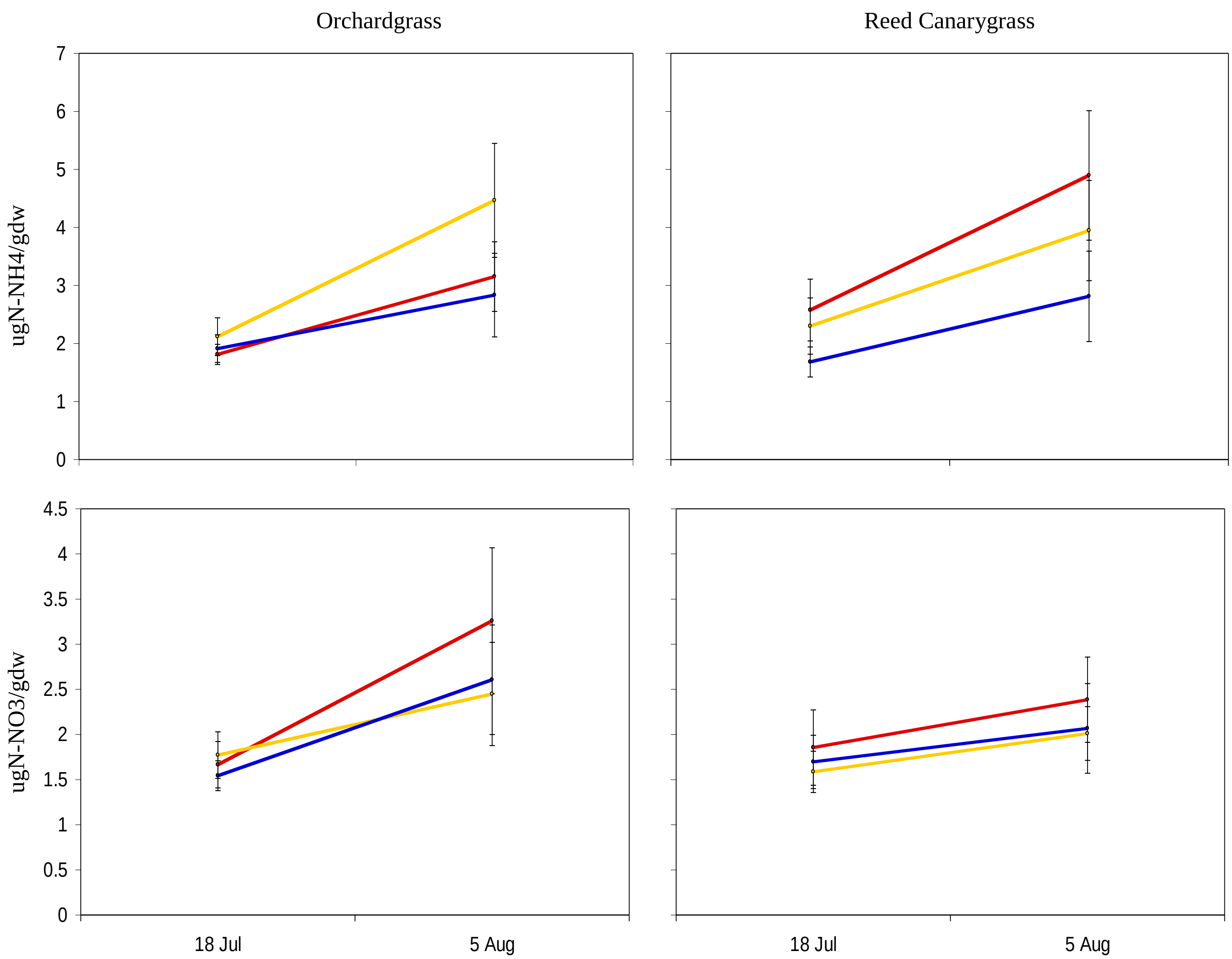

FIGURE 3. Average NH_4 (top) and NO_3 (bottom) amounts at 35 cm depth for both species. Red represents high-density treatments, yellow intermediate-density, and blue low-density.