Emergence and Survival of Pasture Species Sown in Monocultures or Mixtures

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ABSTRACT

Plant–plant interactions during seedling establishment can markedly affect the composition of pasture communities. As each individual within a population germinates and becomes established, spatial and temporal relationships with other seedlings determine the eventual success of that individual. The presence of neighbors changes the environment of a plant and, thus, can change its growth rate or form (Harper, 1977, p. 151). Seedlings may either compete with each other for light, water and nutrients, or facilitate each others’ establishment by ameliorating harsh conditions, depending on the species involved and on the environment into which seeds are sown. The beneficial effects of neighbors most commonly occur when unfavorable environmental conditions can be alleviated by the presence of other plants (Bertness and Hacker, 1994).

The spatial relationships among individuals are critical within plant populations (Harper, 1977, p. 239). The close proximity of other seedlings can sometimes im-

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Abbreviations: BF, birdsfoot trefoil; OG, orchardgrass; PR, perennial ryegrass; WC, white clover.
early growth of perennial ryegrass, orchardgrass, white clover, and birdsfoot trefoil seedlings sown as monocultures or in simple and complex mixtures. The work was part of an ongoing effort to determine if complex mixtures can improve the productivity and stability of pastures in the northeastern USA. An important part of that effort is to understand the interactions that take place among and within species during the earliest stages of stand establishment.

**MATERIALS AND METHODS**

Four forage species commonly found in temperate northeastern USA pastures were selected for the study based on functional group (grass vs. legume) and relative drought tolerance. Drought-tolerant species included ‘Penlate’ orchardgrass and ‘Viking’ birdsfoot trefoil, while drought sensitive species included ‘Basion’ perennial ryegrass and ‘Will’ white clover. Seeds were sown as monocultures of each of the four species, as grass–legume binary mixtures (perennial ryegrass–white clover, perennial ryegrass–birdsfoot trefoil, orchardgrass–white clover, and orchardgrass–birdsfoot trefoil), and as a complex mixture containing all four species for a total of nine treatments (four monocultures, four binary mixtures, and one complex mixture).

Two study sites were selected based on potential susceptibility to drought stress. The first, at the Russell E. Larson Agricultural Research Center near Rock Springs, PA, is located at an elevation of 357 m in the Ridge and Valley province of central Pennsylvania. The soil was a Morrill silt loam (fine, mixed mesic Typic Hapludalf) with an available water holding capacity of 201 mm in the top 1 m of the soil profile. The second site was located at an elevation of 600 m on the Allegheny Plateau near Kylertown, PA. The soil was a Rayne silt loam (fine-loamy, mixed, mesic Typic Hapludult) with a strongly acid aluminum subsoil (pH 4.5–5.0) that limited available water holding capacity in the top 1 m to 90 mm (Stout, 1992). Air temperature and soil moisture at a depth of 10 cm were recorded at weather stations located at each site.

In 1999, seeds were sown on 11 May at Rock Springs and 14 May at Kylertown. Seeds were broadcast onto 60 by 60 cm plots at rates of 538 or 1076 seeds m$^{-2}$ then the soil was rolled with a water-filled drum to improve soil–seed contact. In 1999, maximum temperatures greater than 30°C occurred on 12 occasions in 1999, while only twice in 2000 were there more than 4 d between rainfall events. Rock Springs experienced a long period without rainfall in 2000, beginning about 10 d after sowing. However, the initially wet soil conditions and cooler temperatures meant that the soil was not as dry in 2000 as in 1999. Because of the earlier planting dates, temperatures were also more favorable for seedling emergence in 2000 compared with 1999. In 1999, maximum temperatures greater than 30°C occurred on 12 occasions at each site whereas only 4 d reached 30°C or greater in 2000. Because of low initial soil moisture levels in 1999, emergence was dependent on rainfall received during the experiment. Each significant rainfall event was followed in approximately 7 to 10 d by a flush of new seedling emergence. In 2000, high initial soil moisture and abundant rainfall soon after planting resulted in much greater emergence compared with 1999 (42% in 2000 vs. 20% in 1999, $P < 0.01$).

Combined across years and sites, seedling emergence was greater at the low (35%) compared with the high (30%) sowing density ($p = 0.01$). At the same time, 35% of the seedlings that emerged at the low density died compared with 31% at the high density ($p = 0.07$). The net result was that sowing density had no significant effect on percent establishment (low = 23%, high = 21%, $p = 0.14$). Emergence of birdsfoot trefoil and orchardgrass were most affected by sowing density (Fig. 2), being reduced by 34 and 20%, respectively, at the high density, whereas, emergence of perennial ryegrass de-

**RESULTS**

In 1999 volumetric soil moisture content at planting was 0.22 m$^3$ m$^{-3}$ at both Kylertown and Rock Springs, whereas in 2000 soil moisture content at planting was 0.31 m$^3$ m$^{-3}$ at Kylertown and 0.33 m$^3$ m$^{-3}$ at Rock Springs. In 1999, <2 mm of precipitation was received during the first 9 d after planting at Kylertown (Fig. 1). The interval between storms was 6 d or greater on five occasions in 1999, while only twice in 2000 were there more than 4 d between rainfall events. Rock Springs experienced a long period without rainfall in 2000, beginning about 10 d after sowing. However, the initially wet soil conditions and cooler temperatures meant that the soil was not as dry in 2000 as in 1999. Because of the earlier planting dates, temperatures were also more favorable for seedling emergence in 2000 compared with 1999. In 1999, maximum temperatures greater than 30°C occurred on 12 occasions at each site whereas only 4 d reached 30°C or greater in 2000. Because of low initial soil moisture levels in 1999, emergence was dependent on rainfall received during the experiment. Each significant rainfall event was followed in approximately 7 to 10 d by a flush of new seedling emergence. In 2000, high initial soil moisture and abundant rainfall soon after planting resulted in much greater emergence compared with 1999 (42% in 2000 vs. 20% in 1999, $P < 0.01$).

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creased by only 7% and white clover emergence was unchanged. The greatest reduction in birdsfoot trefoil and orchardgrass emergence at high density occurred in the complex mixture (data not shown).

The effects of mixture complexity on seedling emergence and mortality varied depending on site and year (Fig. 3). Compared with monocultures, seedling emergence was reduced in the complex mixture at Kylertown in 2000 and in the binary mixtures at Rock Springs in 2000. However, when averaged across species, sites, and years, there was no significant difference in seedling emergence between monocultures and either mixture ($p = 0.27$ for contrast between monocultures and the complex mixture, $p = 0.11$ for contrast between monocultures and binary mixtures).

Seedling mortality was reduced in the complex mixture at both sites when drought stress limited seedling emergence in 1999 (Fig. 3). Seedling mortality was lower in the complex mixture at Rock Springs in 2000 as well. Reduced mortality in the complex mixture was particularly evident in the legumes while grass mortality was not affected by mixture complexity (Fig. 4). Overall seedling establishment, that is, the number of surviving plants, was not affected by the number of species in the mixture (23% in monocultures, 22% in the complex mixture, and 21% in binary mixtures).

The distribution of emerged seedlings was clustered to some extent in $>80%$ of the plots that had enough seedlings for analysis, with the greatest degree of clustering occurring at a lag distance of 3.8 cm (Fig. 5). Seedlings in most other plots were randomly distributed with $<1%$ of plots exhibiting a regular distribution. As seedlings died, the percentage of plots with clustered distribution decreased and seedling distribution became more random. There were significant differences among spe-
Fig. 3. Effect of mixture complexity on seedling emergence and mortality (percentage of emerged seedlings) at two sites in central Pennsylvania. Birdseedtrefoil, white clover, orchardgrass, and perennial ryegrass were sown as monocultures, grass–legume binary mixtures, or as a complex mixture containing all four species. Data are averaged across sowing density. Error bars indicate ±1 SE.

Fig. 5. Distribution of emerged (A) and surviving (B) seedlings based on the distribution of distances between all pairs of seedlings. Seedlings are assumed to be randomly distributed if the observed and expected number of seedlings at given distance are similar. If there are more seedlings than expected at a particular distance, the seedlings are clustered, while if there are fewer than expected the seedlings are regularly-dispersed. Less than 1% of all plots showed a regular distribution.

Fig. 4. Effect of mixture complexity on the mortality rate of individual species. Birdseedtrefoil, white clover, orchardgrass, and perennial ryegrass were sown as monocultures, grass–legume binary mixtures, or as a complex mixture containing all four species. Error bars indicate ±1 SE. Data are averaged across sowing density, year, and site.

Fig. 6. Effect of species identity on the proportion of plots containing clustered seedlings at a lag distance of 3.8 cm. Species combinations included perennial ryegrass (pr), orchardgrass (og), white clover (wc), and birdseedtrefoil (bf) monocultures, binary grass–legume mixtures, and a complex mixture containing all four species.
Seeds in this experiment were hand broadcasted onto plots that had been plowed and raked to provide a uniform seed bed free of weeds. This procedure mimicked broadcast planting, which is a common means of sowing forage seeds. If seeds were randomly sown, the emerged seedlings would be expected to be randomly distributed, barring differences in the soil microenvironment or interactions among germinating seeds. However, a random distribution was observed in only about 16% of the plots, whereas most plots exhibited an aggregated or clustered distribution with maximum clustering occurring at a lag distance of 3.8 cm (Fig. 1). When seedling emergence is near 100%, the distribution of emerged seedlings must match the distribution of sown seeds. In these experiments, 94% of the plots showed a clustered distribution when seedling emergence was >80% (Fig. 8). This suggests that the seeds were not randomly sown and that the clustered distribution of emerged seedlings was not due to interactions among seedlings during germination and emergence, but resulted from the clustered distribution of sown seeds.

Generally, seeding density does not affect the rate of seedling emergence, although both positive and negative effects are occasionally found. When differences do occur, they tend to be species specific (Rebollo et al., 2001). In this experiment, birdsfoot trefoil, orchardgrass, and white clover were grouped for data presentation because of a limited number of seedlings and similarity in their response to neighbor proximity.

Fig. 7. Effect of distance to the nearest neighbor on seedling mortality. Each data point is based on 29 to 75 individual plants in 1999 (mean = 47) and 79 to 272 plants in 2000 (mean = 148). Birdsfoot trefoil, orchardgrass, and white clover were grouped for data presentation because of a limited number of seedlings and similarity in their response to neighbor proximity.

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with grass–white clover mixtures, where plants in 100% of the plots were clustered at the time of emergence and nearly 90% remained clustered at the final harvest.

Mortality did not always reduce clustering. Regression of mortality rate vs. distance to the nearest neighbor (Fig. 7) showed that in 1999 perennial ryegrass seedlings were most likely to survive when they emerged within 1 cm of another seedling, while maximum mortality occurred when seedlings were 3 to 4 cm apart. This mortality pattern resulted in increased clustering of perennial ryegrass seedlings in 1999. Forty-four percent of perennial ryegrass seedlings emerged within 2 cm of a neighbor in 1999, whereas 50% of surviving seedlings were within 2 cm of their nearest neighbor. Nearest neighbor analysis of seedling mortality for perennial ryegrass in 2000 and for all other species in both years showed that mortality increased as the distance between neighbors decreased, consistent with the conclusion from spatial pattern analysis that seedling distribution became more random with time.

Regressing seedling growth rates vs. distance to the nearest neighbor showed that perennial ryegrass growth rates in 1999 also increased at both Rock Springs and Kylertown as distance to the nearest neighbor decreased (Table 1). In contrast, birdsfoot trefoil growth rates decreased at Rock Springs in 2000 as the neighborhood became more crowded. Otherwise, neighbor proximity had no influence on seedling growth during the first 2 mo after sowing. Earlier emerging seedlings generally had no growth rate advantage over later emerging seedlings in 2000 when environmental conditions were favorable. However, earlier emerging seedlings had higher growth rates at Rock Springs in 1999 when growth conditions were less favorable. In contrast, growth rates were greater for later emerging perennial ryegrass and birdsfoot trefoil seedlings at Kylertown in 1999.

DISCUSSION

Seeds in this experiment were hand broadcasted onto plots that had been plowed and raked to provide a uniform seed bed free of weeds. This procedure mimicked broadcast planting, which is a common means of sowing forage seeds. If seeds were randomly sown, the emerged seedlings would be expected to be randomly distributed, barring differences in the soil microenvironment or interactions among germinating seeds. However, a random distribution was observed in only about 16% of the plots, whereas most plots exhibited an aggregated or clustered distribution with maximum clustering occurring at a lag distance of 3.8 cm (Fig. 1). When seedling emergence is near 100%, the distribution of emerged seedlings must match the distribution of sown seeds. In these experiments, 94% of the plots showed a clustered distribution when seedling emergence was >80% (Fig. 8). This suggests that the seeds were not randomly sown and that the clustered distribution of emerged seedlings was not due to interactions among seedlings during germination and emergence, but resulted from the clustered distribution of sown seeds.

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Table 1. Correlation between distance to the nearest neighbor or date of emergence and growth rates for seedlings of four cool-season forage species.

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<td>Growth rate vs. distance to nearest neighbor</td>
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<td>Growth rate vs. date of emergence</td>
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<td>$r$‡</td>
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<td>$r$‡</td>
<td>$n$§</td>
</tr>
<tr>
<td>Perennial ryegrass</td>
<td>-0.26**</td>
<td>179</td>
<td>-0.41**</td>
<td>39</td>
</tr>
<tr>
<td>Orchardgrass</td>
<td>0.08 NS</td>
<td>44</td>
<td>-0.27 NS</td>
<td>18</td>
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<tr>
<td>White clover</td>
<td>-0.18 NS</td>
<td>80</td>
<td>-0.17 NS</td>
<td>58</td>
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<tr>
<td>Birdsfoot trefoil</td>
<td>-0.02 NS</td>
<td>25</td>
<td>0.18 NS</td>
<td>21</td>
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<td></td>
<td>Growth rate vs. date of emergence</td>
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<tr>
<td>Perennial ryegrass</td>
<td>-0.58**</td>
<td>216</td>
<td>0.62**</td>
<td>54</td>
</tr>
<tr>
<td>Orchardgrass</td>
<td>-0.42**</td>
<td>63</td>
<td>0.23 NS</td>
<td>33</td>
</tr>
<tr>
<td>White clover</td>
<td>-0.39**</td>
<td>106</td>
<td>0.15 NS</td>
<td>88</td>
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<tr>
<td>Birdsfoot trefoil</td>
<td>-0.46**</td>
<td>40</td>
<td>0.39*</td>
<td>35</td>
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* Significance at 0.05 probability level.
** Significance at 0.01 probability level.
‡ Correlation coefficient.
§ Number of observations in each correlation.

The presence of neighbors can have both negative and positive effects on seedling survival and growth (Bisigato and Bertiller, 1999; Rebollo et al., 2001; Gustafsson and Ehrlen, 2003). In most cases, neighbors had a negative effect on survival in this experiment, as evidenced by reduced clustering in surviving compared with emerged seedlings (Fig. 5 and 6) and by the negative relationship between mortality rate and distance to the nearest neighbor for all species in both years except perennial ryegrass in 1999 (Fig. 7). Plants were still very small at the end of the experiment. Average seedling weights ranged from 2.7 mg plant$^{-1}$ at Kylertown in 1999 to 15.9 mg plant$^{-1}$ at Rock Springs in 2000. Seedlings this small would not be expected to significantly deplete available resources and the distance to neighbors generally had no effect on growth rates (Table 1). However, perennial ryegrass growth was facilitated by the presence of neighbors under the same environmental conditions where neighbors facilitated seedling survival.

Neighboring plants can favorably alter numerous environmental conditions including light, temperature, and soil moisture and nutrient content (Callaway, 1995). When seedlings are only a few millimeters or centimeters apart some shading of the soil surface and of seedling leaves can occur within a few days after emergence. Shading of the soil surface could be expected to reduce evaporation (Bertness and Hacker, 1994) increasing soil water availability. Shade-induced stomatal closure could further improve leaf water status as transpiration is reduced.

Improved plant–water relations will only have a beneficial effect if benefits exceed the costs to photosynthetic uptake associated with increased shading. In some cases, shading can have a positive effect on photosynthesis under drought conditions. For example, Holmgren (2000) grew *Liriodendron tulipifera* seedlings under combinations of low and high light and low and high soil water content. Net photosynthesis on a daily basis and daily carbon gain were greater under low compared with high light when plants were drought stressed, primarily due to a longer period of photosynthetic activity each day under low light. The light compensation point was also lower for plants grown under low light. In well-watered plants, however, daily photosynthesis and C gain were significantly greater under high light. Shumway (2000) also found that net photosynthesis was not significantly reduced while photosynthetic efficiency increased for plants grown beneath shrubs. All the previously cited studies involved plants experiencing relatively large changes in their environmental conditions caused by the presence of other plants. These results suggest that the subtle environmental changes effected by small seedlings can also affect neighbor development.

Even though mixture complexity had significant effects on seedling emergence and mortality, differences were generally small and tended to cancel each other out such that species composition and dry matter production in the binary and complex mixtures could be predicted based on emergence, survival, and growth in...
monocultures. Thus, species composition of the complex mixture was 12% birdsfoot trefoil, 18% orchardgrass, 26% white clover, and 43% perennial ryegrass. Predicted composition based on establishment of monocultures was the same for white clover and perennial ryegrass, while the birdsfoot trefoil component decreased from 12 to 11% and orchardgrass increased from 18 to 19%. In a long-term study at the Rock Springs site, perennial ryegrass also dominated two five-species mixtures at the first spring harvest following a fall seeding, comprising 51 and 59% of harvested biomass in the two mixtures (Skinner et al., 2004). Current results suggest that the initial advantage of perennial ryegrass was due to its higher emergence rate compared with other species in the mixture. It therefore appears that seedling emergence information gleaned from monocultures can be a useful tool for predicting initial species composition of more complex mixtures. At least as far as seedling establishment is concerned, growers can have some confidence that knowledge of species performance in monoculture can be useful in understanding how those species will perform in mixtures.

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REFERENCES