Does sampling resolution influence the relationship between plant community diversity and aboveground productivity at a northern prairie site? An investigation using ground-based radiometry

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Abstract - While recent studies generally support the idea that diverse plant communities function better than depauperate versions, there is less agreement as to whether this is caused by the number of species present, the identities of the species present, the number of functional groups that these species make up, or by which functional groups are represented. In this study, we use ground-based remote sensing and botanical field sampling to address these issues at a northern prairie site. We assess the degree to which observed diversity-productivity relationships are dependent on (a) the measure of diversity used (species richness vs. functional group richness), (b) the presence of particular species or functional groups, and (c) sampling resolution. To achieve this, we collected plant diversity and spectrally-derived productivity information over plots of comparable ground resolution (approx. 0.5m) during the summer of 1998 from three upland grassland communities, then used a spatially nested sampling design to scale each property and their relationships to 2.5m, 10m and 50m sampling resolutions. Our results showed that the overall strengths and shapes of observed diversity-productivity relationships were dependent on all of the above factors. Overall richness-productivity relationships were found to be asymptotic at all observational scales. Multiple regressions indicated that the individual effects of species richness were generally stronger and more significant than functional group richness. The presence of particular species had significant effects on productivity at the plot (0.5m) level, but not at coarser resolutions. These results were consistent with those of other studies, and suggest that the higher productivities of diverse grassland plots in our sites result both from the effects of richness as well as the presence of productive species. However, the lack of species effects at coarser resolutions suggest other mechanisms might be responsible for such relationships at these scales.

II. METHODS

A. Collection of radiometric and botanical data

Species composition and spectral data were collected during the 1998 growing season at three upland grassland sites within Grasslands National Park (GNP), Canada (49° 15' N, 107° 0' W). At each site, 72 square sampling plots of 0.5m resolution were arranged in a nested design (Fig. 1a.).

On nine separate dates during the summer of 1998, spectrally reflected radiation in Landsat TM bands 3 (0.63-0.69 µm) and 4 (0.76-0.90 µm) were measured over each plot using a ground-based radiometer. The radiometer has a 15° Field Of View (FOV) and was mounted at a height of approximately 1.5m, giving a spatial sample resolution of 0.5m (nadir view). On each sampling date, plot reflectances were computed from a ratio of canopy radiance to that of a reference panel, and then transformed into the Normalized Difference Vegetation Index [NDVI = (NIR − R) / (NIR + R)], where NIR and R correspond to reflectances in the near-infrared and red wavelengths, respectively. These values were then used to estimate within-plot aboveground live biomass (ALB, in gm−2) using an empirical relationship derived by [5] [ALB = 2.9(NDVI) − 45.6]. Using the Max-Min biomass method [6], we derived an overall estimate of plot productivity (ANPPMM) from these estimates. ANPPMM was calculated by subtracting the minimum seasonal plot ALB from its maximum.

We estimated the proportional areal coverage of individual species rooted within each diversity plot. Individual species estimates were combined to calculate the proportion of plot area covered by each various functional groupings (C3, C4 grasses; C3, C4 forbs; C3, C4 shrubs;
CAM; lichen; *S. densa*). Plot diversity was then expressed in terms of both its species and functional group richesses (SR and FR, respectively).

**B. Scaling relationships by nested sampling**

We used our nested sampling design to scale these plot-level (0.5m resolution) measurements of ANPP\textsubscript{MM} and diversity – and hence the relationships between them – “up” to coarser spatial resolutions of 2.5m, 10m and 50m. The scaling of diversity and productivity information occurred through the successive aggregation of sampling points in our nested sampling scheme (Fig. 1b). At each site, this resulted in \(n=18\) estimates of each measure of diversity and productivity at 2.5m, \(n=9\) estimates at level 10m and \(n=9\) estimates at level 50m.

**C. Statistical Methods**

We used separate univariate regressions to assess the individual effect of each measure of plant diversity on ANPP\textsubscript{MM}. We then used separate multivariate regressions to assess the overall effects of richness on ANPP\textsubscript{MM}. All regressions were fit by linear least squares. Multiple regression models were specified with two independent terms (i.e. SR and FR).

Where partial regression coefficients from multiple regressions showed the effects of SR to be significant, we tested whether this significance could be attributed to the presence of any particular species. To do this, we repeated the previously described multiple regressions, but replaced our original independent variates with 21 dummy variates, each describing a species as absent or present.

**III. RESULTS AND DISCUSSION**

We found weak and positive relationships between SR and ANPP\textsubscript{MM}, and FR and ANPP\textsubscript{MM}, when univariate regressions were applied to all data, but strong log\textsubscript{e}-linear relationships when similar regressions were applied to the mean observed ANPP\textsubscript{MM} at each level of richness (Fig. 2). These relationships were highly significant at the finest sampling resolutions, but less so at coarser resolutions. While these results are consistent with those reported by many single-location experiments (see [7]), as well as those predicted by theory ([8]), they are less consistent with the study of [9], who reported linear richness-productivity relationships for the a 7-year experiment. However, when we replaced each of our log\textsubscript{e}-linear functions with a linear one at a sampling resolution comparable with theirs (10m, in comparison to their 9m), the total variance in ANPP\textsubscript{MM} explained by our models decreased only by 5% on average with little change in statistical significance. This suggests (a) that linear regression models may be equally appropriate for explaining our richness-ANPP relationships at this sampling resolution, and (b) that the nonlinearity of observed richness-productivity relationships may vary according to the successional stage of the plant community under scrutiny. The non-significant relationships found at coarser scales likely resulted from the small sample sizes generated by data aggregation.

**Fig. 1. Nested sampling scheme used in study.**

**Fig. 2. Effects of sampling resolution on relationship between SR and ANPP\textsubscript{MM}. Regression line fit to mean ANPP at each level of SR. Error bars show variation around mean value. Absence of error bars at coarser resolutions indicate single observations.**
The strong richness-ANPP_{MM} relationships outlined above suggest that both SR and FR might provide a useful measure of grassland community productivity at our site. Nevertheless, the partial regression coefficients generated by multiple regressions indicate that SR may be a stronger determinant of ANPP than FR. Indeed, these results suggest that the productivity of plots containing an equal number of species is independent of the number of functional groups present. These results contradict those of [10], who found that both SR and FR affected productivity, and those of [11], who found that only FR had a significant effect on productivity in their experimental plant community.

Multiple regression analyses suggest that the presence of two dominant species significantly affect upland plant community ANPP_{MM} at the plot-level. These species are *S. comata* and *A. frigida*. The significant effects of *S. comata* may occur because it begins growth during the early summer months when large amounts of water are available for plant uptake. The same is true for *A. frigida*, whose longer rooting systems also allow it to access sources of water from deeper in the soil profile. Significant effects of species identity on productivity have also been reported by other studies, but primarily for nitrogen-fixing species. Partial regression coefficients did not show the effects of functional group richness to be significant at any resolution.

Log_{e}-linear regression models fit to our plot-level data show strong and significant increases in total ANPP_{MM} and its upper and lower bounds of variation with increasing richness. This supports the presence of niche complementarity at our sites. This is especially true for models fit to the mean observed ANPP_{MM} at each level of richness, even when data are aggregated to coarser scales.

Despite these results, our study is limited by its lack of any experimental control of diversity. As a result, our results will always be open to other interpretations. This criticism is not unique to our study. Indeed, it has often been directed at observational approaches in general because of their difficulty in controlling for the many variables that potentially covary with diversity.

IV. CONCLUSIONS

Our study provides a valuable insight into the nature of diversity-productivity relationships of northern mixed grass prairie. We have shown that (a) richness-productivity relationships are generally asymptotic, and dependent on the scale of observation, and (b) that our observed diversity-productivity relationships are likely influenced by both diversity (i.e. niche and complementarity effects) and composition (i.e. sampling effects). These results are consistent with the many diversity-productivity relationships reported to date, as well as with theory, which suggests that both diversity and composition are both likely to matter in natural communities. However, longer-term work in other community types at GNP is needed to determine the overall generality of these results and to better assess the implications of declining biodiversity on grassland ecosystem management.

REFERENCES