Average seasonal phytomass: a temporally independent index of herbaceous plant dominance

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Keywords: Diversity, Dominance, Phenology, Phytomass dynamics

Abstract

Diversity, similarity and dominance in plant communities are usually assessed from data collected at a single date. Herbaceous species have differing periods of growth, making phytomass or cover-weighted indices of diversity, similarity or dominance highly dependent on the timing of data collection. A new way of mathematically expressing residence time is presented. Average seasonal phytomass values can be used to better express dominance throughout a growing season. A similar approach could be used for cover or any other dynamic property of plant growth. These values could then be used in dominance-weighted indices of community similarity and diversity.

Introduction

Similarity and diversity are important structural variables used in comparing plant communities. The more sophisticated ways of expressing similarity and diversity often require the use of 'dominance' estimators. A common way of expressing dominance of a given taxon is its weight (phytomass). Phytomass, however, changes greatly over time, especially for herbaceous species. In some vegetation types different herbs grow at different times and have differing peak standing crops. Thus, timing of sampling can greatly affect phytomass estimates obtained, particularly within species-rich communities. These problems are recognized for calculating diversity (Peet, 1974), but no suggestions are made for overcoming them. Although many have studied the seasonal progression of phytomass or cover contributions by component species, most have plotted either individual species

responses (e.g. Krüsi, 1981) or total community cover and diversity separately (e.g. Hutchings, 1983). None have suggested ways of quantitatively expressing species residence time in combination with a measure of dominance such as weight so that other than visual comparisons of community-wide responses could be made.

Although it is possible to partially overcome the problem of characterizing phytomass dynamics by frequent clipping, increased costs and variance emerge because more area must be sampled. Natural patchiness in native vegetation leads to increased variance because some additional species are encountered and previously encountered species may be missing in additional plots (Singh et al., 1975).

Peak standing crop data are suitable only for comparisons among communities with relatively homogeneous species composition and dynamics. As phenologies of taxa diversify, underestimation of standing crops increases (Singh et al., 1975). Additionally, prediction of community peaks is subjective and can only be determined ex post facto.

Terminal standing crops, especially when they include dead material from the current year are more comparable between diverse communities. The true community value would theoretically be underestimated only if there were undetected losses due to disappearance via decomposition and herbivory. Seemingly ideal approaches are to sum the peak standing crops of each individual plant, accounting for phytomass lost to herbivory and litter (Bradbury & Hofstra, 1976) or to mark plant parts and estimate turnover rates and correct for loss of plant parts while others are simultaneously being produced (Williamson, 1976). Less demanding approximations are to sum the peak standing crops of each individual taxon, or even easier, the peaks of each functional or phenologic group (Kelly *et al.*, 1974). These indices are, however, based on a single dimensional measure-magnitude, and fail to take into account the residence time of taxa or other groups over a season. It would be desirable for some purposes such as comparing similarity or diversity of communities with widely different phenological spectra to have a means of expressing the average phytomass of given taxa over the entire growing season. Such an expression of residence time could be used in indices of similarity, diversity or dominance and thus facilitate the comparison of community-wide structural and functional differences under various natural or treated conditions. The following develops and illustrates a new approach to meeting these needs.

Study area

Since the problems with conventional methodology are most pronounced where high floristic and phenologic diversity prevail, especially in regions with short growing seasons, we chose a subalpine meadow in the Wasatch Mountains of northern Utah (Schimpf *et al.*, 1980) as a site for the testing of our method. Sixty three species of herbs were found on the 'Big Meadow' site in 1977. Only two shrub species were present, both in trace amounts. We were thus dealing with a mixed forb–grass plant community; this included all growth forms from small annuals developing early to waist-high, long-lived *Asteraceae* flowering in late summer.

Methods

A 20 × 20 m macroplot was chosen and fenced in 1975 to exclude large herbivores. Other herbivores (e.g. tree-dwelling mammals and insects) and detritivores were largely eliminated beginning in 1976 through snap trapping and periodic application of pesticides to reduce invertebrate activity. (ca 1.2 kg ha^{-1} of lindane, Isotox®, Chevron Chemical Co., and 1.6 kg ha^{-1} of an aldicarb, Temik®, Union Carbide Co.). The exclusion of herbivory was necessary to minimize losses of plant tissue which could not otherwise be accounted for. Comparison with nearby untreated plots showed that there were no pronounced shifts in plant species composition due to pesticide application over the period considered here.

Net aboveground community standing crop (NCSC) refers to the current year's phytomass of both live standing (green) phytomass and any dead material produced that year by all vascular plant taxa. NCSC was sampled 6 times throughout the snow-free growing season of 1977 (200 days, April 21 to October 29) using double sampling (Reese *et al.*, 1980).

Prior to the first sampling, forty 1 m^2 microplot locations, each consisting of four clustered 1 × 2 ft (30.5 × 61 cm) microplots were selected at random within the sampling grid in the interior of the macroplot. This microplot size was chosen to allow repeated, non-destructive sampling with a herbage capacitance meter constructed in English units (Reese *et al.*, 1980). A subset of ten plot locations (40 microplots) became the species phytomass validation sample. This latter sample was chosen to include, as nearly as possible, the full range in phytomass for the taxa within the meadow. Additionally, an attempt was made to include those quadrats which had the greatest number of taxa. This insured the largest number of (x, y) pairs in the double sampling regression for each taxon.

In subsequent samplings, an additional 10 random plot locations were added to the sample. These replaced the 10 which were destructively sampled for method validation. Thus, the list of sampled plot locations continually advanced, removing 10 locations from the top of the list and adding 10 locations to the bottom. This procedure allowed for repeat sampling of 75% of the quadrats from one sampling to the next and minimized potential dif-

ferences in total community NCSC attributable to anomalies in quadrat coverage. It did not, however, insure the same consistency for individual taxon phytomass estimates, since 100% of these validation quadrats were replaced.

Vegetation on the validation plots was harvested by three-dimensional clipping (Currie et al., 1973) to ground level all phytomass attributed to current year's growth. This included current year's dead material (necromass), which was subjectively separated in the field from previous year's necromass on the basis of color and, especially in fibrous taxa, the degree of fragmentation. In many of the taxa encountered, fragmentation occurred within a few weeks (days?) after senescence and became undistinguishable from previous years' necromass. Hence some weights are likely underestimates of necromass (Williamson, 1976). The weight of the 3–4 m deep winter snowpack and rapid decomposition under it (Bleak, 1970) simplify such problems in this environment, however. What is erect during the growing season is definitely the result of the current year's growth.

All clipped material was bagged by taxon and dried in a forced air oven at 70 ° C for at least 48 h. Weighing was done on an analytical balance with weights recorded to a precision of 0.001 g for those samples less than 1.0 g, and 0.01 g for those greater than 1.0 g. Care was taken to exclude all non-organic matter from the contents of each bag. Current year's necromass was separated from live standing phytomass in the laboratory and weighed separately.

NCSC, as well as individual taxon regressions, were computed using regressions through the origin, for both biological and computational reasons. Since negative standing crop is non-sensical and zero relative weight estimation or zero capacitance meter readings are by definition equal to a standing crop of 0.0, the first order regression model is appropriate.

Regression equations for NCSC were separately computed for each sampling interval. Validation sample weights were computed as the sum of the weight of all taxa in each microplot.

Individual taxon regressions were based on a two-stage sampling procedure. The percentage contributions by weight for each taxon within each microplot were multiplied by the predicted weight for the total vegetation within each quadrat. The

latter were estimated from the NCSC double sampling regression equation (Reese et al., 1980).

Mean current year's necromass was determined by taxa for each sampling interval and based on the $n = 10$ validation sample. These data were used to simplify calculations of mean seasonal live standing phytomass.

Estimation of mean seasonal standing crop, a term which includes current year's necromass, would have entailed determining to species level all such necromass harvested on the last day of the growing season. It is doubtful that such a task could have been accomplished, irrespective of the question of accuracy of the data.

Growth curves were determined by fitting linear regression equations to changes in live standing phytomass between each sampling date. The limits on each equation were defined as either (a) mean date of sampling interval i (minimum limit) to the date prior to the mean day of sampling interval $i + 1$ (maximum limit); (b) the date midway between sampling interval i and $i + 1$ to the date prior to $i + 1$ for cases where the phytomass at date $i = 0.0$ (appearance); or (c) the mean date of sampling interval to the date midway between sampling intervals in cases where the phytomass at date $i + 1 = 0.0$ (disappearance). Mean live standing phytomass ($\bar{x}$) values were determined for each taxon by:

$$\bar{x} = (\overset{d}{\underset{i=1}{\Sigma}} \ Y_i)/d$$

where Y_i is the predicted phytomass on day i and d is the number of snow-free days in 1977 (i.e. 200).

Results and discussion

The seasonal trend in total live standing phytomass in the sampled meadow for 1977 is depicted by the bold, upper line in Figure 1. Species contributions to live standing phytomass change drastically over the season. Figure 1 also shows, via the lighter lines, the values for four major taxa. Curves were hand fit to approximate sigmoid curves between sampling intervals.

The high narrow growth curve of Erigeron speciosus var. macranthus is conspicuous. This taxon bloomed and senesced within a period of approximately two months and is an indicator of peak
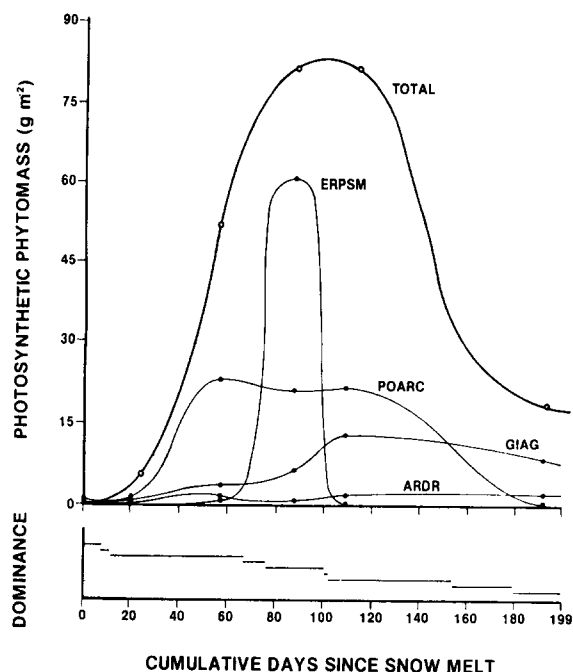
Fig. 1. Thick line on upper part of figure is a hand-fitted curve of seasonal course of total live standing phytomass (net above-ground community standing crop less current year necromass). Thinner lines are seasonal courses of live standing phytomass for four major taxa. ERSPM = *Erigeron speciosus* (Lindl.) D.C. var. *macranthus* (Nutt.) Cronq.; POARC = *Potentilla arguta* Pursh var. *convallaria* (Rydb.) Th. Wolf.; GIAG = *Gilia aggregata* (Pursh) Spreng, and ARDR = *Arabis drummondii* Drummond. Horizontal lines along bottom show when there are changes in the two species which have the most phytomass at a given time in 'Big Meadow' during the 1977 snow-free season.

dominance bars are subject to sampling errors, they serve to stress that dominance on a single date is mainly an artifact for that date. Sampling at the time of peak community production resulted in *Potentilla* and *Gilia* being the co-dominants. Peak community phytomass as an index of production ignores taxa which had peaks at times other than on the sampling date. Using the sum of species peaks, a single dimensional measure which uses the maximum phytomass during the season, the co-dominants would have been *Erigeron* and *Potentilla*.

Reference to Figure 1 shows the limitations of the sum of species peak method. Taxa identified as co-dominants by this method were not necessarily the same taxa that showed large areas beneath their growth curves. These taxa may have bloomed quickly and just as quickly disappeared. They could be considered false dominants in the sense that their residence time is short. This limitation can be compensated for through use of average seasonal phytomass.

Phytomass data are fairly expensive to obtain (see Reese *et al.,* 1980, for costs), therefore a similar approach could be used for cover or other dynamic properties of plants if they are preferred to phytomass in weighting dominance or diversity indices.

This index is not to be recommended to those who want to draw out the details of the seasonal patterns of standing live photomass of individual species in a community. Such information, although important in some types of studies (e.g. Al Mufti *et al.,* 1977), is deliberately submerged here in order to produce a numerical value to express season-long contributions and ease comparisons of similarity and diversity between a variety of nearby communities with widely different phenological spectra.

community standing crop. Curves for *Potentilla arguta* var. *convallaria, Gilia aggregata,* and *Arabis drummondii* were, in contrast, expanded in breadth with live standing phytomass present over much of the snow-free season. This resulted in both *Potentilla* and *Gilia* having higher mean seasonal phytomass (12.2 and 6.9 g m^{-2}, respectively) than *Erigeron* (6.5 g m^{-2}). In contrast, peak standing crops for these taxa were 60.2 g m^{-2} ± 23.9 g m^{-2} (*Erigeron*), 22.9 ± 4.6 g m^{-2} (*Potentilla*), and 12.9 ± 2.4 g m^{-2} (*Gilia*).

Changes in the two most abundant taxa (co-dominants) occurred repeatedly during the season. These shifts are illustrated by segmented, chronological dominance bars in the bottom part of Figure 1. From other related studies (Reese *et al.,* 1980), we know that nine shifts occurred in 1977. While these

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