reasonably well by a long-term variation model. This study, along with other recent criticisms of the testing of magnetic reversal periodicity[10,11], suggests that previous claims that "a statistically significant period of ~30 Myr does formally exist" were premature[4]. Further investigation is necessary to show whether the height of the 30 Myr peak in the spectrum requires a short-term explanation.

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A comparative approach to predicting competitive ability from plant traits

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Decades of study of interspecific competition in community ecology has yielded an overwhelming body of special cases but few general principles[1–3]. This is largely because of the phenomenological, non-predictive approach used[4]. Further progress requires a predictive approach[5] that will enable general principles to be deduced that apply beyond the species and conditions of a particular study or site. General principles are best sought using a comparative approach, that is, the systematic screening of a large number of species under standardized experimental conditions[6,7] We used 44 wetland plant species to test whether competitive ability could be predicted from plant traits. Multiple linear regression showed that there was a strong relationship between plant traits and competitive ability ($r^2 = 0.74$). Plant biomass explained 63% of the variation in competitive ability and plant height, canopy diameter, canopy area and leaf shape explained most of the residual variation. This study represents a major step in escaping the current phenomenological approach to competition in community ecology, and provides a general predictive tool for studying competition in natural communities.

To date there has been no systematic analysis of the relationship between plant traits and experimental measures of competitive ability in a large, morphologically diverse, multi-species community. Several authors have advocated the use of physiological, morphological or behavioural traits to predict competitive ability[1-4,8]. The present study measures the relative competitive ability of 44 herbaceous plant species and tests whether it is correlated with simple measurable plant traits.

A modified additive design[9,10,11] was used to assess competitive ability as the relative ability of each species to suppress the growth of a common indicator species, or phytometer. All 44 species were tested against the phytometer, *Lythrum salicaria*. A subset of 10 species was tested against *Penthorum sedoides* to assess the effect of different phytometers on the results. Single phytometers were planted in the centre of a 1-litre pot in a sterile, organic, high-nutrient mix. Four individuals of each test species were planted in a systematic design around the phytometer (five replicates for each species). Most studies on competitive interference within plant communities are based on considerations of population density, but this obscures variation due to other factors, such as plant size[12,13]. Therefore, this study was conducted at a single density with the effects of distance and angular dispersion kept constant, so that the effects of other parameters could be clearly interpreted. Plants were grown over one growing season, April 1986 to September 1986. Several morphological measurements (Table 1) were made on the test species both under the experimental conditions described above, and on each species grown singly.

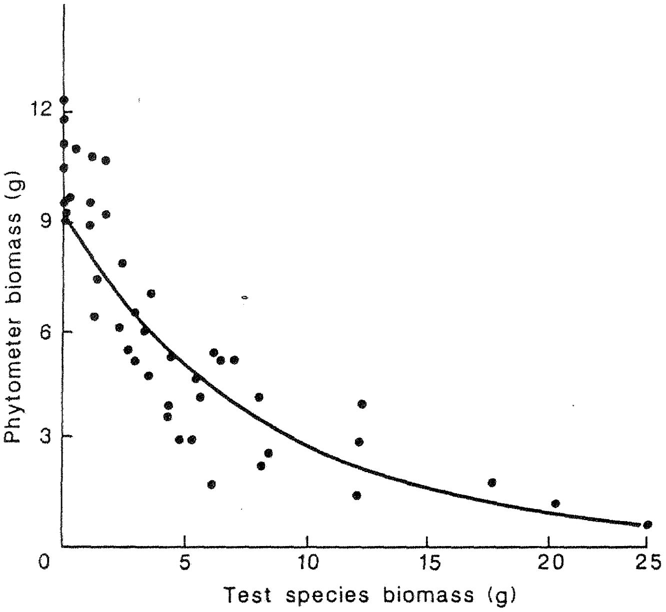

Fig. 1 Phytomer biomass (PB) (*L. salicaria*) as a function of test-species biomass (TSB) ($n = 44$). $\mathrm{PB} = \exp(2.217 - 0.118\,\mathrm{TSB})$; $F = 186.3$, $P < 0.0001$, $r^2 = 0.81$; $b = 0.118 \pm 0.0021$, $p < 0.05$. Test species were (in ascending order of competitive ability): 1, *Ranunculus reptans*; 2, *Lobelia dortmanna*; 3, *Xyris difformis*; 4, *Juncus militaris*; 5, *Eleocharis palustris*; 6, *Juncus filiformis*; 7, *Drosera intermedia*; 8, *Juncus pelocarpus*; 9, *Sabatia kennedyana*; 10, *Anenome canadensis*; 11, *Rhynchospora fusca*; 12, *Eriocaulon septangulare*; 13, *Panicum longifolium*; 14, *Eleocharis erythropoda*; 15, *Dulichium arundinaceum*; 16, *Onoclea sensibilis*; 17, *Lysimachia terrestris*; 18, *Leersia oryzoides*; 19, *Impatiens capensis*; 20, *Viola lanceolata*; 21, *Triadenum fraseri*; 22, *Galium palustre*; 23, *Carex crinita*; 24, *Lysimachia nummularia*; 25, *Spartina pectinata*; 26, *Scirpus validus*; 27, *Polygonum hydropiperoides*; 28, *Hypericum ellipticum*; 29, *Iris versicolor*; 30, *Mentha arvensis*; 31, *Acorus calamus*; 32, *Eupatorium maculatum*; 33, *Rumex verticillatus*; 34, *Potentilla anserina*; 35, *Lysimachia thrysiflora*; 36, *Lysimachia ciliata*; 37, *Carex rostrata*; 38, *Scirpus fluviatilis*; 39, *Pilea pumila*; 40, *Typha latifolia*; 41, *Stachys palustris*; 42, *Phalaris arundinacea*; 43, *Bidens cernua*, 44, *Lythrum salicaria*. Nomenclature follows Fernald[28].

When all 12 measured variables were included, multiple regression showed a strong predictive relationship between plant traits and competitive ability ($r^2 = 0.74$). The biomass of the phytometer was correlated with several traits, but most strongly with the above-ground biomass of the test species (Table 1). Height was also highly correlated with phytometer biomass, but in a stepwise multiple regression it increased r^2 by only 2% over above-ground biomass alone. These relationships can be better described by an exponential equation (Figs 1 and 2).

A major objective was to identify general relationships between plant traits and competitive ability. We therefore conducted several other experiments to determine whether the relationships were robust. The morphological traits discussed above were measured on plants interacting with the phytometer. To examine the influence of the phytometer on morphology, the same traits were measured on each test species grown singly, but under otherwise identical experimental conditions. When regressed against phytometer biomass, similar results were obtained with both sources of measurement and test species biomass was still most strongly correlated with competitive ability ($r^2 = 0.74$; $P < 0.001$).

Changing the phytometer has no measurable effect on the results. Results using *L. salicaria* were compared with results obtained using a smaller species, *P. sedoides*, as a phytometer. Biomass was still the most significant predictor of competitive ability ($r^2 = 0.75$; $p < 0.001$) and the slopes of the regression equations (phytometer biomass as a function of test biomass) were not significantly different (*L. salicaria*, $b = -0.118$; *P. sedoides*, $b = -0.207$; $t = 0.35$).

These results suggest that 'guilds'[14] or 'functional groups'[15] of plants with similar competitive ability may occur along an intergrading continuum of increasing biomass. Within these guilds, that is, where biomass is similar, other factors may become more important in determining the outcome of competitive interactions. Therefore, though our results show that biomass has the best predictive value across this range of species morphologies, in a study that considers a small number of species with a small biomass range, height or other life-history or morphological variables could be the critical determinants of dominance. An inherent assumption of replacement-series experiments[9] is that the species are of similar biomass, so that this traditional approach to measuring competitive ability becomes an assessment of effects 'per biomass'. This may explain why such studies have failed to yield general relationships and patterns.

Though our experiment clearly establishes a predictive relationship between competitive ability and plant traits, it was conducted at a single nutrient level deemed to be most representative of the highly productive conditions of wetlands[16] and those in which competition is presumably most important[8,17]. Our results do not provide a mechanistic interpretation of resource competition. Biomass may simply integrate or summarize other traits, such as high rates of resource capture above and below ground[18,19]. Alternatively, it has been suggested that at high nutrient levels, light becomes the critical limiting resource[20,21] and traits we have identified may be primarily associated with competition for light.

What are the general implications of these results in understanding the organization of natural communities? Published research suggests that size-related variables are pervasive indicators of competitive dominance in a variety of herbaceous plant communities[1,3,22-25] and within forest monocultures[12]. It has been shown that plant biomass or height varies predictably along natural gradients of stress and disturbance[26,27]. Successional and even evolutionary patterns are represented by increases in plant biomass[20]. The occurrence of natural gradients of plant biomass in the field, and the relationship established in this study between plant traits and competitive ability, suggests that competitive ability is an important determinant of community pattern. Our results provide a general predictive tool for testing this relationship. The ultimate value of this research is that it shows the potential for predicting the outcome of multispecies competitive interactions, an important goal if community ecology is to move from a phenomenological to a predictive science.

Table 1 Correlation (r) between traits of 44 test species and biomass of the phytometer (*Lythrum salicaria*)

Plant traits	Correlation with phytometer biomass
Biomass, total (g)	−0.775**
Biomass, above ground (g)	−0.791**
Biomass, below-ground (g)	−0.710**
Height (cm)	−0.659**
Leaf length (cm)	−0.084
Leaf width (cm)	−0.179
Leaf area (cm^2)	−0.302
Leaf number	−0.244
Leaf shape (length:width)	0.356*
Canopy diameter (cm)	−0.455*
Canopy area (cm^2)	−0.593**
Shoot to root ratio (g/g)	−0.016

* $P < 0.05$; ** $P < 0.001$. Correlations are simple linear correlations with phytometer biomass.

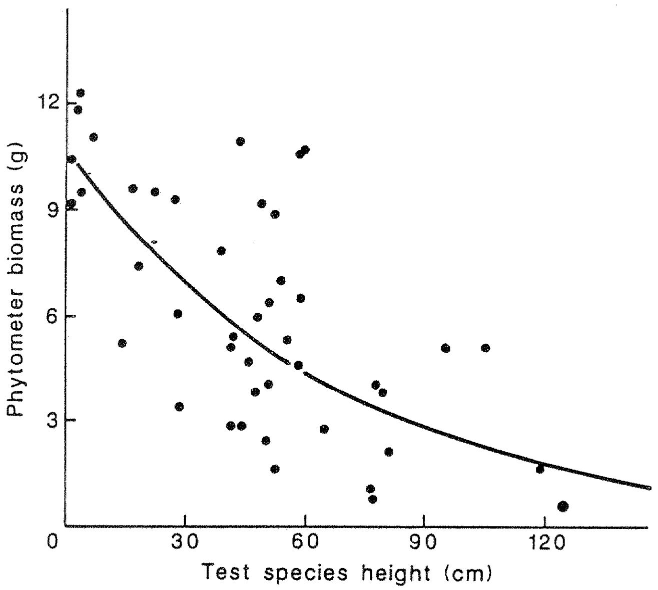

Fig. 2 Phytometer biomass (*L. salicaria*) as a function of test species height (TSH) ($n = 44$). $\text{PB} = \exp(2.392 - 0.016\,\text{TSH})$; $F = 36.263$, $P < 0.05$, $r^2 = 0.64$.

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