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Author(s): Ned Fetcher and Gaius R. Shaver

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## NOTES AND COMMENTS

ENVIRONMENTAL SENSITIVITY OF ECOTYPES AS A POTENTIAL  
INFLUENCE ON PRIMARY PRODUCTIVITY

Since the pioneering studies of Turesson (1922) and Clausen et al. (1948), the notion of ecotypic differences has become an accepted concept in plant ecology. Despite advances in our understanding of physiological and morphological differences between ecotypes (Billings et al. 1971; Osmond et al. 1980), the effect of ecotypic differentiation on ecosystem parameters has received little attention. Here we present an example of ecotypic differentiation in a dominant plant species of the tussock tundra ecosystems of northern Alaska and suggest how such differentiation can affect ecosystem responses such as primary productivity.

*Eriophorum vaginatum* L. is a tussock-forming member of the Cyperaceae with a circumpolar distribution (Wein 1973). Its physiology, demography, and ecology have been the subject of several recent investigations (Shaver and Chapin 1980; Fetcher and Shaver 1983; Chapin and Shaver 1985), including a study of latitudinal variation in growth (Shaver et al. 1986). During the latter study, reciprocally transplanted gardens were established at six sites, three on the northern slope of the Brooks Range in northern Alaska and three on the southern slope (table 1). Each garden contained 60 tussocks, 10 from each site, including local tussocks that were retransplanted. The gardens were established in 1980, except for the Coldfoot garden, which was established in 1982. In August 1983, we measured the length of the longest leaf and counted the number of green leaves in three tillers of each tussock. Tillers were chosen by inserting a pencil into an arbitrary location in the tussock and picking the nearest tiller. We constructed an index of tiller size by multiplying the length of the longest leaf and the number of green leaves. The index is highly correlated with tiller mass (Shaver et al. 1986).

We used the approach originally proposed by Yates and Cochran (1938) and used several times since (Finlay and Wilkinson 1963; reviews in Falconer 1981; Garbutt and Zangerl 1983; Kelley 1985) to reanalyze the data (Shaver et al. 1986). Our objective was to detect genotype-by-environment interaction in the response of the tiller-size index. The gardens were ranked according to the environmental value, which is the value of the tiller-size index averaged over all populations in a garden. The genotypic values are the means of the index for each population within a garden. These were plotted against the environmental value for each garden to produce the response of the population to changes in the environment.

TABLE 1  
CHARACTERISTICS OF SITES AND POPULATIONS OF *ERIOPHORUM VAGINATUM* USED IN  
A RECIPROCAL-TRANSPLANT EXPERIMENT IN NORTHERN ALASKA

CHARACTERISTIC	LOCATION					
	Prudhoe Bay	Sagwon	Toolik Lake	Coldfoot	Eagle Creek	No Name Creek
Latitude (°N)*	70.33	69.42	68.63	67.26	65.17	66.12
Elevation (m)*	5	300	730	300	760	170
Degree-days*	611	904	985	1,622	1,127	1,584
Slope, $\beta$	.80	.79	.41	1.88‡	1.64	1.57
<i>t</i> statistic†	-1.86	-1.63	-5.06	2.53‡	5.07	3.24
df	175	177	178	144‡	178	178
<i>P</i>	.061	.101	<.001	.012‡	<.001	.002

NOTE.— $\beta$  is the slope of the regression of genotypic value on environmental value. All values of *P* are two-tailed.

\* Data from Shaver et al. 1986; long-term averages from May 1 to September 30.

† Values of the *t* statistic for the null hypothesis that  $\beta = 1$ .

‡ From a linear regression using data from Prudhoe Bay, Sagwon, Toolik Lake, Coldfoot, and Eagle Creek.

The slopes ( $\beta$ ) given by the regressions of genotypic value against environmental value give an index of sensitivity to the environment for each population. Since the mean slope is one, populations with a slope greater than one can be considered more sensitive to changes in the environment; those with slopes less than one can be considered less sensitive (Falconer 1981).

The results show considerable heterogeneity in the response of the tiller-size index (fig. 1). The populations from north of the Brooks Range—Prudhoe Bay, Sagwon, and Toolik Lake—generally had smaller tillers; the Coldfoot, Eagle Creek, and No Name Creek populations from south of the Brooks Range had larger tillers. Sensitivity to the environment also differed. The northern populations had slopes less than one, whereas the Eagle Creek and No Name Creek populations had slopes greater than one (table 1). The population from Coldfoot was the only one with a significant ( $P < .0001$ ) quadratic component (fig. 1a). When the value for the Coldfoot population at No Name Creek was excluded from the regression, the slope was significantly greater than one. When genotypic value was plotted against cumulative average degree-days above 0°C between May and September (Shaver et al. 1986), essentially the same results were obtained (fig. 1b). This occurred because the environmental values were positively correlated with degree-days ( $r = 0.798$ ,  $P < .057$ ,  $n = 6$ ).

The populations with the largest tillers also had the greatest slopes of the regression of the genotypic value on environmental value (see the figure). In nearly all studies of genotype-by-environment interaction that used the Finlay-Wilkinson method, a positive correlation has been found between the mean performance of a population as measured by productivity or economic yield and the sensitivity of that population to the environment (Kelley 1985). Kelley (1985) attributed this result to a trade-off between mean yield and stability of production. Such a trade-off could be the result of selection for lower growth rates for plants

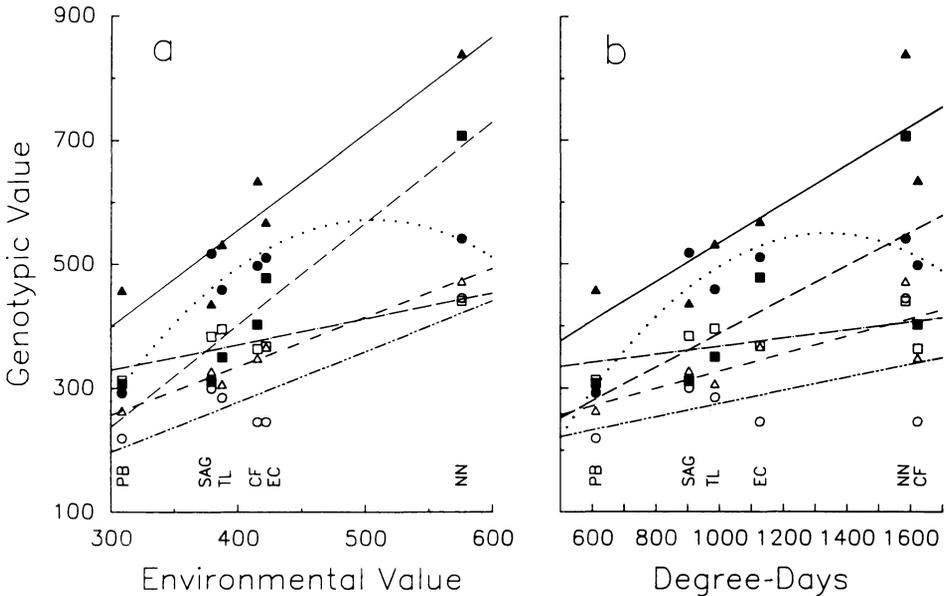


FIG. 1.—*a*, Genotypic value of tiller-size index (length of the longest leaf, in mm, times the number of green leaves) versus environmental value for six populations of *Eriophorum vaginatum* grown in six gardens in northern Alaska. *b*, Genotypic value plotted against cumulative average degree-days above 0°C from May 1 to September 30 at each site. Lines were fitted by least-squares regression. PB, dashed line with double dots, open circles, Prudhoe Bay; SAG, short-dashed line, open triangles, Sagwon; TL, dashed and dotted line, open squares, Toolik Lake; CF, dotted line, solid circles, Coldfoot; EC, long-dashed line, solid squares, Eagle Creek; NN, solid line, solid triangles, No Name Creek.

growing under more-stressful conditions (Grime 1979; Chapin 1980). For the *E. vaginatum* populations in this study, conditions at the northern sites were more severe, as shown by the decline in the number of degree-days with latitude.

Schlichting (1986) criticized the Finlay-Wilkinson approach on the grounds that mean yields were positively correlated, in general, with the regression coefficients ( $\beta$  values) for genotypic value against environmental value. Such a correlation may be a statistical artifact because of a positive correlation between mean yield and its variance. Taylor and Aarssen (1988) argued that the regression method may still be valid if a standardized measure of genotypic variance (coefficient of variation or variance-to-mean ratio) is shown to increase with mean genotypic performance. They found significant positive correlations between the mean and the variance-to-mean ratio for five of the six characters that they studied. For the data in the present study, we also found a significant positive correlation between the mean of the tiller-size index and its variance-to-mean ratio (Spearman  $r = 0.771$ ,  $P < .051$ ,  $n = 6$ ). There was no correlation between the coefficient of variation of the genotypes and their mean tiller-size index, however. When the data were normalized by dividing each value by the mean genotypic value, the Coldfoot and Eagle Creek populations had the highest values of  $\beta$ , and the

Sagwon and Toolik populations had the lowest. The No Name Creek and Prudhoe Bay populations, which had the largest and smallest tillers, respectively, had similar regression coefficients, which were intermediate between the others. In other words, when the data are normalized, the differences between the northern and southern populations of intermediate size become more striking. It appears that a component of the response shown in figure 1a is due to the correlation between mean value of the tiller-size index and its variance but that another component may be attributed to a differential response of the populations independent of size. Clearly, the relationship between mean response and the stability of response requires further investigation under more-controlled conditions.

Several reviews have pointed out the importance of phenotypic plasticity in plants (Bradshaw 1965; Schlichting 1986; Sultan 1987). Our results suggest that ecotypes from colder environments are less plastic in response to an amelioration of the environment. Other studies have found similar results, although they have not used the Finlay-Wilkinson approach (Clausen et al. 1948; Billings et al. 1971; Chapin and Chapin 1981). The differential response of ecotypes represents a genetic limitation on primary productivity in addition to that imposed by climate (Shaver et al. 1986). This situation is analogous to that discussed by Chapin et al. (1986), who proposed that the degree of nutrient limitation of primary productivity depends on both nutrient availability and species composition. Because species that are characteristic of low-nutrient sites often have a limited capacity to respond rapidly to nutrient addition (Chapin 1980), a large increase in nutrient levels at low-nutrient sites often means that the sites must await invasion by more-responsive species to achieve maximum productivity (Chapin et al. 1986).

We propose that ecotypic differentiation may have a similar damping effect on primary productivity. That is, ecotypes from sites where productivity is restricted by cold temperatures may not be able to respond to an increase in temperature as completely as do ecotypes from warmer regions. Alternatively, they may not be able to respond to resources whose availability is controlled by temperature. An example of a resource that would respond to an increase in temperature is the length of the growing season. Leaves on tussocks from northern Alaska were observed to senesce in early August when transplanted to the southern gardens, whereas leaves from the southern populations stayed green for 1–2 wk longer (Fetcher, personal observation), indicating that the northern tussocks were not able to take advantage of the extended growing season completely.

If temperatures were to increase and growing seasons were to lengthen, it seems likely that site productivity in northern Alaska could be limited until ecotypes that show greater response to increases in temperature replace the present populations. *Eriophorum vaginatum* is an important component of tussock tundra (Wein and Bliss 1974) and can contribute 14%–48% of aboveground production in northern Alaska (Chapin et al. 1988). Because of increased concentrations of carbon dioxide and other gases, temperature increases of up to 13°C in the boreal regions have been predicted by several models of global climatic change (Schlesinger and Mitchell 1985).

The replacement of less-responsive ecotypes by more-responsive ecotypes could occur by invasion from warmer areas or by selection of more-responsive,

faster-growing individuals from the population currently occupying the site. The latter possibility is perhaps more likely, in light of the findings of short-term changes in the growth characteristics of plant populations of old fields (Aarssen and Turkington 1985).

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NED FETCHER

DEPARTMENT OF BIOLOGY  
UNIVERSITY OF PUERTO RICO  
RIO PIEDRAS, PUERTO RICO 00931

GAIUS R. SHAVER

THE ECOSYSTEM CENTER  
MARINE BIOLOGICAL LABORATORY  
WOODS HOLE, MASSACHUSETTS 02543

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