Bonnie Heidel

E. Jennifer Christy

and

Amy Jean Gilmartin

Department of Botany
Washington State University
Pullman, Washington 99164

Numerical Phenetic Analysis of Variation in Populations of Poa secunda Presl. and Bromus japonicus Thunb. (Poaceae)

Abstract

Vegetative and floral morphological characteristics appropriate to the Poaceae were assembled, and variabilities between population samples of two grass species from the steppe of eastern Washington were contrasted using multivariate analyses. The species are a native, perennial inbreeder, *Poa secunda*, and an introduced, annual inbreeder, *Bromus japonicus*. Floral differentiation between populations is highest in *Poa secunda*, while our samples of this species show no differentiation vegetatively. Vegetative differentiation between populations of *Bromus japonicus* is evident but is exceeded by floral differentiation between populations of *Poa secunda*. In both taxa, individuals from more mesic sites showed greater intrapopulation variability than those from the drier sites in *Bromus japonicus* and *Poa secunda*. Within-population variability is higher for vegetative than for floral characters in the mesically growing *Bromus* and the xerically growing *Poa*. Results are compatible with the theory which predicts that the facultative apomict, *Poa secunda*, will show a broader range of adaptive variation than the strictly sexually reproducing apomict, *Bromus japonicus*.

Introduction

Among the native and introduced bromegrasses and bluegrasses prominent in western North America are perennials, annuals, inbreeders, and outbreeders. Variability of sympatric populations of inbreeding, annual, and perennial grasses has not been explored intensively with multivariate analyses. Such studies are of value to both systematists and ecologists. We have quantified the pattern of morphological variability between two steppe grasses. The OTUs (operational taxonomic units) are individual plants sampled from local populations.

The following generalizations form a conceptual framework for predicting patterns of differentiation. Phenotypic plasticity, the individual's responses to environmental stimuli (Cook, 1968), is prevalent over fine-tuned adaptation for introduced, annual species (Iman and Allard, 1965), whereas fine-tuned adaptation predominates in native species (Baker, 1972, 1974; McNeil, 1976). Under stable, recurrent conditions, adaptations which are fixed genetically allow for more permanent, finely tuned responses than does phenotypic flexibility or plasticity, and each type of response is present in both inbreeders and outbreeders (Jain and Bradshaw, 1966). Populations of perennial species show more adaptive variation than annual species because the former would be likely to include individuals of different ages which may have been submitted to different environments in their developmental stages (Hamrick *et al.*, 1979). These authors also suggest that species which reproduce both sexually and asexually show a broader range in adaptive variation than more strictly sexually reproducing ones.

The variation patterns will reflect the fact that vegetative characters respond more directly to the environmental factors, while floral traits are more stable, having evolved in response to strong selection pressures such as for fecundity and have become canalized (Bradshaw, 1965; Stebbins, 1974).

The above generalizations and our observations of the two grass species led to the development and testing of the following three hypotheses. (1) The introduced, annual inbreeder, *Bromus japonicus* Thunb., will vary more vegetatively within and between populations than the native perennial inbreeder (and facultative apomict) *Poa secunda* Presl. (2) Within population variability will be higher with vegetative characters than floral ones, and populations of the perennial, facultative apomict *P. secunda* will display higher interpopulation variation with respect to floral characters than vegetative ones. (3) In addition, because mesic sites permit more "experimentation" by the plants, it is predicted that variability within populations from more mesic sites will exceed that for populations of both species from the more xeric habitats.

Application of numerical phenetic techniques has flourished in systematics (Crovello, 1970; Sneath and Sokal, 1973) in which the units of comparison are taxa (e.g., Gilmartin, 1969a, 1974; Jensen and Eshbaugh, 1976; Adams, 1977; Parker *et al.*, 1979; Jacobsen, 1979) or sample sets within the species circumscription (Ellis *et al.*, 1971; Gilmartin, 1977; Riggins *et al.*, 1977; Wilkin, 1978). Related techniques have been applied in ecology for delimiting and evaluating communities (Goodall, 1973; Bray and Curtis, 1957; Williams and Lambert, 1966; Grigal and Goldstein, 1971). Ellis *et al.* (1971) employed large samples (many OTUs from each of seven populations and nine variables) in a biometric analysis of colonization of the introduced *Poa annua* in Australasia. They concluded that while *Poa annua* has been considered to be an inbreeder, their analyses suggest outbreeding. Considerable differences in intrapopulational variabilities among the populations were shown, and the degrees of similarities between members of pairs of different populations in terms of generalized distance varied more than 100 percent in some cases.

Methods and Materials

The two prairie grasses under study occur throughout the Palouse steppe in southeastern Washington and are widespread elsewhere in the Pacific Northwest. *Poa secunda* is a common native species (Weaver, 1917; Daubenmire, 1970) and flowers early. It is a facultative apomict (Hartung, 1946), as are other species of the scabrellae complex (Clausen and Hiersey, 1958), and is typically cleistogamous. *Bromus japonicus* was introduced from Asia and was not recognized in the regional flora (St. John, 1963) until recently (Hitchcock *et al.*, 1969). It is among the latest flowering of the annual bromes in the area (Hulbert, 1955) and is usually cleistogamous (Hitchcock *et al.*, 1969; Smith, 1944). Thus, both species tend to be inbreeders.

The sampling area for each population of *Bromus japonicus* and *Poa secunda* was less than 10 m^2. All four populations are on the same hilly tract five miles west of Colton, Whitman County, Washington. The *Bromus* and *Poa* populations Bx and Px are growing together on a xeric, south-facing slope of the *Agropyron spicatum-Poa secunda* habitat type (Daubenmire, 1970). *Poa* population Pm is on a more mesic north-facing slope, and Bm is growing at a mesic fencerow site between adjacent wheatfields where moisture accumulates. The latter two sites are the *Festuca idahoensis-Symphoricarpos* *albus* habitat type (Daubenmire, 1970). No *B. japonicus* grows at the Pm site, and *P. secunda* does not occur at the Bm site.

Population samples consisted of 12 solitary annual culms of *B. japonicus* collected late in the fruiting stage in October 1978. The two sampling sites (Bx and Bm) were approximately 200 m apart. Twelve caespitose plants of the perennial *P. secunda* were sampled from different clumps to increase the likelihood of each culm belonging to a different clone. These two sampling sites (Px and Pm) were approximately 50 m apart.

The adequacy of the 12-member sample for estimating population variability with a large number of characters has been substantiated among several plant families (Gilmartin, 1974), for *Bromus tectorum* (Bookman, 1980), *Agropyron spicatum* (Dobrowolksi, 1979), and for two species of *Festuca* with a somewhat different character-list (Belsky, 1979). A more extensive character list for the Poaceae is that of Clifford and Goodall (1967).

Data were recorded for each plant with 64 morphological characters applicable to the Poaceae (Dobrowolski, 1979). Twenty vegetative characters (leaf, ligule, culm, and rhizome characters) and 44 floristic characters (inflorescence, spike, and spikelet characters) were treated as character subsets. The ratios of the number of quantitative to qualitative characters were 3:7 for the vegetative set and 1:2 for the floristic set. All characters were scored in one of five mutually exclusive character-states, the mean number of states being three. Data were standardized to a range of 0 to 1 (Crovello, 1963) to calculate phenetic distances from which were calculated the summary statistics, mean phenetic distance (MPD), standard deviation (SD), and coefficient of phenetic variation (CVD). No *a priori* character weighting was applied.

First, principal components analysis (PCA) using NT-SYS (Rohlf *et al.*, 1974) was conducted to determine if the conspecific populations are distinct. It was based on characters which vary between the conspecific population samples; for *Poa* there were six vegetative and eleven floristic; for *Bromus*, eight vegetative and nine floristic. PCA was performed on a product moment correlation matrix. The first three factors were computed.

Second, discriminant analysis on *Bromus* and separately on *Poa* was applied to identify major differences between populations. While not combined in analysis, results are presented on one axis to facilitate comparisons between populations. A maximum of three best discriminating characters delimited the canonical axis, representing a scale of collective character-states. Individual species samples were aligned along the axis (Fig. 2). The best discriminators were determined, and the inter-population distances were compared between species.

Third, phenetic variation was quantified to compare variation within and between conspecific populations. Each population and both pairs of conspecific populations were treated as datasets. Datasets were condensed, and the summary statistics were computed with the DISTA program (Gilmartin, 1969b), which also indicates the actual number of characters employed for each OTU x OTU comparison.

Phenetic distances were computed as the negative log to the base 2 of the similarity index (Rogers and Flemming, 1964). This is a log transformation of the resemblance coefficient (distance) and not of the data, as is more typical. The phenetic distances become new variates; the mean phenetic distance and standard deviation were calculated

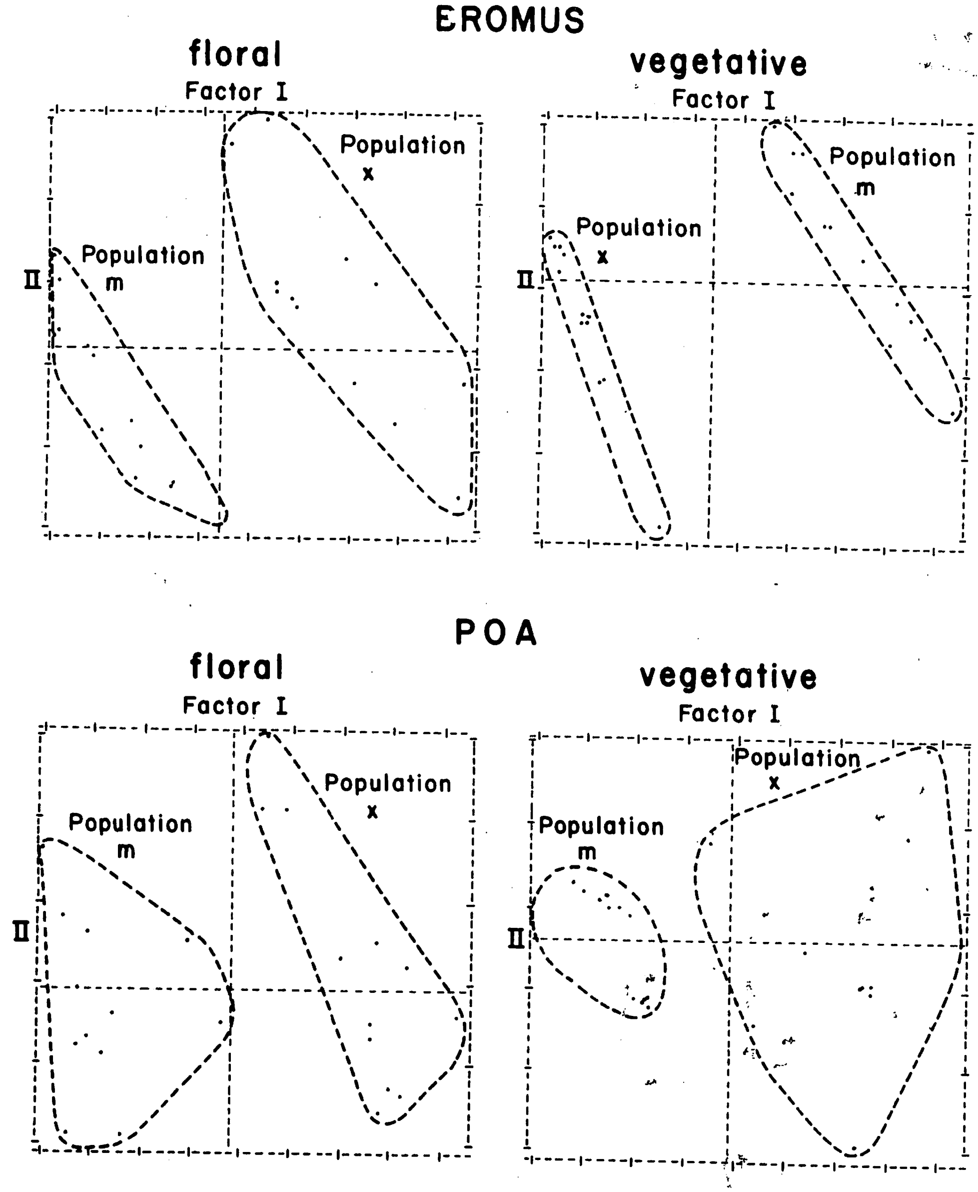

Figure 1. *Bromus japonicus* and *Poa secunda* samples on the first and second axes of a principal components analysis plot using the available 8 vegetative and 9 floristic characters for *Bromus* and 6 vegetative, 11 floral characters in *Poa*. Population X is the xeric site, population M is the mesic site. Proportions of total variance accounted for by each axis are: *Bromus* vegetative dataset: Factor I = 56%, Factor II = 14%, *Bromus* floral dataset: Factor I = 67%, Factor II = 14%. *Poa* vegetation dataset: Factor I = 55%, Factor II = 23%, *Poa* floral dataset: Factor I = 55%, Factor II = 22%.

from a matrix of phenetic distances between all sample members within each dataset. The MPD represents the central tendency of the phenetic dissimilarities, while the SD represents the degree of heterogeneity of the dissimilarities among members of the dataset.

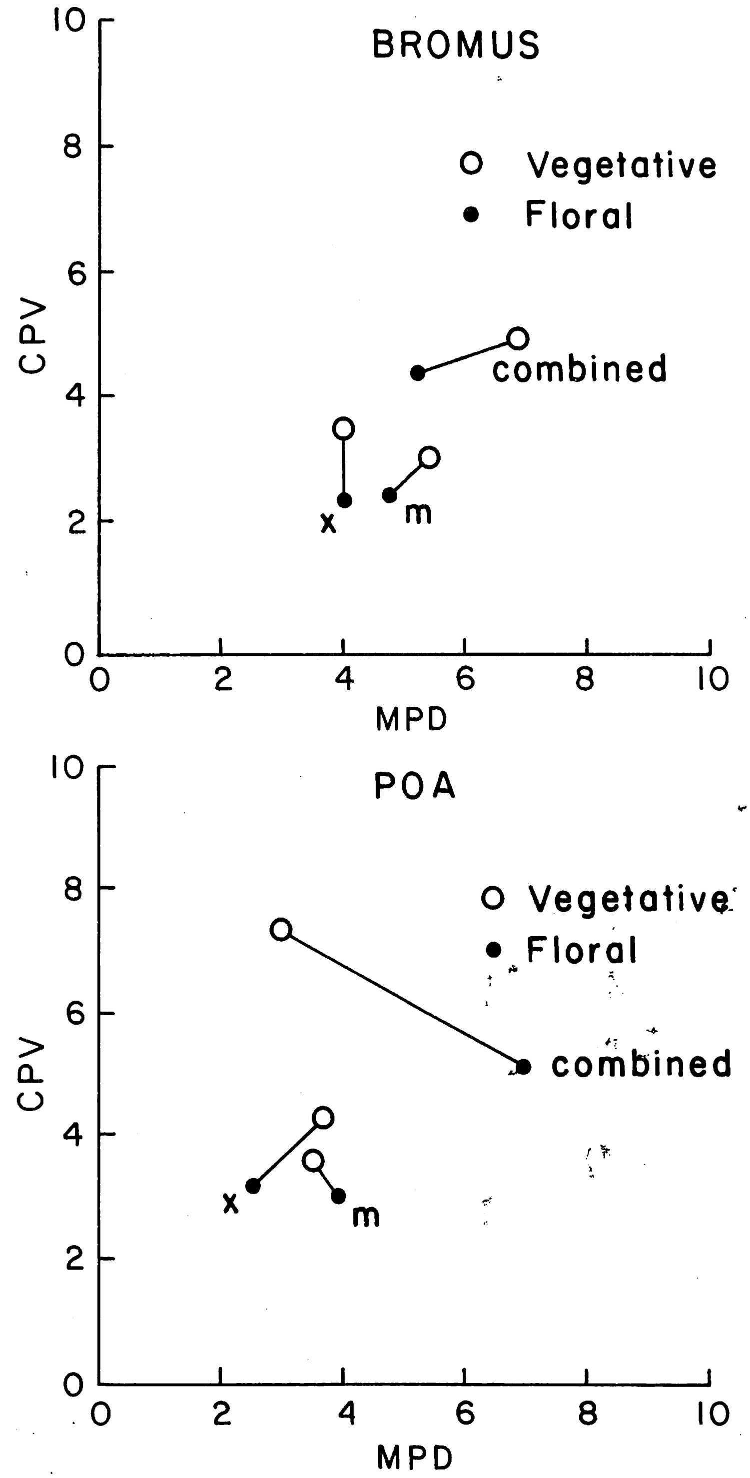

Figure 2. *Bromus japonicus* and *Poa secunda* population members plotted on axes from discriminant analysis using those characters which best discriminate between populations of the species.

A coefficient of phenetic variation (CPV = SD/MPD) was calculated to compensate for scale differences of the MPD when comparing both mean and deviation (Gilmartin, 1974). Were it our goal to discriminate between entities, some other method, such as Mahalanobis D^2, would be appropriate. However, we wish to quantify over all relative amounts of dissimilarity based upon a considerable number of characteristics, rather than test whether two populations are different. The CPV/MPD were plotted for each dataset, displaying the central tendency of variation (the magnitude of the differentiation) and the dispersal (relative degree of uniformity of the dissimilarities among the OTUs). In order to estimate the degree of overall differentiation between two populations, the MPD within each population sample was compared with that obtained from two combined populations. Population pairs which have differentiated will sharply differ in their individual and pooled MPD values. Two populations which have differentiated slightly (or having diverged morphologically, once more have converged) will show little difference in MPD values obtained with pooled and individual samples. However, two populations not distinct in their pooled versus individual MPD values are not necessarily undifferentiated. The two populations may vary in opposing directions, and the counteractive effects may produce a pooled MPD very close to the individual population's MPDs. Such a situation, however, becomes evident if the SDs obtained with pooled and individual samples differ sharply—i.e., if the combined population sample has a much higher SD (less uniformity) than either of the individual samples.

By plotting the CPV against the MPD, a progression of variability (both in terms of magnitude (MPD) and dispersal (SD)) is represented going from the lower left to upper right. While Gilmartin (1980) has done log transformations of such axes in order to portray the linear progression of magnitudes of variation and the dispersal (heterogeneity) of variation within taxa of several categories from species to family, such a transformation is less helpful here because only two levels of variation are included, population and species.

The importance of vegetative and floral variation within and between populations was determined by obtaining the MPD and SD with vegetative and floral characters separately. The presentation technique is modified from Gilmartin (1974) to emphasize character subsets rather than taxonomic levels.

Results

Figure 1 shows the plots for the two factors of PCA which removed at least 70 percent of the variance. The highest character loadings, analogous to correlations between variables and the factor, are shown for Factor I and II in Table 1. The populations of *B. japonicus* (Fig. 1) appear to be more distinct from one another with floral or vegetative characters than the *P. secunda* populations. Ordination accuracy was evaluated by comparing the distances in multidimensional phenetic space with the distances in three-factor space; in all cases, the correlations exceeded 0.95 (reconstructing the original matrix).

Conspecific populations of each species are distinct with respect to the few best discriminating characters (three characters for *B. japonicus* and two for *P. secunda*), but the *B. japonicus* populations showed better separation (Fig. 2). The *B. japonicus*

TABLE 1. Principal component factor loadings obtained with four datasets, floral and vegetative character-sets of **Bromus japonicus** and **Poa secunda**[a]. The first two factors explain at least 70 percent of the correlations.

B. japonicus		**P. secunda**	
Floral Characters			
Factor I loadings (9[b])		Factor I loadings (11[b])	
Inflorescence length	0.94	Lemma length	0.93
Inflorescence diameter	0.92	Shape of first glume apex	0.92
Branch length	0.90	Number of florets per spike	0.89
Lemma texture	-0.88	Number of spikelets per node	0.75
Glume maximum length	-0.87	Length of inflorescence	0.73
Glume maximum width	-0.84	Branch length	0.44
Length of internodes	0.82		
Number of spikelets/node	0.52		
Factor II loadings		Factor II loadings	
Number of spikelets/node	-0.57	Length of internodes	-0.84
Glume maximum width	-0.44	Inflorescence diameter	0.82
Glume maximum length	-0.42	Branch length	-0.80
		Inflorescence length	-0.59
Vegetative Characters			
Factor I loading (8[b])		Factor I loadings (6[b])	
Culm height	0.91	Leaf-blade length maximum	0.94
Culm degree of hollowness	0.86	Leaf-blade width maximum	0.93
Leaf-blade length	0.84	Culm height	0.83
Culm diameter	0.78	Leaf-sheath indumentum type	-0.70
Ligule diameter	0.73	Ligule length	0.70
Culm pulvinus presence	0.44	Culm diameter	0.36
Factor II loadings		Factor II loadings	
Leaf-blade width	-0.84	Degree stoloniferous	-0.84
Culm degree of hollowness	0.43	Ligule length	0.40

[a]The correlation matrices upon which the analyses were based are deposited with the Ownbey Herbarium, Washington State University.

[b]Number of characters available for the analysis.

population discriminators were lemma length, glume length, and glume width. The *P. secunda* population discriminators were glume width and leaf-blade length.

Variation differences using all 20 vegetative and 44 floristic subsets of characters were used in order to sample two kinds of overall divergences. Variabilities were compared by plotting their CPV and MPD values (Fig. 3). The vegetative subset in all cases shows a higher value in CPV than does the floral subset. However, the standard deviation (dispersal of the distances between the OTUs) of Pm is smaller for the combined *P. secunda* population's vegetative set than the floral subset (Table 2). This finding is also evidenced in Fig. 3 by the reversal in the slope from floral to vegetative of the line depicting combined *P. secunda* populations. In one case, *Poa secunda* combined populations, the slope differs significantly from zero.

The relative amounts of differentiation between conspecific populations are shown by the summary statistics for all datasets in Table 2, and change or difference in SD

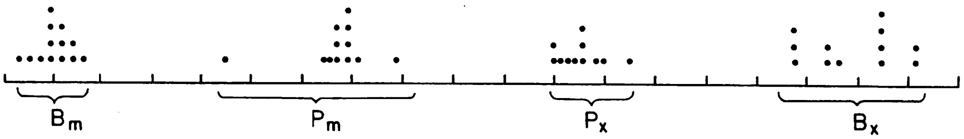

Figure 3. Variability of *Bromus japonicus* and *Poa secunda* datasets using all characters. The ordinant is the coefficient of phenetic variation (CPV), the abscissa is the mean phenetic distance (MPD), each multiplied by a factor of 10.

TABLE 2. Overall variability within and between conspecific populations of **Bromus japonicus** and **Poa secunda** using floral and vegetative subsets of 44 and 20 characters to obtain the MPD (mean phenetic distance), SD (standard deviation) and CPV (coefficient of phenetic variation). Population X is the xeric site, population M is the mesic site.

	B. japonicus		**P. secunda**	
	Floral	Veg.	Floral	Veg.
Population X				
MPD	0.40	0.40	0.25	0.36
SD	0.10	0.14	0.08	0.15
CPV	0.25	0.35	0.32	0.42
Population M				
MPD	0.48	0.53	0.39	0.36
SD	0.12	0.17	0.12	0.13
CPV	0.25	0.32	0.30	0.36
Combined populations				
MPD	0.52	0.67	0.69	0.31
SD	0.23	0.34	0.36	0.23
CPV	0.44	0.50	0.52	0.74
SD from combined populations minus maximum SD within populations	0.11	0.17	0.24	0.08

from within to between samples is given in the last row. For example, 0.11 is the difference between the SD within and between populations of *B. japonicus* with floral data. The degree of differentiation seen in vegetative and floral features is greater in *P. secunda* than in *B. japonicus*.

Discussion

Hypotheses were only partly supported by the data. For clarity, these will be discussed separately under (A) within population variability (anagenesis) and (B) between population variability (cladogenesis). One of the most useful plots is Fig. 3, which portrays the variability within as well as between conspecific populations employing 20 vegetative and 44 floral traits. The techniques of numerical taxonomy are valuable to ecologists as a means of quantifying descriptive relationships within and between populations. It is clear from Table 2 and Fig. 3 that the overall intra-population variation for *P. secunda*, regardless of character-set, is less than that for *B. japonicus*; that vegetative characters are as variable or more so than floral ones; and that mesic populations vary more than xeric ones. We have applied some methods appropriate to questions concerning relative degrees of overall intrapopulational variability and divergence between conspecific populations. We are much less interested here in discriminating populations. Generalized distance, which is designed to help distinguish populations, is inappropriate to our questions and our datasets, which lack multivariate normality.

A. Within Population Variation, Anagenesis

1. An introduced, annual inbreeder, *B. japonicus*, will vary more than the native, perennial inbreeding facultative apomict *P. secunda*. Using 20 vegetative and 44 floral traits, some of the differences between the two species show the predicted trend. With floral information, variability of Bx (MPD = 0.40, SD = 0.10) is 38 percent higher than Px (MPD = 0.25, SD = 0.08). A biologically interesting difference is considered to be at least 15 percent (Gilmartin, 1974; Bookman, 1980). Florally, the variabilities

did not differ particularly between Pm and Bm, but vegetatively they did differ. Specifically, Bm showed variabilities 32 percent higher in MPD (0.53) than Pm (0.36), and Bm's SD (0.17) was 42 percent higher than Pm's SD (0.13). Other differences are within a few percentage points of 15 percent and are not considered because they are likely the result of sampling error. The differences between Bx and Px are the largest and among the most interesting because these two populations were growing together on the same habitat type, a south-facing slope. The drier site produced a similar amount of vegetative response for both species, but there was less floral variation for *P. secunda* than for *B. japonicus*. We will return to this point later.

Summary statistics employ 22 and 44 characteristics for the vegetative and floral subsets, respectively, whereas the PCA used no more than 11 characters. The algorithms for the PCA and discriminant analysis (DA) are designed to use only variables; only a few traits vary within and between conspecific populations. In addition to the degree of variation of each of the variables, the summary statistics incorporate the PROPORTION of the total character set which actually varies, while PCA does not take into account differences in the proportion of characters which vary. For example, 11 out of 44 floral traits vary in *Poa* and 9 vary in *Bromus*. Six out of 20 vegetative traits vary in *Poa*; eight vary in *Bromus*. The summary statistics incorporate the fact—e.g., that in *Poa* 6/66 or 1/11 of the characters vary. Not only do the summary statistics afford a more unbiased estimate of overall variability than PCA, but they also calibrate the variability for population samples relative to other taxa. Our results can be compared with results derived by using a similar character list. For example, Dobrowolski (1979) found that in 15 paired comparisons among populations of *Agropyron spicatum* (Pursh) Scribn., six of the MPD values for vegetative characters were at least 30 percent greater than the MPD values for floral subsets while the other nine were about equal.

2. Populations of the introduced annual *B. japonicus* are expected to show greater overall variability and difference in vegetative characters than in floral ones. Neither the Bx nor Bm population appears to show appreciably greater vegetative than floral variation (Fig. 2; Table 2).

3. Vegetative traits vary more than floral traits. Considering both the magnitude of variability (MPD) and the dispersal of the dissimilarity values (SD), this conclusion is supported by our data (Fig. 3; Table 2). In all cases the vegetative subsets show as high or higher variability than the floral traits.

4. In each species, individuals from the more mesic habitats will be more variable than individuals from the more xeric habitats. While the Pm population was substantially more variable than the xeric Px population for floral characters (Table 2, Fig. 3), the same cannot be said for the vegetative subset of *P. secunda*. Both vegetatively and florally, the Bm population was more variable than the Bx populations; vegetative characters varied the most. Thus, the *Bromus japonicus* mesic population varied more vegetatively, and the *Poa secunda* mesic population varied more florally.

B. Variation between Populations, Cladogensis

This type of variability is of great interest to taxonomists involved in circumscription of taxa and interpretations of the processes of speciation. Each of the hypotheses stated in the introduction will be dealt with as in part (A) above but will also be considered with regard to interpopulation variability.

1. An introduced, annual inbreeder, *B. japonicus* will show more interpopulation variability than the native perennial, *P. secunda*. Results of each of the three methods (PCA, DA, and summary statistics) are pertinent. The PCA plots (Fig. 1) of the first two factors show the *Bromus* populations to be somewhat more distinct for both vegetative and floral traits than the *Poa* populations. The best distinction between *Bromus* populations is based on vegetative traits. The results with PCA with 11 or fewer variates are supported by the summary statistics obtained with 20 and 44 characters.

The relationship (Kluge-Kerfoot phenomenon) between variability within populations and divergence between population has been shown to be significant (Kluge and Kerfoot, 1973; Sokal, 1976) for individual characters for a number of vertebrate and invertebrate taxa. It is not known yet if this holds for plants or for overall variability. Our results with overall variabilities show discrepancies from this association. Table 2 shows the change in CPV and MPD from individual to combined populations for *Poa* with floral traits, and the decrease in MPD with vegetative traits. There is little vegeative change but great floral change for *P. secunda*. This point is illustrated in Fig. 2 by the proximity of the open circles (vegetative subset) for both Px and Pm and the lack of any increase in PMD from within to between populations. Table 2 and Fig. 3 do show, however, that the SD of the *Poa* floral samples differs from within to between populations. The hypothesis must be considered supported by the data only for floral traits, since floral traits of the *Poa* populations are more differentiated than the *Bromus* samples. The next higher differentiation is between the two Bx and Bm populations vegetatively.

2. Populations of *B. japonicus* differ more in vegetative characters than in floral ones; the converse is true for *P. secunda*.

3. Vegetative traits vary more between populations than floral traits. This is true for *B. japonicus* and false for *P. secunda*.

4. Hypothesis number 4 is only applicable to within populational variability and is discussed under (A).

In summary, we find different responses to similar and to differing environments in the two evolutionary lines, with *Poa* differentiating more florally and *Bromus* differentiating more vegetatively.

The high overall variability within the introduced *B. japonicus* populations in both sites was expected, but the greater differentiation between *Poa* populations is especially interesting. While both species are inbreeders, only *P. secunda* is a facultative apomict; this apomixis should result in differentiation between local populations. The fact that it is demonstrated more by floral traits than vegetative ones also suggests an evolutionary derivation for this distinction rather than strict plasticity. In addition, older populations are expected to show greaer interpopulational differentiation. Populations of *P. secunda*, a native of the Pacific Northwest, differ more between populations than do the populations of the introduced *B. japonicus*.

Whereas we hypothesized that the perennial nature of *P. secunda* would impose greater variability among individuals within populations due to individuals being of different ages as suggested by Hamrick *et al.* (1970), we do not find any evidence of this. The explanation could be that this response, while present, is swamped by other factors, or indeed that all of the individuals of the *P. secunda* populations which were sampled were approximately of the same age, a phenomenon which often occurs among some of the perennials of the Pacific Northwest because of grazing practices.

Factor II of PCA (Fig. 1) plays little or no part in grouping together members of a population sample, but Factor I does. We feel that an elongation factor is evidenced by Factor I loadings for floral traits of both species; e.g., lengths of inflorescence, branches, and internodes. Factor I includes some of the variables such as a plant height and inflorescence size used by Iman and Allard (1965) to quantify genetic information (in a study of wild oats). Factor I could be thought of simply as a size factor, as often occurs for the first axis of PCA. Beyond the size element within Factor I, there are in *Poa* a meristic component (number of florets, number of spikelets) and glume apex shape which play a role. These latter three traits are particularly developmental or meristematic and more evident in *P. secunda* than in *B. japonicus.*

The drier sites (Px, Bx) were accompanied by less variability within all datasets, especially for the *Poa* floral set. This is interpretable by recalling that *P. secunda* is a facultative apomict and that variants may survive in the more favorable Pm site and not in the Px site. Vegetatively, the responses of the two *Poa* populations were very similar. As pointed out by Jain and Bradshaw (1966, p. 436), localized differentiation is entirely explicable by a species having ". . . the ability to develop the relevant characters by processes of conditioning in the vegetative phase." Such conditioning (direct responses during the lifetime of the individual) would be a much more potent force in a perennial than in an annual species.

In conclusion, populations of both species have differentiated, but *Poa* demonstrated greater floral differentiation. We interpret this as an evolutionary response. Within-population variability is somewhat greater in *Bromus* than *Poa*, regardless of the character space. We interpret this as a manifestation of acclimation or plasticity within the *Bromus* populations. The PCA plots, which were based on small sets of characters (6-11), were useful for comparing OTUs; but the summary statistics, which include many more characters (20-44) and incorporate an estimate of overall variability (the proportion of the characters which vary out of the total subset of characters being used), provide a calibration of our results for comparisons with results of other studies.

Questions which remain unanswered concern relative influences of: reproductive systems; annual versus perennial habit; and the length of establishment of the populations. Do long-established populations of the annual *Bromus japonicus* growing as a native in Europe show the same degree of interpopulation floral differentiation as the American native populations of the perennial, facultative apomict, *Poa secunda*? While we found that parapatric populations differentiate as predicted (Jain and Bradshaw, 1966), it will be interesting to learn if parapatric populations of *Poa secunda* not from contrasting moisture regimes will show the same degree of floral differentiation. Using the described techniques, the foregoing questions can be answered as well as others; e.g., do allopatric populations of *Poa secunda* in the same and different moisture regimes show the same degree of floral differentiation, and if not, by how much do they differ, and which characters vary? Herein, we have been able to quantify the differing responses of populations of two grass species, and the answers we have provided may have applicability to many species.

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