

# Expanding the View of Emergence in Individuals, Populations, and Species of Stipoid Grasses: A Comparison Including Achnatherum occidentale

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Dedicated to the memory of Mareen S. Kruckeberg, friend to people and plants.

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## ABSTRACT

In our ongoing studies of emergent properties at different hierarchical levels in the grass tribe Stipeae, an additional species, *Achnatherum occidentale*, is included to broaden the comparison. The degree of emergence seen parallels that of previous studies, an increasing trend from populations to individuals and species to related groups of species. The degree of emergence in species pairs that hybridize, *A. hendersonii* and *A. lemmonii*, or *A. occidentale* and *A. lemmonii*, is lower than in non-hybridizing species pairs of *Achnatherum*, including the closely related pair of *A. wallowaensis* and *A. hendersonii*. The degree of emergence assesses the relationship among variables. This relationship, in turn, is the end product of integrated developmental pathways; a lower degree of emergence reveals similar responses among developmental pathways. Similar developmental responses may facilitate hybridiz a-

tion since hybrid survival requires coordinated development. The different developmental pathways inferred for *A. hendersonii* and *A. wallowaensis* argue for the existence of different developmental ways to very similar ends, the spikelets in the two species. The outcome of speciation, as viewed from a developmental perspective, seems best accounted for through theories that relate the dissipation of energy to the transformation of matter along with conceptualizing a species as a virtual code that achieves material expression only when an individual appears. This view of a species is explored through structural relationships within and among grass species.

### 3 INTRODUCTION

This is part of a series of continuing studies where the original intent was to offer an empirically based account attempting to link ontogeny and phylogeny. Both are central events in biology and share the features of irreversibility, the appearance of novelty, increasing complexity and with identifiable beginnings and ends. In addition, ontogeny and phylogeny offer a bridge to the physical sciences through the proposal that they are systems of increasing entropy (Brooks 2001). We wish to offer a continued exposition of ontogeny and phylogeny in a search for common mechanisms of change and to put those mechanisms within a framework of causal connections. We seek answers to the questions, “Why do ontogeny and phylogeny occur?” and “What are the common changes that take place during ontogeny and phylogeny?” We seek an account that makes these biological phenomena as inevitable as water flowing down hill or the rise and fall of tides. We seek the underlying causal generalities or physical laws.

The first step is to offer a universal description of the products of ontogeny and phylogeny, or individuals and aggregations of related individuals. The language of ontogeny, which describes changes that take place within an individual over its lifetime, cannot be directly translated into the language of phylogeny, which infers time from patterns of similarities and differences among natural groups of organisms. So we must first establish a common lexicon that would allow us to compare ontogeny and phylogeny analytically.

To apply a common lexicon we rely on Polanyi’s (1958) concept of emergence, as a difference between parts and wholes, and as a way of describing individuals (Maze and Bohm 1997), populations, species and groups of related species (Maze 1998; Maze *et al.* 2001a,b, 2002b). Once emergence was established, as evaluated by the angular difference between first principal components analysis (PCA) eigenvectors (see Analysis section below for details), it was then used to derive other comparisons among individuals, populations and related species, this comparison being the degree of emergence. The degree of

emergence is a numerical evaluation of how much emergence was seen within any group analyzed and is the difference between parts and wholes. The degree of emergence is a measure we can apply to individuals and aggregations of individuals ranging from populations to parts of phyletic lineages. This has become the main focus of our studies; what inferences about the common features of ontogeny and phylogeny are allowed by a comparison of the degree of emergence seen in individuals, populations, species and related groups of species (Maze 1998; Maze and Bohm 1997; Maze *et al.* 2001a,b, 2002b)?

In our studies there have been consistent findings in the degree of emergence with populations showing the lowest, followed in sequence by the combination of individual plants and species, pairs of species and larger groups of species. The last category shows an increasing degree of emergence as the groups come to comprise more distantly related species. With the exception of individual plants, this trend can be related to inferred historical age with populations being the youngest and the more distantly related species the oldest.

There were some unexpected results in the degree of emergence obtained in comparisons of certain pairs of species (Maze *et al.* 2001a). *Achnatherum hendersonii* (Vasey) Barkworth and *A. wallowaensis* Maze and K. A. Robson are very similar morphologically, so much so that the latter was only recently described as distinct (Maze and Robson 1996). But those two showed a greater degree of emergence than the combination of *A. hendersonii* and *A. lemmonii* (Vasey) Barkworth. The latter two species are very distinct and, to our knowledge, have never been confused with each other. There is an intriguing biological correlate of these results in that *A. hendersonii* and *A. lemmonii* hybridize (Spellenberg 1968). We speculated (Maze *et al.* 2001a) that perhaps a lower degree emergence seen in the two species is related to their ability to hybridize.

The purpose of this study was to expand our comparisons of these grasses by adding another closely related species, *A. occidentale* (Thurber) Barkworth. By adding another species to those analyzed in earlier studies we could test the previous relative ranking of the degree of emergence seen in groups of various inferred ages, from individuals to phyletic lineages comprised of distantly related species. Using *A. occidentale* would also allow us to test our speculations about the degree of emergence in species pairs that hybridize. *Achnatherum occidentale* hybridizes with a species previously studied, *A. lemmonii*, forming, in some cases, sterile hybrids (Maze 1962) and in others a polyploid species *A. latiglumis* (Swallen) Barkworth (Pohl 1954). Based on our comparison of *A. lemmonii* and *A. hendersonii* we would predict that *A. occidentale* and *A. lemmonii*

would show a lower degree of emergence than other species pairs that are not known to hybridize.

## 4 MATERIALS AND METHODS

### 4.1 SPECIES

Achnatherum occidentale, like other taxa and individuals analyzed for emergence, is in the tribe Stipeae of the Poaceae. It is a grass of drier forests of western North America and occurs from British Columbia, Canada, south in the United States to California and east to Montana, Idaho and Nevada (Hitchcock *et al.* 1969). In this study, it was collected throughout part of its range, from California north into Washington. Collection sites are in Table 1.

Table 1: Collection sites for A. occidentale.

| Acronym | Site  |
|---------|---|
| MON     | On both sides of Power House Road, just n. of Calif. St. Highway 167, Mono Co., Calif. growing with sagebrush. 38.05N, 119.17W.   |
| MIL     | On east side of road at eastern edge of Mountain Warfare Training Center along Calif. St. Highway 108, Mono Co., Calif. growing with sagebrush. 38.37N, 119.50W.                          |
| MOI     | 4.5 km e. of Monitor Pass on Calif. St. Highway 89, Alpine Co., Calif. growing with antelope brush. 38.70N, 119.60W.  |
| PRO     | 0.4 km. S. of Prosser Hill Recreation Site on Calif. St. Highway 89, Nevada Co., Calif. growing with ponderosa pine. 38.40N, 120.23W.   |
| SIE     | 2.4 km. s. of Graeagle on Calif. St. Highway 89, Plumas Co., Calif. growing with ponderosa pine. 39.45N, 120.37W.   |
| OLD     | 1.6 km. sw. of junction of Calif. St. Highways 44 and 89 on Calif. St. Highway 89, Shasta Co., Calif. growing with ponderosa pine. 48.70N, 121.5W.  |
| LAK     | 5.4 km from county road on Thomas Creek Road (ultimately U. S. Forest Service Road 28) (nw of Lakeview, OR) at cattle guard, Lake Co., Ore. growing with ponderosa pine. 42.27N, 120.50W. |
| RED     | 16.8 km w. Redmond, OR on Ore. St. Highway 126, Deschutes Co., Ore. growing with junipers. 44.30N, 121.43W  |
| MAR     | At junction Marshal Ave. and Cheney - Spokane Road, Spokane Co., Wash. growing with ponderosa pine. 47.29N, 117.35W   |
| COL     | Along west bank Columbia River just north of bridge carrying U. S. Highway 395 bridge across the Columbia River, Stevens Co., Wash. growing with ponderosa pine. 48.63N, 118.13W.         |

The exact relationships between A. occidentale and the other species of Stipeae studied to date, A. lemmonii, A. hendersonii, A. wallowaensis and Heterostipa comata, are not clear. The consensus is that A. hendersonii and A. wallowaensis form a closely related pair, and they, along with A. lemmonii, form a group of three closely related species. Achnatherum lemmonii is larger than either A. hendersonii or A. wallowaensis but shares with them an indurate lemma, an oblique apex of the lemma where the awn attaches, a blunt callus and a palea almost as long as the lemma. Achnatherum lemmonii also shares some unique developmental features with A. hendersonii: an outer integument that projects into the junction at the base of the style branches and an adaxial meristem at the summit of the floret that develops predominately through events taking place in the protoderm, viz. periclinal divisions, followed by distally and obliquely directed cell elongation (Maze et al. 1972; Mehlenbacher 1970). Achnatherum occidentale is related to the trio of A. lemmonii, A. hendersonii and A. wallowaensis, but differs from them in having a softer lemma, a transverse lemma apex, a longer and much sharper callus and a palea much shorter than the lemma. Achnatherum occidentale is a highly variable taxon, forming a complex that often defies definition. It also has a relationship to another highly variable taxon, A. nelsonii, with which it appears to hybridize, resulting in A. occidentale ssp. californicum (Merril and Burt Davy) Barkworth (Maze 1962). In being part of a complex and highly variable group this species offers a contrast with other species of Achnatherum previously analyzed, all of which are well defined. The other species included in these analyses, Heterostipa comata, is a relative of Achnatherum and in the same tribe, the Stipeae; H. comata was part of a previous study (Maze et al. 2002b). Until recently, many species of Achnatherum and Heterostipa were placed in the genus Stipa, while A. hendersonii and A. wallowaensis were grouped in Oryzopsis, the closely related ricegrasses.

## 4.2 DATA

The structures measured and analyzed were spikelets, each consisting of a single floret. Spikelets are the functional and homologous equivalent of flowers. Morphologically, they are flowers plus accessory structures. Our sampling procedure was the same as in our previous studies on populations and species (Maze 1998; Maze et al. 2001a, 2002b), one spikelet per individual for each of 100 individuals in a population. The variables used to describe those spikelets were: length of the upper and lower glumes (G1L, G2L), floret length (including the callus) and width (FL, FW) and the length of the awn that terminates the floret (AWN). These variables are not the same as those in previous studies on emergence in these grasses (Maze and Bohm 1997; Maze 1998; Maze et al. 2001a,

2002b) which also used width of the upper and lower glumes. There were three reasons for dropping these two width variables: 1) Glume widths have higher coefficients of variation (details not shown to save space) than glume lengths. 2) Measuring the width of one glume requires more time than measuring the other five variables combined. The continuation of these studies and the exploration of initial findings will require larger and larger data sets thus placing a premium on the ability to quickly measure a spikelet. 3) We compared the results from an analysis of seven as opposed to five variables over all previous studies on grasses and both analyses show similar patterns and relationships. These comparisons are not presented, as they are lengthy; they are available from the senior author.

## 5 ANALYSES

The analysis for emergence used here is the same as in previous studies (Maze 1998, 1999; Maze and Bohm 1997; Maze *et al.* 2000, 2001a,b, 2002a,b) to which the reader is referred for details. Briefly, the approach was to generate two hierarchical levels for a group being analyzed, a lower level, which represents the parts, and a higher, which represents the whole. Emergence was a difference between the parts and wholes, where parts and wholes were both described by the angle, in degrees, with a vector of isometry formed by first eigenvectors from a principal components analysis (PCA) of a correlation matrix. Only first eigenvectors were used since they account for the majority of variation in the data. The angles with a vector of isometry were calculated from bootstrapped (Efron 1982) samples; for details see previous studies (see Maze 1998, 1999; Maze and Bohm 1997; Maze *et al.* 2000, 2001a,b, 2002a,b). The analyses involved generating random subsets from a group being analyzed, establishing lower and higher hierarchical levels within each random subset and then calculating angles with a vector of isometry for the two levels within each randomly generated subset. To analyze for emergence in the populations, each population was the group from which random samples were drawn. When we analyzed for emergence in the species all populations were pooled, the population structure eliminated and that pooled sample formed the group from which random samples were drawn. Random samples from each group analyzed were generated using SYSTAT 4.1 (Wilkinson 1988), which uses an algorithm developed by Bebbington (1975). The emergent properties of the group being analyzed was determined by the average of the angles with a vector of isometry, calculated over all the random subsets for that group, for the parts and whole. In our previous studies the data were bootstrapped 50

times. In this study we bootstrapped 10 times since we have discovered that the results achieved after 10 bootstrappings do not differ from those based on 50.

In addition to analyzing for the occurrence of emergence, we also wanted to know the degree of emergence, that is, how much emergence is seen in any group analyzed; individuals, populations and more inclusive assemblages of related taxa. In order to estimate the degree of emergence we calculated the angle formed between each part, the lower level, and the whole, the higher level, for first eigenvectors. These angles are calculated as part of Pimentel's (1993) MPCA program. The degree of emergence for any group analyzed was the average of those angles. A small angle means that first eigenvectors for the parts are similar to the first eigenvector for the whole. As that angle increases, so too does the dissimilarity in eigenvectors. Or, the greater the dissimilarity in eigenvectors the greater the difference between parts and wholes and the greater the degree of emergence. These angles were based on 10 bootstrapped analyses and we call the measure for any group ANG. ANG is designed to replace AVGD, the average degree of emergence, of previous studies (Maze 1998, 1999; Maze and Bohm 1997; Maze *et al.* 2000, 2001a,b, 2002a,b), which was also based on a comparison of first eigenvectors. AVGD suffers from being computationally clumsy, requiring five steps where ANG requires only one. In order to assure that using ANG, and a reduced variable set, does not distort our results we compared all our previous analyses done on grasses, which were based on AVGD, with reanalysis of the same grasses for ANG based on five variables. The results are very similar but the comparison is not presented for economy of space; it is available from the senior author.

ANG, and AVGD of previous studies, are both derived from eigenvectors which are descriptors of a correlation matrix which, in turn, is an estimator of integration or organization, the relationship among parts. Hence when we use ANG to evaluate the degree of emergence we are also evaluating the variation in integration for various levels of biological organization, individuals, populations, species and various species combinations. With the addition of *A. occidentale* to these studies we have added more populations and another species. This will allow us to further test our previous results on the relationship between the degree of emergence and level of biological organization. Also, we can evaluate the within-group degree of emergence in another species pair, *A. occidentale* - *A. lemmonii*, that have formed hybrids, either as sterile hybrids (Maze 1962) or a polyploid species *A. latiglumis* (Pohl 1954) to see if that species pair, like *A. hendersonii* and *A. lemmonii*, show a lower degree of emergence than other species pairs of *Achnatherum* (Maze *et al.* 2002b).

The addition of A. occidentale in this study also allows us to expand our analyses of lineages; we can now analyze a group of species within Achnatherum, consisting of the close relatives A. lemmonii, A. hendersonii and A. wallowaensis and the more distant A. occidentale. Our analysis of the lineage comprised of the more distant H. comata plus Achnatherum now has A. occidentale added to the Achnatherum branch. In the analysis for ANG for the four species of Achnatherum one lower level consisted of A. occidentale and the other of A. lemmonii - A. hendersonii - A. wallowaensis combined. In the analysis including H. comata, that species formed one lower level and all species of Achnatherum the other. In cases where species were combined into a lineage, the entire sample was bootstrapped. Thus, in comparing Achnatherum with H. comata the bootstrapped sample for the former group consisted of all the spikelets measured for all the species of Achnatherum. Species were combined into lineages, as described above, in order to add another dimension to our studies of hierarchical organization and emergence.

In our previous studies (Maze 1999; Maze *et al.* 2000, 2001a,b, 2002b) we related within-group variation in integration to variation in size and shape. That approach is not used here because the samples are so diverse morphologically that first PCA axis, the basis for estimations of variation in size becomes a shape axis.

Our method of analysis is complicated and relies on abstract descriptors of variable relationships, angles between vectors, so we feel a few explanatory words are justified. In our analyses for emergence we wanted to address a unique biological feature, integration. Integration, as used here, sets the living world apart from the non-living. Integration is necessary for survival because it is necessary for functionality and accounts for many significant biological features. The physical differences between men and women are ontogenetically related differences in integration. Because the vectors we use in calculating angles are derived from PCA they describe correlation matrices, one type of estimator of integration.

## 6 RESULTS

### 6.1 RESULTS OF ANALYSES

Table 2 presents the results from analyses to test for emergence in the 10 populations analyzed and the species A. occidentale.

Table 2: Median values (ranges between upper and lower hinges) for bootstrapped angles with a vector of isometry for first MPCA axes for populations of A. occidentale;



same superscripts show like median values based on notched box plots, acronyms for populations as in Table 1.

|     | Subgroup A                       | Subgroup B                        | Pooled data                      |
|-----|----------------------------------|-----------------------------------|----------------------------------|
| MON | 31.9 <sup>a</sup><br>(27.7-34.0) | 29.5 <sup>bc</sup><br>(22.0-54.9) | 26.0 <sup>c</sup><br>(24.7-27.9) |
| MIL | 42.1 <sup>a</sup><br>(38.4-46.3) | 16.8 <sup>b</sup><br>(15.8-18.5)  | 23.8 <sup>c</sup><br>(22.9-25.4) |
| MOI | 24.1 <sup>a</sup><br>(21.2-25.5) | 29.5 <sup>b</sup><br>(26.8-33.0)  | 25.1 <sup>c</sup><br>(23.7-26.2) |
| PRO | 20.6 <sup>a</sup><br>(20.3-21.8) | 11.5 <sup>b</sup><br>(10.5-12.4)  | 15.7 <sup>c</sup><br>(14.8-16.2) |
| SIE | 36.5 <sup>a</sup><br>(34.9-38.6) | 45.4 <sup>b</sup><br>(45.1-46.4)  | 40.3 <sup>c</sup><br>(39.2-41.6) |
| OLD | 17.5 <sup>a</sup><br>(21.6-28.0) | 15.6 <sup>a</sup><br>(18.1-21.2)  | 16.8 <sup>a</sup><br>(18.9-21.7) |
| LAK | 14.7 <sup>a</sup><br>(12.9-15.5) | 7.9 <sup>b</sup><br>(7.4-8.4)     | 11.9 <sup>c</sup><br>(11.8-12.2) |
| RED | 21.4 <sup>a</sup><br>(19.3-24.4) | 7.8 <sup>b</sup><br>(6.2-9.0)     | 14.2 <sup>c</sup><br>(13.6-15.0) |
| MAR | 36.2 <sup>a</sup><br>(34.0-39.2) | 42.8 <sup>b</sup><br>(42.4-43.0)  | 40.4 <sup>c</sup><br>(39.8-41.1) |
| AOC | 17.0 <sup>a</sup><br>(16.9-17.1) | 26.2 <sup>b</sup><br>(26.0-26.2)  | 21.5 <sup>c</sup><br>(21.4-21.6) |

In all populations, except two from California, OLD from Shasta Co. and MON from Mono Co., there is evidence for emergence. (The) the angles with a vector of isometry for the parts, subgroups A and B, are different from the same angles for the whole, pooled data. OLD does not show emergence and MON is equivocal in whether or not emergence is seen, but the species overall shows emergence.

As another means of comparing the plants studied here, Table 3 presents the eigenvectors for each of the populations, and the combination of populations that represents the species, A. occidentale.

Table 3: Eigenvectors for populations of A. occidentale and for the species itself; B, angles between the eigenvectors; G1L, length first glume; G2L, length second glume; FL, floret length; FW, floret width; AWN, awn length. Population acronyms as in Table 1, AOC, all populations combined.

MON MIL MOI PRO SIE OLD LAK

|     |       |       |        |       |        |       |       |
|-----|-------|-------|--------|-------|--------|-------|-------|
| G1L | 0.426 | 0.534 | 0.523  | 0.500 | 0.568  | 0.499 | 0.517 |
| G2L | 0.507 | 0.520 | 0.508  | 0.495 | 0.576  | 0.523 | 0.460 |
| FL  | 0.489 | 0.396 | 0.493  | 0.470 | 0.191  | 0.485 | 0.486 |
| FW  | 0.168 | 0.079 | -0.034 | 0.191 | -0.153 | 0.171 | 0.250 |
| AWN | 0.542 | 0.531 | 0.473  | 0.497 | 0.534  | 0.461 | 0.472 |

|     | RED   | MAR    | COL   | AOC   |
|-----|-------|--------|-------|-------|
| G1L | 0.525 | 0.540  | 0.490 | 0.523 |
| G2L | 0.487 | 0.434  | 0.491 | 0.508 |
| FL  | 0.447 | 0.437  | 0.467 | 0.453 |
| FW  | 0.229 | -0.238 | 0.298 | 0.119 |
| AWN | 0.485 | 0.522  | 0.461 | 0.500 |

The greatest variation in the loadings is seen for floret width (FW) with the greatest difference in values seen between MAR, with -0.238, and COL, with 0.298.

The degree of emergence seen in each of the 10 populations and the species, as represented by ANG, is presented in Table 4.

Table 4: Ranking of median ANG values for each population of A. occidentale and all populations combined as the species. Acronyms as in Table 1, AOC, all populations of A. occidentale combined. Median ANG values to right of each set of acronyms, similar superscripts identify similar ANG values as based on notched box plots.

|     |                   |
|-----|-------------------|
| OLD | 1.5 <sup>a</sup>  |
| MIL | 2.3 <sup>a</sup>  |
| MOI | 2.6 <sup>a</sup>  |
| LAK | 4.0 <sup>b</sup>  |
| MAR | 4.1 <sup>b</sup>  |
| COL | 4.2 <sup>b</sup>  |
| PRO | 4.6 <sup>b</sup>  |
| SIE | 5.2 <sup>bc</sup> |
| MON | 6.7 <sup>bc</sup> |
| RED | 7.7 <sup>c</sup>  |
| AOC | 9.3 <sup>d</sup>  |

There is a gradation in the degree of emergence with OLD, MIL, and MOI being the lowest and the species the highest.

A comparison of the degree of emergence seen in all the species of Stipeae studied to date is presented in Table 5; the values used for all the species, other than A. occidentale, are derived from measurements made for a study already published (Maze *et al.* 2002b).

Table 5: Ranking of median ANG values for species analyzed, A. lemmonii (LEM), A. hendersonii (HEN), A. wallowaensis (WAL), H. comata (COM) and A. occidentale (AOC). Median ANG values to right of each set of acronyms, similar superscripts identify similar ANG values as based on notched box plots. Correlation between median ANG values and variance in first PCA axis scores 0.845 (p=0.072, n=5).

HEN 3.1<sup>a</sup>  
 LEM 3.8<sup>b</sup>  
 WAL 5.1<sup>c</sup>  
 COM 8.0<sup>d</sup>  
 AOC 9.3<sup>e</sup>

All show different degrees of emergence with A. hendersonii being the lowest followed, in sequence, by A. lemmonii, A. wallowaensis, H. comata and A. occidentale. These results are interesting in that the species occupying the low end of this trend, A. hendersonii, is rare and tends to have a lower amount of variation (Rapson and Maze 1994; Robson and Maze 1995), and the species that appears toward the top end, A. occidentale is a highly variable species (Maze 1962).

The degree of emergence seen at the different levels of biological organization is presented in Table 6.

Table 6: Ranking of median values for ANG for all Stipeae analyzed. All individuals (IND), all populations (POP), all single species (SPP), all possible pair-wise combinations of A. hendersonii, A. lemmonii, A. hendersonii, A. wallowaensis and A. occidentale (PAI), closely related trio of species (A. hendersonii, A. lemmonii and A. wallowaensis) (TRI), all species of Achnatherum as two lineages one consisting of the three closely related species and the other of A. occidentale (ACH), two lineages one consisting of the four species Achnatherum and the other of H. comata (ALL). ANG values to right of each set of acronyms, similar superscripts identify similar ANG values as based on notched box plots.

POP 2.9<sup>a</sup>  
 IND 3.9<sup>b</sup>  
 SPP 5.1<sup>b</sup>  
 PAI 6.4<sup>c</sup>  
 TRI 8.4<sup>d</sup>  
 ACH 15.8<sup>e</sup>  
 ALL 21.3<sup>f</sup>

The data used to calculate the degree of emergence for the different levels of organization, in large part, was based on studies previously published (Maze 1998; Maze and Bohm 1997; Maze *et al.* 2001a; 2002b). The data gathered for this study was included in the calculations of the degree of emergence for populations, species, some of the species pairs, all Achnatherum and all Stipeae. Two levels of that organization, individuals and species, show the same degree of emergence. The degree of emergence at the remaining levels of organization are all different with a trend in the degree of emergence paralleling the degree of relationships seen within that level, from populations, each of which are comprised of closely related plants, to the lineage comprised of the more distant relatives, Achnatherum and H. comata.

The comparison of the degree of emergence between all possible species-pairs of Achnatherum is presented in Table 7.

Table 7: Ranking of median values for ANG for all species pairs of Achnatherum combined. Al-Ao (A. lemmonii and A. occidentale); Ah-Al (A. hendersonii and A. lemmonii); Ao-Ah (A. occidentale and A. hendersonii); Al-Aw (A. lemmonii and A. wallowaensis), Ao-Aw, (A. occidentale and A. wallowaensis), Ah-Aw (A. hendersonii and A. wallowaensis). ANG values to right of each set of acronyms, similar superscripts identify similar ANG values as based on notched box plots.

Al-Ao 2.3<sup>a</sup>  
 Ah-Al 5.6<sup>b</sup>  
 Ao-Ah 6.1<sup>d</sup>  
 Al-Aw 6.6<sup>e</sup>  
 Ao-Aw 6.7<sup>f</sup>  
 Ah-Aw 12.2<sup>g</sup>

All are different with the pair A. lemmonii - A. occidentale being the lowest and A. hendersonii - A. wallowaensis the highest. The two species-pairs known to hybridize, A. occidentale - A. lemmonii and A. lemmonii - A. hendersonii have the lowest values. Another contrast was also made, one between the species-pairs that have hybridized taken as one group and the rest as the other group. The differences between those that have hybridized and those that have not remain significant (results not shown).

## 7 DISCUSSION

### 7.1 THE MEANING OF EMERGENCE

When we assess emergence, including the degree of emergence, we are relying on angular comparisons of eigenvectors from PCA. These eigenvectors describe the relationship among the variables measured as expressed in the correlation matrix that was calculated from those same variables. Or, eigenvectors present a description of a correlation matrix which, in turn, reflects the relationships among the variables upon which it is based; how those variables vary in relation to each other, how they covary. The covariation among variables is a function of two things, how strongly integrated they are and the direction of the variable vectors. Strong integration will be indicated by a higher correlation coefficient, an opposite direction of variable vectors will be marked by a negative correlation coefficient.

Thus, when we assess emergence we are also assessing integration. In those cases where emergence occurs, there is sufficient variation in integration within the group showing emergence that descriptive attributes for the parts and the whole are different. The degree of emergence, the angle between first eigenvectors among parts and wholes, estimates the difference in integration between those parts and the whole. As the degree of emergence increases, the number of states of integration, as revealed in first eigenvectors, increases.

The degree of emergence measures one aspect of biological variation, the variation in integration. This use of variation is not the usual definition where it refers to the position of samples around a mean. The variation in integration, in a comparable sense, would be the actual position of eigenvectors relative to some average state of eigenvectors. This would represent the position of vector-random variables around a centroid where both the vector-random variables and the centroid are expressed as vectors and scalars.

Integration in plants is the end result of the growth rates of the variables measured, relative to each other. In cases where the integration is strong, correlations are high and the growth in those particular variables are somehow linked; as one shows a certain response so too does another, whether those responses are positive (changing in a similar fashion) or negative (changing in an opposed fashion). Where integration is weak, correlations decline and the relative growth rates become less powerfully linked.

The phenomenon we are evaluating when we refer to emergence is ontogeny, the series of events whose material expression is in relative growth rates among structures. As

the degree of emergence increases, the greater the divergence among growth rates relative to each other. Relative growth rates can be visualized as developmental trajectories, the paths that plant structures follow through morphological space as they undergo ontogeny.

Some of our results can easily be placed within the context of a relationship between the degree of emergence and divergence among relative growth rates, or developmental trajectories. The greater degree of emergence seen in individuals, as opposed to populations, is one such result. As discussed in Maze and Bohm (1997), the spikelets of an individual grass develop under continually changing external environmental conditions, including temperature, day length, quantity and quality of light and moisture regime. As well, there will be continually changing internal properties as the plant grows and new growth centers, additional sources of factors affecting growth, appear. All of these factors affect the series of events, expressed as developmental trajectories, whereby a mature plant comes to exist. This results in a high level of within-plant variation, i.e., phenotypic plasticity. Or, phenotypic plasticity is due, in part, to variable external and internal environments strongly affecting plant form. Plants are able to express extreme variability and still remain functional. As a point of interest, phenotypic plasticity has a long history with examples of the phenomenon being included in Lamarck (1803). The interest in phenotypic plasticity has been given new impetus through its rediscovery by Lewontin (2000).

Population samples gathered for these studies are represented by a single spikelet per plant. Because of this, fewer factors affecting the growth of spikelets would have had a chance to be expressed. Thus, fewer factors affecting developmental events were captured in the spikelets representing a population. Another way to represent the differences between individuals and populations, in terms of sampling, is time. The spikelets measured for an individual represent a sample of spikelets that developed over a longer period of time than those representing a population. It is also possible that the difference between individuals and populations represent some additional, poorly understood biological property. In order to determine if there is some unique biological property that sets individuals apart from populations in terms of relative growth rates or developmental trajectories, it will be necessary to analyze a population using a sampling scheme that captures as much developmental time for the populations as has been captured for the individuals. This can be accomplished by an analysis where a population represents the whole and the parts are individuals, where each plant is represented by many spikelets. This comparison is underway.

A relationship between the degree of emergence and whether or not species hybridize also makes sense when emergence is seen as reflecting ontogenetic events. In order for interspecific hybrids to survive, the genomes of the parent species must be capable of coordinated function. One genomic function is the control of development, thus arguing that similar ontogenetic controls in different species would be expressed as similar relative growth rates and a lower degree of emergence. The species of Achnatherum that hybridize show lower degrees of emergence and have similar eigenvectors, as based on an angular comparison. Thus, we conclude they have similar developmental pathways.

But there is an oddity in these species-pairs comparisons, the high degree of variation in integration, and in developmental pathways seen in A. hendersonii and A. wallowaensis. These two species are closely related, so much so that the two were only recently discovered to be different (Maze and Robson 1996). The most reasonable account for the disparity in developmental pathways in A. hendersonii and A. wallowaensis is that the two species have used different routes, moving along different developmental paths or trajectories, to an apparently similar end. This interpretation is conjectural and should be subject to testing at both the structural and molecular level.

There are other findings of interest in the context of a relationship between interspecific hybridization and the degree of emergence in species that hybridize. Interspecific hybridization in the subgenus Lepidobalanus of Quercus is a common event (Cottam et al. 1982). One pair of hybridizing species, Q. gambelii Nutt. and Q. macrocarpa Michx. (Maze 1968) has been analyzed for the degree of emergence seen when the two species are treated as a whole, and the parts are comprised of the species. The degree of emergence is lower for the species-pair than it is for either of the species. These results were not presented as they are too preliminary, but Quercus does offer ample opportunity to further test a relationship between the degree of emergence and interspecific hybridization. The same phenomenon exists in Achnatherum where polyploid species (Johnson 1962; Stebbins and Love 1941) as well as interspecific hybrids occur, all with A. hymenoides (Roemer and Schultes) Barkworth as one parent (Johnson 1945).

The comparison of the degree of emergence seen at different levels of biological organization can also be related to different relative growth rates; more distantly related species have first eigenvectors that are more dissimilar. As evolution proceeds, differences between lineages appear as developmental pathways are modified. A basic biological question is captured in this descriptive statement; how do these differences in developmental pathways appear? Differences in the degree of emergence, and in devel-

opmental pathways, are found in populations observed here and in A. lemmonii (Maze et al. 2001a) and H. comata (Maze et al. 2002b). But how do those differences among populations become incorporated into, and appear as differences, among species? As speciation occurs, it appears that there is some sort of closure and all the individuals and populations react in a similar fashion, showing the similar developmental pathways typical of individuals within a species. We can describe the cause of change by following Taborsky (1999), and linking matter transformation (information expression) to the dissipation of energy along gradients. This was done in Maze et al. (2002a) where a positive relationship between matter transformation, as expressed in the degree of emergence, and a measure of energy was demonstrated. Using Matsuno's (1998) approach, we can revisit our results in terms of time, where events further removed from the present are captured within the concept of global time, while those events that occur in the present create local time. Indeed, this approach was used in previous studies (Maze 1998, Maze et al. 2001b). Another way to represent our findings is to infer that the emergence seen with phylogenetic change (speciation) is the result of variation in integration in a constrained system, an argument made in Maze (1998) and Maze et al. (2001b, 2002b).

These concepts may be interesting, but what do they mean to the plants we are studying? It is easy to relate these ideas to the growth of a single plant, the product of ontogeny. As a plant develops there is an increase in complexity as more information is expressed. The expression of that information is the transformation of matter that occurs as energy is dissipated from the plant (Taborsky 1999). The expression of that transformation is determined by the plant itself, its phylogenetic history, and the boundary conditions that harness the laws of physics and chemistry (Polanyi 1976). The most recently expressed features in a plant represent local time built on an ever-expanding foundation of global time, or previously achieved developmental stages. The emergence that occurs with ontogeny, as seen in an individual, is the result of developmental variation in a plant whose constraints are its boundary conditions, *sensu* Polanyi (1976). Most of the empirical and analytical studies that would follow from these ideas would be various approaches to describing energy dissipation, the nature of the boundary conditions in a plant and how both of these change with ontogeny.

Phylogeny, the events that occur in groups of related individuals as they undergo change, is more difficult to approach. The same concepts can be invoked, but a crucial element needed for explanatory completeness, the mechanism whereby those changes occur, is less clear. Again, it is relatively easy to offer an explanation for an individual, where all the changes occur in a single entity with a physical barrier, the cell walls and



membranes of all the cells, epidermal and substomatal mesophyll, in contact with the external environment, separating a plant from its world. This is not the case for assemblages of plants. Because of the lack of a physical boundary in assemblages of plants, the variables used to describe them are not part of a physically integrated system where there is ready interaction among the parts. In this case the boundary conditions, as expressed in the integration of the parts of the plant, are different from those in an individual. A group cannot harness the laws of physics and chemistry that deal with energy dynamics because the events to which those laws apply in an individual cannot occur directly in an assemblage of individuals.

However, there is another important aspect of boundary conditions in an individual; they are historical, and they are generated as the events that mark development accrue. The boundary conditions in an assemblage of plants are also historical. In a population of cross breeding individuals, that history can be shared and expressed through reproduction. In a species, boundary conditions are expressed through the changes that have taken place as the species developed. But a problem still exists. The integration seen in the populations of *A. occidentale* is not the same as that seen in the species itself. The same applies to *A. lemmonii* (Maze et al. 2001a), and *H. comata* (Maze et al. 2002b) and all the others we have studied.

How do we resolve the different patterns of integration seen within the constituent populations of a species with a different pattern for the species itself? The question is especially interesting since the populations of one species, in most cases, are isolated from each other. This is a long-standing problem in concepts of speciation. There is an apparently coordinated reaction of individuals isolated in space when speciation occurs, when one species evolves into two, or more. We are aware of the recent argument (Riesberg and Burke 2001) that gene flow is sufficient to allow the spread of favorable alleles and thereby act as an agent of collective evolution, i.e., evolutionary change in a species that exists as several populations. There are two intractable problems with this interpretation. The first is the geographical range over which an allele will be favorable. Even in the few sites where *A. occidentale* was collected it grew in habitats with different plants, with sagebrush (MON, MIL), antelope bitterbrush (MOI), juniper (RED) and ponderosa pine (PRO, SIE, OLD, LAK, MAR, COL); the distribution was from California to Washington. We doubt that many, if any alleles, would be favorable over such a distance or range of habitats. The second is the distance over which gene exchange is assumed to occur. The greatest distance over which gene exchange had been documented with molecular markers was 4 km for *Pinus flexilis* James (Riesberg and Burke 2001). The distance be-

tween populations of conspecific grasses often greatly exceeds 4 km. The premise that gene flow must be the only link among populations and individuals of a species disallows exploring other possibilities.

It is possible to attribute a common reaction among isolated individuals as the result of historical constraint; they share a history and that is sufficient cause for them to all act in a similar way. Another possibility is that when speciation occurs it is initiated by one, or a few, populations. This would account for the patterns of integration seen here; the “new” species would have the integrative attributes of the few populations that formed the “founder” populations. As those population continue to differentiate they would do so starting from one pattern of integration upon which new ones would be elaborated.

But, to us, these two accounts are still incomplete. Invoking history does not offer an account for the coordinated change or response among the isolated populations in which occurs, it simply uses an alternate lexicon. Invoking a founder effect can offer a known mechanism for speciation which appears to be a coordinated response. But invoking a founder effect, possibly a strong argument for insular species, leaves the disappearance of the many other populations of larger geographic areas unaccounted for.

It is possible that the reason for this problem is in the way species are conceptualized. The traditional view of species has focused on certain attributes that exist because individuals exist; members of a species are individuals that share some properties, morphological similarities and/or the ability to interbreed. It is these individuals that are isolated in space and by emphasizing those individuals, the problem of how there is coordinated reaction among them becomes something that defies understanding. Brooks and Wiley (1988) have offered an account for speciation that relies on the increasing entropy that follows from the second law of thermodynamics. Briefly, the assemblages of individuals in a species increase in variation, an informational representation of increasing entropy, until bifurcation occurs. But that still does not solve the problem of isolated individuals all reacting the same way in a given time period.

Another way to conceptualize species may offer the beginnings of a solution to the problem. If a species is thought of not as a collection of individuals, but as a code with no material existence of its own (Maze *et al.* 2002c) then the emphasis in an account for speciation changes. The code that is a species achieves material expression when an individual is initiated by whatever means. When that individual appears, there is then a physical entity through which energy is dissipated with its attendant transformation of matter (Taborsky 1999). As an individual develops, new expressions of the species code

will appear as ontogeny unfolds, the individual reacts to external environmental cues or, in plants, as somatic mutations occur. These new expressions of the species code will be incorporated into the code for that species. The species code will also change through recombination and mutation expressed when gametes fuse into a zygote. As this species code is expanded its potential will increase; the number of possible expressions of that species code will increase. This expanded species code will produce individuals with a greater amount of variation, and with the passage of time the individuals representing the species code will show more variation. With the continued expansion of the species code in this manner, it will become more and more unstable until, at some stage, it bifurcates. This is related to the argument of Brooks and Wiley (1988) but stated from a different perspective. Instead of increasing variation in individuals being a step on the way to speciation, it becomes a measure of the diversity in the species code. What is seen in individuals is a reflection of a reality, a species code, that cannot be directly observed. Individuals, in this sense, become like tracks in a cloud chamber, observations that reveal something about subatomic properties that themselves are beyond direct human perception.

These ideas are not radically different from previous ideas on species and speciation, but the emphasis has changed from defining a species as a collection of individuals to defining a species as something more abstract. The stimulation for such a change in emphasis away from a species as a collection of individuals has precedence in Coleman and Wiley (2001), while a more detailed argument about the nature of that change is captured in Maze et al. (2002c).

These views are difficult to test and do suffer from elusive qualities in the concept of a species code. But if one uses computers as an analogy, the species code becomes less mystical. The code in a computer itself is not available to human perception but it has a material expression in what the computer does. As well there can be feedback between the material world, through a programmer, and the code within a computer. A specific computer and the code it has at a moment in time could be viewed as analogous to an individual, while the species code could be viewed as corresponding to an operating system or software application, something that exists because of a computer but is independent of any one computer. Of course, one difference between a computer and a species is that the latter is much more labile whereas the former, we hope, is not.

The idea of a species as a code does have one advantage. In offering an account for speciation it includes conventional accounts, the production of variation with reproduc-

tion, but it also includes ontogeny as one source of increasing diversity in the species code. Heretofore, if there has been any reference to ontogeny as an evolutionary force, it has been mainly through the incorporation of developmental features in a set of variables used in analysis, not in the sense of being involved in the evolution of form. One advantage of incorporating ontogeny into evolution is that it offers a mechanism for the increasing complexity that precedes speciation, the transformation of matter that accompanies the energy dynamics that occur within an individual.

It would seem, based on these arguments, that the common feature shared by ontogeny and phylogeny is emergence, a change over time and an increase in complexity in the biota of the world. We realize these views differ from the consensus and they require further testing. Perhaps additional comparisons, based on analysis stressing individuals instead of populations are warranted. Clarification may also be forthcoming from a study that focuses on A. occidentale and its close relative A. nelsonii, since both are variable, and the variation is represented by named varieties. It is possible that incipient speciation is occurring in this case, an inference consistent with A. occidentale having the greatest degree of emergence of all the species studied so far. A more in depth study of that species, stressing individuals and a larger sample for populations, may give insights into speciation as expressed in integration.

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