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Genetics

Rates of evolution in seed plants: Net increase in diversity of chromosome numbers and species numbers through time

(polyploidy/aneuploidy/population structure/speciation/fossil record)

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ABSTRACT **An approach was made to the problem of estimating rates of chromosomal evolution in plants. This was done by considering variability in chromosome number within genera whose ages are known approximately from fossil and biogeographic evidence. The relative increases in chromosome number diversity per lineage per unit time were as follows: herbaceous angiosperms, 100; woody angiosperms, 14; conifers, 2; and cycads, 0. Rates of increase in species diversity were estimated in an analogous way. These rates were strongly correlated with the karyotypic rates.**

These evolutionary rate differences between major groups of seed plants are largely explicable in terms of the breeding structures of populations. Herbs usually have small to moderate effective population sizes, and relatively high dispersability. By contrast, woody angiosperms and gymnosperms are usually obligate outbreeders with large effective population sizes and low dispersability. Thus the probability of fixing and dispersing new karyotypes or novel character ensembles is higher in herbs than in other seed plants.

Rates of chromosomal divergence and speciation appear to vary in plants with different growth forms, rates being high in herbs and low in shrubs and trees, especially in conifers and cycads (1–4). It is desirable to document these impressions and to place these rates on an absolute time scale, because they not only influence historical perception of evolutionary change, but also the interpretation of the processes promoting these changes.

Rates of chromosomal evolution and speciation per genus cannot be estimated without knowledge of gain and loss of diversity in past geological periods. However, knowledge of present diversity and the approximate age of genera does provide a basis for estimating mean net rates of increase in chromosomal diversity and species number per genus. In this paper we test by analytical methods the hypothesis that there are evolutionary rate differentials between plant growth forms.

MATERIALS AND METHODS

The genera considered represent the nine superorders of Angiospermae recognized by Cronquist (5), and the conifers and cycads in the Gymnospermae. The ages of angiosperm and gymnosperm genera were estimated from megafossil and pollen records and from biogeographical distributions as interpreted in recent publications (6–14 and references therein). Only genera with fossil records were considered. The date assigned to a genus is the date for the beginning of the epoch. Although the fossil record is rich in conifers and cycads (15), the date at which a given genus is thought to have emerged is somewhat arbitrary, since similar fossils may be assigned different generic names. We assume that the cycad genera originated at the beginning of the Jurassic period [185 million years (Myr) ago], and that conifer genera originated at the beginning of the lower Cretaceous epoch (135 Myr). We recognize that a small number of conifer genera arose in the mid-Jurassic (6).

We have adopted the time scale used by Raven and Axelrod (8), who regard the epochs to have commenced at the following times before the present: Pleistocene, 2.5 Myr; Pliocene, 10 Myr; Miocene, 27 Myr; Oligocene, 38 Myr; Eocene, 54 Myr; Paleocene, 65 Myr; Upper Cretaceous, 110 Myr; Lower Cretaceous, 135 Myr. The ages of epoch boundaries are accurate to within 1–2 Myr as judged from radiometric dates. The mean ages of angiosperm genera considered herein are judged to be as follows: herbs, 37.4 Myr; shrubs, 67.0 Myr; trees, 74.7 Myr. The herbaceous genera have a weakly bimodal age distribution with peaks in the Pleistocene and Paleocene epochs. Woody genera originated primarily in the Paleocene and Upper Cretaceous epochs.

Chromosome numbers for 8378 angiosperm and 590 gymnosperm species were obtained from chromosome number indices and review articles (16–20). When counts conflicted, the latest one was used. We considered only those genera containing more than five species of known chromosome numbers. Most of the genera examined had at least 20 species of known karyotypes.

From the heterogeneity of chromosome numbers within each genus, we estimated the mean increase in chromosome number diversity along a typical lineage within that genus. This quantity, m, is given by $m = (k - 1)/n$, where n is the number of species sampled per genus and k is the number of chromosome numbers per genus. By dividing m by the putative genus age (t), the mean rate of increase in chromosomal diversity per lineage is obtained. To estimate the average rate of increase in chromosomal diversity per lineage (r_c) for a group of N genera we used the equation

$$r_c = \frac{1}{N} \sum_{i=1}^{N} \frac{(k-1)}{nt}. \qquad [1]$$

This method of computing karyotypic rate differs from that used in a previous paper by one of us (21). It is noteworthy that r_c is a minimum estimate, since all species with the same derived number are considered to have evolved from a single common ancestor bearing that number.

To estimate the net rates of speciation (speciation minus extinction) in plant genera, we used Eq. 2,

$$s = 2^p, \text{ i.e., } p = 3.3 \log s. \qquad [2]$$

where s is the number of living species in a genus and p is an estimate of the average number of speciation events that have occurred along a typical lineage in that genus. This equation is similar to that used for estimation of speciation rates in animals (22). The number of species per genus was taken from Willis (23) for 201 angiosperm genera and 37 gymnosperm genera. To estimate the average net number of speciations per

Abbreviation: Myr, million years.

Table 1. Net rates of chromosomal evolution and speciation in representative genera

Genus	Growth form	Age (Myr) (t)	No. of extant species per genus (s)	Mean increase in species no. per Myr (p/t)	Chromosomal diversity (m)	Mean increase in chromosome number diversity per Myr (m/t)
Bromus	Herb	65	50	0.09	0.07	0.001
Viola	Herb	13	500	0.89	0.12	0.009
Phlox	Herb	2.5	67	2.41	0.14	0.057
Mimulus	Herb	38	38	0.14	0.40	0.011
Arctostaphylos	Shrub	27	71	0.23	0.01	0.001
Vaccineum	Shrub	65	350	0.13	0.05	0.001
Ilex	Shrub	110	400	0.08	0.07	0.001
Diospyros	Tree	110	500	0.09	0.13	0.001
Juglans	Tree	65	15	0.06	0.10	0.001
Alnus	Tree	65	35	0.08	0.18	0.002

lineage per million years for a group of N genera, Eq. 3 was used:

$$r_s = \frac{3.3}{N} \sum_{i=1}^{N} \left(\frac{\log s}{t}\right). \quad [3]$$

The method used to calculate r_s assumes an exponential increase in the number of lineages per genus through time, i.e., a dichotomously branching phylogeny.

To illustrate some of the above methods for calculating net rates of chromosomal evolution and speciation, the results of sample calculations for representative genera are given in Table 1. The table also draws attention to the fact that most of the genera considered were from the temperate zone.

RESULTS AND DISCUSSION

Independence of Diversity and Time. Chromosomal diversity and species numbers are independent of the age of the genus. We plotted m for each genus against t for that genus within herbs, shrubs, and trees. In no case was a significant correlation coefficient observed: the average correlation coefficient was 0.06. We also plotted the number of species per genus against genus age within each superorder. Again no significant correlations were observed: the average correlation coefficient r was 0.09. Accordingly, an old genus is not more variable in chromosome number or more species-rich than a young one. The patterns described in the next sections thus are not attributable to differences in the ages of plant groups.

Consider next the relationship between basic chromosome number of genera and the age of genera. If we treat all dicots collectively and plot their base numbers against their ages, a significant correlation emerges ($r = 0.41$, $P < 0.01$). Genera arising in the Cretaceous and Paleocene epochs have higher basic numbers than genera of more recent derivation. If woody genera and herbaceous ones are treated independently, significant correlations are absent within each group. The mean basic number in the woody genera considered herein is $x = 13.1$ as compared to $x = 9.3$ in the herbaceous genera. Possibly, basic numbers of many modern woody genera were derived by ancient polyploidy, and the original basic numbers of woody and herbaceous genera were similar (3, 24).

Rates of Increase in Chromosomal Diversity. Chromosomal evolution has proceeded much faster in herbs than in shrubs or angiosperm trees. Conifers and cycads have the slowest rates. The average increase in chromosomal diversity per million years is 0.0736 for herbs, 0.0102 for shrubs, 0.0014 for hardwoods, and 0.00012 for conifers (Table 2). There has been no change in cycads. The difference between shrubs and hardwoods is not statistically significant; that between hardwoods and conifers is significant at the 5% level ($t_s = 2.25$). All other differences are significant at the 1% level.

Karyotypic evolution in angiosperms involves both aneuploidy and polyploidy. Aneuploidy refers to the addition or loss of chromosomes through translocations without an alteration in genome size or balance.‡ Polyploidy refers to changes in genome size based upon the addition of one or more complete sets of chromosomes. Both polyploid and aneuploid changes accumulate rapidly in herbs (Table 2). In shrubs the rate of change by polyploidy is about seven times that in angiosperm trees; change by aneuploidy shows a 2-fold difference. Differences between herbs and either shrubs or hardwoods are significant ($P < 0.01$; $t_s > 3.6$). Differences between shrubs and trees are not statistically significant.

The relative importance of polyploidy and aneuploidy differs markedly between herbaceous and woody genera. Aneuploidy accounts for 23% of the mean rate of increase in karyotype diversity in herbs, whereas in woody plants it accounts for only 5%. Since translocations are essential for an increase or decrease in basic chromosome number (2, 3), the relatively unimportant role of aneuploidy in woody plants may relate in large measure to a lower incidence of translocations therein. Congeneric species of herbs with the same basic number are more likely to differ by translocations than are species of shrubs or trees (3, 25–27).

In the gymnosperms, polyploidy is unknown in cycads, and rare in conifers. This is in contrast to angiosperms, where polyploidy is common not only within genera but within many species. The paucity of polyploidy in the gymnosperms ostensibly is due to poor means of vegetative reproduction, little chromosome repatterning in the course of speciation, and the infrequent occurrence of natural interspecific hybridization (28).

Rates of Increase in Species Numbers. Net rates of increase in herbs are higher on the average than in other plants (Table 2). The average rate of increase per lineage in herbs is 1.05 per million years, 0.24 in shrubs, 0.09 in angiosperm trees, and 0.02 in conifers, and 0.01 in cycads. All differences are statistically significant as revealed by t-tests. Note that these values are on a per lineage basis.

The mean net rate of increase in species numbers per lineage equals the speciation rate minus the extinction rate. Stanley (22)

‡ The botanical meaning of *aneuploidy* differs from the medical meaning.

Table 2. Net rates of chromosome evolution and speciation as a function of growth form

Growth form	No. of genera examined	Mean increase in species numbers per lineage per Myr	Mean increase in chromosome number diversity per lineage per Myr		
			Total	Polyploid	Aneuploid
Herbs	99	1.05 ± 1.19	0.073 ± 0.116	0.05 ± 0.09	0.020 ± 0.042
Shrubs	63	0.24 ± 0.45	0.010 ± 0.038	0.01 ± 0.03	0.0005 ± 0.0019
Hardwoods	39	0.09 ± 0.03	0.0014 ± 0.0019	0.001 ± 0.001	0.0003 ± 0.0010
Conifers	26	0.02 ± 0.01	0.0001 ± 0.0002	0.00001	0.0001
Cycads	10	0.01 ± 0.01	0.0000	0.0000	0.0000

Values are given ± standard error of the mean.

has suggested a procedure which permits the estimation of the extinction rate and the true rate of speciation. Looking backward in geological time, we will reach a point at which extant species comprise 50% of the fossil flora. Average species duration will be about twice this value, referred to as D. The extinction rate equals $1/D$. Although the fossil record does not permit the average duration of different growth forms to be determined by empirical means, we can make some approximations based upon paleobotanical observations. We reason that 50% of the late Pliocene herbs are extant, as are 50% of the late Miocene shrubs, 50% of the middle Miocene hardwoods, and 50% of the early Miocene conifer and cycad species. Given these values, the mean extinction rates (per Myr) are: for herbs 0.10, shrubs 0.04, hardwoods 0.03, and gymnosperms 0.02. Adding these values to the mean rate of speciation provides an estimate of the true rate of speciation for each growth form. Estimates of the several rates in question are summarized in Table 3.

The true rate of speciation per lineage in herbs is 1.15 per Myr as compared to 0.28 in shrubs, 0.12 in hardwoods, 0.04 in conifers and 0.03 in cycads. In the angiosperms these values are similar to those for the net rate of speciation, extinction rates being low relative to net speciation rates. The angiosperms are rapidly diversifying, but apparently not at the expense of existing species. From the net speciation and extinction rates, it follows that on the average over 80% of all angiosperm species which evolved in the genera under consideration are extant. In gymnosperms the true rate of speciation is nearly twice that of the net rate. The net rate of speciation has been comparable to that of extinction. Thus, the group has been relatively static in species numbers since early in its development. Net speciation and extinction rates indicate that on the average about 50% of all gymnosperm species that arose in the genera considered are extant. Although this discussion is based upon unestablished species duration times, it is important to realize that increasing or decreasing these values by a factor of two does not alter the general pattern which has emerged.

We do not intend to imply that average rates of increase in species numbers and chromosome number diversity per lineage have been constant from one geological epoch to another or throughout the history of a genus. For example, it is likely that rates of increase in chromosomal variation in the woody genera of the Magnoliidae were much greater during the Upper Cretaceous and Paleocene (especially via polyploidy) than during subsequent ones (3, 24). Phylads generally evolve considerably more rapidly early in their history than in their more mature stages (29–31).

Correlations Between Rates of Evolution. The rates of chromosomal diversification were plotted against those for species numbers for each angiosperm genus. A significant correlation was found ($r = 0.64$; $P < 0.01$). Some striking correlations also are evident when genera are grouped on the bases of growth form: $r = 0.71$ for herbs, 0.89 for shrubs, 0.15 for trees. Accordingly, the genera of herbs and shrubs which have the highest rate of increase in chromosome number diversity also have the highest rate of increase in species number. The lack of significant correlation in trees is not understood. If we take mean rates for each growth form, including conifers and cycads, a striking correlation is obtained; $r = .99$, as illustrated in Fig. 1. We have not attempted to quantify rates of morphological evolution per growth form. However, it is apparent that conifers and cycads are much more conservative than angiosperms (2, 5, 15).

Factors Affecting Evolutionary Rates. Our findings are consistent with the view that the rates of evolution at both karyotypic and organismal levels are related to the breeding structure of species and to environmental predictability. A system of small, semi-isolated populations in transient habitats or ecotonal regions experiencing marked fluctuations in habitat hospitality is most conducive for the fixation of chromosomal and morphological novelties (1, 2, 32–34) and rapid speciation (35). Conversely, systems of large continuous populations where climatic and biotic pressures are stable through time are likely to be much more conservative. Our findings with plants, as well as those reported recently for animals (21), are consistent with these views.

The mean rates of increase in chromosomal diversity and species numbers in plant genera and among plant growth forms are highly correlated. This relationship may be due to the fact that the tempo of both processes is influenced by the same or similar factors, or that karyotypic changes set the stage for

Table 3. Estimates of speciation rate parameters (per Myr)

Growth form	Mean species duration time in Myr (D)	Mean species extinction rate ($1/D$)	Net speciation rate	True speciation rate
Herbs	10	0.10	1.05	1.15
Shrubs	27	0.04	0.24	0.28
Hardwoods	38	0.03	0.09	0.12
Conifers	54	0.02	0.02	0.04
Cycads	54	0.02	0.01	0.03

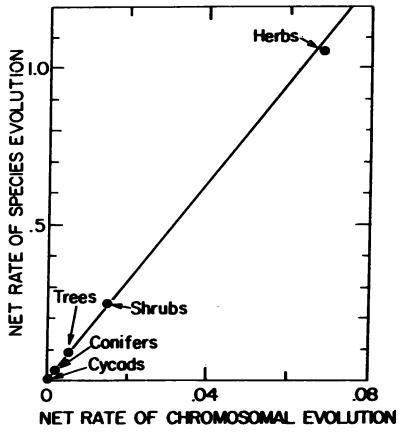

FIG. 1. Correlation between chromosomal evolution and speciation in major groups of seed plants. The ordinate gives the mean net increase in the number of species per lineage per Myr. The abscissa gives the mean net increase in number of karyotypes per lineage per Myr.

speciation either by reducing gene exchange or by altering the regulatory system and thereby providing the species with new phenotypic alternatives that may be selectively favored (36).

Annual and short-lived perennial herbs are the primary occupants of transient or disturbed habitats. Some species are partially or predominantly self-fertilizing, and many have small neighborhood sizes (20 or less). Long-lived perennial herbs, shrubs, and trees occur in long-lived associations or in regions with equable or predictable environments. These plants are almost exclusively outcrossers, and typically have neighborhood sizes exceeding 100 individuals and large neighborhood areas (37). The smaller the neighborhood size and area, the greater is the isolation of populations by distance and the potential for interpopulation differentiation by selection and random drift (38, 39).

Differences in generation time could contribute to differences in rates of chromosomal evolution and speciation, since each generation represents an opportunity for selection or random drift. The shortest generation times probably occur in annual herbs. The annuals are followed by perennial herbs, shrubs, and trees in order of increasing generation time (40, 41).

Differences in seed dispersability also may affect rates of increase in chromosomal diversity and species numbers per genus. Ecotonal regions are climatically intermediate and experience an ebb and flow of climatic and biotic pressures which places a premium on dispersal. Species in such regions tend to have more effective mechanisms for long-distance dispersal than do species inhabiting more stable communities (37, 42). Accordingly, the incidence of colonization episodes per unit time and accompanying genetic bottlenecks is apt to be relatively high in phylads with adaptation for long-distance dispersal. High dispersability also promotes the expansion of novel variants and reduces the probability of their extinction. Seed dispersability tends to be greatest in herbs, and least in cycads and conifers (37).

Finally, differences in the manner in which plants experience the environment in time and space ostensibly affect their rate of increase in species numbers via ecogeographic divergence. Woody plants experience the environment as a succession of many different conditions, the average of which is similar for all members of a population and most members of a population system. Herbs, especially the annuals, experience the environment as a series of alternative states in time and space (43, 44). For woody plants the optimum strategy is more often a genotype specialized for the most frequently encountered set of conditions. For ephemeral herbs, the environment dictates a strategy in which different specialized genotypes occur in proportions dependent upon the frequencies of different environmental patches in time and space. Accordingly, interpopulation differentiation and subsequent divergence to the species level is more likely to occur in short-lived herbs than in shrubs or trees.

CONCLUSIONS

Speciation involves the establishment of distinctive adaptive strategies, and in some instances the fixation of chromosomal variants that confer complete or partial barriers to gene flow from related lineages. The novel character ensemble is unlikely to remain extant and be recorded by systematists unless it is distributed beyond the population in which it was assembled. The probability of establishment and dispersal, and thus the rate of speciation and chromosomal evolution, primarily is a function of breeding structure and dispersability of populations. Populations that are highly inbred by virtue of restricted pollen flow or partial self-fertility, and also have adaptations for long-distance seed dispersal, will have the highest evolutionary rates. It is this combination of characters rather than any single character that promotes rapid interpopulation differentiation. Populations that are inbred, but lack high dispersability, will have relatively few opportunities per unit time to colonize a new habitat where the reorganization of the gene pool requisite for rapid divergence can proceed. Populations that are outbred will experience enough pollen input from neighboring populations to retard the rate of interpopulation differentiation due to divergent selection pressures and genetic drift even if seed dispersability is low. High-seed dispersability will further retard the rate of differentiation in outbreeders.

We propose that the relatively high mean rate of diversification or evolution in herbaceous genera is due to their restricted breeding structure and high dispersability relative to the other growth forms. Correlatively we propose that the low rate of evolution in gymnosperms is due to their open breeding structure and narrow seed dispersability. Small breeding units and high dispersability probably account for the fact that in vertebrates the highest rates are in mammals, especially those with the best developed social structure (e.g., horses) (21). We expect that among invertebrates as well the groups with this character combination will be shown to have the most rapid rates of evolution.

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