Part one

Hawaiian Islands

Introduction

Few islands of the world have received as much attention for evolutionary patterns and processes as the Hawaiian Islands. Reading through Sherwin Carlquist's stimulating *Hawaii: A Natural History* (1970) always elevates our interest. We have also read about fascinating evolutionary phenomena in picture-wing *Drosophila*, studied so successfully by Hampton Carson and colleagues (e.g., Carson & Kaneshiro, 1976; Kaneshiro, Gillespie & Carson, 1995; DeSalle, 1995). It is fitting, therefore, that the initial two chapters of this book deal with the Hawaiian Islands. Recent studies have greatly increased our understanding of patterns and processes in the endemic vascular plant flora of the Hawaiian Islands. A monumental achievement was the publication of the two-volume *Manual of the Flowering Plants of Hawaii* (Wagner, Herbst & Sohmer, 1990) that established for the first time a consistent species concept for the entire archipelago. In the past, some taxa had been split into numerous microspecies and others had been treated broadly, depending upon the perspective of the particular taxonomist. These disparate treatments of plant diversity in the archipelago made it very difficult to approach questions of speciation and biogeography. In fact, publication of the new *Manual* made it possible to conceive and execute a very meaningful project on biogeography in the archipelago, involving both plants and animals (Wagner & Funk, 1995). This would have been impossible without the consistent foundation of species concepts provided by the flora project.

Along with significant recent floristic efforts, detailed biosystematic studies have been carried out on the Hawaiian Islands on many taxa by different workers. Of particular mention are those investigations on Compositae, such as: the bizarre silverswords by Carr and associates (Carr & Kyhos, 1981, 1986; Carr, 1985); *Bidens* by Gillett & Lim

(1970), Ganders & Nagata (1984) and Helenurm & Ganders (1985); *Lipochaeta* by Gardner (Gardner, 1976, 1977) and Rabakonandrianina & Carr (1981); and *Tetramolopium* by Lowrey & Crawford (1985) and Lowrey (1986).

This first part of the book builds on previous studies and summarizes and extends our understanding of the endemic plants of the Hawaiian Islands. Carr (Chapter 1) focuses on chromosomal evolution in the endemic angiosperms and discusses possible reasons for cytological change or lack thereof (stasis) within many groups. Baldwin (Chapter 2) summarizes and extends his recent macromolecular studies with colleagues (e.g., Baldwin *et al.*, 1991) that finally resolved ancestry of the Hawaiian tarweeds from California progenitors. This general biogeographic connection has been known for some time (e.g., Carlquist, 1959), but the particular continental group from which all the Hawaiian diversity came was never determined satisfactorily. Taken together, these two chapters provide an excellent view of recent work on the angiosperm flora of the Hawaiian Islands and they provide a very good beginning to our volume.

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1

Chromosome evolution and speciation in Hawaiian flowering plants

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Abstract

Chromosome numbers available for about 38% of the 956 native species of Hawaiian plants indicate that more than 80% are polyploid. However, support for the occurrence of autochthonous polyploidy is very limited, with fairly clear examples in *Peperomia, Portulaca*, and *Wikstromia*; less certain instances in *Bobea, Lepidium, Plantago* and *Psychotria*; and dubious examples in *Labordia* and *Polygonum*. Likewise, evidence of chromosome evolution in the form of gross structural changes or dysploidy is sparse and clearly demonstrated only in the silversword alliance of *Argyroxiphium, Dubautia* and *Wilkesia*. *Luzula* and *Peperomia* may provide additional examples of dysploidy. In contrast, a large number of groups, most notably *Bidens, Cyrtandra, Hibiscadelphus, Lipochaeta, Pipturus, Scaevola, Tetramolopium, Vaccinium* and the lobelioid genera *Brighamia, Clermontia, Cyanea, Delissea, Lobelia, Rollandia* and *Trematolobelia*, are seemingly characterized by complete chromosome stasis, at least with respect to gross structural alterations, dysploidy and polyploidy. There appears to be little or no indication that chromosome evolution on the Hawaiian Islands has proceeded in a manner particularly different from continental areas. Rather, the examples of insular chromosome evolution appear to reflect the tendencies inherent in their continental ancestors. In light of the evidence accumulating from molecular studies, it is concluded that the overall patterns of chromosome structural evolution and chromosome stasis observed in plants are most readily explained on the basis of structural variants having different selective values that are determined by the relative positions of critical genes in the genome.

Knowledge related to chromosome evolution in Hawaiian plants is very incomplete. Available data are primarily the result of very few general surveys of chromosome numbers (Skottsberg, 1953; Carr 1978, 1985*a*) and several studies of individual species or plant groups. Most of what is known about chromosome numbers of Hawaiian flowering plants was summarized recently by Wagner, Herbst & Sohmer (1990). These data have been extracted (with a few minor adjustments) and combined with several more recent determinations in Table 1.1. Based on the analysis of the Hawaiian flora by Wagner, Herbst & Sohmer (1990), the chromosome determinations for the 359 species recorded in Table 1.1 represent one or more counts for just over one-third of the native Hawaiian plant species (359/956 = 37.6%).

No determinations based on Hawaiian material are available for 53 genera that are native to Hawaii. Most notable in this respect are *Myrsine* (20 species), *Pritchardia* (19 species) and *Mariscus* (10 species). Furthermore, only one determination is available for the third largest genus in Hawaii, *Melicope*, with 47 species. It may also be noted that the chromosome determinations reported for 38 of the non-endemic species are based only on extra-Hawaiian populations. Thus, in addition to filling in the gaps for species and genera with no counts, it would be desirable to have counts for Hawaiian populations of non-endemic taxa.

Based on the counts available for Hawaiian populations, more than 80% (288/359) of the native plant species are polyploid. The frequency of polyploidy is nearly 9% higher in monocots compared to dicots. This estimate relies on the criterion of $n > 13$ denoting polyploidy (Grant, 1963; Goldblatt, 1980) but specifically includes the species of *Dubautia* with $2n = 26$ because they exhibit duplicate gene expression indicative of polyploidy (Witter, 1990). As will be discussed more fully below, the high incidence of polyploidy reported here has not been derived autochthonously. Rather, it reflects mainly paleopolyploidy inherent in the ancestors of Hawaiian species. Nevertheless, the high frequency of polyploidy reported here for the Hawaiian flora considerably exceeds most other general estimates of polyploidy among flowering plants. For example, using the same criterion, Grant (1963) estimated that 47% of the 17 138 flowering plant species he sampled were polyploid (dicots 43%, monocots 58%) and Goldblatt (1980) estimated that 55% of the 10 580 species of monocots he sampled were polyploid. Although the sample is very small, the same criteria applied to the data provided by Sanders, Stuessy & Rodríguez R. (1983) for the flora of the Juan Fernandez Islands produces an estimate of 75% polyploidy. Perhaps the high

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Table 1.1. *Chromosome numbers in Hawaiian flowering plants.*

An asterisk(*) identifies determinations based on populations outside the Hawaiian Islands, which are not referenced

Taxon	No. spp/genus counted : No. spp/genus native	Diploid chromosome number
DICOTS		
AIZOACEAE		
Sesuvium portulacastrum (L.) L.	1 : 1	(8,36,48)*,*c*.48[a]
AMARANTHACEAE		
Achyranthes splendens Mart. ex Moq.	1 : 3	76[b],78[b]
Amaranthus brownii Christoph. & Caum	1 : 6	34[c]
Charpentiera ovata Gaud.	2 : 5	52[d]
C. tomentosa Sohmer		*c*.52[e]
Nototrichium (A. Gray ex Hillebr.) Hillebr.	0 : 2	
ANACARDIACEAE		
Rhus L.	0 : 1	
APIACEAE		
Peucedanum sandwicense Hillebr.	1 : 1	66[f]
Sanicula sandwicensis A. Gray	1 : 4	16[c]
Spermolepis hawaiiensis Wolff	1 : 1	22[h]
APOCYNACEAE		
Alyxia oliviformis Gaud.	1 : 1	*c*.36[b],*c*.39[b]
Ochrosia Juss.	0 : 4	
Pteralyxia K. Schum.	0 : 2	
Rauvolfia sandwicensis A. DC.	1 : 1	44[a]
AQUIFOLIACEAE		
Ilex anomala Hook. & Arnott	1 : 1	80[a]

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Table 1.1. (*cont.*)

Taxon	No. spp/genus counted : No. spp/genus native	Diploid chromosome number
ARALIACEAE		
Cheirodendron trigynum (Gaud.) A. Heller	1 : 5	24[b]
Munroidendron racemosum (C. Forbes) Sherff	1 : 1	48[a,i]
Reynoldsia A. Gray	0 : 1	
Tetraplasandra oahuensis (A. Gray) Harms	1 : 6	48[a]
ASTERACEAE		
Adenostemma lavenia (L.) Kuntze	1 : 1	20*
Argyroxiphium caliginis C. Forbes	4 : 5	28[f]
A. grayanum (Hillebr.) Degener		26[b],28[f,g]
A. kauense (Rock & M. Neal) Degener & I. Degener		28[a]
A. sandwicense DC.		28[a,f,g]
Artemisia australis Less.	2 : 3	18[a,f]
A. mauiensis (A. Gray) Skottsb.		18[a,f]
Bidens conjuncta Sherff	13 : 19	*c.*70[b]
B. cosmoides (A. Gray) Sherff		72[j]
B. forbesii Sherff		72[j]
B. hawaiiensis A. Gray		72[j]
B. hillebrandiana (Drake) Degener		72[j]
B. macrocarpa (A. Gray) Sherff		72[j]
B. mauiensis (A. Gray) Sherff		72[j]
B. menziesii (A. Gray) Sherff		72[j]
B. micrantha Gaud.		72[j]
B. molokaiensis (Hillebr.) Sherff		72[a,j]
B. sandvicensis Less.		72[b]

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B. torta Sherff		72[j]
B. wiebkei Sherff		72[j]
Dubautia arborea (A. Gray) Keck	21 : 21	26[a,g]
D. ciliolata (DC.) D. Keck		26[a,g]
D. dolosa (Degener & Sherff) G. Carr		26[a,g]
D. herbstobatae G. Carr		26[g]
D. imbricata St John & G. Carr		28[g]
D. knudsenii Hillebr.		26[b],28[a,g]
D. laevigata A. Gray		28[g]
D. latifolia (A. Gray) D. Keck		28[a]
D. laxa Hook. & Arnott		28[a,f,g]
D. linearis (Gaud.) D. Keck		26[a,g]
D. menziesii (A. Gray) D. Keck		26[a,g]
D. microcephala Skottsb.		28[a,g]
D. paleata A. Gray		28[a]
D. pauciflorula St. John & G. Carr		28[g]
D. plantaginea Gaud.		28[a,g]
D. platyphylla (A. Gray) D. Keck		26[g]
D. raillardioides Hillebr.		28[g]
D. reticulata (Sherff) D. Keck		26[a]
D. scabra (DC.) D. Keck		28[a,g]
D. sherffiana Fosb.		26[a]
D. waialealae Rock		28[g]
Gnaphalium L.	0 : 1	
Hesperomannia arbuscula Hillebr.	1 : 3	20[a,k]
Lagenifera helenae C. Forbes & Lydgate	2 : 3	54[c]
L. maviensis H. Mann		54[a]
Lipochaeta connata (Gaud.) DC.	15 : 20	52[a,l]
L. heterophylla A. Gray		52[l]
L. integrifolia (Nutt.) A. Gray		30[a,l]

Table 1.1. (*cont.*)

Taxon	No. spp/genus counted : No. spp/genus native	Diploid chromosome number
L. kamolensis Degener & Sherff		30[l]
L. lavarum (Gaud.) DC.		30[a,l]
L. lobata (Gaud.) DC.		52[a,l]
L. micrantha (Nutt.) A. Gray		30[l]
L. remyi A. Gray		30[a,l]
L. rockii Sherff		52[a,l]
L. subcordata A. Gray		30[l]
L. succulenta (Hook. & Arnott) DC.		52[a,d,l]
L. tenuifolia A. Gray		30[l]
L. tenuis Degener & Sherff		30[m]
L. venosa Sherff		30[m]
L. waimeaensis St John		30[l]
Remya mauiensis Hillebr.	1 : 3	36[c]
Tetramolopium consanguineum (A. Gray) Hillebr.	7 : 11	18[n]
T. filiforme Sherff		18[a,n]
T. humile (A. Gray) Hillebr.		14[f],18[a,f,n]
T. lepidotum (Less.) Sherff		18[n]
T. remyi (A. Gray) Hillebr.		18[n]
T. rockii Sherff		18[n]
T. sylvae Lowrey		18[n]
Wilkesia gymnoxiphium A. Gray	2 : 2	*c*.24[f],28[a,g]
W. hobdyi St John		28[g]
BEGONIACEAE		
Hillebrandia sandwicensis Oliver	1 : 1	48[f]
BORAGINACEAE		