Revista Chilena de Historia Natural
*62:* 43-60, 1989

# Fruit and seed characteristics of woody species in mediterranean-type regions of Chile and California

## Características de frutos y semillas de especies leñosas en regiones de tipo mediterráneo: una comparación entre Chile y California

ALICIA J. HOFFMANN, SEBASTIAN TEILLIER and EDUARDO R. FUENTES

Departamento de Ecología, Facultad de Ciencias Biológicas,
Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago, Chile

ABSTRACT

The distribution and characteristics of propagules of woody species were compared in four community types along a gradient of increasing annual rainfall, between 30° and 38° latitude in Chile and California. The hypothesis tested was that in these two regions climatic constraints determine similar responses in phylogenetically unrelated organisms. The abundance of fleshy fruits less than 15 mm in diameter (corresponding to the syndrome of bird-dispersal), their sizes, and the frequency of black fruits increased from xeric towards mesic communities, both in Chile and in California; the largest variety of fruit colors was found in the evergreen scrub in both regions. These trends support the convergence hypothesis. In contrast, the distribution and characteristics of wind-dispersed propagules and of "small" dry, not wind-dispersed propagules showed different, apparently non-convergent trends, in Chile and California.

Key words: California, Chile, convergence, seed dispersal, propagules, mediterranean-type climates.

RESUMEN

Se comparó la distribución y características de las diásporas de especies leñosas presentes en cuatro comunidades en un gradiente de aumento progresivo de la precipitación media anual entre 30° y 38° de latitud, en Chile y California. Se evaluó la hipótesis de que en estas dos regiones condiciones climáticas limitantes determinan respuestas similares en organismos filogenéticamente no relacionados. La abundancia de frutos carnosos de menos de 15 mm de diámetro (que corresponden al síndrome de dispersión por aves), su tamaño y la frecuencia de frutos negros, aumentan desde el extremo más xérico hacia el más húmedo del gradiente climático tanto en Chile como en California; el mayor número de colores de frutos se encuentra en el matorral esclerófilo en ambas regiones. Estas tendencias apoyan la hipótesis de convergencia. En cambio, la distribución y características de las diásporas dispersadas por viento y de las diásporas secas "pequeñas" no dispersadas por viento (con mecanismos múltiples de dispersión) aparentemente no presentan tendencias convergentes en Chile y California.

Palabras claves: California, Chile, convergencia, dispersión de semillas, diásporas, climas de tipo mediterráneo.

## INTRODUCTION

Several studies have found correlations between seed dispersal mechanisms and environmental conditions (e.g. moisture availability). Howe and Smallwood (1982) documented a significant negative correlation between the percentage of wind-dispersed canopy trees and annual rainfall and Gentry (1982) found that in neotropical forests mammal- and bird-dispersal increase regularly with rainfall, while wind dispersal decreases. It has been reported[1] that the proportions of different types of propagules change with latitude in the mediterranean region of Chile. Finally, in the same region, Fuentes *et al.* (1986) indicated that the seed rain is richer in fleshy fruits at higher latitudes.

These studies suggest that climate might have an influence on the evolution of dispersal mechanisms, although the influence of climate could not be separated from the floristic histories of the communities. The mediterranean regions of Chile and California were considered suitable for this kind of study. There is evidence that in these regions, as a result of comparable environmental conditions, structural and

[1] HOFFMANN AJ and S TEILLIER (1986) Síndromes de dispersión de especies leñosas, en la región mediterránea de Chile. VI Reunión de la Sección Botánica, Sociedad de Biología, Valdivia: 95.

(Received 27 September 1988. Accepted 15 May 1989).

functional similarities have evolved in phylogenetically unrelated organisms. Both regions have comparable climatic gradients, with winters becoming wetter and cooler and summer-droughts decreasing in length and severity at higher latitudes (Mooney *et al.* 1977). Various convergent trends in vegetation structure have been established in Chile and California (Mooney *et al.* 1970, Parsons and Moldenke 1975, Mooney *et al.* 1977, Cowling and Campbell 1980), although several dissimilarities have also been found (Mooney *et al.* 1970).

If dispersal modes are related to the climatic conditions, they should show similar tendencies in comparable climatic gradients in Chile and California. This would be particularly interesting because there is little floristic overlap between these two geographic areas.

In this study we assess the characteristics of propagules of woody species in plant communities found along similar climatic gradients in Chile and California. Propagules were first sorted, according to morphology and size, into types corresponding to dispersal syndromes (Van der Pijl 1982, Wheelwright 1985, Janzen 1986). Then we determined (a) the proportions of species with different types of propagules; (b) the size distribution (by species) of the propagules; and (c) the distribution of colors of fleshy fruits at each community in the Chilean and Californian regions. For each of these attributes we tested the hypothesis that they should follow parallel trends along similar climatic gradients in Chile and California.

## METHODS

### *Plant communities*

We studied the flora of four community types, as defined by Mooney *et al.* (1970), distributed between 30° and 38° latitude in Chile and California: (1) semi-arid scrub with succulents; (2) semi-arid coastal scrub; (3) evergreen scrub; and (4) evergreen forest. The general characteristics of these community types, the features of the vegetation and their location in the aridity gradients of Chile and California are discussed in detail in Mooney *et al.* (1970). Both Chile and California have comparable climatic gradients, with precipitation increasing and temperature decreasing at higher latitude (Table 1). We considered primarily the vegetation of the slopes, omitting species occurring along streams or ravines. The rationale for this decision was that distribution of species along streams is more azonal because of abundant water availability and therefore is not constrained by the regional climate.

### *Species sample*

We used the most complete species lists possible, to reduce biases resulting from small sample sizes. Thus, the lists of woody species for each community type from Mooney *et al.* (1970) were expanded by accepting as valid the distribution of woody taxa in Reiche (1934), Johow (1948), Oberdorfer (1960), Mooney and Schlegel (1966) and Rodríguez *et al.*

TABLE 1

Mean annual rainfall and temperature data of four community types in Chile and California. Source: Mooney *et al.* 1970, di Castri and Hajek 1976; Thrower and Bradbury 1977; Barbour and Major 1988.

Promedios anuales de precipitaciones y temperaturas en cuatro tipos de comunidades de Chile y California. Fuentes: Mooney *et al.* 1970; di Castri and Hajek 1976; Thrower and Bradbury 1977; Barbour and Major 1988

| Community type | | Latitudinal Range (°) | Annual Rainfall (mm) | Temperature (°C) |
|---|---|---|---|---|
| Semi-arid scrub with succulents | Chile | 30 - 32½ | 125- 400 | 15.3 |
| | California | 30 - 32½ | 80- 280 | 22.3 |
| Semi-arid coastal scrub | Chile | 31 - 34 | 150- 500 | 14.5 |
| | California | 32½ - 37½<br>33 - 38 | 280- 440 | 15.8 |
| Evergreen scrub | Chile | 30 - 41 | 320-1500 | 13.4 |
| | California | 32 - 37 | 250-1150 | 13.4 |
| Evergreen forest | Chile | 35 - 43 | 380-1300 | 12.6 |
| | California | | 640-1600 | 11.4 |

(1983) for Chilean species; and in Munz and Keck (1965) and Kuechler (1977) for Californian species. A few species were added to the Chilean lists based on our personal observations and the species list for the semi-arid scrub with succulents in California (Baja California) was supplemented by J. Delgadillo, curator of the BCMEX Herbarium. Thus the list in our study includes most woody species present at each community type. In taking species lists for large areas, there is the risk that some species may be included that are geographical replacements for each other within a same habitat type. To clear out this issue, both the proportions of species and of genera were determined for each plant community. With the only exception of *Arctostaphylos,* all species mentioned for each of the genera had only one type of propagule. Although the fruits of *Arctostaphylos* are berries (Jepson 1975), they are extremely dry in several species (Munz & Keck 1965); the latter were listed as nutlets in our study, since we felt these morphological differences probably reflected their dispersal modes.

*Propagule characteristics*

The characteristics of propagules were determined from data in the literature; those of Chilean species were supplemented by field collections. Propagules were first sorted into fleshy and dry and then grouped according to morphology and size.

Fleshy propagules were berries, drupes, fleshy perigonia and arillate seeds. There is evidence (Herrera 1984) indicating that fleshy fruits, with diameters closely related to the gape-width of the predominant local frugivorous species, are typically dispersed by birds. Although we do not have data on the gape-widths of frugivorous birds in our study sites, we assumed that fleshy fruits measuring 15 mm in diameter or less could be bird-dispersed. This assumption is based on data available on the sizes of fruits dispersed by birds in other temperate and mediterranean regions. In New Zealand, 85% of ornithochorous species have fruit measuring less than 15 mm in diameter (fide Armesto 1986); in Illinois, 95% of fruits of ornithochorous species measure 5.1-10 mm (Johnson *et al.* 1985); in Spain, 50-60% of species produce fleshy fruit, but the percentage of fruit crop removed by birds declines significantly when the fruit diameter exceeds 10 mm (Herrera 1984, 1987); in the southern temperate region of Chile, 74% of fruits of ornithochorous species range from 5.1 to 10 mm in diameter (Armesto 1986), and the mean gape-width of the local frugivorous birds species is 8.6 mm (range 6.2-12.0, n= 12) (Armesto *et al.* 1987). We called *"small" fleshy propagules* measuring up to 15 min in diameter (Table 2).

In both regions there was a number of fleshy fruits with diameters larger than the gape-width of all birds present in the region. It has been postulated (Janzen & Martin 1982, Herrera 1985, Janzen 1986) that the Pleistocene herbivorous megafauna might have had a major impact on the evolution of these usually thick-husked, large fleshy fruits. We considered a category of *"large" fleshy propagules,* including all those measuring over 15 mm in diameter, for which no present-day bird dispersers are available, and included them into a broader group of *"large" propagules* (Table 2).

Dry propagules having wings, plumes, a many-barbed pappus, or very light seeds, were considered as wind-dispersed (Van der

TABLE 2

Propagule types and potential dispersal agents

Tipos de diásporas y agentes potenciales de dispersión

| PROPAGULE TYPE | | | POTENTIAL DISPERSAL AGENT |
|---|---|---|---|
| 1) Fleshy | small (< 15 mm wide) | | avian frugivores |
| 2) Fleshy | large (> 15 mm wide) | | large vertebrates, extinct megafauna? |
| 3) Dry | winged or plumed | | wind |
| 4) Dry | not winged or plumed | small (< 20 mm) | multiple, mainly birds, small mammals and water |
| | | large (> 20 mm) | large vertebrates, extinct megafauna? |

Pijl 1982). This group was classified as *"winged or plumed" propagules* (Table 2).

Another group of dry fruits and seeds lacking morphologies suited for wind dispersal included nuts and nutlets, achenes without pappus, dry berries and drupes, pods, loments, and seeds released from capsules and legumes. Dispersal mechanisms of these propagules are not well understood. Some may be dispersed through diverse mechanisms (e.g. autochory, epizoochory). However, in many species the spherical seeds or fruits lack morphological features for dispersal and probably drop to the ground when ripe. Ellner & Shmida (1981) also report that, in desert regions in Israel, many seeds lack mechanisms for dispersal. We propose a fourth group of *"small", dry, not wind-dispersed propagules,* including all those propagules under 20 mm. This group probably encompasses multiple dispersal mechanisms (including ground-feeding birds and rodents) (Table 2).

There was a group of "large" (> 20 mm in length) dry, not wind-dispersed propagules (mainly indehiscent, pulp-filled pods) which according to Van der Pijl (1982) may be dispersed by large mammals. It has also been postulated that some of these large, dry propagules would have evolved in connection with the extinct Pleistocene megafauna (Janzen & Martin 1982, Janzen 1986). We grouped in one category of *"large" propagules the "large" fleshy* and the *"large" dry* propagules (Table 2).

*Statistics.*

Relationships between community type and propagule frequencies were analyzed with chi-square tests on two-way contingency tables and by fitting a log-linear model to the contingency tables (Fienberg 1980).

## RESULTS

We analyzed the characteristics of fruits and seeds of 101 species (in 38 families and 75 genera) from Chile, and 206 species (in 39 families and 87 genera) from California. The lists of species present in each of the community types of Chile and California, as well as various characteristics of the diaspores of each species are presented in Appendix 1. Only six genera, *Baccharis, Berberis, Encelia, Haploppapus, Lycium,* and *Solanum,* were common to both regions.

### 1. *Proportions of propagule types*

The four types of propagules (Table 2) were present in all communities in Chile and California, although in different proportions. In general, trends in the distribution of species and genera are similar in both regions (Tables 3 and 4). Fitting a log-linear model to the data showed that for certain types of propagules there are significant differences in their distribution between communities, both in Chile and California (Table 3 and 4).

The percentages of both species and genera with "small" fleshy fruit increase along the rainfall gradient, following similar tendencies in Chile and California (Spearman rank correlation, $r_s = 1, P < 0.05$, Tables 3 and 4), thus supporting the convergence hypothesis. Both in Chile and in California the percentages differ significantly between community types ($X^2$, $P < 0.001$).

The percentages of species with "large" propagules decrease from the semi-arid scrub with succulents through the evergreen scrub, to remain roughly equal in the evergreen forest, both in Chile and in California (Spearman rank correlation, $r_s = 1$, $P<0.05$, Table 3).

The percentages of species and genera with "winged or plumed" and "small", dry, not wind-dispersed propagules tend to decrease in Chile as rainfall increases, although differences are statistically non-significant (Tables 3 and 4). No such tendencies are discernible in California, where the proportion of "winged or plumed" propagules is significantly higher in the semi-arid coastal scrub. Therefore, no convergent trends are apparent in these characteristics.

### 2. *Size variation of propagules*

The average sizes of some types of propagules differ between community types in Chile and in California (Table 5).

The cross diameter of fleshy fruit varies from 2 to almost 33 mm, with a bimodal distribution of sizes in both regions. This is consistent with our distinction of "small" and "large" fleshy fruits. The bimodal distribution patterns is more marked in Chile than in California (Fig. 1). In Chile

TABLE 3

Distribution of propagule types in four analogous plant communities in Chile and California. The number of species (N), and the proportion (%) in which each propagule type occurs in relation to the total number of species at each site are indicated.

Distribución de los tipos de diásporas en cuatro comunidades análogas de Chile y California. Se indica el número de especies (N) y la proporción (%) de cada tipo de diáspora en relación al número total de especies en cada sitio

| Propagule type | Semi-arid scrub with succulents | | Semi-arid coastal scrub | | Evergreen scrub | | Evergreen forest | | $X^2$ | Significance level |
|---|---|---|---|---|---|---|---|---|---|---|
| | N | % | N | % | N | % | N | % | | |
| CHILE | | | | | | | | | | |
| Small fleshy | 6 | 13.3 | 6 | 20.0 | 11 | 31.4 | 15 | 65,2 | 21.49 | 0.0005 |
| Small dry | 14 | 31.1 | 9 | 30.0 | 10 | 28.6 | 2 | 8,7 | 4,52 | NS |
| Large (fleshy or dry) | 8 | 17.8 | 5 | 16.7 | 3 | 8.6 | 12 | 8.7 | 4.75 | 0,1 |
| Winged or plumed | 17 | 37.8 | 10 | 33.3 | 11 | 31.4 | 4 | 17.4 | 2.97 | NS |
| TOTAL | 45 | | 30 | | 35 | | 28 | | | |
| CALIFORNIA | | | | | | | | | | |
| Small fleshy | 4 | 19.1 | 10 | 23.8 | 39 | 31.7 | 33 | 52.3 | 13.22 | 0.005 |
| Small dry | 7 | 33.3 | 12 | 28.6 | 65 | 52,9 | 19 | 30.2 | 3.29 | NS |
| Large (fleshy or dry) | 6 | 28.6 | 4 | 9.5 | 2 | 1.6 | 2 | 3.2 | – | |
| Winged or plumed | 4 | 19.0 | 16 | 38.1 | 17 | 13.8 | 9 | 14.3 | 13.14 | 0.005 |
| TOTAL | 21 | | 42 | | 123 | | 63 | | | |

TABLE 4

Distribution of propagule types in four analogous plant communities in Chile and California. The number of genera (N), and the proportion (%) in which each propagule type occurs in relation to the total number of genera at each site are indicated.

Distribución de los diferentes tipos de diásporas en cuatro comunidades análogas de Chile y California. Se indican el número de géneros (N) y la proporción (%) de cada tipo de diáspora en relación al número total de géneros en cada sitio.

| Propagule type | Semi-arid scrub with succulents | | Semi-arid coastal scrub | | Evergreen scrub | | Evergreen forest | | $X^2$ | Significance level |
|---|---|---|---|---|---|---|---|---|---|---|
| | N | % | N | % | N | % | N | % | | |
| CHILE | | | | | | | | | | |
| Small fleshy | 6 | 15.8 | 6 | 23.1 | 11 | 33.3 | 12 | 63.2 | 14.36 | 0.0005 |
| Small dry | 14 | 36.8 | 7 | 26.9 | 9 | 27.3 | 2 | 10.5 | 4.24 | NS |
| Large | 6 | 15.8 | 5 | 19.2 | 3 | 9.1 | 2 | 10.5 | – | – |
| Winged or plumed | 12 | 31.6 | 8 | 30.8 | 10 | 30.3 | 3 | 15.8 | 1.79 | NS |
| TOTAL | 38 | | 26 | | 33 | | 19 | | | |
| CALIFORNIA | | | | | | | | | | |
| Small fleshy | 4 | 20.0 | 7 | 30.4 | 18 | 40.9 | 22 | 53.7 | 6.78 | 0.005 |
| Small dry | 4 | 20.0 | 8 | 34.8 | 13 | 29.5 | 9 | 21.9 | 1.87 | NS |
| Large | 6 | 30.0 | 1 | 4.4 | 2 | 4.6 | 3 | 7.3 | – | – |
| Winged or plumed | 6 | 30.0 | 7 | 30.4 | 11 | 25.0 | 7 | 17.1 | 1.98 | NS |
| TOTAL | 20 | | 23 | | 44 | | 41 | | | |

there is one mode in the size range 4.1-6 mm (33% of fruits), and one in the range 26.1-30 mm (12.1% of fruits). In California there is one mode in the size range of 6.1-8 mm (39.2% of fruits), and one in the range 26.1-35 mm (7.6% of fruits). Fig. 1 also shows that "small" fleshy fruits are larger on the average in California than in Chile.

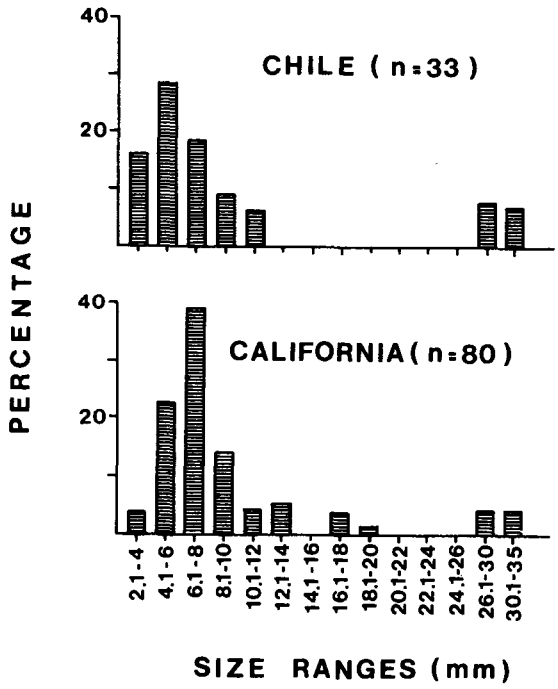


*Fig. 1:* Size (diameter) ranges of fleshy fruits in the mediterranean regions of Chile and California.

Distribución de tamaños (expresados como diámetro) de frutos carnosos presentes en las regiones mediterráneas de Chile y California.

In Chile, the diameter of "small" fleshy fruits of the three more arid communities is smaller than that of the more humid community in the climatic gradient ($P<0.05$, ANOVA; Table 5A). In California, the diameter of fruits of the two more arid communities is smaller than that of the two more humid communities ($P<0.05$, ANOVA). Differences in fruit sizes between the semi-arid coastal scrub and the evergreen scrub, as well as those between the semi-arid coastal scrub and evergreen forest, are significant. Therefore, although in both regions fleshy fruits are larger at the wet end of the gradient, significant variation occurs in different parts of the gradients (Table 5A).

Dry, not wind-dispersed propagules vary between 0.1 and over 25 mm in diameter (Fig. 2). A first group, measuring 0.1 to 16 mm in diameter ("small" dry, not wind-dispersed propagules), comprises 70% of the propagules of the Chilean list and 90% of those in the Californian list. Within this size range, the largest frequency in Chile (almost 30%) falls in the 4.1-8 mm range, whereas in California (74%) it falls in the 0.1-4 mm range. Propagules measuring over 25 mm, included in the class "large" dry, not wind-dispersed propagules, represent 30% of the propagules in Chile, and 10% in California. Their size ranges from 30 to 120 mm in length and from 10 to 30 mm in width.

The diameters of "small", dry not wind-dispersed propagules change along the climate gradient, both in Chile and California (Table 5B). There is no apparent relation between the average size of this type of propagules and the precipitation gradient in Chile, whereas in California average size increases from dry to wet communities. Therefore this type of propagules shows no convergent trends.

The average length and width of the "large" propagules differs between sites, both in Chile and in California (Table 5 C and D), but no convergent trends are apparent in relation to the precipitation gradient.

### 3. *Colors of fleshy fruits*

The overall color distributions of ripe fleshy fruits under 15 mm in diameter (including seeds with colored arils) are shown in Fig. 3. In Chile, violet/black is the most frequent color (48%). Red, green and pink hues occur in similar proportions (10-15% of the species) and other colors are less frequent. In California, red is the predominant color, occurring in 42% of the species, while violet/black is found in 30%, and brown in 15% of the species; other colors are less frequent.

The proportions of fruits with different colors vary between communities in both regions (Table 6). The percentage of species with violet/black fruits increases from the arid towards the mesic communities, both in Chile and California (Spearman rank correlation $r_s = 1$, $P<0.05$), thus supporting the convergence hypothesis.

Changes in the proportions of the other colors bear no relationship to the climatic

TABLE 5

Average sizes (in mm) of "small" fleshy, "small" dry not wind-dispersed and "large" propagules at four analogous plant communities of Chile and California. N = sample size. Letters a and b designate means that are different from each other at 0.05 level by ANOVA and multiple comparison.

Tamaño promedio (en mm) de diásporas "pequeñas" carnosas, "pequeñas" secas, no dispersadas por viento, y "grandes", en cuatro comunidades análogas de Chile y California. N = tamaño de muestra. Las letras a y b designan promedios que son diferentes entre sí al nivel de 0.05, según ANDEVA y test de comparación múltiple.

| Propagule type | Semi-arid scrub with succulents | | Semi-arid coastal scrub | | Evergreen scrub | | Evergreen forest | |
|---|---|---|---|---|---|---|---|---|
| | N | X ± SD | N | X ± SD | N | X ± SD | N | X ± SD |
| A. SMALL FLESHY | | | | | | | | |
| Chile | 6 | 5.9 ± 2.2a | 6 | 5.7 ± 0.8a | 12 | 5.0 ± 1.1a | 15 | 7.0 ± 2.2b |
| California | 2 | 6.3 ± 3.7a | 10 | 5.8 ± 1.5a | 34 | 7.4 ± 2.4b | 24 | 9.0 ± 3.2b |
| B. SMALL DRY | | | | | | | | |
| Chile | 5 | 6.0 ± 3.3a | 8 | 1.9 ± 1.4b | 12 | 4.5 ± 3.1a | 1 | 5.0 – |
| California | 3 | 2.6 ± 0.1a | 6 | 2.8 ± 0.5a | 51 | 4.8 ± 3.2b | 11 | 5.4 ± 3.7b |
| C. LARGE (width) | | | | | | | | |
| Chile | 11 | 16.8 ± 7.5 | 5 | 21.0 ± 9.2 | 4 | 17.5 ± 8.3 | 1 | 20.0 – |
| California | 4 | 25.0 ± 5.0 | 3 | 23.3 ± 4.7 | 3 | 40.0 ± 20.4 | 2 | 15.0 ± 5.0 |
| D. LARGE (length) | | | | | | | | |
| Chile | 11 | 50.5 ± 33.6 | 5 | 39.0 ± 17.0 | 4 | 42.5 ± 17.9 | 1 | 30.0 – |
| California | 4 | 40.0 ± 10.0 | 3 | 40.0 ± 14.1 | 3 | 43.3 ± 16.5 | 2 | 32.5 ± 7.5 |

gradient in either region. However, the widest variety of colors was found in the evergreen scrub both in Chile and in California (Table 6).

## DISCUSSION

The convergence hypothesis states that if the environments impose similar restrictions to the evolutionary responses of organisms, species living in geographically disjunct places should display structural and functional similarities. When the distributions of propagule types of woody species are compared along similar climatic gradients in the mediterranean regions of Chile and California, several traits follow similar patterns of variation, suggesting convergent responses to similar climatic constraints. In contrast, other traits do not show convergent tendencies.

On the one hand, the proportions of "small" fleshy propagules, as well as their sizes, increase from xeric to mesic communities, in both regions. The frequency of black fleshy fruits also increases along this precipitation gradient, while the proportion of "large" fruits decreases in the same direction. In addition, our results indicate that the largest number of traits following convergent tendencies in Chile and California are found in "small" fleshy fruits.

On the other hand, while in Chile the percentage of "winged or plumed" propagules decreases with annual rainfall, a pattern similar to that described for other regions (Howe and Smallwood 1982, Gentry 1982), no such pattern is discernible in California. In a similar way, while the proportion of "small" dry, not wind-dispersed propagules decreases with increasing rainfall in Chile, this is not the case in California. Finally, "small" fleshy propagules also show some differences between Chile and California: (1) the average diameter of "small" (<15 mm) fleshy fruits is smaller in Chile; (2) the frequencies of fruit colors other than black do not show similar distributions along the climatic gradients; (3) black is the most frequent fruit color in Chile, while red predominates in California.

It appears, therefore, that propagules do not respond evolutionally as a whole to climatic limitations, but that independent responses are likely in structural and functional attributes of a particular type of propagule. Some types of propagules show more convergent responses than others. In fact, when the characteristics of propagules are compared with those of other medite-

rranean regions (e.g. southern Spain), the largest number of convergent traits also appear in fleshy fruits. Thus, plant/bird interactions might facilitate convergent evolutionary changes in fleshy fruits. However, predominance of certain traits differs among regions. Such is the case with the color of fleshy fruits: whereas black is the most frequent color in Peru, Costa Rica, Florida (Wheelwright and Janson 1985), South Africa (Knight and Siegfried 1985) and in the mediterranean regions of southern France (Anonymous 1986 and pers. obs., A.H.), red is more common in the Iberian Peninsula (Herrera 1987) and in Central Europe (Wheelwright and Janson 1985). In turn, it is still unclear why there is only a weak convergence in wind-dispersed propagules.

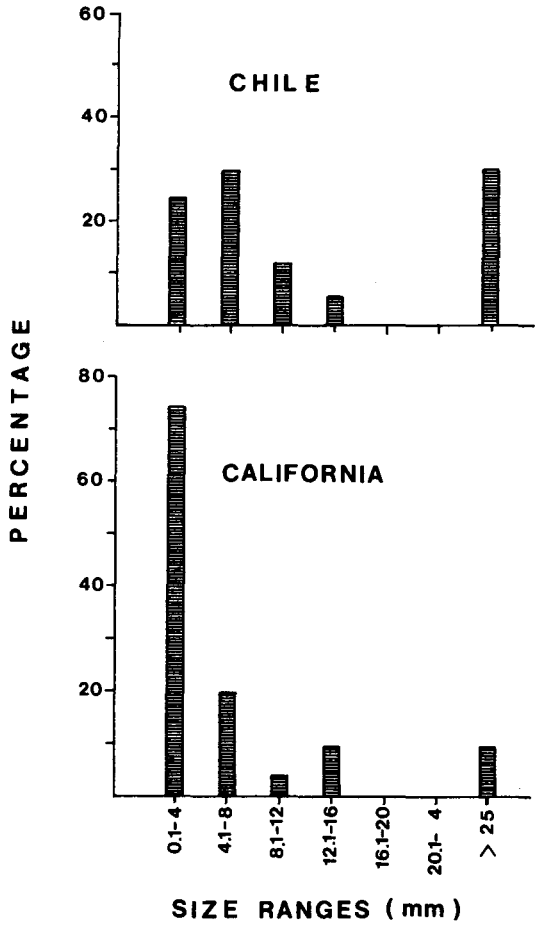


*Fig. 2:* Size ranges of dry, not wind-dispersed propagules, in the mediterranean regions of Chile and California.

Distribución de tamaños de las diásporas secas, no dispersadas por viento, en las regiones mediterráneas de Chile y California.

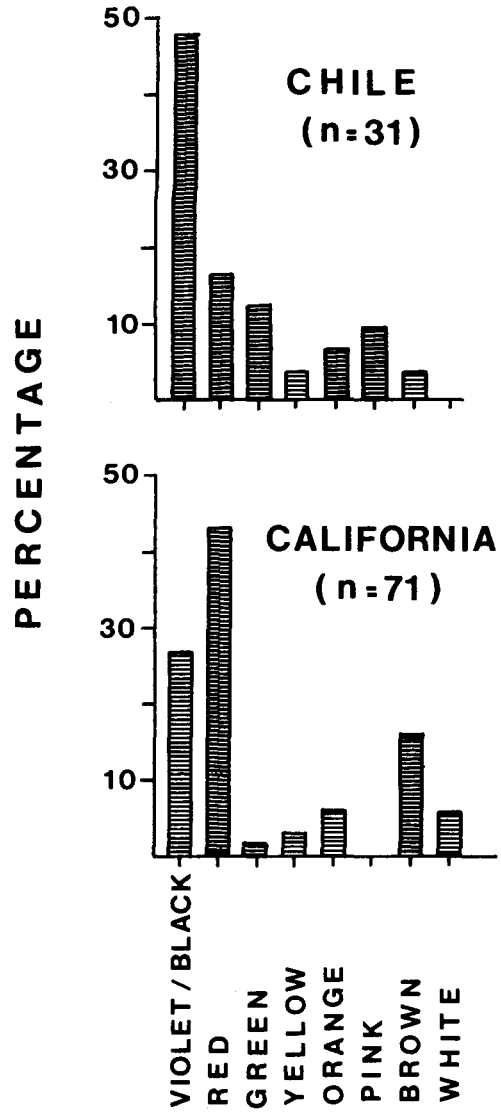


*Fig. 3:* Distribution of colors of "small" (< 15 mm) fleshy fruits in the mediterranean regions of Chile and California.

Distribución de los colores de los frutos carnosos "pequeños" (<15 mm), en las regiones mediterráneas de Chile y California.

When other syndromes are considered additional questions arise. There are several species in which the fruit traits cannot be associated with the extant potential dispersers. Some of these species might correspond to ancient large-fruited taxa that failed to overlap with fruit-eating dispersers of appropriate sizes since the onset of mediterranean conditions in the Pleistocene (Herrera 1985). We recognized three types of

TABLE 6

Distribution of colors in "small" fleshy fruits, in four analogous plant communities in Chile and California.

Distribución de los colores de frutos carnosos "pequeños", en cuatro comunidades análogas de Chile y California.

| Fruit color | Semi-arid scrub with succulents | | Semi-arid coastal scrub | | Evergreen scrub | | Evergreen forest | |
|---|---|---|---|---|---|---|---|---|
| | N | % | N | % | N | % | N | % |
| CHILE | | | | | | | | |
| Violet/Black | 2 | 25.0 | 2 | 28.6 | 4 | 30.8 | 11 | 64.8 |
| Green | 2 | 25.0 | 2 | 28.6 | 3 | 23.1 | 2 | 11.8 |
| Yellow | – | | – | | 1 | 7.7 | – | |
| Orange | – | | – | | 1 | 7.7 | 1 | 5.9 |
| Pink | 2 | 25.0 | 1 | 14.2 | 3 | 23.1 | – | |
| Red | 2 | 25.0 | 2 | 28.6 | 1 | 7.1 | 2 | 11.8 |
| Brown | – | | – | | – | | – | |
| White | – | | – | | – | | 1 | 5.9 |
| Total N° of species | 8 | | 7 | | 13 | | 17 | |
| Total N° of colors | 4 | | 4 | | 6 | | 5 | |
| CALIFORNIA | | | | | | | | |
| Violet/Black | 1 | 25.0 | 2 | 25.0 | 8 | 26.7 | 15 | 50.0 |
| Green | – | | – | | – | | 1 | 3.3 |
| Yellow | 1 | 25.0 | 1 | 12.5 | 2 | 6.7 | – | |
| Orange | – | | – | | 1 | 3.3 | – | |
| Pink | – | | – | | – | | – | |
| Red | 1 | 25.0 | 4 | 50.0 | 15 | 50.0 | 11 | 36.7 |
| Brown | – | | – | | 1 | 3.3 | 1 | 3.3 |
| White | 1 | 25.0 | 1 | 12.5 | 3 | 10.0 | 2 | 6.7 |
| Total N° of species | 4 | | 8 | | 30 | | 30 | |
| Total N° of colors | 4 | | 4 | | 6 | | 5 | |

such "large" fruits: (1) fleshy fruits with diameters larger than the gape-width of the local avian frugivores (e.g., *Opuntia, Trichocereus*); (2) large berries or drupes with thick, leathery husks, mostly of brown or greenish color (e.g., *Beilschmiedia, Lardizabala, Umbellularia*); (3) large indehiscent, pulp-filled pods (e.g., *Balsamocarpum, Senna, Cercis*). Janzen and Martin (1982), Herrera (1985) and Janzen (1986) have proposed that dispersal of large propagules might have evolved in connection with extinct megafauna. We believe, though, that "large" fruits may have had diverse evolutionary origins. Although for some propagule types (e.g., *Lardizabala*) the extinct megafauna hypothesis seems reasonable, for others (e.g., *Prosopis, Acacia*) at least in Chile, evolution could have occurred in association with modern mammals, such as the guanaco.

Propagules that evolved in association with particular dispersal agents can be eventually consumed by other animals that may have some influence on their dispersal. For instance, the pods and seeds of several species (*Prosopis, Acacia*) are dispersed by cattle (Gutiérrez and Armesto 1981), and seeds of *Balsamocarpum* are consumed and possibly dispersed by rodents such as the chinchilla (*Chinchilla chinchilla*) (Burkart 1952). The large berries of *Opuntia* are currently eaten by cattle (Janzen 1986), and those of *Trichocereus* by tenca (*Mimus thenca*). Some "small" fleshy fruits are also eaten by mammals. In Chile, the drupes of *Cryptocarya alba* and *Lithrea caustica* are consumed by foxes (Jaksić *et al.* 1980) and those of *Peumus boldus* by the introduced rabbit, *Oryctolagus cuniculus* (E F, pers. obs.). However, little evidence is available on the effectiveness of such "secondary" dispersers. Probably tencas, that consume portions of the fleshy pulp, with small seeds included and later void the seeds, may be effective dispersers. In contrast, the

effectiveness of foxes is doubtful, because they leave their droppings, often containing dozens of seeds, mostly in open spaces, where it has been shown that seedling survival is low when unprotected from drought (Fuentes *et al.* 1986).

ACKNOWLEDGEMENTS:

We are grateful to J. Delgadillo and A. Walkowiak for valuable information on the vegetation of Baja California. We also thank M.F. Willson and two anonymous reviewers for very helpful comments and suggestions. The study was funded by Grant 93/87, DIUC.

REFERENCES

ANONYMOUS (1986) Guide des arbres et arbustes. Sélection du Reader's Digest, S.A. 212, Boulevard Saint-Germain, Paris, 351 pp.

ARMESTO JJ (1986) Mecanismos de diseminación de semillas en el bosque de Chiloé: una comparación con otros bosques templados y tropicales. Anales del IV Congreso Latinoamericano de Botánica, Medellín, Colombia: 7-24.

ARMESTO JJ, R. ROZZI, P MIRANDA & C SABAG (1987) Plant/frugivore interactions in South American temperate forests. Revista Chilena de Historia Natural 60: 321 - 336.

BARBOUR MG & J MAJOR (1988) Terrestrial vegetation of California. California Native Plant Society. Special Publication Nº 9, 939 pp.

BURKART A (1952) Las leguminosas argentinas. Acme Agency, Buenos Aires, 590 pp.

COWLING RM & BM CAMPBELL (1980) Convergence in vegetation structure in the mediterranean communities of California, Chile and South Africa. Vegetatio 43: 191-197.

DI CASTRI F & ER HAJEK (1976) Bioclimatología de Chile. Imprenta Editorial Universidad Católica de Chile, Santiago, 128 pp.

ELLNER S & A SHMIDA (1981) Why are adaptations for long-range dispersal rare in desert plants? Oecologia 51: 133-144.

FIENBERG SE (1980) The analysis of cross-classified categorical data. Second Edition. The MIT Press, Cambridge, Massachusetts.

FUENTES ER, AJ HOFFMANN, A POIANI & C. ALLIENDE (1986) Vegetation change in large clearings: patterns in the Chilean matorral. Oecologia (Berlin) 68: 358-366.

GENTRY AH (1982) Patterns of neotropical plant species diversity. Evolutionary Biology 15: 1-84.

GUTIERREZ JR & J ARMESTO (1981) El rol del ganado en la dispersión de las semillas de *Acacia caven* (Leguminosae). Ciencia e Investigación Agraria 8: 3-8.

HERRERA CM (1984) A study of avian frugivores, bird-dispersed plants, and their interaction in mediterranean scrublands. Ecological Monographs 54: 1-43.

HERRERA CM (1985) Determinants of plant-animal coevolution – the case of mutualistic dispersal of seeds by vertebrates. Oikos 44: 132-141.

HERRERA CM (1987) Vertebrate dispersed plants of the Iberian Peninsula: a study of plant characteristics. Ecological Monographs 57: 305-331.

HOWE HF & J SMALLWOOD (1982) Ecology of seed dispersal. Annual Review of Ecology and Systematics 13: 201-228.

JAKSIC FM, RP SCHLATTER & JL YAÑEZ (1980) Feeding ecology of central Chilean foxes, *Dusicyon culpaeus* and *Dusicyon griseus*. Journal of Mammalogy 61: 254-260.

JANZEN DH (1986) Chihuahuan desert nopaleras: defaunated big mammal vegetation. Annual Review of Ecology and Systematics 17: 595-636.

JANZEN DH & PS MARTIN (1982) Neotropical anachronisms: the fruits the gomphothers ate. Science 215: 19-27.

JEPSON WL (1975) A manual of the flowering plants of California. University of California Press, Berkeley, California, 1238 pp.

JOHNSON RA, MF WILLSON, JN THOMPSON & RI BERTIN (1985) Nutritional values of wild fruits and consumption by migrant frugivorous birds. Ecology 66: 819-827.

JOHOW E (1948) Flora de Zapallar. Revista Chilena de Historia Natural 49: 1-566.

KNIGHT RS & WR SIEGFRIED (1983) Interrelationships between type, size and color of fruits and dispersal in Southern African trees. Oecologia (Berlin) 56: 405-412.

KUECHLER AW (1977) The map of the natural vegetation of California. Department of Geography, University of Kansas, Lawrence, Kansas, 31 pp.

MARTICORENA C & M QUEZADA (1985) Catálogo de la flora vascular de Chile. Gayana 42: 1-155.

MOONEY HA & F SCHLEGEL (1966) La vegetación costera de Los Molles en la provincia de Aconcagua. Boletín Universidad de Chile 75: 27-32.

MOONEY HA, EL DUNN, F SHROPSHIRE & L SONG (1970) Vegetation comparisons between the mediterranean climatic areas of California and Chile. Flora 159: 480-496.

MOONEY HA, J KUMMEROW, AW JOHNSON, DJ PARSONS, S KEELEY, A HOFFMANN, RI HAYS, J GILIBERTO & C CHU (1977) The producers– their resources and adaptive responses. In: HA Mooney (ed) Convergent evolution in Chile and California: 144-19. Dowden, Hutchinson & Ross, Stroudsburg, PA.

MUNZ PA & DD KECK (1965) A California Flora. University of California Press, Berkeley, California, 1681 pp.

OBDERDORFER E (1960) Pflanzensoziologische Studien in Chile. Ein Vergleich mit Europa. In: Tuexen R (ed) Flora et Vegetatio Mundi: 1-198. Verlag von J Cramer, Weinheim.

PARSONS DJ & R MOLDENKE (1975) Convergence in vegetation structure along analogous climatic gradients in California and Chile. Ecology 56: 950-957.

PIJL L VAN DER (1982) Principles of dispersal in higher plants. 2nd edition, Springer, New York. 214 pp.

REICHE K (1934) Geografía Botánica de Chile, Imprenta Universitaria, Santiago. Tomo I, 424 pp, Tomo II, 150 pp.

RODRIGUEZ R, O MATTHEI & M QUEZADA (1983) Flora arbórea de Chile. Edit. Universidad de Concepción, Concepción, 408 pp.

THROWER NJW & DE BRADBURY (1977) Chile-California Mediterranean Scrub Atlas. Dowden, Hutchinson & Ross, Stroudsburg, Pennsylvania 273 pp.

WHEELWRIGHT NT (1985) Fruit size, gape width, and the diets of fruit-eating birds. Ecology 66: 808-818.

WHEELWRIGHT NT & CH JASON (1985) Colors of fruit displays of bird-dispersed plants in two tropical forests. American Naturalist 126: 777-799.

Appendix 1. Woody species present in four analogous communities in the mediterranean regions of Chile and California. The kinds of propagules, the colors of fleshy fruits and sizes, are indicated. Propagule type codes: 1= "small" fleshy; 2= "small" dry, without morphologies for wind-dispersal; 3= "large" fleshy or dry; 4= "winged or plumed". Aril.= arillate; Lom.= Loment. Sources for nomenclature of taxa: Chile: Marticorena and Quezada 1985; California: Munz and Keck 1965.

Apéndice 1. Especies leñosas presentes en cuatro comunidades análogas de las regiones mediterráneas de Chile y California. Se indican sus tipos de diásporas, color de los frutos carnosos y tamaño. Código de tipos de diásporas: 1= carnosas "pequeñas"; 2= secas "pequeñas", sin morfologías para dispersión por viento; 3= carnosas o secas "grandes"; 4= "aladas o plumosas". Ari.= ariladas; Lom.= lomento. Fuentes de nomenclatura de los taxa: Chile: Marticorena y Quezada 1985; California: Munz and Keck 1965.

| | Propagule type | Color | Size (mm) | Type code |
|---|---|---|---|---|
| **CHILE** | | | | |
| *Semi-arid scrub with succulents* | | | | |
| Adesmia argentea Meyen | Lom. | | 30x10 | 4 |
| Adesmia glutinosa Hook. et Arn. | Lom. | | 30x10 | 4 |
| Adesmia microphylla Hook. et Arn. | Lom. | | 30x10 | 4 |
| Bahia ambrosioides Lag. | Achene | | | 4 |
| Baccharis linearis (R. et Pav.) Pers. | Achene | | | 4 |
| Balsamocarpon brevifolium Clos | Lom. | | 40x10 | 3 |
| Bridgesia incisifolia Bert. ex Cambess. | Seed | | | 2 |
| Calliandra chilensis Benth. | Seed | | | 2 |
| Caesalpinia spinosa (Mol.) O.K. | Seed | | 6-8 | 2 |
| Cestrum parqui L'Herit. | Berry | black | 5.6 | 1 |
| Chuquiraga acicularis D. Don | Achene | | | 4 |
| Colliguaja odorifera Mol. | Seed | | 5 | 2 |
| Cordia decandra Hook. et Arn. | Nut | | 10 | 2 |
| Encelia canescens Lam. | Achene | | | 4 |
| Eulychnia acida Phil. | Berry | green | | 3 |
| Eulychnia spinibarbis (L. Pfeiffer) Britton et Rose | Berry | green | | 3 |
| Eupatorium salvia Colla | Achene | | | 4 |
| Ephedra andina (Poepp.) ex C. A. Mey. | Aril. seed | pink | | 1 |
| Fagonia chilensis Hook. et Arn. | Seed | | | 2 |
| Fluorensia Thurifera (Mol.) DC | Achene | | | 2 |
| Geoffroea decorticans (Gill. ex H. et A.) Burk. | Drupelike | | 20-30 | 3 |
| Gochnatia foliolosa (D. Don) D. Don ex H. et A. | Achene | | | 4 |
| Gutierrezia resinosa (H. et A.) Blake | Achene | | | 2 |
| Haplopappus ischnos (Phil.) Reiche | Achene | | | 4 |
| Heliotropium stenophyllum Hook. et Arn. | Achene | | | 2 |
| Larrea nitida Cav. | Nutlike | | | 2 |
| Lobelia polyphylla Hook. et Arn. | Seed | | | 4 |
| Lycium stenophyllum (Miers) Remy | Berry | red | 3-4 | 1 |
| Oxalis gigantea Barn. | Seed | | 1-1.5 | 2 |
| Phrodus microphyllus (Miers) Miers | Berry | | 10 | 1 |
| Pleocarphus revolutus D. Don | Achene | | | 4 |
| Podanthus mitiqui Lindl. | Achene | | | 2 |
| Porlieria chilensis Johnst. | Nutlike | | 8.7 | 2 |

Appendix 1 (Cont.)

| | Propagule type | Color | Size (mm) | Type code |
|---|---|---|---|---|
| Proustia cuneifolia D. Don fma. cinerea (Phil.) Fabris | Achene | | | 4 |
| Proustia ilicifolia H. et A. fma. bacharioides (D. Don) Fabris | Achene | | | 4 |
| Prosopis chilensis (Mol.) Stuntz | Lom. | | 150x15 | 3 |
| Puya berteroniana Mez | Seed | | | 4 |
| Puya chilensis Mol. | Seed | | | 4 |
| Schinus polygamus (Cav.) Cabrera | Berry | violet | 3-4 | 1 |
| Senna cumingii (H. et A.) Irwin et Barneby | Lom. | | 70x15 | 3 |
| Trevoa trinervis Miers | Drupe | green | | 2 |
| Trichocereus chilensis (Colla) Britton et Rose | Berry | green | 50x30 | 3 |
| Trichocereus coquimbanus (Mol.) Britton et Rose | Berry | green | 40x30 | 3 |
| Tristerix aphyllus (Miers ex DC.) Van Tiegh. ex Barlow et Wiens | Berry | pink | 6.0 | 1 |
| *Semi-arid coastal scrub* | | | | |
| Adesmia microphylla Hook. et Arn. | Hairy Lom. | | 30x10 | 4 |
| Anisomeria littoralis (Poeppig et Endlicher) Moq. en DC. | Berrylike | | 7 | 1 |
| Adenopeltis serrata (W. Aiton) Johnst. | Seed | | 5 | 2 |
| Azara celastrina D. Don | Berry | orange | 5.0 | 1 |
| Baccharis concava (R. et Pav.) Pers. | Achene | | | 4 |
| Bahia ambrosioides Lag. | Achene | | | 2 |
| Eupatorium salvia Colla | Achene | | | 4 |
| Eupatorium glechonophyllum Less. | Achene | | | 4 |
| Escallonia pulverulenta (R. et Pav.) Pers. | Seed | | | 4 |
| Eulychnia castanea Phil. | Berry | green | | 3 |
| Fuchsia lycioides Andr. | Berry | red | | 1 |
| Flourensia thurifera (Mol.) DC. | Achene | | | 2 |
| Haplopappus foliosus DC. | Achene | | | 4 |
| Heliotropium stenophyllum H. et A. | Nutlet | | | 2 |
| Lithrea caustica (Mol.) H. et A. | Drupe | green | 5.9 | 1 |
| Lobelia excelsa Bonpl. | Seed | | 1-1.5 | 4 |
| Lobelia polyphylla Hook. et Arn. | Seed | | 1-1.5 | 4 |
| Neoporteria subgibbosa (Haw.) Britton et Rose | Berry | | | 3 |
| Oxalis gigantea Barn. | Seed | | 1-1.5 | 2 |
| Peumus boldus Mol. | Berry | green | 6.3 | 1 |
| Podanthus mitiqui Lindl. | Achene | | | 2 |
| Pouteria splendens (A. DC.) O.K. | Drupe | brown | 25-30 | 3 |
| Proustia pyrifolia DC. | Achene | | | 4 |
| Puya chilensis Mol. | Seed | | | 4 |
| Puya venusta Phil. | Seed | | | 4 |
| Schinus latifolius (Gill. ex Lindl.) Engler | Berry | violet | 5.0 | 1 |
| Senna candolleana (Vogel) Irwin et Barneby | Lom. | | 20x10 | 3 |
| Sphacele salviae (Lindl.) Briq. | Nutlet | | | 2 |
| Trichocereus litoralis (Johow) Looser | Berry | | | 3 |
| *Evergreen scrub* | | | | |
| Acacia caven (Mol.) Mol. | Lom. | | 60x20 | 3 |
| Adesmia confusa Ulib. | Hairy Lom. | | 30x10 | 4 |
| Azara dentata R. et Pav. | Berry | orange | 5.6 | 1 |
| Baccharis linearis (R. et Pav.) Pers. | Achene | | | 4 |
| Baccharis paniculata DC. | Achene | | | 4 |
| Berberis chilensis Gillies ex Hook. | Berry | blue | 5 | 1 |

Appendix 1 (Cont.)

| | Propagule type | Color | Size (mm) | Type code |
|---|---|---|---|---|
| Centaurea chilensis H. et A. | Achene | | | 2 |
| Cestrum parqui L' Herit. | Berry | black | 5.6 | 1 |
| Colletia spinosa Lam. | Nutlet | | 4-5 | 2 |
| Colliguaja odorifera Mol. | Seed | | 5 | 2 |
| Ephedra andina Poepp. ex C.A. Mey. | Berry | pink | 4-5 | 1 |
| Eccremocarpus scaber R. et Pav. | Seed | | 3 | 4 |
| Escallonia pulverulenta (R. et Pav.) Pers. | Seed | | | 4 |
| Eupatorium salvia Colla | Achene | | | 4 |
| Gochnatia foliolosa (D. Don) D. Don | Achene | | | 4 |
| Kageneckia oblonga R. et Pav. | Seed | | | 4 |
| Lithrea caustica (Mol.) H. et A. | Drupe | green | 5.9 | 1 |
| Lobelia excelsa Bonpl. | Seed | | | 4 |
| Maytenus boaria Mol. | Aril. Seed | red | | 1 |
| Muehlenbeckia hastulata (J. E. Sm.) Johnst. | Berry | pink | 3.5 | 1 |
| Podanthus mitiqui Lindl. | Achene | | | 2 |
| Porlieria chilensis Johnst. | Nutlike | | 8.7 | 2 |
| Proustia cuneifolia D. Don fma. cinerea (Phil.) Fabris | Achene | | | 4 |
| Quillaja saponaria Mol. | Seed | | | 4 |
| Retanilla ephedra (Vent.) Brongn. | Drupe | green | 3 | 1 |
| Satureja gilliesii (Graham) Briq. | Nutlet | | 1.5-2 | 2 |
| Schinus polygamus (Cav.) Cabrera | Berry | violet | 3.0 | 1 |
| Senna candolleana (Vogel) Irwin et Barneby | Legume | | 20x10 | 3 |
| Solanum ligustrinum Lodd. | Berry | black | 6.8 | 1 |
| Talguenea quinquinervia (Gill. et Hook.) Johnston | Nut | | 5 | 2 |
| Teucrium bicolor J. E. Sm. | Nutlet | | 2-2.5 | 2 |
| Trevoa trinervis Miers | Drupe | green | 4.0 | 2 |
| Trichocereus chilensis (Colla) Britton et Rose | Berry | | 50x30 | 3 |
| Tristerix aphyllus (Miers ex DC.) Van Tiegh ex Barlow et Wiens | Berrylike | pink | 6.0 | 1 |
| Tristerix tetrandrus (R. et Pav.) Mart. | Berrylike | yellow | 5.8 | 1 |
| *Evergreen forest* | | | | |
| Adenopeltis serrata (W. Aiton) Johnst. | Seed | | 5 | 2 |
| Aextoxicon punctatum R. et Pav. | Berry | violet | 11.0 | 1 |
| Azara celastrina D. Don | Berry | orange | 5.0 | 1 |
| Azara petiolaris (D. Don) Johnst. | Berry | black | 4.0 | 1 |
| Beilschmiedia miersii (Gay) Kosterm. | Drupe | brown | 20x30 | 3 |
| Chusquea cumingii Nees | Seed | | | 2 |
| Cissus striata R. et Pav. | Berry | blue | 5-6 | 1 |
| Citronella mucronata (R. et Pav.) D. Don | Drupe | black | 10-12 | 1 |
| Cryptocarya alba (Mol.) Looser | Drupe | red | 9.6 | 1 |
| Dasyphyllum excelsum (D. Don) Cabr. | Achene | | | 4 |
| Eupatorium glechonophyllum Less. | Achene | | | 4 |
| Eupatorium salvia Colla | Achene | | | 4 |
| Lardizabala biternata R. et Pav. | Berry | green | 55x22 | 3 |
| Lithrea caustica (Mol.) H. et A. | Drupe | green | 5.9 | 1 |
| Luma chequen (Mol.) A. Gray | Berry | black | 9.6 | 1 |
| Myrceugenia obtusa (DC.) Berg | Berry | black | 7.0 | 1 |
| Persea lingue (R. et Pav.) Nees ex Kopp | Drupe | black | 7-8 | 1 |
| Persea meyeniana Nees | Drupe | black | 7-8 | 1 |
| Peumus boldus Mol. | Berry | green | 6.3 | 1 |
| Proustia pyrifolia DC. | Achene | | | 4 |
| Rhaphithamnus spinosus (A. L. Juss.) Mold. | Berrylike | violet | 5.0 | 1 |

Appendix 1 (Cont.)

| | Propagule type | Color | Size (mm) | Type code |
|---|---|---|---|---|
| Schinus latifolius (Gill. ex Lindley) Engler | Berry | violet | 5.1 | 1 |
| S. velutinus (Turcz.) Johnst. | Berry | violet | | 1 |
| **CALIFORNIA** | | | | |
| *Semi-arid scrub with succulents* | | | | |
| Adenothamnus validus (Bdg.) Keck | Achene | | | 4 |
| Aesculus parry A. Gray | Seed | | | 4 |
| Agave shawii Engelm. | Seed | | 6-8 | 4 |
| Artemisia californica Less. | Achene | | | 4 |
| Bergerocactus emoryi Britt. et Rose | Berry | | | 3 |
| Cleome isomeris Greene | Seed | | | 2 |
| Cneoridium dumosum (Nutt.) Hoof. F. | Drupelike | red | 5-6 | 1 |
| Eriogonum fasciculatum Benth. | Achene | | | 4 |
| Euphorbia misera Benth. | Seed | | 2.5 | 2 |
| Franseria chenopodiifolia Benth. | Bur | | | 2 |
| Lophocereus schotii (Engelm.) Britt. & Rose var. schotii | Berry | | | 3 |
| Lycium brevipes Benth. | Berry | | 10 | 1 |
| Machaerocereus gummosus (Engelm.) Britt. et Rose | Berry | | | 3 |
| Myrtillocactus cochal (Orcutt) Britt. et Rose | Berry | | | 3 |
| Opuntia prolifera Engelm. | Berry | green | 30x15 | 3 |
| Rosa minutifolia Engelm. | Hip | | | 1 |
| Rhus integrifolia (Nutt.) Benth. & Hook. var. integrifolia | Drupe | | 10 | 1 |
| Salvia apiana Jeps. | Nutlet | | | 2 |
| Salvia munzii Epl. | Nutlet | | | 2 |
| Simmondsia chinensis (Link) C.K. Schneid. | Seed | | 18-20 | 3 |
| Viguiera laciniata Gray | Achene | | | 4 |
| *Semi-arid coastal scrub* | | | | |
| Arctostaphylos rudis Jeps. & Wiens | Nutlet | brown | 6-9 | 2 |
| Artemisia californica Less. | Achene | | | 2 |
| Baccharis plummerae Gray | Achene | | | 4 |
| Baccharis viminea DC. | Achene | | | 4 |
| Baccharis emoryi Gray | Achene | | | 4 |
| Baccharis pilularis DC. | Achene | | | 4 |
| Baccharis sarothroides Gray | Achene | | | 4 |
| Berberis nevinii Gray | Berry | red | 6-8 | 1 |
| Ceanothus spinosus Nutt. in T. & G. | Seed | | 3 | 2 |
| Cneoridium dumosum (Nutt.) Hook. | Drupelike | | 5-6 | 1 |
| Crossosoma californicum Nutt. | Aril. Seed | yellow | | 1 |
| Encelia farinosa Gray | Achene | | | 2 |
| Encelia californica Nutt. | Achene | | | 2 |
| Eriogonum fasciculatum Benth. | Achene | | | 4 |
| Euphorbia misera Benth. | Seed | | | 2 |
| Euphorbia ocellata Dur. et Hilg. | Seed | | | 2 |
| Forestiera neomexicana Gray | Drupe | blue | 5-7 | 1 |
| Haplopappus venetus ssp. vernonioides (Nutt.) Hall | Achene | | | 4 |
| Haplopappus canus (Gray) Blake | Achene | | | 4 |
| Haplopappus squarrosus H. et A. | Achene | | | 4 |
| Haplopappus palmeri Gray | Achene | | | 4 |
| Haplopappus pachylepis Hall | Achene | | | 4 |

Appendix 1 (Cont.)

| | Propagule type | Color | Size (mm) | Type code |
|---|---|---|---|---|
| Isomeris arborea Nutt. | Seed | | 6-7 | 2 |
| Lepidospartum squamatum (Gray) Gray | Achene | | | 4 |
| Lycium andersonii Gray | Berry | red | 4-8 | 1 |
| Lycium californicum Nutt. | Berry | red | 3-6 | 1 |
| Opuntia prolifera Engelm. | Berry | | >30 | 3 |
| Opuntia parryi Engelm. | Berry | green | >30 | 3 |
| Opuntia serpentina Engelm. | Berry | | 10-15 | 3 |
| Opuntia occidentalis var. littoralis Engelm. | Berry | red | >25 | 3 |
| Pluchea cerisea (Nutt.) Cov. | Achene | | | 4 |
| Rhus trilobata Nutt. ex T. & G. | Drupe | red | 4-5 | 1 |
| Rhus integrifolia (Nutt.) Benth. et Hook. | Drupe | | 7 | 1 |
| Rhus laurina Nutt. in T & G. | Drupe | white | 2-3 | 1 |
| Solanum douglasii Dunal in DC. | Berry | black | 6-9 | 1 |
| Salvia apiana Jeps. | Nutlet | | | 2 |
| Salvia leucophylla Greene | Nutlet | | | 2 |
| Salvia mellifera Greene | Nutlet | | | 2 |
| Salvia munzii Epl. | Nutlet | | | 2 |
| Senecio lyonii Gray | Achene | | | 4 |
| Senecio douglasii DC. | Achene | | | 4 |
| Tetradymia comosa Gray | Achene | | | 2 |
| Yucca whipplei Torr. | Seed | | 6-8 | 4 |
| *Evergreen scrub* | | | | |
| Adenostoma fasciculatum H. et A. | Achene | | | 4 |
| Adenostoma sparsifolium Torr. | Achene | | | 4 |
| Amorpha californica Nutt. | Pod. | | | 2 |
| Arctostaphylos andersonii Gray | Nutlet | red | 6-8 | 2 |
| Arctostaphylos auriculata Eastw. | Nutlet | orange | 5-7 | 2 |
| Arctostaphylos canescens Eastw. | Berry | | 7-8 | 1 |
| Arctostaphylos edmunsii J. T. Howell | Nutlet | brown | 8 | 2 |
| Arctostaphylos elegans Jeps. | Berry | red | 8-10 | 1 |
| Arctostaphylos glandulosa Eastw. | Nutlet | red | 8 | 2 |
| Arctostaphylos glauca Lindl. | Nutlet | brown | 12-15 | 2 |
| Arctostaphylos glutinosa Schreib. | Berry | orange | 9-14 | 1 |
| Arctostaphylos insularis Greene | Nutlet | brown | 6-8 | 2 |
| Arctostaphylos manzanita Parry | Berry | red | 8-12 | 1 |
| Arctostaphylos morroensis Wies. & Schreib. | Nutlet | orange | 10 | 2 |
| Arctostaphylos myrtifolia Parry | Nutlet | green | 4-5 | 2 |
| Arctostaphylos nissenana Merriam | Nutlet | red | 4 | 2 |
| Arctostaphylos otayensis Wies. & Screib. | Nutlet | brown | 5-8 | 2 |
| Arctostaphylos parryana Lemmon | Berry | red | 8-12 | 1 |
| Arctostaphylos pechoensis Dudl. ex Abrams. | Nutlet | brown | 8-10 | 2 |
| Arctostaphylos pilosula Jeps. & Wies. | Nutlet | orange | 8-10 | 2 |
| Arctostaphylos pringlei Parry | Berry | red | 6-10 | 1 |
| Arctostaphylos pungens HBK | Nutlet | brown | 5-8 | 2 |
| Arctostaphylos rudis Jeps. & Wies. | Nutlet | brown | 6-9 | 2 |
| Arctostaphylos silvicola Jeps. & Wies. | Nutlet | brown | 6-8 | 2 |
| Arctostaphylos stanfordiana Parry | Berry | red | 5-7 | 1 |
| Arctostaphylos viscida Parry | Nutlet | brown | 6-8 | 2 |
| Berberis dictyota Jeps. | Berry | blue | 6-7 | 1 |
| Berberis higginsae Munz | Berry | yellow | 6-7 | 1 |
| Castanopsis chrysophylla var. minor (Benth.) A. DC. | Nut | | | 2 |
| Ceanothus arboreus Greene | Seed | | 2 | 2 |

Appendix 1 (Cont.)

| | Propagule type | Color | Size (mm) | Type code |
|---|---|---|---|---|
| Ceanothus crassifolius Torr. | Seed | | 3.5-4 | 2 |
| Ceanothus cuneatus (Hook.) Nutt | Seed | | 4 | 2 |
| Ceanothus cyaneus Eastw. | Seed | | | 2 |
| Ceanothus dentatus T. & G. | Seed | | | 2 |
| Ceanothus divergens Parry | Seed | | | 2 |
| Ceanothus ferrisae McMinn. | Seed | | | 2 |
| Ceanothus foliosus Parry | Seed | | | 2 |
| Ceanothus insularis Eastw. | Seed | | 4 | 2 |
| Ceanothus impressus Trel. | Seed | | 2.5 | 2 |
| Ceanothus jepsonii Greene | Seed | | | 2 |
| Ceanothus leucodermis Greene | Seed | | 2.5-3 | 2 |
| Ceanothus masonii McMinn. | Seed | | | 2 |
| Ceanothus megacarpus Nutt. | Seed | | | 2 |
| Ceanothus oliganthus Nutt. in T. & G. | Seed | | 3 | 2 |
| Ceanothus palmeri Trel. | Seed | | 3 | 2 |
| Ceanothus parryi Trel. | Seed | | 2 | 2 |
| Ceanothus pumilus Greene | Seed | | 3.5 | 2 |
| Ceanothus purpureus Jeps. | Seed | | 3 | 2 |
| Ceanothus ramulosus (Greene) McMinn. | Seed | | 3 | 2 |
| Ceanothus sonomensis J. T. Howell | Seed | | | 2 |
| Ceanothus spinosus Nutt. in T. & G. | Seed | | 3 | 2 |
| Ceanothus sorediatus H. et A. | Seed | | | 2 |
| Ceanothus thyrsiflorus Esch. | Seed | | | 2 |
| Ceanothus velutinus Dougl. ex Hook. | Seed | | | 2 |
| Cercis occidentalis Torr. ex Gray | Pod | | 65x22 | 3 |
| Cercocarpus betuloides Nutt. ex T. & G. | Achene | | | 4 |
| Cercocarpus minutiflorus Abrams. | Achene | | | 4 |
| Chrysothamnus nauseusus ssp albicaulis (Nutt.) Hall & Clem. | Achene | | | 4 |
| Cneoridium dumosum (Nutt.) Hook | Drupelike | | 5-6 | 1 |
| Comarostaphylis diversifolia (Parry) Greene | Drupe | red | 5-6 | 1 |
| Crossosoma californicum Nutt. | Aril. Seed | yellow | | 1 |
| Encelia californica Nutt. | Achene | | | 2 |
| Eriodictyon californicum (H. et A.) | Torr. | Seed | 1-1.5 | 2 |
| Eriodictyon crassifolium Benth. | Seed | | 1 | 2 |
| Eriodictyon tomentosum Benth. | Seed | | 1-1.5 | 2 |
| Eriodictyon trichocalyx Heller | Seed | | 1-1.5 | 2 |
| Forestiera neomexicana Gray | Drupe | blue | | 1 |
| Fraxinus dipetala H. et A. | Samara | | | 4 |
| Fremontia californica Torr. | Seed | | 3-4 | 2 |
| Fremontia mexicana (A. Davids.) Macbr. | Seed | | 4-5 | 2 |
| Garrya buxifolia Gray | Berry | black | 4-6 | 1 |
| Garrya elliptica Dougl. | Berry | white | 7-11 | 1 |
| Garrya fremontii Torr. | Berry | black | 6 | 1 |
| Garrya veatchii Kell. | Berry | purple | 7-8 | 1 |
| Haplopappus arborescens (Gray) Hall | Achene | | | 4 |
| Haplopappus parishii (Greene) Blake | Achene | | | 4 |
| Haplopappus pinifolius Gray | Achene | | | 4 |
| Haplopappus squarrosus H. et A. | Achene | | | 4 |
| Haplopappus stenolepis Hall | Achene | | | 4 |
| Hymenoclea monogyra T. & G. | Achene | | | 4 |
| Heteromeles arbutifolia M. Roem. | Pome | red | 5-6 | 1 |
| Lepechinia calycina (Benth.) Epl. in Munz | Nutlet | | | 2 |
| Lepechinia cardiophylla Epl. | Nutlet | | | 2 |

Appendix 1 (Cont.)

| | Propagule type | Color | Size (mm) | Type code |
|---|---|---|---|---|
| Lepechinia fragrans (Greene) Epl. | Nutlet | | | 2 |
| Lepechinia ganderi Epl. | Nutlet | | | 2 |
| Lepidospartium squamatum (Gray) Gray | Achene | | | 4 |
| Lycium andersonii Gray | Berry | red | 4-8 | 1 |
| Lyonothamnus floribundus Gray | Seed | | | 4 |
| Lonicera interrupta Benth. | Berry | red | 5-7 | 1 |
| Lonicera subspicata H. et A. | Berry | red | 5-7 | 1 |
| Opuntia serpentina Engelm. | Berry | | 10-15 | 2 |
| Osmaronia cerasiformis (T. & G.) Greene | Drupe | black | 10 | 1 |
| Pickeringia montana Nutt. | Legume | | 40x10 | 2 |
| Psoralea californica Wats. | Nutlet | | | 2 |
| Purshia glandulosa Curran. | Achene | | | 4 |
| Quercus chrysolepis Liebm. | Nut | | | 2 |
| Quercus dumosa Nutt. | Nut | | | 2 |
| Quercus durata Jeps. | Nut | | | 2 |
| Rhamnus californica Esch. | Drupe | | | 1 |
| Rhamnus ilicifolia (Kell.) C.B. Wolf. | Drupe | | 8 | 1 |
| Ribes amarum McClat. | Berry | | 15-20 | 1 |
| Ribes californicum H. et A. | Berry | red | 9-10 | 1 |
| Ribes canthariforme Wiggins | Berry | | 5-6 | 1 |
| Ribes glutinosum (Benth.) Loud. | Berry | black | | 1 |
| Ribes indecorum Eastw. | Berry | | 6-7 | 1 |
| Ribes malvaceum Sm. | Berry | purple | 6 | 1 |
| Ribes viburnifolium Gray | Berry | red | 6 | 1 |
| Rhus integrifolia (Nutt.) Benth. & Hook. | Drupe | | 7 | 1 |
| Rhus laurina Nutt. in T. & G. | Drupe | white | 2-3 | 1 |
| Rhus ovata Wats. | Drupe | red | 7-8 | 1 |
| Rhus trilobata Nutt. ex T. & G. | Drupe | red | 4-5 | 1 |
| Salvia apiana Jeps. | Nutlet | | | 2 |
| Salvia clevelandii (Gray) Greene | Nutlet | | | 2 |
| Salvia spathacea Greene | Nutlet | | | 2 |
| Salvia sonomensis Greene | Nutlet | | | 2 |
| Senecio douglasii DC. | Achene | | | 4 |
| Simmondsia chinensis (Link.) C.K. Schneid. | Seed | | 18 | 3 |
| Solanum umbelliferum Esch. | Berry | white | 10-15 | 1 |
| Staphylea bolanderi Gray | Seed | | 5-7 | 2 |
| Styrax officinalis var. californica (Torr.) Rehd. | Berry | brown | 12-14 | 1 |
| Tetradymia comosa Gray | Achene | | | 4 |
| Viburnum ellipticum Hook. | Drupe | | 10-12 | 1 |
| Xyloccocus bicolor Nutt. | Drupe | red | 5-8 | 1 |
| *Evergreen forest* | | | | |
| Abies bracteata (D. Don) Nutt. | Seed | | | 4 |
| Abies grandis (Dougl.) Lindl. | Seed | | | 4 |
| Acer macrophyllum Pursh. | Samara | | | 4 |
| Amelanchier florida Lindl. | Pome | black | 10-13 | 1 |
| Arbutus menziesii Pursh. | Berry | red | 8-10 | 1 |
| Arctostaphylos cinerea Howell | Berry | red | 6-8 | 1 |
| Arctostaphylos columbiana Piper. | Berry | red | 7-10 | 1 |
| Baccharis pilularis ssp. consanguinea (DC) C.B. Wolf | Achene | | | 4 |
| Berberis pinnata Lag. | Berry | blue | 6 | 1 |
| Berberis piperiana (Abrams.) McMinn. | Berry | blue | 6-7 | 1 |
| Castanopsis chrysophylla (Dougl.) A. DC | Nut | | | 2 |
| Ceanothus dentatus T. & G. | Seed | | | 2 |

Appendix 1 (Cont.)

| | Propagule type | Color | Size (mm) | Type code |
|---|---|---|---|---|
| Ceanothus foliosus Parry | Seed | | | 2 |
| Ceanothus incanus T. & G. | Seed | | 3 | 2 |
| Ceanothus integerrimus H. et A. | Seed | | 2.5 | 2 |
| Ceanothus sorediatus H. et A. | Seed | | 2 | 2 |
| Ceanothus papillosus T. & G. | Seed | | 2 | 2 |
| Ceanothus parryi Trel. | Seed | | 2 | 2 |
| Ceanothus thyrsiflorus Esch. | Seed | | 2 | 2 |
| Chamaecyparis lawsoniana (A. Murr.) Parl. | Seed | | | 4 |
| Crataegus douglasii Lindl. | Pome | black | 10-12 | 1 |
| Cornus nuttallii Aud. | Drupe | red | 10-15 | 1 |
| Corylus cornuta var. californica (A. DC.) Sharp. | Nut | | | 2 |
| Dirca occidentalis Gray | Drupe | | | 1 |
| Eriodictyon californicum (H. et A.). Torr. | Seed | | 1-1.5 | 2 |
| Euonymus occidentalis Nutt. ex Torr. | Aril. Seed | | | 1 |
| Garrya buxifolia Gray | Berry | black | 4-6 | 1 |
| Garrya elliptica Dougl. | Berry | white | 7-11 | 1 |
| Garrya fremontii Torr. | Berry | black | 6 | 1 |
| Gaultheria shallon Pursh. | Berry | purple | 7-8 | 1 |
| Libocedrus decurrens Torr. | Seed | | | 4 |
| Lithocarpus densiflora (H. et A.) Rehd. | Nut | | | 2 |
| Lonicera hispidula Dougl. | Berry | red | 5-6 | 1 |
| Malus fusca (Raf.) C. K. Schneid. | Pome | black | 12-14 | 1 |
| Myrica californica Cham. & Schlecht. | Drupe | brown | 6-8 | 1 |
| Osmaronia cerasiformis (T. & G.) Greene | Drupe | black | 10 | 1 |
| Pickeringia montana Nutt. | Legume | | 40x10 | 3 |
| Pseudotsuga menziesii (Mirb.) Franco | Seed | | | 4 |
| Quercus agrifolia Neé | Nut | | | 2 |
| Quercus chrysolepis Liebm. | Nut | | | 2 |
| Quercus garryana Dougl. | Nut | | | 2 |
| Quercus kelloggii Newb. | Nut | | | 2 |
| Rhamnus californica Esch. | Berry | red | | 1 |
| Rhamnus crocea Nutt. in T. & G. | Drupe | | | 1 |
| Rhododendron macrophyllum D. Don | Seed | | 3 | 2 |
| Rhododendron occidentale (T. & G.) Gray | Seed | | 2.5 | 2 |
| Rhus diversiloba T. & G. | Drupe | white | 4-7 | 1 |
| Ribes bracteosum Dougl. ex Hook. | Berry | black | 8-10 | 1 |
| Ribes californicum H. et A. | Berry | red | 9-10 | 1 |
| Ribes divaricatum Dougl. | Berry | black | 6-10 | 1 |
| Ribes glutinosum (Benth.) Loud. | Berry | black | | 1 |
| Rosa gymnocarpa Nutt. in T. & G. | Hip | red | 5-10 | 1 |
| Rosa nutkana Presl. | Hip | red | 15-18 | 1 |
| Rosa spithamea Wats. | Hip | | 7-8 | 1 |
| Rubus spectabilis Pursh. | Drupe | red | 15-20 | 1 |
| Salix scouleriana Barr. | Seed | | | 2 |
| Symphoricarpus rivularis Suksd. | Berry | white | 8-12 | 1 |
| Torreya californica Torr. | Drupelike | | > 25 | 3 |
| Tsuga heterophylla (Ref.) Sarg. | Seed | | | 4 |
| Umbellularia californica (H. et A.) Nutt. | Drupe | green | > 25 | 3 |
| Vaccinium ovatum Pursh. | Berry | black | 6-9 | 1 |
| Vaccinium parviflorum Sm. in Rees. | Berry | red | 6-10 | 1 |
| Vitis californica Benth. | Berry | purple | | 1 |
| Wipplea modesta Torr. | Seed | | | 2 |